Effects of Canopy Disturbance and Fire on Vegetation and Fuel Dynamics in Oak Forests of the Mid-South USA

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Andrew Lee Vander Yacht
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DEDICATION

"*If I speak with a silver tongue, convince a crowd but don't have love, I leave a bitter taste with every word I say. So let my life be the proof, the proof of your love, let my love look like You, and what You're made of. How You lived, how You died. Love is sacrifice. So let my life be the proof, the proof of Your love.*"

-For King & Country.

To my God and creator. Like the roots of *Pinus echinata*, let my life be the proof.

"I put the rage in a river, roll in a thunder. But you kept me from going under when that current got too heavy. I always thought I'd be a heap of metal, and a cloud of smoke, foot stuck to the pedal. Sold for parts like a junkyard rusted-out Chevy. Fear I've had none. What the hell made you wanna love…A man who was gonna die young?"

-Eric Church, A Man Who Was Gonna Die Young

To my best friend, who makes everything in my life sweeter.

"*It is very important to a lot of people to make unmistakably clear to themselves and to the universe that they love the universe but are not intimidated by it and will not be shaken by it, no matter what it has in store. Moreover, they demand something from themselves early in life that can be taken ever after as a demonstration of this abiding feeling.*"

-Norman Maclean, Young Men and Fire

To my father and mother, who molded me into the man I am today.

"*It is an incalculable added pleasure to any one's sum of happiness if he or she grows to know, even slightly and imperfectly, how to read and enjoy the wonder-book of nature.*"

-Theodore Roosevelt, Nature at Home, 1905

To all past, present, and future conservationists.

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ABSTRACT

Removing fire's influence from Southern Appalachian and Central Hardwood forests (Mid-South) has 1) virtually eliminated communities defined by shortleaf pine (*Pinus echinata*) and native warm-season grasses, 2) greatly altered fuel-bed properties, 3) limited the regeneration of shade-intolerant and fire-adapted woody species, and 4) decreased herbaceous groundcover and diversity. We evaluated the ability of canopy-disturbance (none, 7, and 14 m^2 ha^{-1} residual basal area) and fire-season (none, October, and March) combinations to reverse such trends by monitoring vegetation and fuels from 2008 to 2016 at three sites located across the Mid-South. Shortleaf pine regeneration and native warm-season grasses occurred when canopy closure was reduced below 65 % and the dominance of understory woody vegetation was reduced. Regardless of degree, thinning doubled (+19.6 Mg ha^{-1}) coarse woody fuels (diameter >0.66 cm) and 3 biennial fires did not affect this difference. A net reduction of fine-fuels (reduced woody [litter and 1-hour], increased herbaceous) followed thinning and burning; however, maintenance of this reduced level required biennial burning, and the rate of herbaceous fuel increase under the biennial burning regime suggested future compensation for reductions in fine woody-fuels. Thinning and fire shifted understory woody communities towards shade-intolerant and fire-tolerant woody species. Management nearly doubled (+2,256 stems ha^{-1}) oak (*Quercus* spp.) seedling density across all sites, but mesophytic species (largely red maple [*Acer rubrum*]) persisted and perhaps precluded an even greater response of disturbance adapted woody species. Herbaceous diversity increased 3.4- to 5.2- fold across sites from pre- to post-treatment. Fire-season did not have strong effects on any monitored components of this system. Overall, our results question restoration associated thinning and burning as regionally effective

fuel reduction treatments but demonstrate the ability of such disturbance to increase diversity, function, and sustainability of oak communities throughout the Mid-South region.

Keywords: fire suppression; fire season; canopy disturbance; shortleaf-bluestem restoration; fuel treatment; mesophication.

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INTRODUCTION

Removing fire from its historic role in shaping oak (*Quercus* spp.) and pine (*Pinus* spp.) community development throughout the Mid-South (Abrams 1992; Guyette et al. 2007) has yielded many negative effects (Nowacki & Abrams 2008). Once extensive shortleaf-bluestem communities, defined by a sparse overstory of shortleaf pine and robust groundcover of native C_4 grasses, have been virtually eliminated east of the Mississippi River (NatureServe 2013; Anderson et al. 2016). Decreased fuel-bed flammability limits the restoration success associated with fire reintroduction (Nowacki & Abrams 2008). Mesophication has promoted dark, moist, and cool micro-environments dominated by species with physical and chemical leaf-litter (hereafter, litter) properties not conducive to fire (Kreye et al. 2013; Alexander & Arthur 2014; Varner et al. 2015). Alternatively, accumulating heavy fuels, climate-change, and associated increases in fire activity (Mitchell et al. 2014) could combine to promote catastrophic wildfires that degrade regional ecosystems (Vose & Elliott 2016). Shortleaf pine and oak overstories, the remnants of fire's regional legacy, are approaching senescence (Abrams 2003; South & Harper 2016) while an extended absence of disturbance has rendered regeneration of these shade-intolerant and fire-tolerant woody species non-competitive (Oswalt 2012; Brose et al. 2014). Once diverse understories of native grasses, forbs, and legumes have been reduced to continuous leaf litter as the result of light reductions and resource gradient eliminations (Hutchinson et al. 2005; Lettow et al. 2014).

Restoring the composition, structure, and function of these communities, which are among the most imperiled in North America (Nuzzo 1986; Noss et al. 1995), will require addressing altered fuel dynamics and the return of appropriate disturbance regimes. Canopy disturbance and fire promote shortleaf pine regeneration and C_4 grasses, the key components for sustaining shortleaf-bluestem communities (Stambaugh et al. 2007; Maynard & Brewer

2013). Such restoration alters fuel-beds and increases their ability to support a long-term regimen of repeated fire, which increases coarse woody fuel (CWF) consumption (Fernandes & Botelho 2003) and decreases smoke emissions (Goodrick et al. 2010) and wildfire risk (Stambaugh et al. 2011). In conjunction, canopy disturbance and fire can reverse mesophication effects by shifting composition toward shade-intolerant and fire-adapted species (Iverson et al. 2017; Vander Yacht et al. 2017). Canopy-disturbance increases the light available for herbaceous germination and growth (Nielsen et al. 2003; Brewer 2016), and a long-term regimen of biennial fire can maximize herbaceous groundcover and diversity by suppressing woody competition (Peterson et al. 2007; Peterson & Reich 2008).

Despite this knowledge, our understanding of how to efficiently and accurately correct altered fuel and vegetation dynamics remains limited. Specifically, knowledge gaps involving recommended overstory reduction rates (Jackson et al. 2006), fire-season effects (Knapp et al. 2009), and the tracking of long-term management outcomes require attention. Most knowledge regarding shortleaf-bluestem communities comes from west of the Mississippi river (Anderson et al. 2016). Applying this information in the east, where only limited research with largely disappointing results has occurred (Elliott et al. 2012), is complicated by differences in climate, duration of fire suppression, presence of remnant shortleaf pine, and hardwood competition. Fuel-treatments have been understudied and ineffective in the Mid-South (Waldrop et al. 2016), and long-term studies often lack canopy-disturbance (Arthur et al. 2017). Also, the contributions of herbaceous fuels have been largely ignored. Recent evaluations of repeated fire on woody vegetation in the Mid-South have not occurred in conjunction with canopy disturbance (Hutchinson et al. 2012; Arthur et al. 2015; Keyser et al. 2017). Growing-season fire can result in comparatively greater woody plant mortality and herbaceous layer gains than

traditionally used dormant-season fire (Knapp et al. 2009). This could increase its use, but the effects of such a transition on fuels and vegetation has not been documented in the Mid-South.

Before investing additional resources into joint vegetation management and fuels treatments, it is imperative that effective management options are identified. Therefore, we monitored fuel and vegetation response from 2008 to 2016 within a replicated experiment at three sites located across the Mid-South. Treatments were combinations of canopy disturbance (none, 7, and 14 m^2 ha^{-1} residual basal area) and prescribed fire-season (none, October, and March). Our goal was to elucidate management capable of efficiently restoring the fire-dependent components of oak and pine communities while reducing fuel loading to levels that could reduce wildfire risk and severity. Effective fuel treatments were defined as those reducing the loading (Mg ha^{-1}) of fine-fuels (litter, 1-hour, and herbaceous), which drive fire-behavior, and coarse woody fuels (CWF; 10-, 100-, and 1000-hour fuels), which influence wildfire severity. We focused our evaluation of restoration on 1) the promotion of shortleaf pine (*Pinus echinata*) regeneration and native C_4 grasses (shortleaf-bluestem community components), 2) the reversal of mesophication effects on understory woody vegetation, and 3) increases in herbaceous groundcover and diversity. We had the following specific hypotheses:

Shortleaf-bluestem community restoration: Simultaneous promotion of shortleaf pine regeneration and native C_4 grasses would involve multivariate relationships between canopy openness, reduced woody density in the understory, and site conditions conducive to restoration (*e.g.*, xeric aspects, proximity to overstory shortleaf).

Fuel-dynamics: Thinning would increase CWF (10-, 100-, and 1000-hour) loads, subsequent fire would reduce CWF and fine woody fuel (FWF – litter and 1 hour) loads, and the drier conditions associated with March (vs. October) burning would lead to greater fuel

reductions. Herbaceous fuel loads would increase and compensate for FWF loss.

Understory woody vegetation: The density of shade-intolerant woody species would increase with increasing canopy disturbance, and burning would promote fire-tolerant woody species. Repeated fire prior to leaf-abscission (October) would result in greater reductions in understory woody density than fire conducted prior to bud-break (March). Canopy disturbance and fire-season would interact such that heavy thinning and October fire would result in the greatest reversal of mesophication effects on understory woody communities.

Herbaceous groundcover and diversity: Herbaceous community measures would increase with increasing canopy disturbance, but a peak in diversity would occur at an intermediate level of overstory density. Fire applied prior to leaf abscission (October) would result in greater reductions in woody groundcover, and, therefore, greater increases in herbaceous metrics, than fires occurring prior to bud-break (March). Herbaceous groundcover and diversity would be best promoted by heavy thinning and October fire.

Each of these four questions, and associated research, is addressed in the following four chapters. They have each been formatted for publication as separate journal articles.

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CHAPTER I
PINUS ECHINATA AND WARM-SEASON GRASSES: ESTABLISHMENT OF CRITICAL COMPONENTS INFORMS THE RESTORATION OF AN IMPERILED FIRE-DEPENDENT COMMUNITY

This chapter is original work by Andrew L. Vander Yacht with contributions from co-authors Patrick D. Keyser, Charles Kwit, Mike C. Stambaugh, and Wayne K. Clatterbuck. It is in review with the journal "*Applied Vegetation Science*".

ABSTRACT

Questions: Are critical *Pinus echinata*-bluestem (hereafter, shortleaf-bluestem) community components (herbaceous groundcover, native C_4 grasses, and *P. echinata* regeneration) promoted equally across differences in canopy disturbance and fire-season? Are there site-condition thresholds informative to the restoration of shortleaf-bluestem communities?

Location: Cumberland Plateau, Tennessee, USA.

Methods: We defined shortleaf-bluestem community response using variables related to the herbaceous-layer (groundcover, diversity, and height), native C_4 grasses (density, groundcover), and *P. echinata* regeneration (density, root collar and sprout diameter, basal sprout number, height, and midstory crown class). These metrics and explanatory factors (n = 17) related to canopy-closure, woody-understory density, groundcover, topography, and proximity to overstory *P. echinata* were measured at 345 plots spanning a range of restoration conditions. Canonical correspondence and multivariate regression tree analyses explored multivariate relationships, effect hierarchies, and thresholds associated with restoration response. We then examined differences in identified response groups using ANOVA and zero-inflated negative binomials.

Results: In places, canopy disturbance and fire promoted diverse herbaceous groundcover (205 species), abundant C_4 grasses (>40,000 stems ha^{-1}), and substantial *P. echinata* regeneration (>3,000 stems ha^{-1}). However, shortleaf-bluestem community response was negligible when canopy closure exceeded 65 %. Subordinate effects of understory vertical woody cover and woody groundcover reduced shortleaf-bluestem community metrics when greater than 48 and 85

%, respectively. Conditions where herbaceous response was robust but *P. echinata* regeneration was limited in quantity and quality were also identified by analyses. Overall, structural characteristic effects were greater in magnitude than any effect of fire-season, aspect, slope position, and distance to overstory *P. echinata*.

Conclusions: Sequentially acting effects of canopy closure, understory thickness, and site condition appeared to regulate observed variation in shortleaf-bluestem community response. Our results suggest effective restoration begins with heavy canopy disturbance and continues with frequently applied fire. Fire limited hardwood competition, and thus increased herbaceous development and *P. echinata* regeneration, but moderating fire intensity could further improve results (e.g., strip-head firing). Our observations of unmanaged, closed-canopy forests suggest that without intervention, these communities will continue to decline in the eastern United States.

Keywords: shortleaf pine; warm-season grass; fire suppression; woody encroachment; fire season; canopy disturbance; shortleaf-bluestem; restoration; Tennessee.

Nomenclature: USDA Plants Database (http://plants.usda.gov, 24 June 2017) for plants, for plant associations.

Abbreviations: CWMA = Catoosa Wildlife Management Area; TWRA = Tennessee Wildlife Resources Agency; Sp = spring (March) fire; Fa = fall (October) fire; W = woodland basal area (14 m^2 ha^{-1}); S = savanna basal area (7 m^2 ha^{-1}); AS = advanced savannas; CCA = canonical correspondence analysis; MRT = multivariate regression tree; ZINB = zero-inflated negative binomial.

INTRODUCTION

For nearly 500 million years, fire has shaped the distribution, composition, and structure of the world's vegetation communities (Pausas & Keeley 2009). This is clearly demonstrated on

the North American Coastal Plain, where globally significant levels of biodiversity are largely associated with fire-dependent *Pinus palustris* communities (Noss et al. 2015; Guldin et al. 2016). However, fire's influence extended northward to more temperate climates where *P. echinata* supplanted *P. palustris* in dominance (Lafon et al. 2017). Throughout northern Alabama and Georgia, Tennessee, Kentucky, and North Carolina of the US (hereafter Mid-South), fire historically maintained robust native warm-season (C_4) grass (e.g., *Andropogon gerardii* and *Schizachyrium scoparium*) and forb groundcover under a well-spaced (< 20 m^2 ha^{-1}) overstory dominated by *P. echinata* (hereafter, shortleaf-bluestem communities, Delcourt et al. 1998; NatureServe 2013). Early European explorers of the Cumberland Plateau described herds of *Cervus canadensis* and *Bison bison* grazing under sparse, *P. echinata* dominated overstories (Michaux 1805; Coffey 2012).

Pinus echinata and C_4 grasses arguably promote the very fires responsible for maintaining their dominance, and in doing so play a critical role in determining overall community structure (Mitchell et al. 2009). While direct evidence in shortleaf-bluestem communities is scarce, it has been argued that *Pinus palustris* and *Aristida stricta* similarly perpetuate a fire regime that essentially makes a disturbance-dependent community non-successional (Platt & Connell 2003). Some have even suggested this role is worthy of the keystone species label (Noss 1989). Low canopy interception and regeneration requirement legacies, including limited shade (Lawson 1990; Kabrick et al. 2015) and frequent fire (Stambaugh et al. 2007), result in the typically light-rich environments of *P. echinata* stands. Such conditions facilitate C_4 grass dominated ground-layers that can assist in controlling woody encroachment through substantial and annual contributions of highly flammable fuels (Maynard & Brewer 2013). *Pinus echinata* and C_4 grasses provide a pathway to maintaining structural and

compositional diversity where closed-canopy forests would otherwise develop. Thus, *P. echinata* and C_4 grasses are critical to maintaining disturbance-dependent plant and wildlife species throughout the Mid-South, including the federally endangered *Picoides borealis* (Kabrick et al. 2007; Masters 2007).

Modern fire suppression and exclusion has virtually eliminated shortleaf-bluestem communities east of the Mississippi River (NatureServe 2013; Anderson et al. 2016) through negative effects on critical community components. Development and conversion has occurred, but declines have been largely driven by succession in the absence of disturbance (South & Harper 2016). Increasing canopy closure and understory woody density suppresses herbaceous plants (Hanberry et al. 2014), including shade-intolerant C_4 grasses (Peterson et al. 2007). This reduces fuel-bed flammability, decreases fire frequency and/or intensity, and subsequently, the control of invading woody plants (Maynard & Brewer 2013). Nearly half of the >60% loss in *P. echinata* cover types since the 1950s can be attributed to hardwood encroachment (Oswalt 2012). Community sustainability is further threatened by the lack or non-competitive position of *P. echinata* regeneration as overstory trees approach senescence (South & Harper 2016). Fire's absence has also degraded the genetic integrity of *P. echinata* populations (Stewart et al. 2012), and led to severely overstocked stands that contributed to the unprecedented severity and ≥$1 billion in regional economic loss of the *Dendroctonus frontalis* outbreak of 1999 to 2003 (Nowak et al. 2008).

Shortleaf-bluestem community restoration could reduce wildfire risk, moderate future insect outbreaks (Nowak et al. 2008), support pollinator populations (Hanula et al. 2015), and increase resiliency to impending environmental change (Vose & Elliott 2016). However, most knowledge comes from a disconnected portion of the communities' range west of the Mississippi

River (Anderson et al. 2016). Comparatively little research has occurred in the east, where a wetter climate, longer history of fire suppression, few mature *P. echinata*, and dense hardwood regeneration limit the application of regionally disparate research. A few studies have occurred in the southern Appalachians, but restoration success has remained elusive (Jenkins et al. 2011; Elliott et al. 2012). Before accepting costly artificial regeneration (*i.e.*, planting) as necessary (Elliott et al. 2012; South & Harper 2016), two understudied options should be evaluated: canopy reductions exceeding 40% and repeated, growing-season fire. Heavy canopy disturbance increases light availability in the understory (Kabrick et al. 2015), and fire removes germination inhibiting leaf-litter (Lashley et al. 2011) and releases nutrients associated with plant-growth (Elliott et al. 2012). Growing-season fire could accelerate restoration through greater control of competing hardwoods relative to dormant-season fire (Knapp et al. 2009).

Our goal was to understand how variation overstory, understory, and site characteristics affect the occurrence of critical, shortleaf-bluestem community components (robust and diverse herbaceous groundcover, native C_4 grass groundcover and density, and healthy levels of *P. echinata* regeneration). We also desired to identify thresholds in important regulatory variables, and compare the efficiency of management options in reaching those conditions. Management on the Cumberland Plateau, spanning a range of canopy-disturbance levels and prescribed-fire seasons, has resulted in a positive, but highly variable, *P. echinata* and C_4 grass response (Bowers et al. 2016; Vander Yacht et al. 2017) which we use to explore these questions. We hypothesized that the establishment of shortleaf-bluestem community components would be related to multivariate relationships between canopy openness, reduced woody density in the understory, and conducive site conditions (*e.g.*, xeric aspects, proximity to overstory shortleaf).

METHODS

Study Area

Our research occurred at Catoosa Wildlife Management Area (CWMA), 32,374 ha of the Cumberland Plateau and Mountains physiographic region managed by the Tennessee Wildlife Resources Agency (TWRA). Elevations ranged from 437-521 m and soils were Mesic Typic Hapludults over weathered sandstone and conglomerate (Soil Survey Staff, NRCS 2014). Annual mean precipitation and temperature from 1981 to 2010 was 140 cm and 13 °C for nearby Crossville, TN (NCDC 2014). Forests established in the 1920's and are currently dominated by *Quercus* spp. *Pinus echinata* was dominant prior to the *D. frontalis* outbreak of 1999-2000. In 2000, TWRA began salvage logging and prescribed burning. Such action promoted *P. echinata* (Bowers et al. 2016), prairie-associated flora, and C_4 grasses (Vander Yacht et al. 2017).

Prior to management (2000 or 2008, dependent on site), *Quercus alba*, *Q. falcata*, *Q. velutina*, and *Q. coccinea*, as well as *Acer rubrum*, *Oxydendrum arboreum*, and *Carya* spp., dominated the overstory (Vander Yacht et al. 2017). Mean canopy cover was 85% (± 3.3 SE). Understory woody density (stems >1.37 m tall, <12.7 cm DBH) was 1,936 stems ha^{-1} (± 182 SE), and *Nyssa sylvatica*, *Amelanchier arborea*, *Acer rubrum*, *Oxydendrum arboreum*, and *Sassafras albidum* dominated the midstory. Groundcover included little herbaceous vegetation (4.4% ± 0.7 SE), and was dominated by *Vaccinium* spp., woody regeneration, and leaf-litter.

Experimental Design and Restoration Treatments

We delineated two 20-ha replicates of six treatments in 2014. Each replicate was configured to maximize core area, and treatments included: 1) unmanaged stands (Control); 2) spring burned woodlands (14 m^2 ha^{-1} residual basal area, SpW); 3) fall burned woodlands (FaW); 4) spring burned savannas (7 m^2 ha^{-1} residual basal area, SpS); 5) fall burned savannas (FaS); and

5) advanced savannas (AS) burned eight times since 2000. Commercial logging was completed in June 2000 for AS, and in the winter of 2008-2009 for other treatments. *Quercus* spp., *Carya* spp., and *P. echinata* were retained while fire-intolerant species (*Acer spp.*, *Liriodendron tulipifera*, and *Liquidambar styraciflua*) were removed. After canopy disturbance, >75% of overstory trees were *Quercus* spp. Canopy closure in 2014 and 2015 was comparable within controls (97.6 % ± 0.2 SE), woodlands (70.2 % ± 2.5 SE), and savannas (32.8 % ± 1.9 SE).

Burns in FaW and FaS occurred prior to leaf abscission (mid-October) in 2010, 2012, and 2014, and burns in SpW and SpS occurred prior to bud-break (mid-March) in 2011, 2013, and 2015. Advanced savannas were burned late-February to mid-March in 2000, 2003, 2004, 2005, 2006, 2009, 2013, and 2014. The TWRA used ring-firing techniques, and backing-fires rarely burned >50-m into stands. Weather, fuel moisture, and fire behavior were monitored using the methods in Vander Yacht et al. (2017), and a two-sample t-test assuming unequal variance compared data between fire-seasons. Heading fires in the spring were more intense, likely because of seasonal differences in wind (Appendix SI1). Burns were otherwise comparable, including fire temperature as recorded by ceramic tiles painted with Tempilaq® liquids. We did not monitor fires in AS stands, but TWRA burn descriptions aligned with spring burn data.

Sampling Design and Data Collection

We monitored 17 explanatory and 14 response variables (Appendix SI2). Explanatory variables described overstory and understory structure, and topography and proximity to mature *P. echinata* (site-condition variables). Response variables described herbaceous groundcover, native C_4 grass density and cover, and *P. echinata* regeneration characteristics. We measured variables in June and July of 2014 (second growing-season post-fire) and 2015 (first growing-season post-fire). Sampling occurred at 15 plots (Appendix SI3) per stand per year (n = 345)

located along a 70 X 70 m grid in stand cores (50-m buffer). Live and dead tree basal area, canopy closure, percent slope, aspect, slope position, and vertical understory woody cover was measured at three locations within each plot. Basal area and canopy closure was determined using 2-factor metric prisms and convex spherical densiometers, respectively. Plots were assigned numerical values, 1-6, corresponding to alluvial, cove, toe-slope, mid-slope, shoulder, and ridge slope positions. Vertical woody cover in the understory was the mean percent obstruction estimated across five, 50-cm strata on a Nudds (1977) profileboard placed 15-m up- and down-slope. Individual C_4 grass plants were tallied within three 1.5 m radius sub-plots.

Woody undergrowth was monitored in seven nested sets of 1-m^2 and 3-m radius sub-plots at each plot. We tallied all seedling (trees ≥30.5 cm tall but <1.4 m tall) and shrubs (mutli-stemmed species <4 m tall at maturity) in 1-m^2 sub-plots. In 3-m radius sub-plots, we tallied small- (≥1.4 m tall and <7.6 cm DBH) and large- (≥1.4 m tall and ≥7.6 but <12.7 cm DBH) saplings (tree species), and all *P. echinata* ≥30.5 cm tall but < 12.7 cm DBH. We also recorded root collar diameter, height, largest basal sprout diameter, number of basal sprouts, and midstory crown-class (dominant, co-dominant, intermediate, or suppressed) for each *P. echinata*, and recorded location using a Trimble Recon® GPS. Because distance and direction from seed sources can influence regeneration (Baker 1992), we similarly recorded overstory *P. echinata* (>12.7 cm DBH) locations during a winter (2015) census of the study area (150-m buffer). We used ArcMap (v 10.5, ESRI, Redlands, CA) to calculate distance and direction to the nearest overstory *P. echinata* from each regeneration stem.

At three locations within each plot, we centered the intersection of two perpendicular 9-m transects and characterized groundcover using the point-intercept method at 1-m intervals (Bonham 1989). All vegetation below 1.4 m at each interval was identified to species and

categorized as native C_4 grass, other graminoid, forb, fern, or woody vegetation (all trees, vines, and shrubs). From these data we determined herbaceous diversity using Shannon-Wiener's Index (Magurran 1988). When no vegetation was present, cover was classified as litter or bare ground. We calculated percent groundcover for each category, and visually estimated the mean height of understory woody (< 3.2 m tall) and herbaceous vegetation along each 9-m transect.

DATA ANALYSIS

Explanatory Gradients and Shortleaf-Bluestem Response

All analyses were conducted in RStudio version 1.0.143 (2016, RStudio, Inc., Boston, MA). We transformed aspect and direction to nearest overstory *P. echinata* using Beers et al. (1966). This is routine for aspect data, and was justified for the latter variable based on disparity in frequency of wind from southwesterly or northeasterly directions (160˚-340˚ = 79.8%, 160˚-340˚ = 20.2%) in nearby Crossville, Tennessee from 1981-2010 (National Climatic Data Center 2014) during the peak shortleaf seed-fall months of October-January (Baker 1992). All variables were z-score standardized (mean = 0, standard deviation = 1), and explanatory variables were normal (Wilk's test, W > 0.90).

Shortleaf-Bluestem Response Ordination

Canonical correspondence analysis (CCA, ter Braak 1986) was conducted using package vegan version 2.4-3 (Oksanen et al. 2017). We chose CCA because it is robust to collinearity, allowing for simultaneously testing of many explanatory variables. We concluded all explanatory and response relationships were unimodal after visually inspecting scatterplots. Year was initially included as a conditioning factor, but only accounted for 1.1 % of total inertia and was therefore dropped. All forms of variable selection (forward, backward, step-wise; $\alpha = 0.05$) yielded the same final model with no observable collinearity. Permutation tests (n = 1,000)

indicated significance of selected variables, final model, and each canonical axis. We then plotted constrained ordinations and interpreted relationships.

Clusters in Shortleaf-Bluestem Response

Thresholds in explanatory effects on shortleaf-bluestem response were identified using multivariate regression tree (MRT) analysis. We only included variables identified as important by CCA, and a year effect. Litter groundcover was not included because of high correlation (Pearson's) with other retained variables that were more intuitive management targets (canopy closure: 0.73; woody groundcover: -0.78). We retained all remaining variables based on hierarchical clustering results of package ClustOfVar (Chavent et al. 2012); Rand criterion continuously increased across all explanatory variable partitions (stability analysis, 1,000 sample bootstrap approach). The MRT analysis then repeatedly selected cut-off values within explanatory variables that minimized resulting within-group multivariance of response (De'Ath 2002). Euclidean distances were used based on our data and research questions. Package mvpart (Therneau et al. 2014) selected final MRTs based on minimum cross-validated relative error (CVRE). Each terminal node contained a minimum of 10 plots, and we used a complexity parameter of 0.01. Forward and backward selection resulted in the same tree.

We then explored differences across MRT groups. Explanatory ($H = 406.3$, $P < 0.001$) and response ($H = 1{,}272.1$, $P < 0.001$) data lacked multivariate normality (Royston's test), so we tested for multivariate differences using a nonparametric comparison (1,000 permutations) in package npmv (Ellis et al. 2017). After observing multivariate differences, explanatory variables were subjected to ANOVA and Tukey mean separation because data were univariate normal (Wilk's test, $W > 0.90$) and displayed equality of group variance. Response data lacked normality, were overdispersed, and had excessive zeroes, and so were modeled using zero-

inflated negative binomials (ZINB). Such models use a logistic function (occurrence) to predict whether a count occurs and a negative binomial (count) function to predict count variation (Zeileis et al. 2008). We transformed response variables (√[Y×10,000]) and rounded to the nearest integer. We included all explanatory variables and year within occurrence and count functions using package pscl (Zeileis et al. 2008). Explanatory variables were retained when significant (Wald test, $\alpha = 0.05$). Backward selection determined final models based on AIC and χ^2 goodness of fit. Models predicted mean response variables at each plot. Predicted values met ANOVA assumptions, and Tukey mean separation assessed differences across MRT groups.

RESULTS

Explanatory Gradients and Shortleaf-Bluestem Response

Explanatory data spanned closed to open canopies, sparse to dense woody-understories, mesic to xeric sites, and many proximities to overstory *P. echinata* (Appendix SI2). We encountered 205 herbaceous species. *Piptochaetium avenaceum* accounted for 17.6 % of those encounters, more than triple the next most common species (5.7 %, *Dichanthelium dichotomum*). *Chasmanthium sessiliflorum* (4.6 %), *Carex albicans* (3.8 %), and *D. latifolium* (2.7 %) were also common, allowing graminoids to dominate the herbaceous layer. Forbs were relatively less common, but included *Solidago odora* (4.2 %), *Lysimachia quadrifolia* (3.3 %), *Lespedeza repens* (2.6 %), and *Coreopsis major* (2.2 %). Ferns were 6.4 % of herbaceous encounters.

In places, shortleaf-bluestem response was robust (Fig. I1). We observed six species of native C_4 grass that collectively accounted for 8.2 % of herbaceous encounters. *Andropogon virginicus* was 64.5 % of C_4 grass plants counted in density plots, followed in dominance by *Schizachyrium scoparium* (18.5 %), *Andropogon gerardii* (10.5 %), *Sorghastrum nutans* (6.4 %), *Andropogon gyrans* (0.1 %), and *Andropogon ternarius* (0.1 %). These grasses were observed at

Fig. I1 Shortleaf-bluestem community response at Catoosa Wildlife Management Area after overstory thinning and eight prescribed fires. Note the midstory dominance of natural *Pinus echinata* regeneration and abundance of native C_4 grasses.

184 of 345 plots. When present, C_4 grasses were a much more dominant component of the herbaceous community (mean groundcover 12.7 %; density 5,033 plants ha^{-1}) than overall means indicated (Appendix SI2).

We located 512 stems *P. echinata* regeneration at 68 of the 345 plots, where related means were: density, 378.9 stems ha^{-1} (± 90.0 SE); root collar diameter, 5.9 cm (± 0.4 SE); height, 195.0 cm (± 18.2 SE); diameter largest basal sprout, 3.5 cm (± 0.5 SE); sprouts $plant^{-1}$, 6.7 (± 1.0 SE); and midstory crown class, 2.4 (± 0.2 SE). Mortality was 4.7 % following fire and appeared equally distributed between fire-seasons (Fa: 5; Sp: 7). *Pinus echinata* regeneration and and C_4 grass density increased with increasing disturbance (woodland: 80.8 stems ha^{-1}, 1,199 plants ha^{-1}, savanna: 107.8 stems ha^{-1}, 3,170 plants ha^{-1}, and advanced: 70.3 stems ha^{-1}, 8,805 plants ha^{-1}), but neither occurred in controls.

Shortleaf-Bluestem Response Ordination

The final CCA model ($F_{9,335} = 10.7$, $P = 0.001$) had four axes ($F_{1,335} \geq 3.9$, $P \leq 0.016$), nine constraining variables ($F_{1,335} \geq 3.5$, $P \leq 0.018$), and explained 22.4 % of the multivariance in shortleaf-bluestem response. Despite some overlap, axes were related to either overstory, understory, or site-condition variables (Appendix SI4). Axis 1 explained 58.4 % of constrained variation through an overstory gradient positively related to litter groundcover and canopy closure. Variables describing the density, groundcover, vertical cover, and height of understory woody vegetation were negatively related to axis 2, which explained an additional 21.5 % of constrained variation. The third axis explained 11.6 % of constrained variation using a xeric to mesic gradient in slope and aspect positions. The fourth axis only explained 4.1 % of constrained variation related to aspect and distance from overstory *P. echinata*.

The top 3 axes explained 91.5 % of constrained variance and ordinated shortleaf-bluestem response in explanatory space (Appendix SI4). Control plots were ordinated far from any association with shortleaf-bluestem community components, and variation was limited relative to other treatments. Similarity between woodlands and controls, and savannas and AS, was observed. Controls and AS were distinct (Fig. I2A). Fall burns were characterized by less woody undergrowth and were more similar to AS (burned eight times) than spring burns. The presence, cover, and density of C_4 grasses was concentrated toward open canopies, sparse woody understories, ridges, and southwesterly aspects (Fig. I2B). *Pinus echinata* related variables were associated with greater canopy closure and a denser woody understory (Fig. I2B), but vigor-related variables (RCD, Mclass, slpHT, and LBSD) were associated with sparser woody understories than less vigor indicative variables (dSLP and #BS). Plots where C_4 grass and *P. echinata* co-occurred straddled the region where each was commonly present (Appendix SI4). Response variables were often associated with neutral to xeric site conditions (Fig. I2B).

Clusters in Shortleaf-Bluestem Response

The best fit MRT (CVRE = 0.767, SE = 0.077) identified five response groups and explained 31.0 % of shortleaf-bluestem response multivariance (Fig. I3). The first split explained 52% of this variation by recognizing limited shortleaf-bluestem response where canopy closure was ≥ 65.5 %. This node mainly included control and woodland plots. Remaining splits involved woody understory characteristics. An additional 26 % of model R^2 was explained by vertical woody cover, which when ≥ 48.6 % was associated with reduced herbaceous and *P. echinata* response. These plots (n = 123) were predominantly located in SpS and FaS. The final two splits discriminated between AS plots. If woody groundcover exceeded 85.8 %, herbaceous development was modest but *P. echinata* response was below average. The final split used

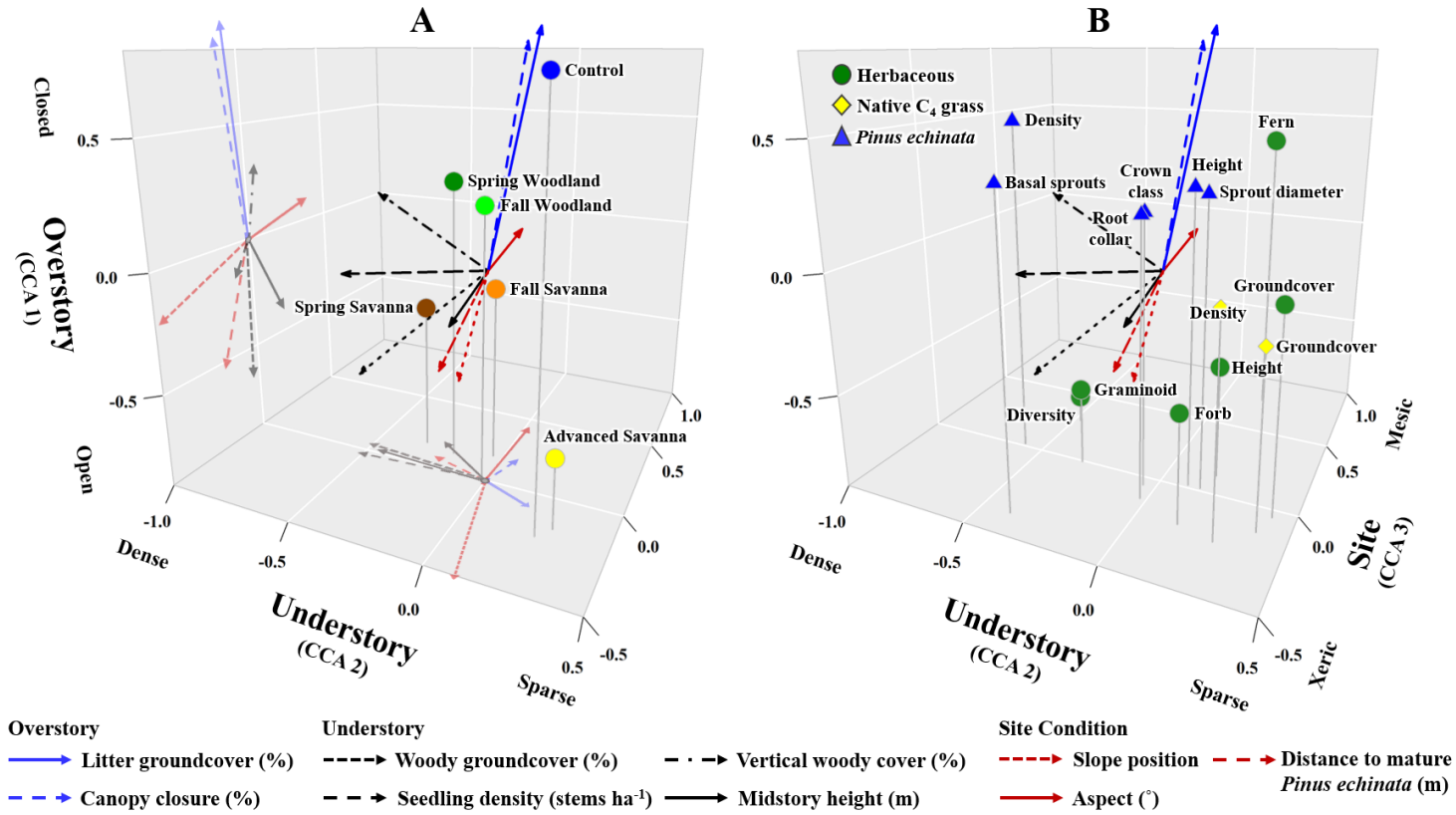

Fig. I2. Shortleaf-bluestem community response along three gradients (CCA, $P \leq 0.016$) describing open to closed canopies, dense to sparse woody understory, and xeric to mesic site conditions on the Cumberland Plateau, TN. A) Centroids of restoration treatments. B) Centroids of shortleaf-bluestem response variables. Arrows depict the explanatory variable correlations and were reflected in A to improve interpretation. Treatments include unmanaged stands (Control), spring (Sp) or fall (Fa) fire with woodland (14 m^2 ha^{-1}, W) or savanna (7 m^2 ha^{-1}, S) residual basal area, and advanced savannas (AS).

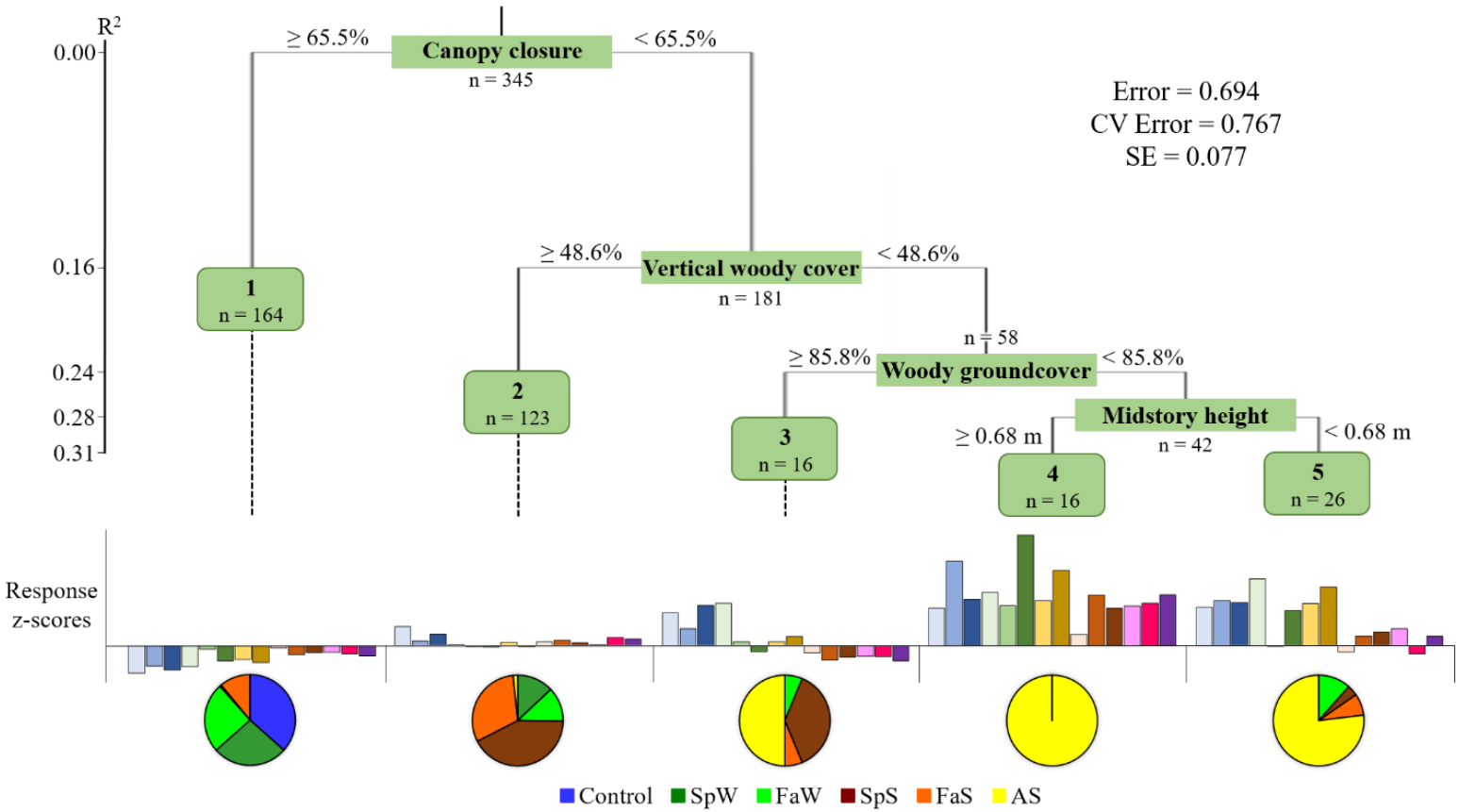

Fig. I3. Multivariate regression tree for shortleaf-bluestem community response to restoration on the Cumberland Plateau, TN. Response z-scores, from left to right: herbaceous diversity and height; graminoid, forb, fern, and herbaceous groundcover; C_4 grass density and groundcover; density, root collar diameter, height, largest basal sprout diameter, number of basal sprouts, and midstory crown class of *Pinus echinata* regeneration. Explanatory variables include; canopy closure (%), vertical woody cover (%), woody groundcover (%), and woody midstory height (m). Tree selected by minimum cross-validated relative error. Treatments: unmanaged stands (Control), spring (Sp) or fall (Fa) fire with woodland (14 m^2 ha^{-1}, W) or savanna (7 m^2 ha^{-1}, S) residual basal area, and advanced savannas (AS).

midstory height to discriminate plots where both herbaceous and *P. echinata* response was robust (≥ 0.68 m) from plots where only the herbaceous response was robust (< 0.68 m). Together, these final two splits explained the remaining 22.6 % of model R^2 (Fig. I3).

We observed multivariate differences in explanatory ($F_{21,697} = 22.5$, $P < 0.001$, Fig. I4 A-B) and response ($F_{13,436} = 29.2$, $P < 0.001$, Fig. I4 C-E) variables across MRT groups. Probability of an excessive absence increased with increasing canopy closure for all response variables (Appendix SI5). Slope coefficients were larger for herbaceous relative to *P. echinata* variables. The absence of an herbaceous response often involved many variables, but *P. echinata's* absence was more simply a function of increasing canopy closure and northeasterly aspects. Seedling density was never a significant predictor of response absence. In count functions, canopy closure was rarely retained in *P. echinata* models but routinely had negative effects on herbaceous response (Appendix SI6). As seedling density increased, *P. echinata* density and basal sprouts increased. In contrast, *P. echinata* height and midstory crown class decreased with increasing seedling density. Vertical woody cover negatively affected all but three response variables.

Differences across MRT groups in all explanatory variables ($F_{4,340} \geq 7.9$, $P < 0.001$, Fig. I4 A-B) except slope position ($F_{4,340} = 1.0$, $P = 0.430$), and predicted (ZINB models) response variables (Fig. I4 C-E), described transitions in vegetation composition and structure. Group 1 had nearly closed canopies (89.4% ± 0.7 SE), greater litter groundcover, and northeasterly aspects that were associated with limited herbaceous and *P. echinata* response. Group 1 was also, on average, 63 m closer to overstory *P. echinata* than all other groups except group 4. Woody understories were more robust in the second relative to first group, and so was herbaceous and *P. echinata* response. Group 2 had greater vertical woody cover in the midstory than group 3, and this was associated with reduced herbaceous height, less graminoid and forb

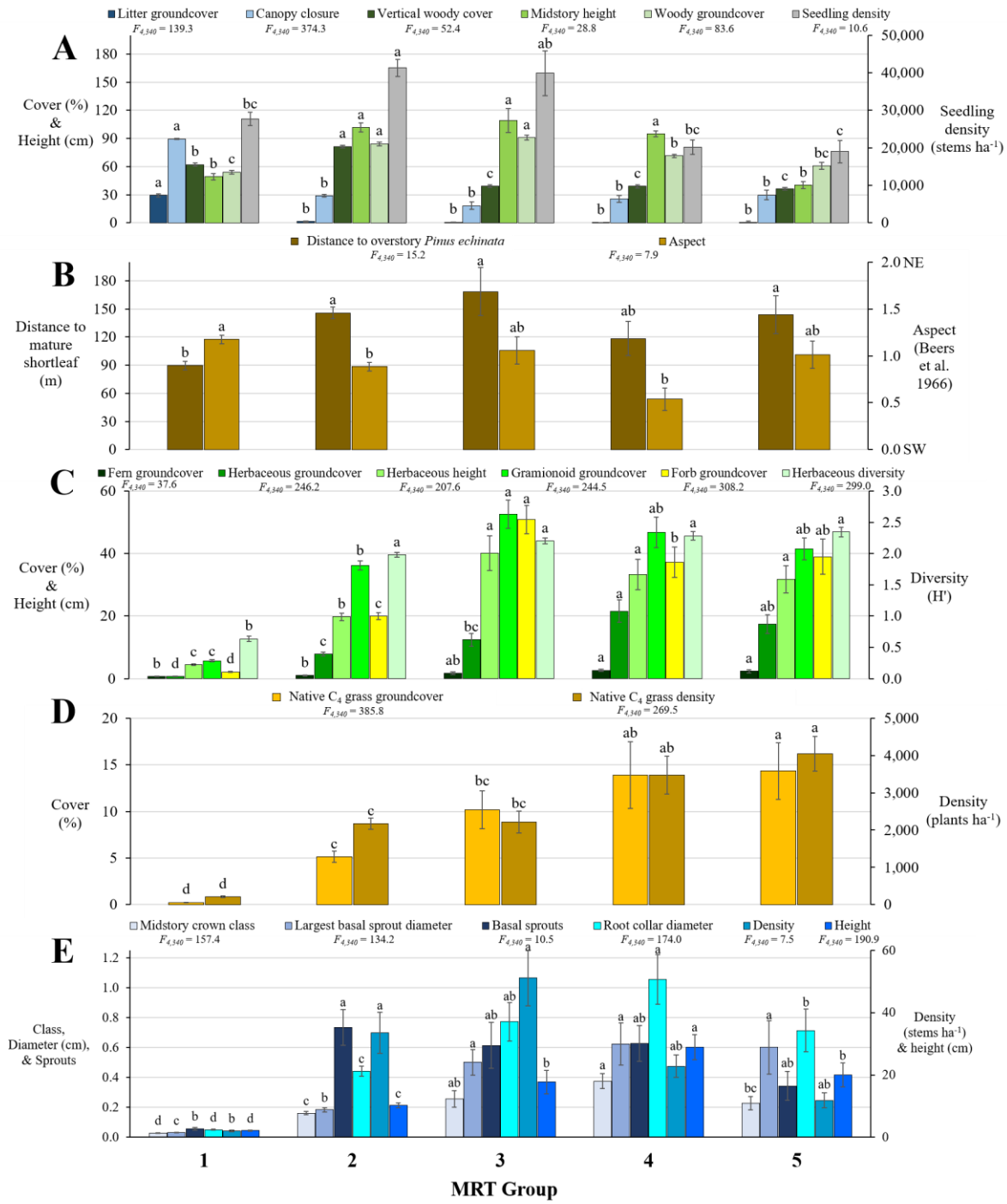

Fig. I4. ANOVA determined differences in explanatory and shortleaf-bluestem response variables across multivariate regression tree identified groups on the Cumberland Plateau, TN. Only variables differing ($\alpha = 0.05$) across groups are presented. A) Overstory and understory explanatory variables. B) Site-condition explanatory variables. C) Herbaceous response variables. D) C_4 grass response variables. E) *Pinus echinata* regeneration response variables. Response variables predicted by ZINB modeling. Lowercase letters represent within variable differences across groups (Tukey mean separation).

groundcover, and suppressed *P. echinata* variables. Group 4 had 19.3% less woody groundcover than group 3, and this was associated with increased herbaceous and decreased forb groundcover, and increased height of *P. echinata* regeneration. All *Pinus echinata* variables in group 4 were greater or equal to other groups. A 0.5 m reduction in mean midstory height distinguished group 5. Herbaceous and C_4 grass variables were equal or greater in this group relative to others, but some *P. echinata* variables were reduced relative to group 4.

DISCUSSION

In descending importance, canopy closure, woody understory density, and site characteristics influenced the occurrence of shortleaf-bluestem community components. Response was negligible where canopy closure, vertical woody understory cover, and woody groundcover exceeded 65, 48, and 85 %, respectively. These thresholds can direct the restoration of these imperiled communities east of the Mississippi river, where work has been scarce, ineffective (Elliott et al. 2012), or focused on more montane pine communities (Jenkins et al. 2011). Closed-canopy forest conditions, which dominate much of the eastern US, had strong, negative influences; however, manipulating those conditions achieved positive results. Under prerequisite conditions, fire and canopy disturbance could be effective alternatives to expensive plantings (Anderson et al. 2016). Disturbance long after the cessation of regular burning resulted, at times, in a robust *P. echinata* (>3,000 stems ha^{-1}) and C_4 grass (>40,000 stems ha^{-1}) response. This demonstrates community resiliency after correcting altered disturbance regimes.

Shortleaf-bluestem response was closely associated with canopy closure. The variable explained nearly 60% of CCA recognized variation, 52% recognized by MRT, and was always a predictor of response absence in ZINB models. Where shortleaf-bluestem components were absent (canopy closure > 65 %), residual basal area was ≥16 m^2 ha^{-1}. Jenkins et al. (2011)

similarly reported the absence of yellow pine seedlings until overstory density was <15 m^2 ha^{-1} (estimated from presented data). Naturally regenerating *P. echinata* often involves overstory reductions that meet or exceed this threshold (Baker 1992; Shelton & Cain 2000). Overstory reductions using fire alone can require 60 years of repeated burning (Knapp et al. 2015). The limitations partial canopies place on *P. echinata* growth may be balanced by similar or greater reductions in the growth of hardwood competition (Shelton & Cain 2000; Kabrick et al. 2015). Our results demonstrate the sensitivity of herbaceous species to canopy closure (Bowles & McBride 1998; Peterson et al. 2007). Recognizing herbaceous species may be more shade intolerant than *P. echinata* has important implications for restoration that aims to promote both.

Subsequently, shortleaf-bluestem response was influenced by understory woody vegetation. Canopy closure was comparable across MRT groups 2 through 5, but robust woody understories in group 2 appeared to suppress response variables. Vertical woody cover was particularly influential, followed by woody groundcover. Woody encroachment is a severe threat to shortleaf woodlands and savannas (Oswalt 2012; Hanberry et al. 2014). In the Mid-South, restoration sites are typically characterized by abundant and well-established hardwoods. Under such circumstances, *P. echinata*'s survival necessitates hardwood control with fire (Stambaugh et al. 2007). A unique basal crook shelters dormant buds beneath an insulating layer of soil to allow for sprouting after top-kill by fire (Lilly et al. 2012; Clabo 2014). Historical fire regimes are informative (Guyette et al. 2006), but our results support fire management that reduces vertical woody cover in the understory (< 48 %) and woody groundcover (< 85 %). Jenkins et al. (2011) similarly enhanced *P. echinata* regeneration after reducing understory woody density (-80 %) and shrub cover (-90 %). Fire also promotes and perpetuates herbaceous understories, including C_4 grasses, that define shortleaf-bluestem communities (Sparks et al. 1998).

Frequent fire (at least once every 4 years) can promote *P. echinata* regeneration (Stambaugh et al. 2007) and increase herbaceous cover and diversity (Peterson et al. 2007) by increasing soil nutrient availability (Elliott et al. 2012) and removing thatch and litter that prevents the seeds of both groups from extending roots into the soil (Jenkins et al. 2011; Lashley et al. 2011). Litter groundcover was influential (CCA axis 1), but highly correlated with canopy closure ($r = 0.73$). Bare mineral soil often promotes shortleaf pine (Baker 1992), but we did not observe any such relationship. We suggest this variable faded in importance prior to our monitoring because few *P. echinata* seedlings have established since initial salvage harvests (Bowers et al. 2016). At the same time, hardwoods persist after fire through basal sprouting (Ward 2015) and this can competitively limit *P. echinata* and herbaceous species. Long-term studies in eastern US forests show many fires are required to decrease hardwood sprouting capacity, and only then if applied without gaps ≥ 3 years during which below-ground resources can be replenished (Arthur et al. 2015). In our study, all plots where shortleaf-bluestem response was the greatest (MRT group 4) were burned eight times over the last 15 years.

Beyond repeated burning, transitioning from dormant- to a late growing-season fire could provide greater hardwood control (Knapp et al. 2009). Top-kill during the growing-season could disrupt carbohydrate translocation to the roots more so than top-kill during dormancy, resulting in less reserves to fuel resprouting (Loescher et al. 1990). While perhaps true, the periodicity of root growth and carbohydrate allocation varies widely by species and region (Pallardy 2010) and root carbohydrate content is maximized in the late fall (Loescher et al. 1990). In our study, spring fires spread consistently faster than fall fires. Perhaps differences in residence time – a factor known to influence woody stem mortality (Michaletz & Johnson 2007) – contributed to

the greater similarity between Fa and AS relative to Sp and AS treatments. Regardless, fire frequency influenced shortleaf-bluestem community response more so than fire-season.

Robust herbaceous response where *P. echinata* vigor was reduced (MRT group 5) suggests restoration may need to balance herbaceous groundcover promotion with ensuring *P. echinata* survival. Clabo (2014) documented substantial fire-induced mortality of *P. echinata* seedlings (up to 55%), and Stambaugh et al. (2007) suggested recruitment may require an 8 to 15 year respite from fire. Locally intense fire resulting from ring-firing, or perhaps edaphic conditions, could explain herbaceously dominated microsites. Late growing-season fire could also have a greater negative affect on *P. echinata* than dormant-season fire. Of the plots only burned 3 times in MRT group 5, 83% were burned in October. Density of *P. echinata* was also 2X greater in SpS than any other treatment. Clabo (2014) observed greater shortleaf seedling mortality (51.3 %) following burns in November than Shelton and Cain (2002) observed following burns in January (< 5 %). Promoting *P. echinata* regeneration with fire involves a tradeoff between induced mortality and hardwood control. At CWMA, recruitment appears to be occurring during a biennial fire regime (Fig. I1). The wetter climate and greater hardwood competition of the eastern US may increase the utility of fire relative to past cautionary advice derived from drier regions (Shelton & Cain 2000).

Site-conditions did not strongly influence shortleaf-bluestem response. Ridges, proximity to mature *P. echinata*, and southwesterly aspects were positively influenced response variables (CCA), but such factors only accounted for 16 % of variation and were absent from the final MRT. Clustering of response variables perhaps resulted in the contradictory relationships in ZINB models (*e.g.*, increasing *P. echinata* variables as aspect increased). Multivariate approaches better identify subtle, secondary trends (ter Braak 1986; De'Ath 2002). Shortleaf-

bluestem communities are often associated with southwesterly aspects and ridges where solar radiation, fire frequency, and fire intensity is greatest (Kabrick et al. 2007), but historically fire's influence extended beyond dry ridges (Stambaugh et al. 2016). As long as competition is controlled, *Pinus echinata* is adaptable to a variety of aspects, soils, annual temperatures (9-21˚C), total precipitation (102-152 cm) and elevations (up to 915 m, Lawson 1990). Results at our relatively flat site suggest site-conditions only minimally influenced restoration success.

Scheduling management to coincide with adequate seed production and weather favoring regeneration can be difficult. To illustrate, drought, severe fire, and a *D. frontalis* outbreak that killed seed sources contributed to the failure of appropriate management to improve *P. echinata* regeneration (Elliott et al. 2012). Seeds only remain viable for a single season, only disperse 60-90 m downwind from parent trees (Baker 1992), and production can be erratic and infrequent (Lawson 1990). Stands with significant seed loading are rare in the eastern US (Oswalt 2012; South & Harper 2016). Although proximity to mature *P. echinata* did not strongly influence response variables, we caution against dismissing this factor. At our site, *P. echinata* was dominant in the overstory just prior to canopy disturbance. Most *P. echinata* seedlings probably established after this harvest (Bowers et al. 2016), and saplings were probably also present. At plots where *P. echinata* regeneration occurred, stocking was well below (378.9 stems ha^{-1} ± 33.5 SE) that recommended for successful cohort establishment (2,472 stems ha^{-1}, Baker 1992). Such an observation recognizes the importance of overstory seed sources.

Warm-season grasses can virtually disappear following fire suppression (Bowles & McBride 1998) and may not persist in the seedbank (Leck & Leck 1998). At CWMA, a robust C_4 grass response was stimulated from a seedbank that persisted under a closed-canopy for many years. The growth of C_4 grasses to >2 m tall in the growing-season following canopy disturbance

also suggests the presence of dormant rhizomes. Early response was dominated by *Andropogon virginicus*. Seeding or planting could diversify composition, and may even be necessary where seedbanks are depauperate (Elliott et al. 2012; Maynard & Brewer 2013). In such situations, our results could inform site-prep to increase planting success, but our results also suggest succession of C_4 grass species. In non-AS stands, *A. virginicus* increased from 0.2 to 6.8 % of herbaceous encounters (2008 to 2016). In AS stands during 2014 and 2015, the reasonable future of non-AS stands with continued burning, *A. virginicus* was only 0.3 % of herbaceous encounters and composition of other C_4 species was greater (*Schizachyrium scoparium*: 0.7 vs 8.7 %, *A. gerardii*: 0.9 vs. 3.7 %, *Sorghastrum nutans* 0.2 vs 2.3 %). Characteristics of old-growth grassland plant traits describe all but *A. virginicus* (Veldman et al. 2015). These trends in adjacent AS and non-AS stands suggest that reducing the dominance of *A. virginicus*, and increasing more conservative C_4 grasses, may only require continued burning.

CONCLUSIONS

A cascade of canopy closure, understory thickness, and site-condition effects were associated with the response of critical shortleaf-bluestem community components. Promoting *P. echinata* and C_4 grasses begins with reducing the overstory below 65 % closure or 16 m^2 ha^{-1} basal area. Repeated fire can then target threshold understory conditions, including vertical woody cover in the understory (< 48 %) and woody groundcover (< 85 %). Intense fire can create these conditions; however, moderating intensity with strip-head firing could retain more *P. echinata* than the intense ring-firing used at CWMA. Late growing-season fire may harm *P. echinata* vigor, but this should be weighed against the potential for increased competition control and herbaceous development. Restoration should be most effective along ridges, southwest aspects, and downwind from mature *P. echinata*. Unmanaged forests were consistently far from

any association with shortleaf-bluestem community response; however, management alone is not a guarantee for success. Site history and the adequacy of site seedbanks or seed sources need serious consideration. At our site, canopy disturbance and fire simultaneously promoted *P. echinata* and C_4 grass, reflecting their historically intimate association. While our results demonstrate community resiliency, they also suggest that without active management shortleaf-bluestem communities could continue to decline in the eastern US.

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APPENDICES

Appendix SI1. Seasonal comparison of weather, fuel moisture, and fire behavior during prescribed fires (2010-2015) at Catoosa Wildlife Management Area, Tennessee. Statistics based on a two-sample t-test assuming unequal variance.

		Fire season[1]				
Variable	Units	Fall	Spring	*t*	*df*	*p*
Ambient temperature	˚C	25.3 ± 0.6	19.9 ± 1.3	3.75	35	**0.001**
Relative humidity	%	39.0 ± 1.6	35.5 ± 1.5	1.61	52	0.114
Wind speed	m s^{-1}	1.3 ± 0.2	3.6 ± 0.3	6.38	44	**< 0.001**
Wind direction	˚	232.4 ± 22.0	209.6 ± 17.7	0.81	50	0.424
Fine fuel moisture	%	13.7 ± 0.7	17.0 ± 1.5	1.98	84	0.051
10-hour fuel moisture	%	10.7 ± 1.0	10.1 ± 0.6	0.58	17	0.572
Flanking fire rate-of-spread	m min^{-1}	0.8 ± 0.1	1.8 ± 0.5	1.77	12	0.102
Flanking fire flame-length	m	0.4 ± 0.1	0.9 ± 0.3	1.42	14	0.176
Heading fire rate-of-spread	m min^{-1}	1.7 ± 0.1	3.0 ± 0.6	2.19	19	**0.041**
Heading fire flame-length	m	0.7 ± 0.1	1.5 ± 0.2	3.86	22	**0.001**
Fire temperature	˚C	177.2 ± 8.1	158.6 ± 6.4	1.80	147	0.075

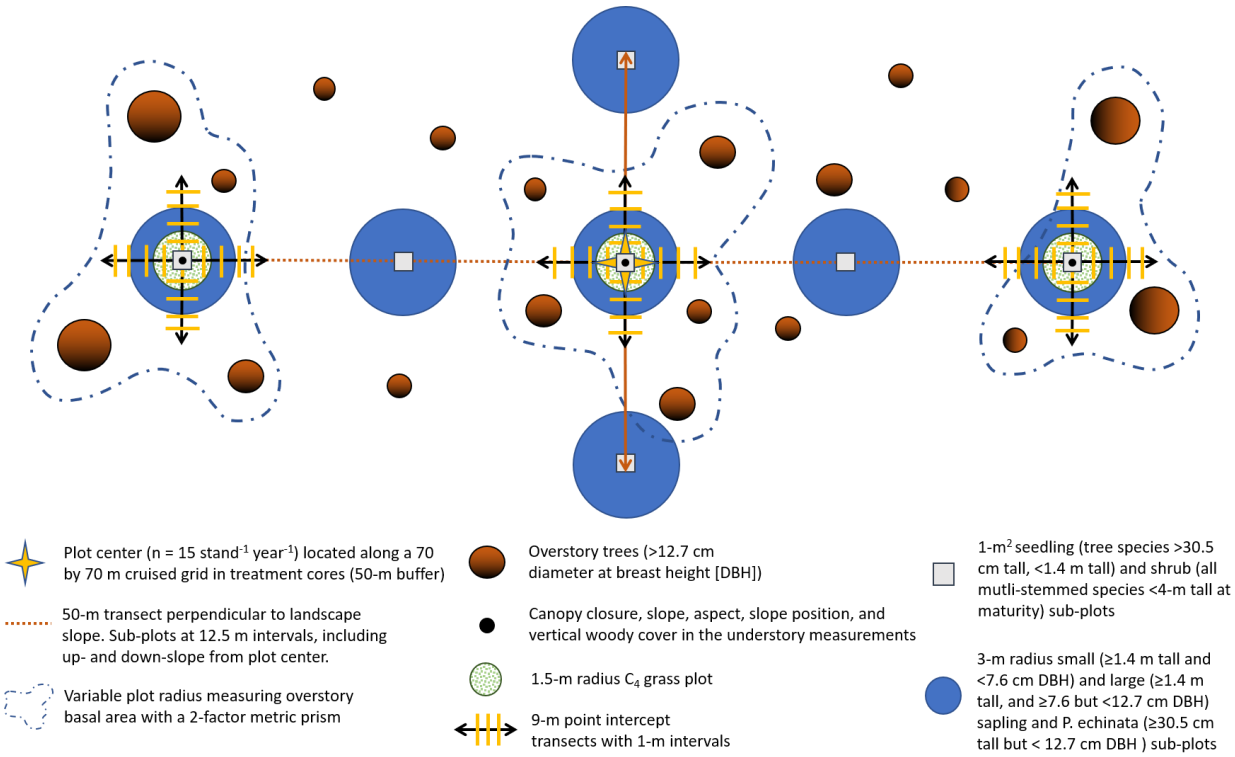
[1]Fall fires occurred 11 Oct 2010, 24 Oct 2012, and 24 Oct 2014. Spring fires occurred 22 Mar 2011, 15 Mar 2013, and 18 Mar 2015. This table does not include data for burns conducted in the advanced savanna treatment.

Appendix SI2. Mean, range, and median of explanatory and response variables across 345 individual plots located along a gradient from closed-canopy forest to heavily thinned and repeatedly burned stands on the Cumberland Plateau, TN. Minimum and maximums represent a single plot.

Variable Type	Variable Category	Variable	Units	Abbreviation	Mean[2]	SE	Minimum	Maximum	Median
Explanatory	Overstory	Live basal area	m^2 ha^{-1}	LBA	9.8	0.4	0	28.7	8.0
		Canopy closure	%	CC	57.1	1.9	0	100.0	59.3
		Snag basal area	m^2 ha^{-1}	DBA	2.5	0.1	0	11.3	2.0
	Understory	Large sapling density[1]	stems ha^{-1}	LgSapDen	123.2	12.4	0	1,516.8	0
		Small sapling density[1]	stems ha^{-1}	SmSapDen	7,189	338	0	43,199	5,457
		Shrubby vegetation density	stems ha^{-1}	ShrubDen	45,732	2,018	0	235,714	37,143
		Seedling density[1]	stems ha^{-1}	SeedDen	32,106	1,273	0	147,143	27,143
		Midstory height	Cm	MidHT	72.0	2.9	1.5	313.3	60.0
		Vertical woody cover	%	Nudd	64.9	1.3	20.0	100.0	64.0
		Woody groundcover	%	pWoody	88.9	2.2	3.9	100.0	85.3
		Litter groundcover	%	pLitter	17.5	1.2	0	94.1	5.9
		Bare groundcover	%	pBare	1.4	0.2	0	23.5	0
	Site conditions	Aspect[1]	Beers et al. 1966	Aspect	1.02	0.03	0.01	2.00	1.05
		Slope position[1]	Numerical	Position	4.07	0.04	1.00	6.00	4.00
		Slope	%	Slope	10.1	0.3	0.7	44.7	8.5
		Distance to mature shortleaf	M	DtoSLP	118.6	4.0	2.3	380.4	105.8
		Azimuth to mature shortleaf	Beers et al. 1966	AztoSLP	1.08	0.04	0.00	2.00	1.09
Response	Herbaceous	Diversity[1]	H´	Hdiver	1.50	0.05	0	3.00	1.67
		Height	Cm	Hhght	16.2	1.0	0	92.5	11.67
		Graminoid groundcover[1]	%	Grass	26.7	1.5	0	96.1	17.6
		Forb groundcover	%	Forb	18.3	1.4	0	100.0	5.9
		Fern groundcover	%	Fern	3.1	0.4	0	60.8	0
		Herbaceous groundcover	%	VegG	10.4	1.2	0	97.1	2.0
	Native C_4 grasses	Density	plants ha^{-1}	dNWSG	2,684	295	0	42,130	0
		Groundcover	%	pNWSG	6.8	0.7	0	72.8	0
	Pinus echinata[2]	Density	stems ha^{-1}	dSLP	74.7	19.3	0	3,082.0	0
		Root collar diameter	Cm	RCD	1.154	0.153	0	17.145	0
		Height	Cm	SLPhght	38.4	6.4	0	975.4	0
		Largest basal sprout diameter	Cm	LBSD	0.687	0.124	0	17.221	0
		Number of basal sprouts	stems $plant^{-1}$	#BS	1.33	0.23	0	32.00	0
		Midstory canopy class[1]	Numerical	Mclass	0.48	0.06	0	4.00	0

[1]Seedlings: ≥30.5 cm, <1.4 m tall; small-saplings: ≥1.4 m tall, <7.6 cm DBH; large-saplings: ≥1.4 m tall, ≥7.6 but <12.7 cm DBH. Directions scaled from 0 (SW) to 2 (NE). Alluvial, cove, toe-slope, mid-slope, shoulder, and ridge slope positions were 1-6, respectively. Diversity was Shannon-Wiener's Index. Graminoid groundcover excluded native C_4 grasses. Crown classes 1-4 corresponded to suppressed, intermediate, codominant, and dominant. [2]Plot-level, calculated from multiple measures (see methods). Minimum and maximums represent single plots.

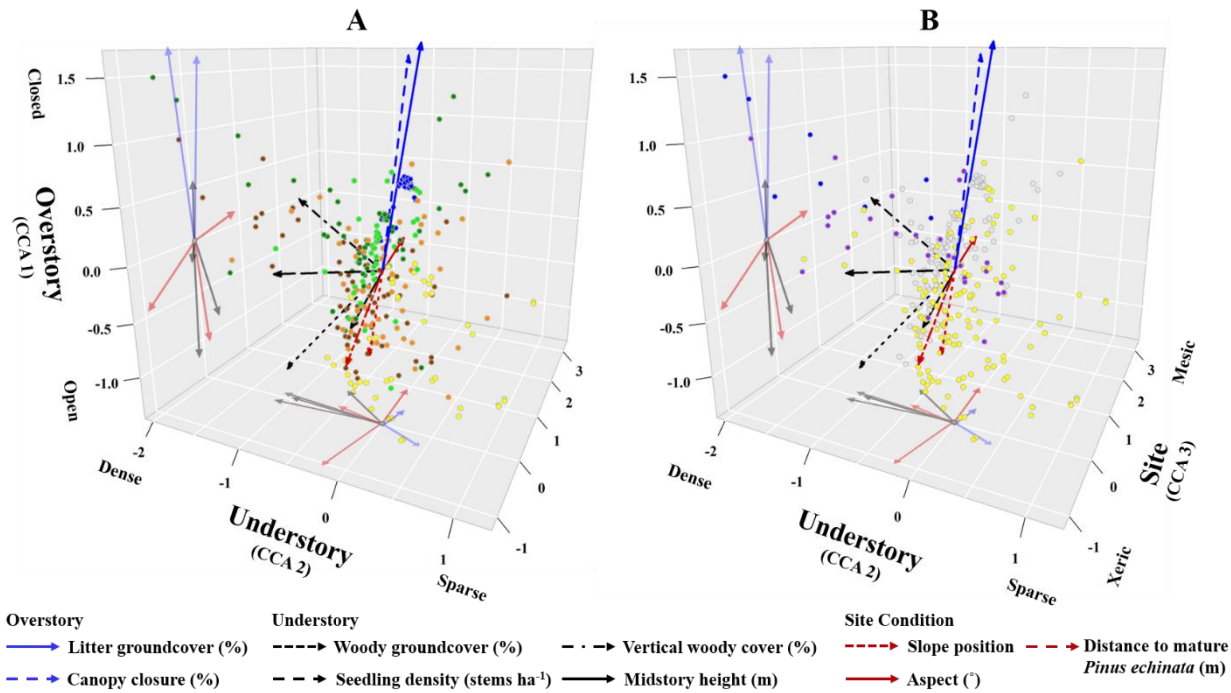
Appendix SI3. Layout of sampling plots used to collect shortleaf-bluestem response and explanatory variables.



Appendix SI4. Canonical correspondence axis scores for explanatory variables and CCA ordinations of shortleaf-bluestem community response along three gradients ($P \leq 0.016$) describing open to closed canopies, dense to sparse woody understory, and xeric to mesic site conditions on the Cumberland Plateau, TN. A) Sampling plots color coded by treatment. B) Sampling plots color coded by *Pinus echinata* and C_4 grass presence. Arrows depict the magnitude and direction of explanatory variable correlations and were reflected in A and B to improve axis interpretation. Appendix SI2 details variables. Treatments include unmanaged stands (Control), spring (Sp) or fall (Fa) fire with woodland (14 m^2 ha^{-1}, W) or savanna (7 m^2 ha^{-1}, S) residual basal area, and advanced savannas (AS).

Explanatory variable	CCA1	CCA2	CCA3	CCA4
Litter groundcover (%)	**0.878**	0.197	-0.115	-0.138
Canopy closure (%)	**0.832**	0.063	0.156	-0.144
Seedling Density (stems ha^{-1})	-0.089	**-0.564**	-0.026	0.098
Woody groundcover (%)	**-0.568**	**-0.550**	0.040	0.086
Vertical woody cover (%)	0.251	**-0.433**	0.032	0.132
Midstory height (m)	-0.358	-0.246	**0.218**	0.167
Slope position (numeric, alluvial to ridge)	-0.188	0.092	**-0.421**	-0.119
Aspect (0 to 2, Beers et al. 1966)	0.063	-0.011	**0.327**	**-0.295**
Distance to overstory *Pinus echinata* (m)	-0.436	-0.190	0.045	**-0.236**

*Values ± 1 standard deviation from 0 are shaded.



Appendix SI5. Occurrence component of zero-inflated negative binomial models for *Pinus echinata*-bluestem response variables as modeled by overstory, understory, and site variables. Parameter estimates (SE), log likelihood, *df*, and a chi square goodness of fit test are presented.

	Explanatory Variables[1]												
Response Variable	Intercept	CC	MidHT	Nudd	pWoody	Aspect	Position	DtoSLP	Year	LL	*df*	Critical χ^2	Model χ^2
Hdiver	-3.41 (0.49)	1.95 (0.47)	-	0.71 (0.20)	-1.20 (0.34)	-	0.51 (0.20)	-	0.94 (0.40)	-1,315	9	379.8	281.2
Hhght	-3.90 (0.56)	1.66 (0.62)	-	-	-0.83 (0.38)	-0.48 (0.21)	-	-	-	-2,092	11	377.6	320.7
Grass	-3.18 (0.44)	2.02 (0.50)	-	0.51 (0.21)	-1.33 (0.34)	-	-0.40 (0.20)	-	-	-1,938	10	378.7	316.4
Forb	-1.79 (0.22)	1.47 (0.27)	-	-	-0.64 (0.23)	-0.48 (0.16)	-	-	-	-1,794	9	379.8	325.3
Fern	1.26 (0.15)	0.74 (0.18)	-0.81 (0.21)	0.66 (0.16)	0.75 (0.26)	-	0.62 (0.14)	-	-	-751	10	378.7	370.8
VegG	-0.38 (0.13)	1.24 (0.16)	0.31 (0.14)	-	-	-	-	-	-	-1,433	12	376.6	346.4
dNWSG	0.13 (0.13)	1.37 (0.17)	0.43 (0.16)	-	-	0.28 (0.14)	-	-0.42 (0.15)	-	-1,695	10	378.7	306.4
pNWSG	0.11 (0.14)	1.58 (0.16)	-	-	-	-	-	-	-	-1,188	8	380.8	299.6
dSLP	1.57 (0.16)	0.55 (0.15)	-	-	-	0.40 (0.15)	-	-	-	-697	8	380.8	337.2
RCD	1.57 (0.16)	0.55 (0.15)	-	-	-	0.40 (0.15)	-	-	-	-542	7	381.9	366.9
SLPhght	1.69 (0.16)	0.53 (0.15)	-	-	-	0.41 (0.16)	-	-	-	-622	7	381.9	337.0
LBSD	1.69 (0.16)	0.53 (0.15)	-	-	-	0.41 (0.16)	-	-	-	-504	7	381.9	377.8
#BS	1.69 (0.16)	0.53 (0.15)	-	-	-	0.41 (0.16)	-	-	-	-507	11	377.6	343.9
Mclass	1.69 (0.16)	0.53 (0.15)	-	-	-	0.41 (0.16)	-	-	-	-444	9	379.8	330.9

[1]Variables defined in Appendix SI2. SeedDEN was also included, but never significant. ZINB coefficients reflect binomial distribution with logit link. Before analysis, explanatory variables were z standardized and response variables were rounded to integers after a $\sqrt{y * 10{,}000}$ transformation. Parameter significance determined by Wald test ($\alpha = 0.05$). LL (log-likelihood), *df*, and χ^2 values are for the overall model (occurrence and count components).

Appendix SI6. Count component of zero-inflated negative binomial models for *Pinus echinata*-bluestem response variables as modeled by overstory, understory, and site variables. Parameter estimates (SE) and log of theta are presented for each model.

Response Variable[1]	Explanatory Variables[1]										
	Intercept	CC	SeedDen	MidHT	Nudd	pWoody	Aspect	Position	DtoSLP	Year	Log(theta)
Hdiver	4.87 (0.01)	-0.14 (0.01)	-	-	-	-	-	-	-	-	4.04 (0.13)
Hhght	5.99 (0.04)	-0.38 (0.03)	-	-	-0.16 (0.03)	-	-	-0.07 (0.03)	0.06 (0.03)	-0.44 (0.05)	1.55 (0.08)
Grass	6.22 (0.03)	-0.34 (0.03)	-	-	-0.05 (0.02)	-	-	-	-	-0.19 (0.05)	1.84 (0.08)
Forb	5.83 (0.03)	-0.42 (0.03)	-	-	-0.19 (0.03)	-	-	-	0.07 (0.03)	-	1.74 (0.09)
Fern	5.72 (0.08)	-	-	-	-	-	-	-0.20 (0.05)	-	-0.24 (0.11)	1.32 (0.15)
VegG	5.85 (0.06)	-0.43 (0.05)	-	0.22 (0.06)	-0.12 (0.04)	-0.31 (0.07)	-	-0.10 (0.04)	-0.07 (0.04)	-0.40 (0.08)	1.49 (0.10)
dNWSG	8.75 (0.05)	-0.20 (0.05)	-	-	-	-0.23 (0.05)	-	-	-0.09 (0.04)	-	1.38 (0.11)
pNWSG	5.80 (0.06)	-0.29 (0.05)	-	-	-0.17 (0.04)	-0.20 (0.05)	-	-	-	-0.33 (0.07)	1.75 (0.11)
dSLP	7.13 (0.07)	-	0.27 (0.07)	-	-0.17 (0.08)	0.32 (0.09)	-	-	-	-	1.18 (0.16)
RCD	5.38 (0.05)	-0.12 (0.05)	-	-	-0.13 (0.04)	-	-	-	-	-	2.33 (0.18)
SLPhght	7.20 (0.05)	-	-0.13 (0.05)	-	-0.12 (0.06)	-	-	-	-	-	1.81 (0.18)
LBSD	5.12 (0.06)	-	-	-	-0.28 (0.06)	-	-	-	0.20 (0.08)	-	1.43 (0.18)
#BS	4.99 (0.08)	-	0.10 (0.05)	-0.25 (0.10)	-	0.36 (0.09)	-0.30 (0.07)	-	-0.17 (0.07)	0.43 (0.12)	2.01 (0.18)
Mclass	5.07 (0.02)	-	-0.09 (0.03)	0.08 (0.03)	-0.09 (0.03)	-	-	-0.05 (0.02)	-	-	3.65 (0.23)

[1]Variables defined in Appendix SI2. Count model coefficients reflect negative binomial distribution with log link. Before analysis, explanatory variables were z standardized and response variables were rounded to integers after a $\sqrt{y * 10{,}000}$ transformation. Parameter significance determined by Wald test ($\alpha = 0.05$).

CHAPTER II
LIMITED EFFECTIVENESS OF WOODLAND AND SAVANNA RESTORATION AS FUEL REDUCTION TREATMENTS IN OAK FORESTS OF THE MID-SOUTH

This chapter is original work by Andrew L. Vander Yacht with contributions from co-authors Patrick D. Keyser, Charles Kwit, Mike C. Stambaugh, Wayne K. Clatterbuck, and Dean M. Simon. It has been submitted to "*International Journal of Wildland Fire*".

ABSTRACT

Thinning and fire can restore disturbance-dependent communities in the southern Appalachian and Central Hardwood regions of the US, but simultaneous reductions in fuel loading have not been substantiated. At 3 sites from 2008 to 2016, we monitored fuel-load response to restoration treatments including controls, burn-only in fall (October) or spring (March), and such fires paired with woodland (14 m^2 ha^{-1}) or savanna (7 m^2 ha^{-1}) residual basal area. All treatments except burn-only increased total fuel-loading. Thinning, regardless of degree, doubled (+20 Mg ha^{-1}) coarse-woody (diameter >0.66 cm) fuel-loads relative to controls. Burning 3 times in 6 years did not affect this difference. In combination, thinning and burning reduced fine fuel-loads. Biennial burning maintained reduced loading of woody fine-fuels (leaf litter and 1-hr twigs), but herbaceous fuel-loads increased at a rate suggestive of compensation for losses in woody fine-fuels within 10 years. Thus, fire may only reduce fine fuel-loads during the early stages of a transition in composition from woody to herbaceous dominance. The implications of this transition on fire behavior deserves exploration, but the potential lack of ultimate effects on fine fuel-loads and observed doubling of coarse-woody fuel-loads suggests restoration associated thinning and burning are not regionally effective fuel-reduction treatments.

Keywords: fuel treatment; thinning; prescribed fire; fire season; and herbaceous fuel.

INTRODUCTION

Fire has long regulated the world's plant communities (Bond and Keeley 2005; Pausas and Keeley 2009), including the oak (*Quercus* spp.) and pine (*Pinus* spp.) dominated portions of the southern Appalachian and Central Hardwood regions of the U.S. (hereafter, Mid-South;

Lafon et al. 2017). Fire-scar analyses (Guyette *et al.* 2006; Aldrich *et al.* 2014), charcoal and pollen in sediment and soil cores (Delcourt *et al.* 1998), witness tree records (Thomas-Van Gundy and Nowacki 2013), and patterns in the age structure of trees (Flatley *et al.* 2015) all demonstrate a strong, historical influence of fire on the region's vegetation. Frequent burning created and maintained mosaics of open woodlands (30-80% canopy cover) and savannas (10-30% canopy cover, Nelson 2010) where closed-canopy forests would otherwise develop (Abrams 1992; DeSelm 1994; Noss 2013). A positive feedback between recurring fires and the fuel properties of promoted plants sustained these disturbance-dependent communities (Mitchell *et al.* 2009). Highly flammable, warm-season grasses were abundant and potentially limited mesophytic woody encroachment (Maynard and Brewer 2013) under oaks well prepared to endure the fires their leaf litter (hereafter, litter) facilitated (Varner *et al.* 2016).

The historical influence of fire was nearly eliminated from the Mid-South during the early 20th century. The "Great Cutover" promoted catastrophic wildfires that threatened national forest resources (Pyne 2015). In response, fire suppression became federal policy (Stephens and Ruth 2005), and consequently, vegetation succession transformed open communities into closed-canopy forests dominated by fire-sensitive species (Abrams 1998; Nowacki and Abrams 2008). Woodlands and savannas of pine and oak now occupy only a minor fraction of their pre-European settlement extent (Nuzzo 1986; Fralish *et al.* 2000; Hanberry *et al.* 2014; South and Harper 2016). Widespread densification of forests threatens diverse herbaceous ground-layers (DeSelm 1994; Leach and Givnish 1999), disturbance-dependent wildlife (Hunter *et al.* 2001; Harper *et al.* 2016), and the regeneration potential of many tree species (Masters 2007; McShea *et al.* 2007). Such loss of biodiversity can decrease resistance and resilience to invasive species

and disease, and irrevocably alter ecosystem productivity, sustainability, and function (Tilman *et al.* 1996; Knops *et al.* 1999; Liang *et al.* 2016).

Reversing such effects with prescribed fire is complicated by widespread changes in fuel-bed properties (Spetich *et al.* 1999; Nowacki and Abrams 2008). Departure from historical fire regimes has 1) increased fuel accumulation and the occurrence of uncharacteristically severe wildfires, or 2) reduced fuel-bed flammability by shifting forest structure and composition (Ryan *et al.* 2013). This second phenomenon is increasingly associated with the eastern U.S. Regionally, mesophication has promoted environments and species with physical and chemical properties not conducive to burning (Kreye *et al.* 2013; Alexander and Arthur 2014; Varner *et al.* 2015). Alternatively, prolonged fire suppression has possibly upset the balance between fuel production and decomposition that is typically observed in eastern ecosystems (Onega and Eickmeier 1991; Graham and McCarthy 2006). Oak and pine dominated overstories, often a legacy of historical fire and harvesting, are aging into senescence (Abrams 2003; South and Harper 2016). Over-stocking, promoted by fire-suppression and widespread decreases in forest harvesting, has led to unprecedented tree mortality during recent insect outbreaks (Coulson and Stephen 2006). If forest senescence proceeds in the absence of management, heavy fuel-loads could combine with climate-change induced increases in fire activity (Mitchell *et al.* 2014) to promote catastrophic wildfires that degrade regional ecosystems (Vose and Elliott 2016). Thus, there exists a need for effective fuel-management in the Mid-South.

Restoring fire-dependent communities could reverse declines in fuel-bed flammability that succession in the absence of fire has promoted. Mechanical thinning promotes combustion by increasing ground-level light, temperature, and wind speed; decreasing fine-fuel moisture content and relative humidity; stimulating herbaceous growth; and shifting tree composition

toward species that contribute flammable litter (Nielsen *et al.* 2003; Brewer 2016). Thus, canopy reduction alters fuel-beds and increases their ability to support a long-term regimen of repeated fire. Such burning regimes can then advance restoration by promoting herbaceous dominance of the understory (Peterson *et al.* 2007; Dey *et al.* 2015), and are simultaneously better positioned to consume woody fuels. Fire severity, the risk it poses to local communities (Hardy 2005; Stambaugh *et al.* 2011), and smoke emissions that reduce air-quality (Goodrick *et al.* 2010) generally exhibit a positive relationship with fuel-loading. Prescribed fire and mechanical surrogates can successfully reduce fuel-loading and lower wildfire risk and severity (Fernandes and Botelho 2003; Agee and Skinner 2005; Stephens *et al.* 2012). Such management techniques have also shown promise in restoring fire-dependent communities in the Mid-South (Vander Yacht *et al.* 2017; Vander Yacht *et al.* In Review).

Fuel treatments have been successful in the western U.S. (Stephens *et al.* 2012), but comparatively little research has occurred in the Mid-South. Substantial differences in climate and species composition limit extrapolating between regions. The few evaluations of thinning and fire as fuel treatments in the Mid-South have concluded short-term reductions in fine-fuel loads but limited effects on larger fuel classes (Graham and McCarthy 2006; Loucks *et al.* 2008; Waldrop *et al.* 2010). More recent and long-term monitoring has reached similar conclusions (Waldrop *et al.* 2016; Arthur *et al.* 2017), but only one of these studies involved canopy disturbance (Waldrop *et al.* 2016). Improving fuel-bed flammability by replicating historical woodland and savanna overstory conditions could increase the combustion of large fuels and thereby address past failures of regional fuel-treatments (McIver *et al.* 2013). Growing-season fire may have advantages over dormant-season fire in promoting understory woody stem mortality and herbaceous dominance (Brose and Van Lear 1998; Knapp *et al.* 2009), but the

effects of seasonal variability in fire on fuel loads has not been documented in the Mid-South. Further, potentially important contributions of herbaceous fuels have been overlooked in past studies. An increased understanding of how canopy disturbance, fire-season, and herbaceous fuels influence fuel-dynamics should lead to regionally effective fuel-treatments.

We applied oak woodland and savanna restoration management to closed-canopy forest stands at 3 sites located across the Mid-South and documented effects on a range of fuel categories. Applied management included thinning to woodland (14 m^2 ha^{-1}) or savanna (7 m^2 ha^{-1}) residual basal area paired with burning, sometimes repeatedly, in the fall (October) or spring (March). We hypothesized that 1) thinning would initially increase coarse woody fuels (10, 100, and 1000 hour), and these increases would be positively related to the degree of canopy disturbance 2) thinning would decrease fine-fuels (l hour and litter), and these decreases would be positively related to canopy disturbance 3) fire would reduce all fuel categories, and these reductions would be greatest during the drier conditions associated with fall burning 4) increases in herbaceous fuels over time would compensate for reductions in other fine-fuels. Our overall goal was to understand the effects of woodland and savanna restoration on fuel-load dynamics, and isolate regional generalities informative to related management decisions.

METHODS

Study Areas

Our research occurred at 3 sites located across the Mid-South. Catoosa Wildlife Management Area (CWMA) is 32,374 ha of the Southwestern Appalachians ecoregion (all ecoregions: Level III, U.S. EPA 2013) managed by the Tennessee Wildlife Resources Agency (TWRA). Moderately rolling ridges and dissecting ravines ranged from 437-521 m in elevation. Soils were Mesic Typic Hapludults (Soil Survey Staff NRCS 2014) over weathered sandstone

and conglomerate (Nicholson *et al.* 2005). Annual precipitation and temperature averaged 140 cm and 13 °C, respectively, from 1981 to 2010 (National Climatic Data Center 2014). Forests were established in the 1920's following agricultural abandonment and were dominated by oaks (Vander Yacht *et al.* 2017). Shortleaf pine (*Pinus echinata* Mill.) became a minimal overstory component after the southern pine bark beetle (*Dendroctonus frontalis* Zimmermann) outbreak of 1999-2000 that created an abundance of shortleaf snags and downed logs. Oak savanna management was initiated by TWRA in 2002 using salvage logging and prescribed fire.

To the east, Green River Game Lands (GRGL) is 5,726 ha managed by the North Carolina Wildlife Resources Commission (NCWRC) at the interface between the Blue Ridge and Piedmont ecoregions. Narrow ridges and steep ravines range from 366 – 640 m in elevation. Soils are deep (>1 m), well-drained, and mostly in the Evard Series (fine loamy, oxidic, Mesic Typic Hapludults, Keenan 1998) over gneiss, schist, and phyllite rock (Clark 2008). Annual precipitation and temperature from 1981 to 2010 averaged 139 cm and 14 °C, respectively, for nearby Hendersonville, NC (National Climatic Data Center 2014). Forests were 80 to 120 years old and unmanaged for at least 50 years (Dean Simon, NCWRC, pers. comm.). Oaks and yellow poplar (*Liriodendron tulipifera* L.) dominated canopies over a dense, ericaceous understory (*i.e.*, mountain laurel [*Kalmia latifolia* L.] and rosebay rhododendron [*Rhododendron maximum* L.]).

Furthest west, Land Between the Lakes National Recreation Area (LBL) is 68,797 ha situated between Kentucky Lake and Lake Barkley in the Western Highland Rim of the Interior Plateau and managed by the U.S. Forest Service. Research occurred at two adjacent sites (Buffalo Trace and Cemetery Ridge) just south of the Kentucky border in Tennessee. Elevations ranged from 122–198 m across rolling ridges and broad valleys. Limestone bedrock underlies the LBL peninsula, and soil series include Bodine, Baxter and Hammock with loess caps on

ridgetops and mid-slopes (Franklin *et al.* 2003). Mean annual precipitation and temperature from 1981 to 2014 was 134 cm and 14 ˚C, respectively. Oak species dominated the overstory, and research sites were located within LBL's Oak-Grassland Restoration and Demonstration Area.

Experimental Design and Restoration Treatments

Prior to treatments, selected stands were representative of regional, oak-dominated forests (Vander Yacht *et al.* 2017). Canopy closure averaged 90.7 % (± 2.5 SE) and live basal area was 20.1 m^2 ha^{-1} (± 2.0 SE). Snag basal area was greatest at CWMA (3.9 m^2 ha^{-1} ± 0.7 SE), lowest at LBL (0.7 m^2 ha^{-1} ± 0.4 SE), and intermediate at GRGL (1.5 m^2 ha^{-1} ± 0.5 SE). Sapling (woody stems >1.4 m tall, < 12.7 cm diameter at breast height [DBH]) density descended from east to west across sites (GRGL: 2,423 stems ha^{-1} ± 391 SE, CWMA: 1,936 stems ha^{-1} ± 182 SE, LBL: 985 stems ha^{-1} ± 219 SE). Understories were dominated by ericaceous shrubs, woody plant regeneration, and litter. Herbaceous groundcover was minimal (5.7 % ± 2.0 SE).

We treated sites as independent experiments because of differences in the timing and type of management, and non-synchronous data collection. At each site, 20-ha forested stands were configured to maximize core area and assigned a treatment using a completely randomized design. At CWMA and GRGL, treatments included: 1) spring burning (prior to bud-break) after thinning to woodland residual basal area (14 m^2 ha^{-1}, SpW), 2) fall burning (prior to leaf abscission) after woodland thinning (FaW), 3) spring burning after thinning to savanna residual basal area (7 m^2 ha^{-1}, SpS), 4) fall burning after savanna thinning (FaS), and unmanaged, closed-canopy forests (Control). We also included a fall burning only treatment (FaO) at GRGL. Each treatment was replicated twice at CWMA, and once at GRGL. We established 2 replicates of 6 similar, but unique, treatments at LBL. Target residual basal area for savanna treatments at LBL was slightly greater (9 m^2 ha^{-1}) than at other sites. Also, burning treatments at LBL included

Buffalo Trace (BT), a site with 2 woodland and savanna replicates burned in the fall before thinning and again in the spring after thinning, and Cemetery Ridge (CR), a site with 2 woodland and savanna replicates only burned in the spring after thinning (Fig. II1). The CR site also had 2 replicates of a spring burn only treatment (SpO).

Canopy reductions were completed commercially at each site during the dormant season (Fig. II1). Where possible, oaks, hickories, and shortleaf pine were retained while mesophytic species including maples (*Acer* spp.), yellow poplar, and sweetgum (*Liquidambar styraciflua* L.) were removed. The generation and placement of logging slash was typical of state and federal timber contracts. Most slash accumulated near log landings on the periphery of stands, but some limbing and topping occurred within stand cores (50-m buffer). Comparatively little slash was generated at LBL. At GRGL, a substantial portion of slash was placed in skid trails to prevent erosion. After thinning, but before burning, residual basal area and canopy closure was comparable across sites within control and burn only treatments (21.4 m^2 ha^{-1} ± 1.1 SE, 97.6 % ± 0.4 SE), woodlands (14.6 m^2 ha^{-1} ± 1.5 SE, 77.7 % ± 4.6 SE), and savannas (9.3 m^2 ha^{-1} ± 1.6 SE, 53.7 % ± 4.2 SE, Vander Yacht *et al.* 2017).

Site managers conducted all prescribed fires (Fig. II1, Table II1). Ring firing was used at CWMA to burn FaW and FaS 3 times in mid-October (2010, 2012, and 2014), and SpW and SpS 3 times in mid-March (2011, 2013, and 2015). Strip-head firing was used at GRGL (October 2015 and March 2016), and at LBL during the CR fire (April 2015) and the fall BT fire (November 2009). The BT site at LBL was ignited aerially using a helicopter (March 2016). Burning conditions and fire behavior were monitored similarly at all sites following Vander Yacht *et al.* (2017). This included oven drying fuel samples to determine moisture content, on-site weather recording, and systematic measurements of fire spread and flame lengths. We also

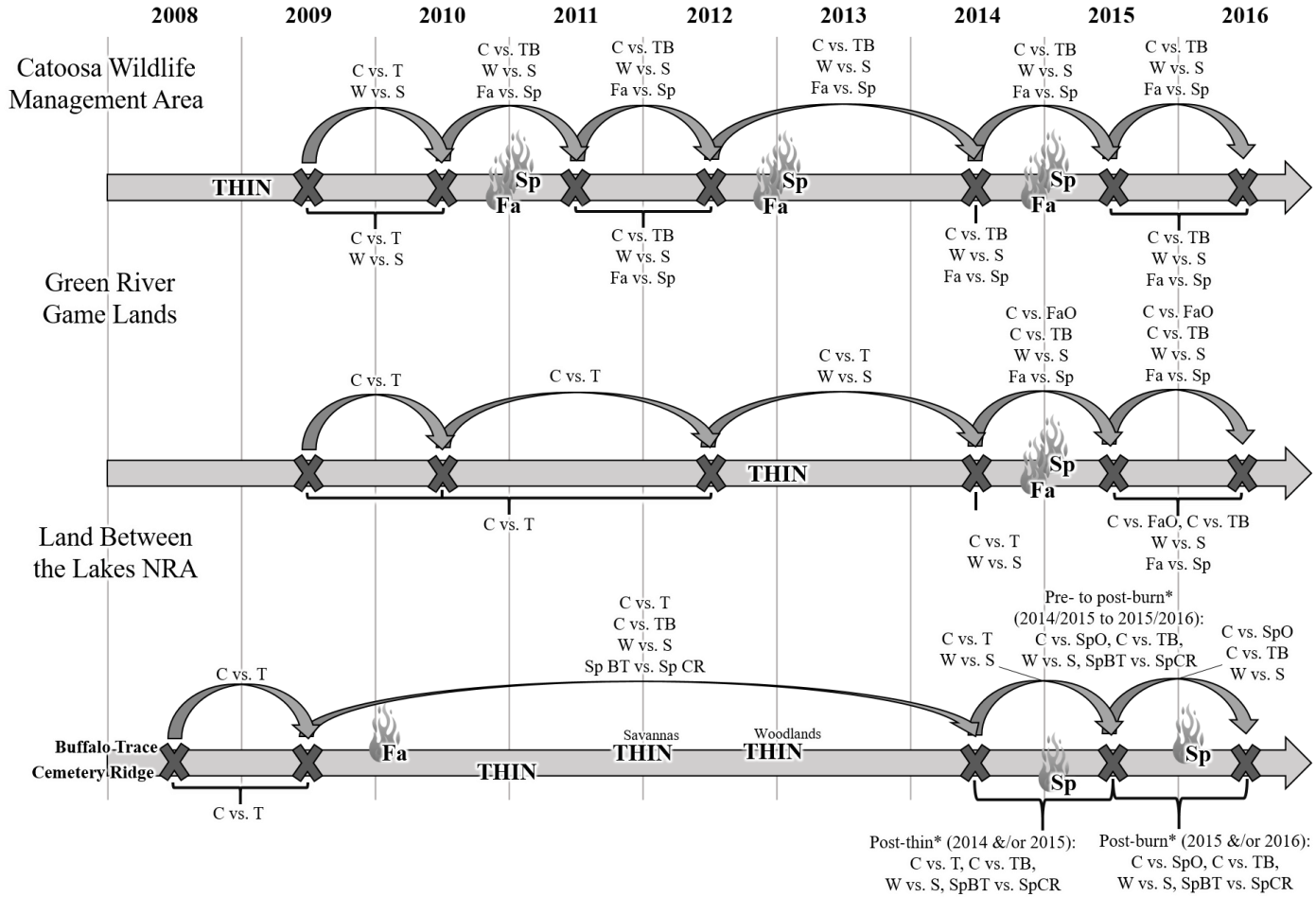


Fig. II1. Timelines depicting treatment implementation, data collection (X's), and tested comparisons during (2008 to 2016) an oak woodland and savanna restoration experiment at 3 sites located across the Mid-South. Treatment (below timeline) and interaction (above timeline) contrasts evaluated differences between replicate stands (20-ha) that were: unmanaged or thinned (C vs. T), unmanaged or burned only in the fall (C vs. FaO) or spring (C vs. SpO), unmanaged or thinned and burned (C vs. TB), reduced to woodland (14 m^2 ha^{-1}) or savanna (7 m^2 ha^{-1}) residual basal area (W vs. S), burned in the fall or spring (Fa vs. Sp), and burned in separate spring fires (SpBT vs. SpCR). *Data from 2014 to 2016 at Land Between the Lakes were compiled as indicated to allow for contrasts among fires not conducted within the same year.

Table II1. Seasonal comparison of weather, fuel moisture, and fire behavior for prescribed fires during an oak woodland and savanna restoration experiment at Catoosa Wildlife Management Area (CWMA), Green River Game Lands (GRGL), and Land Between the Lakes (LBL). Statistics based on a two-sample t-test assuming unequal variance.

		Fire season				
Variable	Units	Fall	Spring	*t*	*df*	*p*
Ambient temperature	˚C	24.6 ± 0.5	17.6 ± 0.6	8.80	101	**< 0.001**
Relative humidity	%	39.0 ± 1.2	38.6 ± 1.5	0.17	110	0.867
Wind speed	m s^{-1}	1.6 ± 0.2	3.5 ± 0.2	6.86	102	**< 0.001**
Wind direction	˚	214.8 ± 15.8	204.5 ± 14.4	0.48	94	0.631
Fine-fuel moisture	%	12.5 ± 0.8	17.0 ± 1.5	2.67	90	**0.009**
10-hour fuel moisture	%	9.2 ± 0.9	10.1 ± 0.6	0.78	22	0.446
Flanking fire rate-of-spread	m min^{-1}	0.6 ± 0.1	1.1 ± 0.3	1.45	25	0.159
Flanking fire flame-length	m	0.4 ± 0.1	0.6 ± 0.1	1.55	44	0.127
Heading fire rate-of-spread	m min^{-1}	1.6 ± 0.1	2.9 ± 0.4	3.03	30	**0.005**
Heading fire flame-length	m	0.7 ± 0.1	1.3 ± 0.1	3.61	37	**< 0.001**
Fire temperature	˚C	170.6 ± 7.7	210.2 ± 15.3	2.32	122	**0.022**

[1]Fall burns at CWMA: 11 Oct 2010, 24 Oct 2012, and 24 Oct 2014. Spring burns at CWMA: 22 Mar 2011, 15 Mar 2013, and 18 Mar 2015. Fall burn at GRGL: 27 Oct 2014. Spring burn at GRGL: 18 March 2015. Buffalo Trace spring burn at LBL: 29 Mar 2016. Cemetery Ridge spring burn at LBL: 22 Apr 2015.

sampled fire temperature using foil-wrapped ceramic tiles (n = 181) painted with Tempilaq® indicating liquids. Monitored burning condition and fire behavior variables are summarized by season (Table II1) based on the relatively few observations of single fires at LBL and GRGL. Conditions were warmer (+7˚ C) and less windy (-1.9 m s^{-1}), and fine-fuels (litter and 1-hour twigs) were nearly 5% drier, during fall relative to spring burning. Heading fires in the spring were nearly double the rate-of-spread and flame length of heading fires in the fall. Spring fires also burned nearly 40 ˚C hotter, on average, than fall fires.

Sampling Design and Data Collection

We monitored the loading of dead and down woody fuels (logs and twigs), litter, and herbaceous vegetation using >60,240 m of planar-intercept transects (Brown 1974) and 6,300 samples of litter and herbaceous fuels collected during 1,916 unique plot visits. Data collection across all sites occurred at different intervals from 2008 to 2016 based on the sequence of management activities (Fig. II1). This occurred at permanent plots located along a 70 X 70 m grid (Avery and Burkhart 2002) within the core (50-m buffer) of each treatment stand. At each plot, planar intercept techniques monitored woody fuels by diameter size classes that corresponded to hourly rates of change in moisture content, including 1-h (0.0–0.64 cm), 10-h (0.66–2.54 cm), 100-h (2.55–7.62 cm), and 1,000-h (>7.62 cm) fuels (Cohen and Deeming 1985). A fuel piece was tallied if its central axis was completely crossed by the transect plane (height: 1.83 m), it was not self-supporting, and had a lean angle >45˚ from vertical (Brown *et al.* 1982; Woodall and Monleon 2008). As is common practice, all intersections were counted regardless of piece connectiveness outside of the plane (*e.g.*, double counting forked pieces).

We conducted two 20-m planar-intercept transects at 15 plots per stand, oriented in the upslope and perpendicular to slope directions. For all intersected 1000-h fuels, we recorded

diameter and binary decay class (rotten, class 1 to 3; sound, class 4 and 5 as described in Waddell 2002). We tallied 100-h fuel intersections between 5 and 15 m on each transect. Transect length for 1000-h and 100-h fuels was extended until a piece was encountered, or a maximum of 85 m was traveled. Intersections with 1-h and 10-h surface fuels were tallied between 5 and 8 m. We measured up-hill transect slope using a clinometer. At 5 locations per plot (center, 10-, and 20-m positions along each transect), we collected all fine and herbaceous fuels present within a 0.25-m^2 sample. We separately collected litter and unexposed 1-h twigs, native C_4 grasses, and other herbaceous fuels. Herbaceous fuel categories were additionally sorted into live and dead categories. These samples were dried in ovens for 5 days at 55˚C and then weighed to the nearest 0.1 g. We collected biomass, 1-h, and 10-h fuel data just prior to intended fires (August or February) based on seasonal dynamics in smaller fuel classes (Stambaugh *et al.* 2011). Less dynamic and larger fuel classes were always measured in August.

From 2008 to 2012, woody fuels were similarly monitored but only one randomly oriented transect was conducted at 6 to 8 plots per stand. Standard error for these estimates was consistently 1.5X greater than 2014 to 2016 estimates, but otherwise appeared to match trends in data derived from expanded methods. We did not collect fine and herbaceous fuel biomass from 2008 to 2012. Herbaceous fuels were rare during the early stages of restoration, and litter depth during these years was measured at 10 locations (2-m intervals) along each fuel transect. We defined litter as freshly fallen leaves that were taxonomically and morphologically identifiable. We also measured duff depths, but do not present this data because fires rarely consumed duff.

Fuel Load Calculation and Analysis

Plot-level woody fuel-loads were determined using squared diameter sums by decay class (1000-h) or the number of transect intercepts (1-h, 10-h, 100-h) and Brown (1974) equations. We

calculated slope correction factors by transect, and assumed a non-horizontal correction factor of 1.00 for 100-h and 1000-h fuels and 1.13 for 1-h and 10-h fuels (Chojnacky *et al.* 2004; Parresol *et al.* 2012). For 1000-h fuels, we calculated sound and rotten specific gravity constants using estimates presented in Harmon *et al.* (2008) and data on overstory (>12.7 cm DBH) species composition during our experiment (2008 to 2016, see Vander Yacht *et al.* 2017). This involved averaging the species-specific estimates presented in Appendix 2 of Harmon *et al.* (2008) to our sound (class 1-3) and rotten (class 4-5) categories, and then calculating sound and rotten estimates for each stand weighted by observed species composition. For 1000-h fuels, sound specific gravity values ranged from 0.385 to 0.479 g/cm^3, and rotten from 0.187 to 0.231 g/cm^3.

For smaller woody fuels, we used oak and pine forest type estimates of quadratic mean diameters (1-h: 0.22 cm, 10-h: 1.22 cm, 100-h: 4.30 cm) determined by Woodall and Monleon (2010) in Brown (1974) equations. Similar to 1000-h fuels, we calculated stand-level estimates of 100-h fuel specific gravity (range: 0.569 to 0.664 g/cm^3) and decay constants (range: 0.869 to 0.901 dimensionless, defined in Waddell 2002) using Appendix 4 in Harmon *et al.* (2008) and overstory composition data. The same process was used for 10-h and 1-h fuels, but estimate calculations also incorporated overstory (weight = 75% for 10-h, 50% for 1-h) and midstory (weight = 25% for 10-h, 50% for 1-h) composition. Midstory (woody stems >1.4 m tall, ≤ 12.7 DBH) and overstory composition was documented at fuel plot locations in association with concurrent vegetation monitoring (Vander Yacht *et al.* 2017). Resulting specific gravity (10-h: 0.660 g/cm^3 ± 0.03 SE; 1-h: 0.727 g/cm^3 ± 0.01 SE) and decay constants (10-h: 0.855 g/cm^3 ± 0.01 SE; 1-h: 0.829 g/cm^3 ± 0.00 SE) varied little across stands. We calculated litter loading in 2008 to 2012 from depth measurements using a bulk density factor (12.2 kg/m^3) quantified in hardwood forests throughout the southern U.S. (Ottmar and Andreu 2007). Although litter depth

and loading relationships can be complicated by variability in litter type, age, and cycles of wetting and drying, data calculated in this fashion (2008-2012) aligned well with patterns in data based directly on mass sampling (2014-2016).

We calculated annual plot-level means for dependent variables, including loading of coarse woody fuels (CWF: sum of 10-h, 100-h, and 1000-h), loading of fine woody fuels (FWF: leaf litter and 1-h), and herbaceous fuel loading. We transformed dependent variables using a square root function, tested for normality (Wilk's test, $W > 0.90$), and graphically observed equality of variance. Separate mixed-effect ANOVA models were developed for each dependent variable. Fixed-effects included treatment, year, and treatment × year interactions. Year was a fixed-effect because treatments were applied over time. Replicates within a treatment were included as a random-effect. We used Kenward-Roger degree of freedom method but dropped autoregressive correlation between annual data (repeated measures) because treatments were applied over time and differences in model fit were small (<5, -2 residual log likelihood per covariance parameter) between inclusion and omission (Littell et al., 2006).

We expected difficult to interpret treatment × year interactions because treatments were applied over time. Therefore, we used orthogonal contrasts to test specific, *a priori* hypotheses (Fig. II1). Orthogonal contrasts are independent statistical tests that do not depend on overall ANOVA results. We included treatment contrasts that tested for differences within specific management intervals (*e.g.*, post-thin and pre-burn) and interaction contrasts that tested for differences across each available year interval (*e.g.*, control versus treatment from 2009 to 2010). Comparisons included control to thinned (C vs. T), control to burned only (C vs. FaO and C vs. SpO), control to thinned and burned (C vs. TB), woodland to savanna residual basal area (W vs. S), October to March burns (Fa vs. Sp), and separate spring fires (SpBT vs. SpCR at LBL).

Because fire treatments did not occur in the same year at LBL, we compiled a pre- and post-burn data set to allow for similar contrast tests. Except for C vs. T, which was always tested, contrasts were only evaluated following the implementation of compared management (Fig. II1). We limit discussion of insignificant ($\alpha > 0.05$) contrasts to those of interest. All analysis was conducted in SAS 9.4 using PROC MIXED (SAS Ins., Cary, N.C., USA).

RESULTS

Coarse Woody Fuels

We observed a similar CWF response to applied management across the three sites (Fig. II2). Loading of CWF in controls was similar at CWMA (23.5 Mg ha^{-1} ± 2.4 SE) and GRGL (20.4 Mg ha^{-1} ± 2.1 SE), about half this level at LBL (12.0 Mg ha^{-1} ± 2.3 SE), and more constant over time relative to other treatments at all sites. Thinning consistently doubled CWF loading (Fig. II3, CWMA: 1.9 X, GRGL: 2.0 X, and LBL: 2.5 X) relative to controls. Post-thinning but pre-fire, CWF loads were a consistent 19.6 Mg ha^{-1} (± 4.6 SE) greater in thinned relative to control stands averaged across all three sites (Table II2). Significant contrasts indicated this difference was the result of increases in CWF from pre- to post- thinning that were 20.9 Mg ha^{-1} (± 7.65 SE) greater, on average, than any increase observed in controls (Table II3). Burning at LBL just prior to thinning resulted in a 57% smaller increase in CWF relative to thinning alone (Fig. II3, Table II2). There was no consistent difference in CWF load response across woodland and savanna treatments immediately following thinning (Fig. II3, Tables II2-II3).

Effects of fire on CWF were site dependent (Fig. II3). Following initial fires at CWMA, stands that were thinned and burned contained more than double the CWF present in controls. Also, CWF in savannas was 19.3 Mg ha^{-1} (29.8%) less than that observed in woodlands at CWMA (Table II2). The opposite was observed at GRGL; loading of CWF in woodlands was

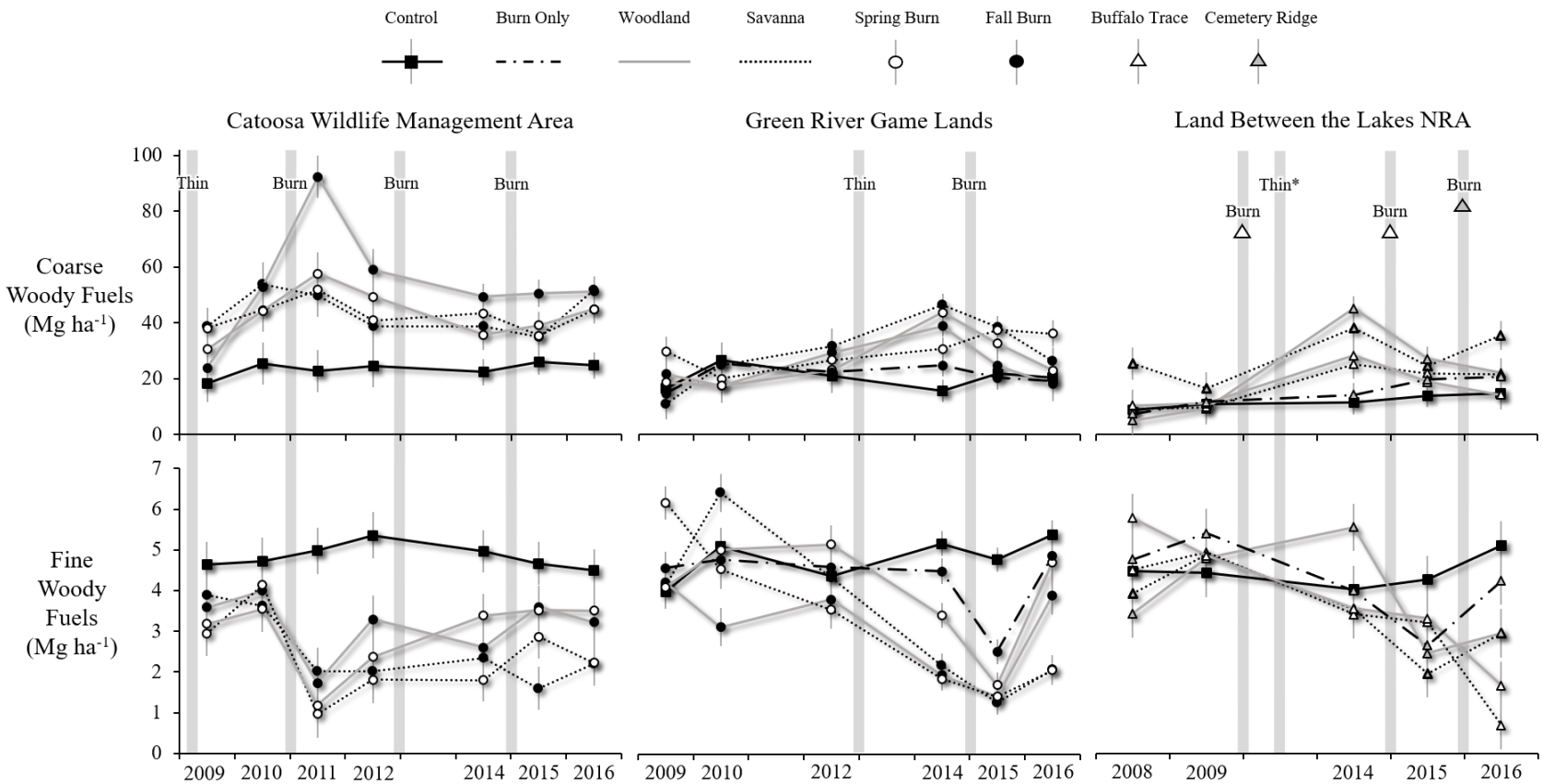


Fig. II2. Observed dynamics in coarse (1000-, 100-, and 10- hour) and fine (1-hour and litter) fuels by oak woodland and savanna restoration treatment during (2008 to 2016) an experiment at 3 sites in the Mid-South. Treatments included unmanaged controls, burn-only in the fall (October) or spring (March), and fall or spring fire paired with woodland (14 m^2 ha^{-1}) or savanna (7 m^2 ha^{-1}) residual basal area. All fires at Land Between the Lakes (LBL) were conducted in the spring, but timing differed between two sites: Buffalo Trace (March) and Cemetery Ridge (April). For LBL and Catoosa, each treatment line represents two 20-ha replicates. Green River had one 20-ha replicate per treatment. *Thinning at LBL occurred over a 3-year period (Fig. II1).

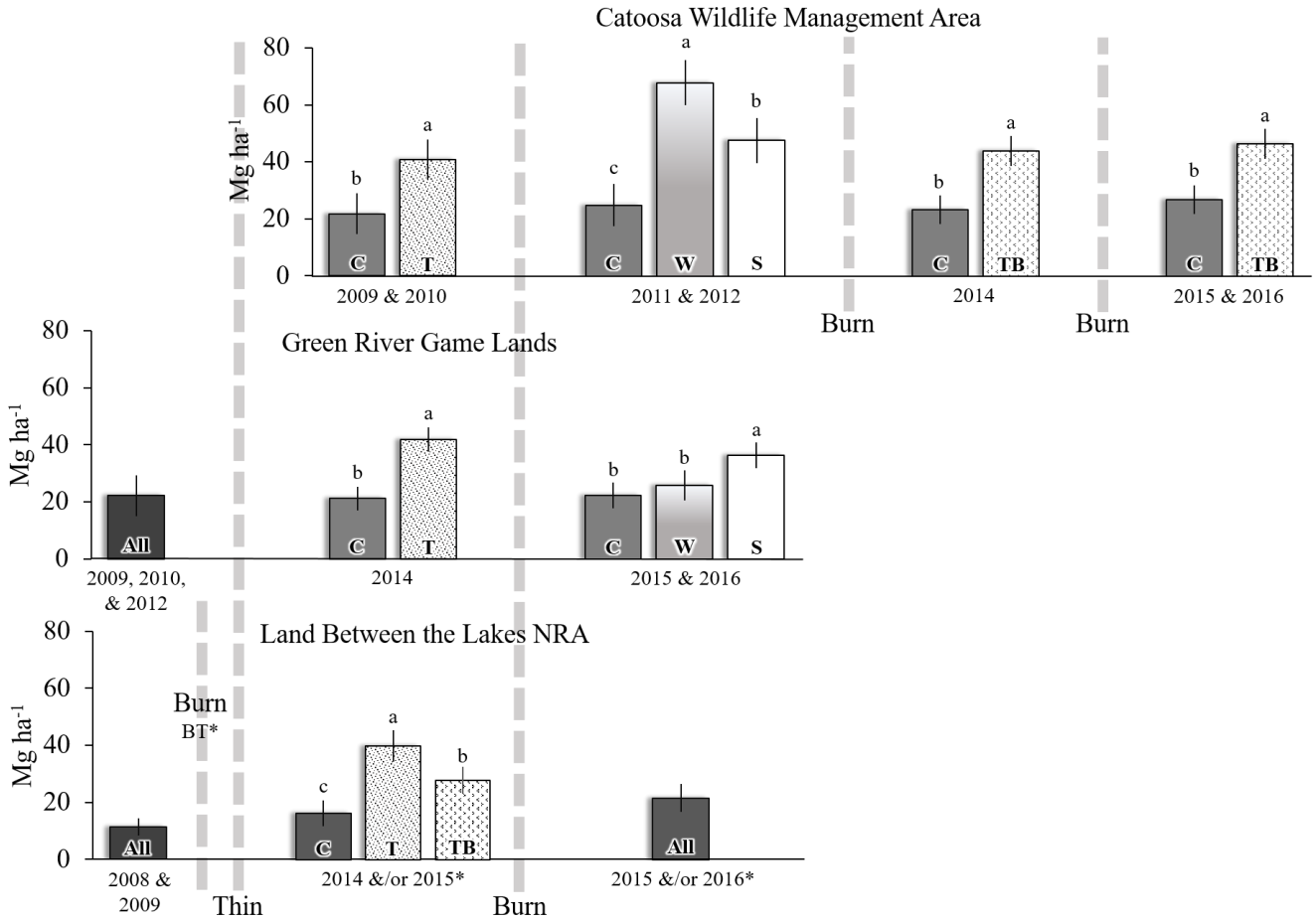


Fig. II3. All significant (α = 0.05) differences in coarse (1000-, 100-, and 10- hour) fuel loading across treatments during (2008 to 2016) an oak woodland and savanna restoration experiment at 3 sites in the Mid-South. Lowercase letters represent differences within a period as indicated by contrasts between stands that were unmanaged or thinned (C vs. T), unmanaged or thinned and burned (C vs. TB), and reduced to woodland (14 m^2 ha^{-1}) or savanna (7 m^2 ha^{-1}) residual basal area (W vs. S). When no differences were observed, the overall mean in presented (All). *At Land Between the Lakes, only the Buffalo Trace (BT) site was burned in 2009 and 2014 to 2016 data was compiled as indicated to compare burns not conducted within the same year.

Table II2. All differences (α = 0.05) in coarse (1000-, 100-, and 10- hour), fine (1-hour and litter), and herbaceous fuel-loads before and after thinning, and before and after subsequent burning, during (2008 to 2016) an oak woodland and savanna restoration experiment at 3 sites in the Mid-South. Treatment contrasts compared stands that were: unmanaged or thinned (C vs. T), unmanaged or only burned in the fall (C vs. FaO) or spring (C vs. SpO), unmanaged or thinned and burned (C vs. TB), reduced to woodland (14 m^2 ha^{-1}) or savanna (7 m^2 ha^{-1}) residual basal area (W vs. S), burned in the fall or spring (Fa vs. Sp), and burned in separate spring fires (SpBT vs. SpCR). Except for C vs. T, which was always tested, contrast evaluation followed the implementation of involved management.

Site	Fuel category	Period	Year(s)[1]	Contrast	*F*	*p*	Estimate[1] Mg ha^{-1} (SE)
Catoosa WMA	Coarse	Post-thin	2009 & 2010	C vs. T	12.0	0.006	+19.0 (6.0)
		Post-burn 1	2011 & 2012	C vs. TB	16.6	0.002	+31.3 (8.1)
				W vs. S	5.6	0.040	-19.3 (7.2)
		Post-burn 2	2014	C vs. TB	13.1	0.015	+19.4 (5.3)
		Post-burn 3	2015 & 2016	C vs. TB	30.1	< 0.001	+18.7 (3.3)
	Fine	Post-thin	2009 & 2010	C vs. T	15.3	0.003	-1.1 (0.3)
		Post-burn 1	2011 & 2012	C vs. TB	95.3	< 0.001	-3.3 (0.3)
				Fa vs. Sp	7.7	0.020	-0.7 (0.3)
		Post-burn 2	2014	C vs. TB	9.6	0.027	-2.4 (0.8)
		Post-burn 3	2015 & 2016	C vs. TB	10.0	0.010	-1.7 (0.5)
				W vs. S	7.2	0.023	-1.2 (0.5)
	Herbaceous*	Post-burn 2	2014	C vs. TB	10.8	0.022	+0.3 (0.2)
				W vs. S	14.1	0.013	+0.4 (0.1)
		Post-burn 3	2015 & 2016	C vs. TB	46.9	< 0.001	+0.3 (0.1)
				W vs. S	19.7	0.001	+0.2 (0.1)
Green River Game Lands	Coarse	Post-thin	2014	C vs. T	35.9	< 0.001	+19.7 (3.8)
		Post-burn	2015 & 2016	W vs. S	10.2	0.002	+10.1 (3.1)
	Fine	Post-thin	2014	C vs. T	99.2	< 0.001	-2.5 (0.2)
				W vs. S	6.0	0.016	-0.7 (0.3)
		Post-burn	2015 & 2016	C vs. FaO	15.0	< 0.001	-1.4 (0.3)
				C vs. TB	94.3	< 0.001	-2.5 (0.3)
				W vs. S	31.8	< 0.001	-1.2 (0.2)
	Herbaceous*	Post-thin	2014	C vs. T	35.0	< 0.001	+0.4 (0.1)
		Post-burn	2015 & 2016	C vs. TB	171.6	< 0.001	+0.5 (0.1)
				W vs. S	94.9	< 0.001	+0.7 (0.1)
				Fa vs. Sp	18.2	< 0.001	+0.2 (0.1)
Land Between the Lakes	Coarse	Post-thin	2014 &/or 2015*	C vs. T	27.5	< 0.001	+20.2 (4.1)
				C vs. TB	7.6	0.017	+8.7 (3.8)
	Fine	Post-burn	2015 &/or 2016*	C vs. SpO	34.7	0.001	-1.3 (0.2)
				C vs. TB	307.5	< 0.001	-2.8 (0.2)
				W vs. S	30.4	0.002	-0.6 (0.2)
				SpBT vs. SpCR	106.3	< 0.001	+1.4 (0.2)
	Herbaceous*	Post-thin	2014 &/or 2015*	C vs. T	18.8	0.005	+0.1 (0.0)
				C vs. TB	25.0	0.003	+0.1 (0.0)
		Post-burn	2015 &/or 2016*	C vs. SpO	88.8	< 0.001	+0.3 (0.0)
				C vs. TB	208.7	< 0.001	+0.4 (0.0)
				SpBT vs. SpCR	22.9	0.003	-0.2 (0.0)

[1]Estimates given in terms of the second treatment relative to the first within contrast labels.
*Data from 2014 to 2016 at Land Between the Lakes were compiled as indicated to allow for contrasts among fires not conducted within the same year. Herbaceous fuels only monitored 2014-2016.

Table II3. All interactions (α = 0.05) between treatment and year effects on coarse (1000-, 100-, and 10- hour), fine (1-hour and litter), and herbaceous fuel-loading during (2008 to 2016) an oak woodland and savanna restoration experiment at 3 sites in the Mid-South. Interaction contrasts compared changes in fuel-loading across all available year intervals between: unmanaged or thinned (C vs. T), unmanaged or only burned in the fall (C vs. FaO) or spring (C vs. SpO), unmanaged or thinned and burned (C vs. TB), reduced to woodland (14 m^2 ha^{-1}) or savanna (7 m^2 ha^{-1}) residual basal area (W vs. S), burned in the fall or spring (Fa vs. Sp), and burned in separate spring fires (SpBT vs. SpCR). C vs. T was always tested, but other contrasts followed the implementation of involved management.

Site	Fuel category	Period	Interval[1]	Contrast	*F*	*p*	Estimate[1] Mg ha^{-1} (SE)
Catoosa WMA	Coarse	-	-	-	-	-	-
	Fine	Pre- to post- burn 1	2010 to 2011	C vs. TB	9.8	0.004	-2.6 (0.9)
	Herbaceous*	Pre- to post- burn 3	2014 to 2015	Fa vs. Sp	6.2	0.025	+0.4 (0.1)
Green River Game Lands	Coarse	Pre- to post- thin	2012 to 2014	C vs. T	4.6	0.033	+13.7 (6.4)
		Pre- to post- burn	2014 to 2015	C vs. TB	4.3	0.038	-13.0 (6.3)
				W vs. S	4.2	0.041	+12.0 (5.9)
	Fine	Pre- to post- thin	2012 to 2014	C vs. T	22.5	< 0.001	-2.2 (0.5)
		Pre- to post- burn	2014 to 2015	C vs. FaO	6.5	0.011	-1.6 (0.6)
		1 to 2 years	2015 to 2016	C vs. FaO	6.7	0.010	+1.8 (0.7)
		post- burn		C vs. TB	6.5	0.011	+1.1 (0.5)
				W vs. S	19.1	< 0.001	-2.0 (0.5)
	Herbaceous*	Pre- to post- burn	2014 to 2015	W vs. S	6.2	0.014	+0.3 (0.1)
				Fa vs. Sp	22.2	< 0.001	+0.5 (0.1)
		1 to 2 years post- burn	2015 to 2016	C vs. TB	9.1	0.003	+0.5 (0.2)
				W vs. S	12.4	0.001	+0.7 (0.1)
Land Between the Lakes	Coarse	Pre- to post- thin	2009 to 2014	C vs. T	8.3	0.007	+28.1 (8.9)
	Fine	Pre- to post- burn	2014/2015 to 2015/2016*	C vs. SpO	6.0	0.021	-1.8 (0.8)
				C vs. TB	32.4	< 0.001	-2.6 (0.6)
				SpBT vs. SpCR	4.2	0.050	-0.3 (0.6)
	Herbaceous*	Pre- to post- burn	2014/2015 to 2015/2016*	C vs. SpO	30.1	< 0.001	+0.3 (0.1)
				C vs. TB	40.7	< 0.001	+0.2 (0.0)

[1]Estimates given in terms of the second treatment relative to the first within contrast label. *Data from 2014 to 2016 at Land Between the Lakes were compiled as indicated to allow for contrasts among fires not conducted within the same year. Herbaceous fuels only monitored 2014-2016.

29.1% less than that observed in savannas post-fire (Fig. II3, Table II2). A post-hoc contrast on GRGL data revealed that CWF in woodlands was no different from controls post-fire (F = 0.75, p = 0.387). Burning reduced CWF in thinned and burned stands at GRGL by one third (32.6 %) from pre- to post-burn, but decreases in woodlands were greater (>4X) than decreases observed in savannas (Table II3). At LBL, CWF loads were similar in all treatments following fire (Fig. II3, Tables II2 and II3). Woodlands and savannas had similar CWF loads at CWMA after the second prescribed fire, but thinned and burned stands remained nearly double the CWF in controls even after 3 prescribed fires (Fig. II3, Tables II2 and II3). Loading of CWF did not differ between controls and burn-only treatments, or between fire-seasons.

Fine Woody Fuels

Restoration management affected the loading of leaf litter and 1-h fuels (FWF) similarly across sites (Fig. II2). Controls, on average, contained 4.7 Mg ha^{-1} (± 0.5 SE) of FWF. This level remained relatively constant over time compared to other treatments. Thinning reduced FWF loads by 33.0% at CWMA, and 51.6% at GRGL, relative to unmanaged controls, but did not cause any differences among treatments at LBL (Fig. II4, Table II2). At GRGL only, FWF loading was also greater in woodlands than savannas after thinning but prior to burning.

After burning, FWF differences were related to thinning level, whether burning occurred, and the seasonal timing of fire (Fig. II4, Tables II2 and II3). Fire alone reduced FWF relative to controls by a mean of 27.1% (GRGL and LBL). Post-hoc contrasts revealed greater FWF loading in FaO (GRGL; F = 7.90, p = 0.006) and SpO (LBL; F = 42.00, p = 0.001) relative to woodlands. At all sites, thinning and burning reduced FWF loading relative to controls after one fire. This difference ranged from 2.5 Mg ha^{-1} (± 0.3 SE) at GRGL to 3.3 Mg ha^{-1} (± 0.3 SE) at CWMA. After burning, FWF loading also decreased with increasing canopy disturbance at

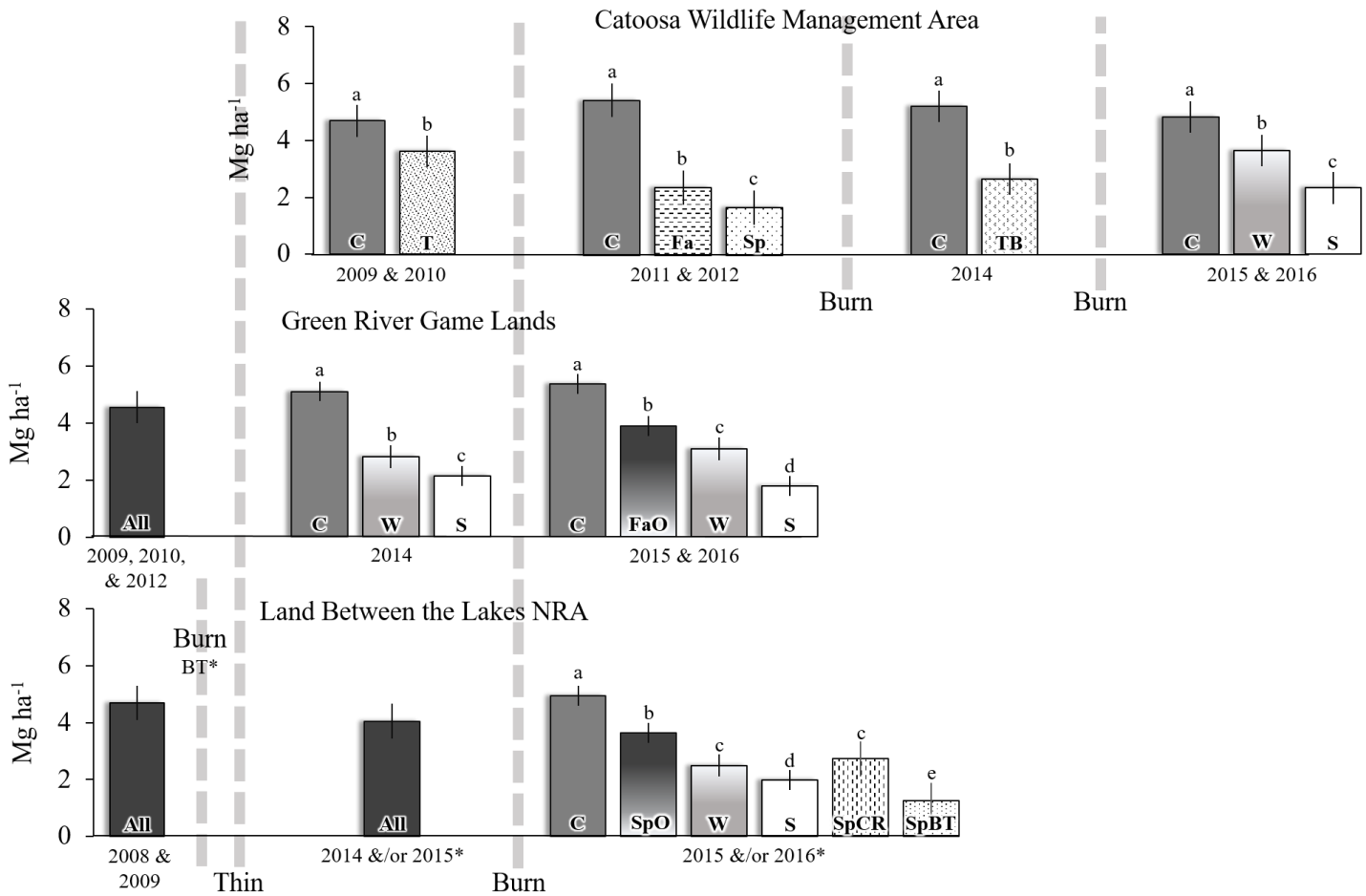


Fig. II4. All differences (α = 0.05) in fine (1- hour and litter) fuel loads across treatments during (2008 to 2016) an oak woodland and savanna restoration experiment at 3 sites in the Mid-South. Lowercase letters represent differences within a period as indicated by contrasts between stands that were unmanaged or thinned (C vs. T), unmanaged or burned only in the fall (C vs. FaO) or spring (C vs. SpO), unmanaged or thinned and burned (C vs. TB), reduced to woodland (14 m^2 ha^{-1}) or savanna (7 m^2 ha^{-1}) residual basal area (W vs. S), burned in the fall or spring (Fa vs. Sp), and burned in separate spring fires (SpBT vs. SpCR). No differences are represented by the overall mean (All). *At Land Between the Lakes, only the Buffalo Trace site was burned in 2009 and 2014 to 2016 data were compiled as indicated to compare burns not conducted within the same year.

GRGL and LBL, but not at CWMA. Instead, FWF loading differed by fire-season at CWMA; stands burned in the spring had 30.0% less FWF than stands burned in the fall. Similarly, the timing of fire at LBL was influential; stands burned in April contained double the amount of FWF observed after March fires. Neither woodland and April burns ($F = 0.96$, $p = 0.328$), or savannas and March burns ($F = 14.48$, $p < 0.001$), differed at LBL. After the second fire at CWMA, FWF no longer differed between spring and fall fires, but FWF in treatments was half that observed in controls. This difference remained after the third burn at CWMA, and FWF in woodlands and savannas became distinct; savannas had 35.8% less FWF than woodlands.

Herbaceous Fuels

Herbaceous fuel loads were commonly greater in thinned and burned stands relative to controls, and in savannas relative to woodlands (Tables II2 and II3, Fig. II5). Post-thinning but pre-burn, herbaceous fuels were greater in thinned than control stands at GRGL (13X) and LBL (nearly 3X). Herbaceous fuel loading in Buffalo Trace and Cemetery Ridge stands differed from controls similarly in 2014 despite the 2009 burn of Buffalo Trace. Burning alone in the spring at LBL increased herbaceous fuel loading for a single season relative to controls, but no such difference followed burning alone in the fall at GRGL. After burning, herbaceous fuels at GRGL increased with increasing canopy openness, whereas differences at LBL were a function of whether thinning occurred and differences between Buffalo Trace and Cemetery Ridge.

Herbaceous fuel loading following fall fire at GRGL was only 72.5% of what it was after spring burning. After the third fire at CWMA, herbaceous fuel loading in managed stands was >10X that observed in controls. At the same time, savannas contained slightly more than double the herbaceous fuel observed in woodlands. The third round of spring burning caused greater increases in herbaceous fuels than the third round of fall burning (Table II3, Fig. II5).

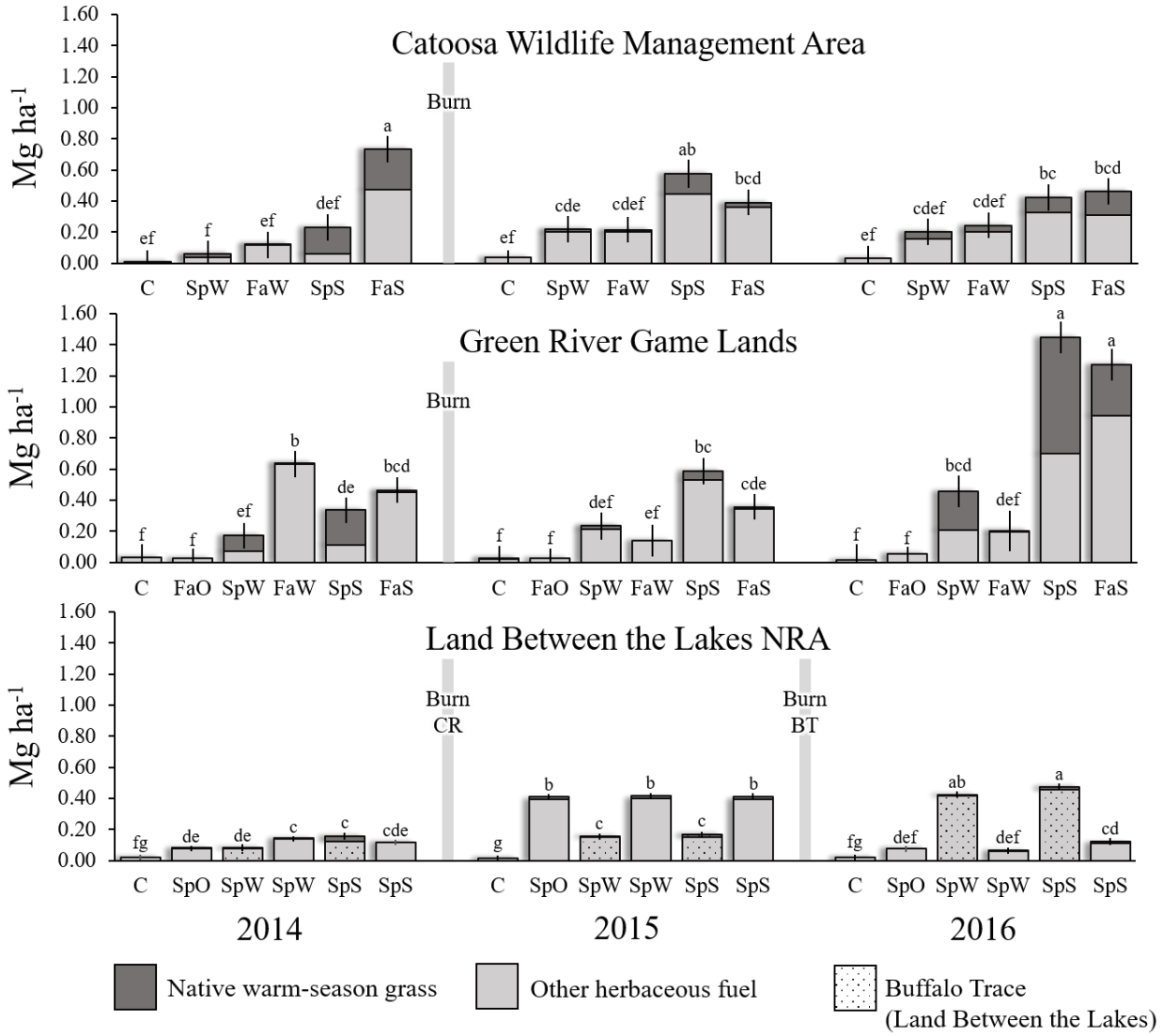


Fig. II5. Herbaceous fuel-loading by treatment and year from 2014 to 2016 of an oak woodland and savanna restoration experiment at 3 sites in the Mid-South. Bars depict fuel composition relative to native warm-season grasses and other herbaceous vegetation. Lowercase letters are differences within a site (2014-2016) by LSD mean separation ($\alpha = 0.05$). Implemented treatments included unmanaged controls (C), burn-only in the fall (FaO) or spring (SpO), and fall or spring fire paired with woodland (FaW or SpW, 14 m^2 ha^{-1}) or savanna (FaS or SpS, 7 m^2 ha^{-1}) residual basal area. All fires at Land Between the Lakes (LBL) were conducted in the spring, but timing differed between two sites: Buffalo Trace (BT) and Cemetery Ridge (CR). For LBL and Catoosa, each treatment bar represents two 20-ha replicates. Green River had one 20-ha replicate per treatment.

Herbaceous fuel composition, in terms of live and dead, differed by fall and spring sampling periods at GRGL post-fire, and at CWMA before and after fire ($F > 20.3$, $p < 0.006$). When different, spring sampling had 31.5% (± 4.5 SE) more dead herbaceous fuel than fall sampling.

Native C_4 grasses were rarely collected in controls and burn only treatments, but were common in thinned and burned stands (Fig. II5). Contrasts related to C_4 grasses were significant before (2014) and after (2015 and 2016) applied fire at all sites ($F > 13.4$, $p < 0.015$) except for at LBL pre-fire ($F = 0.0$, $p = 0.975$), where native C_4 grasses were rare. Averaged across sites and post-burn years (2015-2016), thinned and burned stands had 0.08 Mg ha^{-1} (± 0.01 SE) more native C_4 grass fuel than stands lacking canopy disturbance. Loading of native C_4 grass fuels never differed between woodlands and savannas at LBL, only differed at GRGL post-fire ($F = 9.9$, $p = 0.002$), and differed at CWMA before and after fire ($F > 10.0$, $p < 0.010$). In these cases, savannas contained more native C_4 grass fuel than woodlands, and estimates of differences were 0.22 Mg ha^{-1} (± 0.01 SE) and 0.12 Mg ha^{-1} (± 0.01 SE) for GRGL and CWMA, respectively. Fire-season affected native C_4 grass loading at GRGL, where such fuel loads were 22.9% (± 3.3 SE) greater following spring relative to fall burning.

DISCUSSION

In agreement with similar regional work (Graham and McCarthy 2006; Waldrop *et al.* 2016), mechanical thinning and prescribed fire reduced fine-fuels but increased coarse woody fuels. Through this combination of effects, most treatments increased total fuel loading. Only burning alone decreased total fuel loads. Thinning, regardless of degree, doubled coarse woody fuels by adding nearly 20 Mg ha^{-1}. Burning, even 3 times in 6 years, had little effect on coarse woody fuels. In contrast, treatments reduced leaf litter and 1-h fuels which are key determinants of fire behavior in eastern oak ecosystems (Varner *et al.* 2015). Accumulation of FWF from the

first to second year following initial fires occurred at all sites, but increases did not equal loadings observed prior to burning. This allowed biennial fire at CWMA to maintain FWF reductions. Herbaceous fuel loading was consistently sparse (< 1.5 Mg ha^{-1}) and did not compensate for losses in leaf litter; however, increases in herbaceous fuels with thinning and burning suggest this is possible in the future. Thus, we conclude: (1) thinning and burning reduced FWF, but maintaining reductions required repeated fire, and (2) more intensive or prolonged management will be necessary to reduce CWF loading.

Support for mechanical thinning and prescribed fire as effective methods of fuel reduction is largely derived from work in the western U.S. (Fernandes and Botelho 2003; Andrews and Butler 2006; Stephens *et al.* 2012). At one of only two sites characterized by eastern hardwoods within The National Fire and Fire Surrogate study (McIver *et al.* 2013), Waldrop *et al.* (2010) concluded combining burning and thinning improved short-term (<3 years) resiliency to wildfire by reducing fine-fuels. Our reductions in fine-fuels were comparable, suggesting a similar decline in future wildfire incidence and spread. However, the increases in coarse woody fuels we documented could greatly increase future wildfire severity if fine-fuel reductions are not maintained with repeated fire. Such maintenance will be increasingly important as air temperatures, drought frequency, and drought duration increase throughout the Mid-South (Mitchell *et al.* 2014). Proactive management could ease ecological transitions, promote forest health and productivity, preserve ecosystem services, and safeguard communities (Vose and Elliott 2016). Unfortunately, little regionally specific fuel treatment knowledge exists (Waldrop *et al.* 2016). Our results increase this understanding, but also add urgency. Reducing coarse fuels before climate change effects arrive could require decades of intense management.

Coarse Woody Fuels

Other manipulations of fuels in eastern hardwoods have shown thinning to similarly increase CWF. Relative to controls, Graham and McCarthy (2006) observed greater CWF loading four years after thinning or thinning and burning in south-eastern Ohio and the difference (+19.0 Mg ha^{-1}) was nearly identical to that observed in our study. Mechanical treatments in the Southern Appalachians increased all measured fuels for three years (Waldrop *et al.* 2016). Degree of thinning (woodland vs. savanna) was also influential, but the effect was not consistent (absent at LBL, opposite at CWMA and GRGL), apparent only after burning, and not present after a second fire.

We propose intense ring-firing, which led to overstory tree mortality and toppling, contributed to relatively high CWF loading in woodlands at CWMA. From pre- to post- initial fires in CWMA woodlands, live basal area declined (-2.1 m^2 ha^{-1} ± 0.9 SE) and snag basal area increased (+0.7 m^2 ha^{-1} ± 0.4 SE) to nearly 11X that observed at GRGL (0.3 m^2 ha^{-1} ± 0.1 SE) where strip-head firing was utilized. Also, 45% of snags in CWMA woodlands post first fire were fire-sensitive species (*i.e.*, red maple and sourwood). In comparison, fire-sensitive species were only 9% of documented snags at GRGL. Fires also burned hotter at CWMA (169.5 ˚C ± 5.5 SE) than other sites (143.8 ˚C ± 11.1 SE). Based on these observations, we conclude the contradictory results at CWMA and GRGL related to thinning intensity and CWF loading were a result of differences in fire intensity. Regardless, our CWF estimates aligned well with previous studies, and controls were consistent with reported ranges for eastern oak forests (Onega and Eickmeier 1991; Chojnacky *et al.* 2004; Waldrop *et al.* 2010; Stambaugh *et al.* 2011).

Others have similarly concluded minimal fire effects on larger woody fuels in eastern hardwoods (Graham and McCarthy 2006; Waldrop *et al.* 2016). No identified treatment

differences in CWF involved burning alone. It is likely that fire consumes some CWF, but it also creates snags that slowly break apart and contribute to the fuel-bed for decades (Stephens *et al.* 2012). This effect could be a substantial in the eastern U.S. where mesophication has promoted an abundance of fire-sensitive tree species (Nowacki and Abrams 2008). During 3 biennial fires at CWMA, CWF initially spiked, decreased, and then reached an equilibrium that was double levels observed in controls. This suggests a balance between fire's consumption and creation of CWF that may continue with the continued use of intense fire. Alternatively, a single fire at GRGL reduced CWF by 13.0 Mg ha^{-1} (± 6.3 SE). Given this, two additional fires, applied biennially to allow for fine-fuel re-accumulation (6 years since initial burn), could reduce CWF loads below control levels. This represents more frequent fire than suggested nationally to reduce CWF (2 to 3 fires in a 10 to 20-year period, Stephens *et al.* 2012). Fire-induced reductions of CWF at LBL (6.8 Mg ha^{-1} ± 4.4 SE) were less substantial, variable, and insignificant because wind events in May-July of 2016 increased fuel loading in controls. Season of fire never caused differences in CWF at any of our sites. Fall burning conditions were warmer and dryer relative to spring, but differences in wind caused spring fires to be slightly more intense. Regardless of season, managers conduct prescribed fires under similar weather parameters. Thus, fire intensity and fuel consumption may not differ with season in eastern forests (Knapp *et al.* 2009).

Fine Woody Fuels

We estimated a remarkably consistent 4.7 Mg ha^{-1} of leaf litter and 1-h fuels in unmanaged oak forests across sites. This was comparable to estimates made in undisturbed forests throughout the Mid-South region (Chojnacky *et al.* 2004; Waldrop *et al.* 2007; Waldrop *et al.* 2016). Fine-fuels are the drivers of fire behavior and spread in eastern ecosystems (Varner *et al.* 2015), and thinning generally decreased their loading. The removal of overstory trees

probably reduced FWF deposition and accelerated decomposition by increasing air flow, light, and rain penetration at the forest floor (Zheng *et al.* 2000). Although it often required fire before becoming apparent, all sites eventually exhibited a decreasing trend in FWF as the degree of thinning increased (controls > woodlands > savannas). This challenges the assertion that thinning, and the degree of thinning, fails to affect FWF (Agee and Skinner 2005). Mechanically felling all woody stems >1.8 m tall and <10 cm DBH increased litter and small twigs for 4 years relative to controls (Waldrop *et al.* 2016), and such conditions were associated with an increased risk of intense wildfire (Waldrop *et al.* 2010). Based on our results, overstory reductions may more efficiently and safely reduce FWF loads than understory thinning.

Fire alone reduced FWF loading, and combining thinning with burning nearly doubled such reductions. Reductions in FWF typically last less than 3 years (Graham and McCarthy 2006; Waldrop *et al.* 2016). The rate of increase in FWF we observed from the first to second year post initial fires suggests an even faster recovery, but the magnitude of these re-accumulations appeared to decline with repeated burning at CWMA. Biennial fire at this site appeared to equilibrate FWF loads at a reduced level. The initially greater rate of recovery in FWF could be the result of top-killed seedlings, saplings, and shrubs adding limbs and stems to the fuel-bed after burning (Waldrop *et al.* 2016). Such additions should decline, and FWF consumption should be more complete, as the understory transitions from dense woody vegetation to dominance by highly flammable C_4 grasses and other herbaceous fuels (Vander Yacht *et al.* 2017). Differences in FWF by fire season were rare, but where observed appeared to be driven by differences in fire intensity. Loading of FWF was greater after less intense fall (CWMA) and Cemetery Ridge (LBL) fires relative to more intense spring and Buffalo Ridge fires at each site, respectively. Also, the difference at CWMA was not maintained over further

seasonal burning. Thinning and burning reduced FWF loads, but our long-term monitoring in controls at all three sites supports the lack of accumulation of such fuels noted by others in eastern ecosystems (Onega and Eickmeier 1991; Graham and McCarthy 2006).

Herbaceous Fuels

Herbaceous fuels have not been studied in the Mid-South, perhaps partly because of the misconception that the region was historically unbroken, closed-canopy forest (Denevan 1992). Canopy disturbance and prescribed fire are precisely the tools required to promote a robust and diverse ground-layer of native grasses and forbs during oak woodland and savanna restoration (Peterson *et al.* 2007; Vander Yacht *et al.* 2017). A significant portion of the increase in herbaceous fuels we observed was highly flammable, native warm-season grasses, which may play a key role in interacting with fire to reverse mesophication and thwart woody encroachment (Maynard and Brewer 2013). The high surface area-to-volume ratio, maintenance of upright positions, and perching fallen leaf litter to facilitate drying allows herbaceous groundcover to create a well-ventilated and easily ignited fuel bed (Mitchell *et al.* 2009). Further regional research is required to assess whether such characteristics moderate fire behavior and increase the consumption of hazardous woody fuels, or increase the risk of wildfire spread.

Regardless, the greatest quantity of herbaceous fuel we observed (SpS at GRGL, 2016) was less than 1.5 Mg ha^{-1}. This did not compensate for the leaf litter and 1-h fuels that thinning and burning removed (2.0 Mg ha^{-1} averaged across sites). Post hoc, we averaged herbaceous fuels from 2014 to 2016 across sites separately for woodlands and savannas. Simple linear regression through each set of 3 annual points provided an indication of how long it would take to replace the average post-fire gap in woody fine-fuels between treatments and controls (2.0 Mg ha^{-1}) with herbaceous fuels. Biennial fire for another 55.7 years in woodlands, and 9.1 years in

savannas, could result in total fine-fuel loading comparable to controls. In addition to being highly speculative, this calculation fails to account for differences in energy output during combustion across fine-fuel categories. In other words, lesser amounts of highly flammable C_4 grasses could support fire behavior similar to that generated by greater amounts of woody fine-fuels. Such differences in burning characteristics across fine-fuel categories deserves greater research attention (Varner *et al.* 2015).

CONCLUSIONS

Oak woodland and savanna restoration requires thinning and prescribed fire, and these techniques have been widely used to reduce fuels and wildfire risk. However, our results clearly demonstrate that returning historically appropriate disturbance after its prolonged absence can increase total fuel loading, at least in the short-term. Thinning added 20 Mg ha^{-1} of coarse woody fuels that remained even after 3 fires in 6 years. To reduce this addition, restoration associated thinning could be more intentionally designed to remove fuels (*e.g.*, limbing and topping outside of stands) or supplemented with management that enhances fuel combustion and decomposition rates (*e.g.*, mulching). Also, fire-sensitive tree species should be removed from the overstory to prevent future fuel inputs from snags. Moderately intense fire, capable of consuming fuel while limiting overstory mortality, could make a critical contribution to a long-term reduction in loading of heavier fuels. Restoration management reduced fine-fuels during our study, but maintenance may have relied on burning repeatedly every 2 to 3 years. Even then, herbaceous fuel-loading increased at a rate that suggests compensation for the loss of leaf litter and twigs is possible within 10 years under open (7 m^2 ha^{-1}) canopies. Future research should regionally explore whether this transition in fine-fuel compositional dominance, from leaf litter and twigs to grasses and forbs, moderates fire behavior through the increased consumption of coarse woody

fuels or promotes wildfire spread through increases in fuel-bed flammability. Regardless, the doubling of coarse woody fuel-loads and potentially short-lived reductions in fine-fuels we observed suggest that restoration associated thinning and burning may not be regionally effective fuel reduction treatments.

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CHAPTER III
REVERSING MESOPHICATION EFFECTS ON WOODY VEGETATION IN OAK FORESTS OF THE MID-SOUTH

This chapter is original work by Andrew L. Vander Yacht with contributions from co-authors Patrick D. Keyser, Seth A. Barrioz, Charles Kwit, Mike C. Stambaugh, Wayne K. Clatterbuck, and Dean M. Simon. It has not yet been published, but the authors intend on submitting it to "*Forest Science*".

ABSTRACT

Mesophication has reduced fuel-bed flammability throughout the southern Appalachian and Central Hardwood regions of the US (Mid-South), thus limiting the effectiveness of fire, when used apart from other management tools, to address limited regeneration of disturbance-adapted woody species. We applied combinations of canopy disturbance (none, 7, and 14 m^2 ha^{-1} residual basal area) and seasonally varied fire (none, October, and March) at 3 sites and monitored understory woody response from 2008 to 2016. In combination, thinning and fire preferentially promoted shade-intolerant and fire-tolerant woody species at all sites. Compositional shifts were directly related to management effects on overstory and midstory density. Across sites, thinning and fire increased shrub density, nearly doubled (+2,256 stems ha^{-1}) oak (*Quercus* spp.) seedling density, and similarly increased other disturbance-adapted species. For such species, sapling response was more moderate but still associated with thinning and fire. Except for red maple (*Acer rubrum* L.), shade-tolerant, mesophytic species across all size-classes were most often associated with controls. Fire-season effects were not strong, but more species and greater understory densities were associated with March relative to October burning. Observed dissimilarities in understory woody vegetation between unmanaged and managed stands demonstrate both the effects of mesophication and how such effects can be reversed using canopy disturbance and fire.

Keywords: mesophication; oak regeneration; fire-season; canopy disturbance; Tennessee; North Carolina; woody encroachment; savanna; woodland.

INTRODUCTION

Fire regulates the distribution, structure, and composition of plant communities throughout the world (Bowman et al. 2009; Pausas and Keeley 2009). In the southern Appalachian and Central Hardwood regions of the U.S. (hereafter, Mid-South), the historical relationship between fire and forested ecosystems is becoming increasingly apparent (Lafon et al. 2017). Fire-scar analyses (Aldrich et al. 2014; Guyette et al. 2006), charcoal and pollen in sediments and soils (Delcourt et al. 1998), witness tree records (Thomas-Van Gundy and Nowacki 2013), and patterns in overstory age structure (Flatley et al. 2015) all demonstrate a strong influence of fire on the region's vegetation. Frequent burning created and maintained mosaics of open woodlands (30-80% canopy cover) and savannas (10-30% canopy cover, Nelson 2010) dominated by fire-adapted vegetation where closed-canopy forests would have otherwise developed (DeSelm 1994; Noss 2013; Nuzzo 1986).

Perhaps the greatest evidence of fire's regional influence on vegetation comes in the form of fire-adapted traits exhibited by dominant tree species. Oaks (*Quercus* spp.) have dominated eastern forests since the beginning of the Holocene epoch when drying and warming climates increased the prevalence of fire (Abrams 1992). Hypogeal germination, an emphasis on root over shoot growth, heat insulating properties of bark, and efficient wound compartmentalization all promote the survival and recruitment of oaks in recurrent fire environments (Brose et al. 2014). Co-occurring shortleaf pine (*Pinus echinata* Mill.) exhibits a unique basal crook that shelters dormant buds beneath a layer of insulating soil, allowing for vigorous sprouting after top-kill by fire (Lilly et al. 2012). Other tree species common to the region (*e.g.*, hickories [*Carya* spp.] and sassafras [*Sassafras albidum* Nutt. Nees]) are well suited to sparse overstories maintained by fire

(Burns and Honkala 1990b), and sprout readily or establish quickly after fire (Abrams 2007; Keyser et al. 2017). Many of these woody species also promote the fires they are adapted to by contributing highly flammable and decay-resistant fuel (Varner et al. 2016).

During the early 20th century, logging debris generated during the "Great Cutover" fueled catastrophic wildfires that solidified the perception that fire was a threat to national forest resources (Stephens and Ruth 2005). Consequently, federally supported suppression policies nearly eliminated fire from the Mid-South (Pyne 2015) and allowed succession to transform open communities into closed-canopy forests (Fralish et al. 2000; Nuzzo 1986) dominated by fire-sensitive species (Abrams 1998; South and Harper 2016). This began the self-reinforcing process of mesophication (Nowacki and Abrams 2008), where microenvironmental conditions for shade-tolerant and fire-sensitive woody species continually improve while conditions that favor shade-intolerant and fire-adapted (collectively, disturbance-dependent) species deteriorate. Forest understories are now dominated by dark, moist, and cool conditions and species with physical and chemical leaf-litter properties not conducive to fire (Alexander and Arthur 2014; Kreye et al. 2013; Varner et al. 2015). In contrast, economically and ecologically important species like oaks (McShea et al. 2007) and shortleaf pine (Masters 2007) routinely fail to regenerate (Johnson et al. 2009; Schuler and Gillespie 2000; South and Harper 2016). Reduction in future forest biodiversity could increase susceptibility to invasive species and disease, and alter the productivity, sustainability, and function of regional ecosystems (Knops et al. 1999).

The continually escalating costs and effort required to reverse mesophication creates an urgency for management intervention. Canopy disturbance can provide the understory light required to promote shade-intolerant species (Brudvig and Asbjornsen 2009; Iverson et al. 2017). Prescribed fire can then shift understory composition toward fire-adapted species (Brose et al.

2013; Vander Yacht et al. 2017a). However, knowledge gaps related to correcting mesophication effects on woody vegetation remain. Recent evaluations of repeated fire on woody vegetation in the Mid-South have not occurred in conjunction with canopy disturbance (Arthur et al. 2015; Hutchinson et al. 2012; Keyser et al. 2017). Combining partial harvests and repetitive burning can increase the presence of advanced disturbance-dependent regeneration (Brose and Van Lear 1998; Iverson et al. 2017). Positive results, however, are often partially attributable to intense fire and associated tree mortality. Overstory maintenance and safety concerns can preclude such management. At comparably moderate fire-intensity, growing-season fire can promote disturbance-dependent over mesophytic species more so than dormant-season fire (Brose and Van Lear 1998). The mechanism behind this is unclear, especially for late growing-season fire (Huddle and Pallardy 1999), but greater allocation of resources to root over shoot growth in fire-adapted species is commonly implicated (Knapp et al. 2009). Regardless, the potential for growing-season fire to accelerate the reversal of mesophication deserves research attention.

We implemented an experiment at three sites across the Mid-South, and documented the response of shrubby, seedling, and sapling vegetation to combinations of canopy disturbance (none, 7, and 14 m^2 ha^{-1} residual basal area) and season of prescribed fire (March, prior to leaf expansion, and October, prior to leaf abscission). We hypothesized that canopy disturbance and fire-season would interact such that heavy thinning and late growing-season fire would result in the greatest reversal of mesophication effects on understory woody communities. We use shade and fire tolerance to identify generalities for groups of similar species, but tracked the response of individual species. Our overall goal was to inform management strategies for reversing the effects of mesophication on understory woody communities throughout the Mid-South.

METHODS

Study Areas

Our first site was Catoosa Wildlife Management Area (CWMA), a 32,374 ha property managed by the Tennessee Wildlife Resources Agency (TWRA) on the Cumberland Plateau in the Southwestern Appalachians ecoregion (all ecoregions: Level III, U.S. EPA 2013). Broad ridges and dissecting ravines ranged 437-521 m in elevation. Soils are Mesic Typic Hapludults (Soil Survey Staff NRCS 2014) over weathered sandstone and conglomerate (Nicholson et al. 2005). Annual precipitation and temperature averaged 140 cm and 13 °C, respectively, from 1981 to 2010 (National Climatic Data Center 2014). Forests were established in the 1920's following agricultural abandonment and at study initiation were dominated by oaks, including white (*Q. alba* L.), southern red (*Q. falcata* Michx.), black (*Q. veluntina* Lam.), and scarlet (*Q. coccinea* Münchh.). Red maple (*Acer rubrum* L.), sourwood (*Oxydendrum arboreum* L.), and hickories were also abundant. Shortleaf pine became a minimal overstory component after the southern pine bark beetle (*Dendroctonus frontalis* Zimmermann) outbreak of 1999-2000. In response, TWRA began managing for oak savannas using salvage cutting and prescribed fire. The site's floral (Barrioz et al. 2013; Vander Yacht et al. 2017a) and faunal (Cox et al. 2016; Vander Yacht et al. 2016) response indicate restoration progress.

Our second site was Land Between the Lakes (LBL), a 68,797 ha National Recreation Area in western Kentucky and Tennessee managed by the U.S. Forest Service and situated in the Western Highland Rim of the Interior Plateau. Rolling topography ranged 122–198 m in elevation over limestone bedrock. Soil series are Bodine, Baxter and Hammock with loess caps on ridgetops and mid-slopes (Franklin et al. 2003). Mean annual precipitation and temperature

from 1981 to 2010 was 134 cm and 14 ˚C, respectively. Relative to other sites, forest composition lacked pines and included more white oak, chestnut oak, hickories, and post oak (*Quercus stellata* Wangenh.).

Our third site was Green River Game Lands (GRGL), a 5,726 ha North Carolina Wildlife Resources Commission (NCWRC) property situated at the interface between the Blue Ridge and Piedmont ecoregions. Narrow ridges and steep ravines ranged from 366 – 640 m in elevation. Soils are deep (>1 m), well-drained, and mostly in the Evard series (fine loamy, oxidic, mesic Typic Hapludults, Keenan 1998) over gneiss, schist, and phyllite rock (Clark 2008). Annual precipitation and temperature averaged 139 cm and 14 °C, respectively, from 1981 to 2010 (NCDC 2014). Forests were 80-120 years old with no recent disturbance history. Canopies were also dominated by oaks, but chestnut oak (*Q. montana* Willd.), northern red oak (*Q. rubra* L.), and yellow poplar (*Liriodendron tulipifera* L.) were relatively more common. A dense understory of ericaceous shrubs (*i.e.*, mountain laurel [*Kalmia latifolia* L.] and rosebay rhododendron [*Rhododendron maximum* L.]) occurred throughout the site.

Experimental Design and Management Treatments

We treated sites as independent experiments because of differences in species composition, management, and data collection. At each site, 20-ha forested stands were configured to maximize core area and assigned treatments using a completely randomized design. Treatments included: 1) unmanaged (Control), 2) thinned to woodland residual basal area (14 m^2 ha^{-1}) and burned during spring (SpW), 3) thinned to woodland residual basal area and burned during fall (FaW), 4) thinned to savanna residual basal area (7 m^2 ha^{-1}) and burned during spring (SpS), and 5) thinned to savanna residual basal area and burned during fall (FaS). At LBL, all fires occurred in spring (no FaS, FaW) including an additional treatment: 6) burn-only during

spring (SpO). Target residual basal area for savannas at LBL was greater (9 m^2 ha^{-1}) than at other sites due to administrative constraints. At GRGL, we included 7) burn-only in the fall (FaO, in place of SpO). Treatments were replicated twice at CWMA, four times at LBL (except only 2 replicates of SpO and Control), and once at GRGL. Prior to management, canopy closure averaged 90.7 % (± 2.5 SE) and live basal area was 20.1 m^2 ha^{-1} (± 2.0 SE). Herbaceous groundcover was minimal (5.7 % ± 2.0 SE), and understories were dominated by ericaceous shrubs, woody regeneration, and litter (Vander Yacht et al. 2017a).

Canopy reductions were completed commercially during the dormant season (Fig. III1). Where possible, oaks, hickories, and shortleaf pine were retained while fire-intolerant species including maples (*Acer* spp.), yellow poplar, and sweetgum (*Liquidambar styraciflua* L.) were harvested. After thinning, but before burning, residual basal area and canopy closure was comparable across sites within control and burn-only stands (21.4 m^2 ha^{-1} ± 1.1 SE, 97.6 % ± 0.4 SE), woodlands (14.6 m^2 ha^{-1} ± 1.5 SE, 77.7 % ± 4.6 SE), and savannas (9.3 m^2 ha^{-1} ± 1.6 SE, 53.7 % ± 4.2 SE). Site managers conducted prescribed fires. At CWMA, ring firing burned FaW and FaS 3 times in mid-October prior to bud-break (2010, 2012, and 2014), and SpW and SpS 3

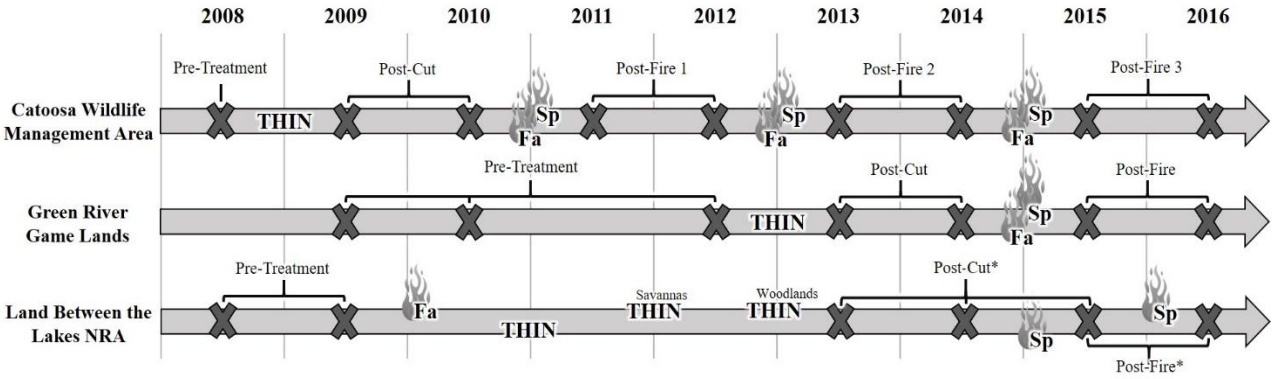


Fig. III1. Timelines depicting treatments, data collection (X's), and periods during (2008 to 2016) mesophication reversal experiments at 3 sites located across the Mid-South. Treatments included canopy disturbance (THIN) and prescribed fire in the fall (Fa) or spring (Sp). *Data from 2014 to 2016 at Land Between the Lakes were compiled into post-cut and post-fire periods in response to differences in when some replicates were burned.

times in mid-March prior to leaf abscission (2011, 2013, and 2015). Strip-head firing was utilized at GRGL (October 2015 and March 2016). At LBL, half of SpW and SpS replicates and all SpO replicates were burned using strip-head firing in late April, 2015. Remaining SpW and SpS replicates were burned in late March, 2016 using aerial ignition from a helicopter. These latter stands were also burned in November of 2009 prior to canopy disturbance.

Burning conditions and fire behavior were monitored following Vander Yacht et al. (2017a). This included determining fuel moisture, on-site weather recording, and systematic measurements of fire spread and flame lengths. We sampled fire temperature using foil-wrapped ceramic tiles (n = 181) painted with Tempilaq® indicating liquids and placed in stands along a 70 × 70 m grid. Monitoring indicated consistency by season across sites, so we present burning condition and fire behavior variables accordingly for simplicity (Appendix SIII1). Conditions were warmer (+7˚ C) and less windy (-1.9 m s^{-1}), and fine-fuels (litter and 1-hour twigs) were nearly 5% drier, during fall relative to spring burning. However, heading fires in spring had nearly double the rate-of-spread and flame length of those in fall. Spring fires also burned nearly 40 ˚C hotter, on average, than fall fires.

Sampling Design and Data Collection

Data collection occurred from 2008-2016 in late May though early August and included sampling within all management intervals at each site (Fig. III1). We systematically located plots (n = 15 $stand^{-1}$) along a 70 X 70 m grid within the core (50-m buffer) of each stand. Woody vegetation was monitored in seven nested 1-m^2 and 3-m radius sub-plots at each plot. Five sub-plots were located at 12.5-m intervals along a 50-m transect running through plot center and perpendicular to landscape slope. Two additional sub-plots were 12.5 m up- and down-slope from plot center. In 1-m^2 sub-plots, all seedling and shrubby stems were tallied by species.

Seedlings were tree species (typically ≥4 m tall at maturity) ≥30.5 cm tall but <1.4 m tall. Shrubby vegetation included lianas, woody, and semi-woody (*e.g.*, *Rubus* spp.) species that were typically multi-stemmed and rarely >4 m tall. Sapling stems (trees ≥1.4 m tall and <7.6 cm DBH) were tallied by species in 3-m radius sub-plots. Larger saplings (≥7.6 cm DBH) were rare (< 150 stems ha^{-1}, Vander Yacht et al. 2017a) and not analyzed. Only one and three sets of nested sub-plots were measured per plot in 2008 and 2009, respectively. We measured live and dead tree basal area (2-factor metric prism), canopy closure (spherical densiometer), percent slope (clinometer), aspect, and slope position at the ends and center of each plot's 50-m transect. A numerical value, 1-6, was assigned to each location within a plot corresponding to alluvial, cove, toe-slope, mid-slope, shoulder, and ridge slope positions, respectively.

DATA ANALYSIS

Analyses were conducted in RStudio version 1.0.143 (2016, RStudio, Inc., Boston, MA). We evaluated differences in shrubby, seedling, and sapling vegetation across treatments and time using restricted, non-parametric, and permutation-based multivariate analysis of variance (PERMANOVA, Anderson 2001). Differences were visualized using non-metric multi-dimensional scaling (NMDS, Kruskal 1964), and indicator analysis (Dufrene and Legendre 1997) and mixed-effect analysis of variance (ANOVA) identified species driving differences in woody vegetation across treatments and time. Finally, structured additive regression (STAR, Umlauf et al. 2015) was used to relate observed patterns in woody vegetation to gradients in overstory and understory density. In all analyses, we aggregated *Vaccinium*, except *Vaccinium arboreum*, and *Carya* species based on identification certainty concerns.

Differences in Understory Woody Community Across Treatments and Time

We conducted PERMANOVA tests using function adonis from R's vegan package (Oksanen et al. 2017). We focused on management periods (*i.e.*, pre-management, post-cut, and post-fire, Fig. III1) because of an interest in long-term effects rather than variation associated with biennial fire cycles. This reduced sampling variance and improved interpretability. We calculated yearly stand means of shrubby, seedling, and sapling density (stems ha^{-1}) by species, and only included species that were ≥1% of total category density in ≥10% of stands within a year and site. This captured ≥95% of total density across all categories and sites. We used a ln(x + 1) transformation on site-specific matrices to moderate the influence of abundant species as is common practice in multivariate compositional analyses (McGarigal 2000).

A significant PERMANOVA result could indicate a difference in either location or dispersion of multivariate data (Warton et al. 2012). Therefore, we used function betadisper (vegan package) to test multivariate homogeneity of distance dispersions across treatments and periods. We used Bray-Curtis distances in PERMANOVA tests and compared observed R^2 to a distribution of R^2 values calculated from 4,999 data permutations. Permutations were variously restricted according to evaluated effect; we preserved temporal order of annual observations within blocked stands during period tests, freely permuted within blocked years during treatment tests, and freely permuted stand groups while preserving internal temporal order during treatment × period interactions. These constraints accounted for our nested study design and the non-independence of annual observations of woody communities within stands.

We progressed through an *a priori* set of post-hoc PERMANOVA contrasts after observing significant main or interaction effects. Treatment contrasts included comparing controls to managed stands, woodlands versus savannas, and fall versus spring fire. At LBL and

GRGL, we also included a control versus burn-only contrast. Period contrasts included comparing pre-management to post-cut and post-cut to post-fire. At CWMA, we also evaluated post-fire 1 versus post-fire 2 (2013 and 2014) and post-fire 2 versus post-fire 3 (2015-2016). We avoided multiple testing problems by re-computing R^2 values during each permutation (Dufrene and Legendre 1997), but also chose to conservatively use Bonferroni *p*-value adjustment within each set of PERMANOVA tests (overall, treatment, and period).

Prior to PERMANOVA, we addressed the uniqueness of management at LBL where burning following thinning did not occur in the same year for all stands (Fig. III1). We compiled data into pre- and post- burn to allow for similar analyses as performed at other sites. In addition, PERMANOVA tests indicated shrubby ($F_{1,14}$ = 1.9, p = 0.063), seedling ($F_{1,14}$ = 2.2, p = 0.055), and sapling ($F_{1,14}$ = 1.8, p = 0.056) communities did not differ in 2013 and 2014 between SpS and SpW replicates that were burned in November 2009 and SpS and SpW replicates that were not. This, and recognizing that the 2009 fire's influence was equally present within SpS and SpW means, warranted analyzing LBL data in a similar fashion as other sites.

Identifying Species Driving Observed Woody Community Differences

We performed indicator analysis (Dufrene and Legendre 1997) using the multipatt function in the indicspecies R package (De Caceres and Legendre 2009). The test calculated an indicator value as the product of two components: specificity (*A*), the probability that a site belongs to the target group given the species has been found, and sensitivity (*B*), the probability of encountering the species in sites belonging to the group. This identified patterns in species occurrence across treatments and periods that varied more than expected by chance. We used PERMANOVA results to inform the suite of potential treatments and periods with which species could be associated. For example, if PERMANOVA results only indicated differences between

woodlands and savannas, only associations with those treatments were evaluated. We examined associations for all species included in PERMANOVA tests, although we do not report results for species with $B < 0.05$. We recomputed indicator values during 4,999 permutations, and only tested associations for which the indicator value was the highest. Permutations during indicator analysis were restricted in the same manner as PERMANOVA tests.

We evaluated univariate differences across treatments and periods in the stem density (stems ha^{-1}) of species accounting for ≥5% of the total stem density within any one treatment using mixed-effect ANOVA. We also evaluated oaks and remaining species (other) in aggregation, and the total density of shrubs, seedlings, and saplings. We square root transformed all variables, assessed each for normality (Wilk's test, W > 0.90), and graphically observed equality of variance prior to ANOVA. Fixed-effects included treatment, period, and treatment × period interactions. Year was a fixed-effect because treatments were applied over time. We included a random effect of replicate stand except where replication did not occur (GRGL). We used Kenward-Roger degree of freedom method, but dropped autoregressive correlation between periods (repeated measures) because the application of treatments over time minimized differences in model fit (<5, -2 residual log likelihood per covariance parameter) between inclusion and omission (Littell et al. 2006).

Ordination and Relationships with Density Gradients

We completed NMDS using metaMDS (vegan package, Oksanen et al. 2017). We restricted this analysis, and subsequently relating it to density gradients, to CWMA based on the advanced state of management at the site. Regarded as the most robust unconstrained ordination, NMDS is free from assumptions concerning normality and linear relationships (Kruskal 1964; Minchin 1987). We again used a ln(x + 1) transformation on abundance matrices, and only

included species evaluated by PERMANOVA. We requested a two-axis solution (k = 2) and used Bray-Curtis distances. Twenty random starts for each iteration avoided local optima. We visualized PERMANOVA identified interactions by plotting and connecting the average position of treatments during each period in ordinated explanatory space.

Changes in woody vegetation were then related to canopy disturbance effects on overstory density, and fire effects on understory density. We used STAR models (Umlauf et al. 2015) to project a non-linear explanatory surface of predicted overstory and understory metrics onto ordination results. This process was comparable to more commonly used thin-plate spline general additive models (Oksanen et al. 2017; Wood 2003). The advantage of STAR models was their ability to handle random and nested effects present within our experiment. We predicted live basal area and sapling density from random stand effects and the tensor product of NMDS ordination axis scores (n = 2) for each woody community of interest (shrubby, seedling, and sapling; 6 models). Stepwise procedures in package R2BayesX (Umlauf et al. 2015) then selected from treatment, year, period, slope, slope position, and aspect effects to generate a top model for each initial model. When predicting sapling density, we also included canopy closure, live basal area, and dead basal area in selection procedures. Smoothing functions were used if trends were non-linear. Prior to analysis, we transformed aspect into a continuous variable between 0 (southwest) and 2 (northeast) using Beers et al. (1966), and all non-categorical variables were z-score standardized (mean = 0, standard deviation = 1).

We then dropped NMDS tensor terms from top STAR models and calculated the change in Akaike's information criterion (AIC). An increase of >2.0 in ΔAIC (Burnham and Anderson 2002) was considered evidence of a relationship between density metrics and ordinated woody community properties. We further examined the significance and strength (R^2) of relationships

by modeling density metrics as a function of NMDS axis scores using multiple regression. We projected density gradients significantly related by both AIC and multiple regression to variation in shrubby, seedling, and sapling communities as contour surfaces underlying ordinations. This depicted relationships between understory woody community change and density gradients.

RESULTS

Differences in Understory Woody Vegetation Across Treatments and Time

We encountered 67 shrubby, and 69 tree, species across all three sites and 9 years of monitoring (Appendix SIII2). Multivariance dispersion across treatment groups was comparable at all sites and for all vegetation except saplings at CWMA (Table III1). The spread of sapling data at CWMA in savannas was 1.5X greater than that observed in controls. Except for GRGL, the dispersion of woody community data differed by period (Table III1). This difference involved increasing multivariance over time, and post-management periods were nearly 3X as variable as pre-management periods. The lack of replication at GRGL probably contributed to the greater observed dispersion relative to other sites.

Understory woody communities differed by treatment and period at all sites, but these effects interacted at CWMA and LBL (Table III2). Such interactions explained, on average, 54% of woody community variation. At GRGL, treatment effects explained 3X as much variation (36%) as period effects (12%). Except for shrubby and seedling communities at GRGL, understory woody vegetation differed in managed and unmanaged stands. This difference explained more variation than other treatment contrasts. Woodlands and savannas commonly differed, but fire-season effects were only observed where fire was applied three times (CWMA). The transition from pre- to post- canopy disturbance explained more variation than the transition from pre- to post- fire, even when fire was applied multiple times (CWMA). Biennial burning (3

Table III1. Multivariate homogeneity of variance dispersions across treatments and periods during mesophication reversal experiments at Catoosa Wildlife Management Area (CWMA), Land Between the Lakes National Recreation Area (LBL), and Green River Game Lands (GRGL). Bold indicates significance and lowercase letters depict differences as determined by Tukey mean separation (α = 0.05 for both). Commonly observed differences by period are presented. Only sapling community dispersion at CWMA differed by treatment (Control: 0.14 b, SpW: 0.20 ab, FaW: 0.19 ab, FaS: 0.21 a, SpS: 0.21 a).

		Treatment Groups			Period Groups			Dispersion estimates by period				
Site	Vegetation[1]	*df*	*F*	*p*	*df*	*F*	*p*	Pre-Mng	Post-Cut	Post-Fire (1)	Post-Fire 2	Post-Fire 3
CWMA	Shrubby	4, 85	0.68	0.617	4, 85	4.13	**0.004**	0.07 b	0.18 a	0.20 a	0.19 a	0.21 a
	Seedlings	4, 85	0.78	0.540	4, 85	13.75	**< 0.001**	0.06 c	0.13 b	0.18 a	0.17 ab	0.19 a
	Saplings	4, 85	3.36	**0.013**	4, 85	18.19	**< 0.001**	0.09 c	0.16 b	0.24 a	0.25 a	0.22 a
LBL	Shrubby	5, 66	1.83	0.119	2, 69	25.37	**< 0.001**	0.09 b	0.23 a	0.28 a	-	-
	Seedlings	5, 66	0.73	0.606	2, 69	103.91	**< 0.001**	0.08 c	0.22 b	0.25 a	-	-
	Saplings	5, 66	0.30	0.911	2, 69	56.61	**< 0.001**	0.09 b	0.25 a	0.28 a	-	-
GRGL	Shrubby	5, 36	0.54	0.745	2, 39	0.94	0.399	0.31 a	0.32 a	0.27 a	-	-
	Seedlings	5, 36	0.48	0.791	2, 39	2.78	0.074	0.24 a	0.22 a	0.16 a	-	-
	Saplings	5, 36	2.54	0.054	2, 39	0.64	0.531	0.19 a	0.21 a	0.21 a	-	-

[1]Shrubby vegetation included multi-stemmed woody and semi-woody (e.g., *Smilax* and *Rubus* spp.) species rarely >4 m tall and lianas. Seedlings (≥30.5 cm tall but <1.4 m tall) and Saplings (≥1.4 m tall and <7.6 cm diameter at breast height) were tree species ≥4 m in height at maturity. Treatments referenced in table include unmanaged oak forests (Control) and savanna (7 m^2 ha^{-1}, S) and woodland (14 m^2 ha^{-1}, W) residual basal area stands burned in the spring (Sp) or fall (Fa). Period associations were prior to management (Pre-Mng), after canopy disturbance (Post-Cut), or after prescribed fires (Post-Fire, multiple at Catoosa).

Table III2. Differences in the composition and/or density of shrubby, seedling, and sapling vegetation during mesophication reversal experiments at Catoosa Wildlife Management Area (CWMA), Land Between the Lakes National Recreation Area (LBL), and Green River Game Lands (GRGL) as determined by restricted PERMANOVA (4,999 permutations). Significant Bonferroni adjusted *p*-values in bold (α = 0.05).

	Overall Tests:	Treatment				Period				Treatment × Period			
Site	Vegetation	*df*	*F*	*p*	R^2	*df*	*F*	*p*	R^2	*df*	*F*	*p*	R^2
CWMA	Shrubby	4, 85	9.04	**0.001**	0.30	4, 85	9.25	**0.001**	0.30	24, 65	6.58	**0.001**	0.71
	Seedlings	4, 85	6.60	**0.001**	0.24	4, 85	6.00	**0.001**	0.22	24, 65	3.50	**0.001**	0.56
	Saplings	4, 85	9.43	**0.001**	0.31	4, 85	4.61	**0.001**	0.18	24, 65	3.84	**0.003**	0.59
LBL	Shrubby	5, 66	2.97	**0.001**	0.18	2, 69	8.31	**0.001**	0.19	17, 54	3.22	**0.001**	0.50
	Seedlings	5, 66	1.94	**0.001**	0.13	2, 69	10.95	**0.001**	0.24	17, 54	2.62	**0.001**	0.45
	Saplings	5, 66	2.45	**0.001**	0.16	2, 69	8.41	**0.001**	0.20	17, 54	2.59	**0.001**	0.45
GRGL	Shrubby	5, 36	4.12	**0.001**	0.36	2, 39	3.78	**0.001**	0.16	17, 24	2.41	1.000	0.63
	Seedlings	5, 36	3.66	**0.001**	0.34	2, 39	2.03	**0.002**	0.09	17, 24	1.87	0.934	0.57
	Saplings	5, 36	4.27	**0.001**	0.37	2, 39	2.33	**0.002**	0.11	17, 24	2.61	0.110	0.65
	Treatment Contrasts[1]:	Control vs. Managed				Woodland vs. Savanna				Fall vs. Spring Fire			
		df	*F*	*p*	R^2	*df*	*F*	*p*	R^2	*df*	*F*	*p*	R^2
CWMA	Shrubby	1, 88	29.12	**0.001**	0.25	1, 70	2.88	**0.001**	0.04	1, 70	1.92	**0.013**	0.03
	Seedlings	1, 88	15.36	**0.001**	0.15	1, 70	1.76	**0.030**	0.02	1, 70	6.13	**0.001**	0.08
	Saplings	1, 88	22.46	**0.001**	0.20	1, 70	2.78	**0.002**	0.04	1, 70	4.81	**0.001**	0.06
LBL	Shrubby	1, 70	7.89	**0.001**	0.10	1, 46	2.66	**0.001**	0.05	-	-	-	-
	Seedlings	1, 70	5.74	**0.001**	0.08	1, 46	1.15	0.355	0.02	-	-	-	-
	Saplings	1, 70	6.62	**0.001**	0.09	1, 46	1.17	0.240	0.02	-	-	-	-
GRGL	Shrubby	1, 40	2.17	0.157	0.05	1, 26	5.80	**0.002**	0.18	1, 26	2.55	0.090	0.09
	Seedlings	1, 40	2.57	0.074	0.06	1, 26	3.09	**0.028**	0.11	1, 26	2.27	0.103	0.08
	Saplings	1, 40	3.61	**0.009**	0.08	1, 26	2.39	**0.024**	0.08	1, 26	1.54	0.222	0.06
	Period Contrasts[2]:	Pre-Management vs. Post-Cut				Post-Cut vs. Post-Fire				Post-Fire 1 vs. Post-Fire 2			
		df	*F*	*p*	R^2	*df*	*F*	*p*	R^2	*df*	*F*	*p*	R^2
CWMA	Shrubby	1, 28	10.53	**0.001**	0.27	1, 78	10.97	**0.001**	0.12	1, 38	2.27	**0.001**	0.06
	Seedlings	1, 28	7.52	**0.003**	0.21	1, 78	8.13	**0.001**	0.09	1, 38	1.17	0.284	0.03
	Saplings	1, 28	4.52	**0.002**	0.14	1, 78	6.97	**0.001**	0.08	1, 38	1.21	**0.006**	0.03
LBL	Shrubby	1, 50	14.35	**< 0.001**	0.24	1, 46	3.02	**0.001**	0.06	-	-	-	-
	Seedlings	1, 50	21.98	**< 0.001**	0.32	1, 46	3.21	**0.001**	0.07	-	-	-	-
	Saplings	1, 50	17.50	**< 0.001**	0.28	1, 46	2.99	**0.006**	0.06	-	-	-	-
GRGL	Shrubby	1, 28	4.67	**< 0.001**	0.14	1, 22	4.59	**0.001**	0.17	-	-	-	-
	Seedlings	1, 28	1.60	0.121	0.05	1, 22	1.46	0.164	0.06	-	-	-	-
	Saplings	1, 28	1.27	0.192	0.04	1, 22	1.72	**0.006**	0.07	-	-	-	-

[1]Tests of Control vs. burn-only at LBL and GRGL were never significant ($F < 6.72$, $p > 0.05$). Only spring fire was conducted at LBL. [2]Period contrasts at CWMA included post-fire 1 vs. post-fire 2 (presented) and post-fire 2 vs. post-fire 3. The latter was only significant for shrubby vegetation ($F = 4.39$, $p = 0.001$, $R^2 = 0.10$). Shrubby: multi-stemmed, woody and semi-woody (*e.g.*, *Rubus* and *Smilax* spp.) species rarely >4 m tall and lianas. Seedlings: tree species (≥4 m in height at maturity) ≥30.5 cm tall but <1.4 m tall. Saplings: trees ≥1.4 m tall and <7.6 cm diameter at breast height.

fires) at CWMA resulted in 1) changes in the shrubby community after each application of fire, 2) changes in the seedling community only after the first fire, and 3) changes in the sapling community after the first and second fires. The seedling community at GRGL was stable across management periods, and the sapling community only changed after fire.

Identifying Species Driving Observed Woody Community Differences

Indicator analysis associated most tested species of shrubs (Appendix SIII3.1), seedlings (Appendix SIII3.2), and saplings (Appendix SIII3.3) with specific treatments and/or management periods. Nearly all shrubby species were indicative of managed treatments and post-management periods (Appendix SIII3.1). Mountain laurel at CWMA was the only shrubby species indicative of controls. Shrubby species with indicator values >0.16 at CMWA (5 species) were exclusively associated with managed stands. Across these stands, the presence and abundance of northern dewberry (*Rubus flagellaris* Willd.) appeared to be a primary driver of shrubby community differences between woodlands and savannas and fall and spring fire. Bristly greenbrier (*Smilax tamnoides* L.) was indicative of post-cut periods at CWMA, but all other shrubby species were associated with post-fire periods. Treatment associations of shrubby species at LBL and GRGL were distributed near equally among woodlands and savannas. Eleven of the twelve species indicative of a management period at LBL were associated with post-cut periods. A more equal distribution of indicators between post-cut and post-fire periods was observed at GRGL.

Eastern white pine (*Pinus strobus* L.) seedlings were relatively strong indicators of controls at CWMA (Appendix SIII3.2). Seven seedling species were indicative of management at the site, including 3 of the 5 treatment-associated oak species. Five seedling species were associated with spring burns. Yellow poplar was associated with fall burns, but *B* was only 0.09.

Scarlet oak, flowering dogwood (*Cornus florida* L.), and Virginia pine (*Pinus virginiana* Mill.) seedlings indicated post-cut periods. All other period associations for seedlings at CWMA were with post-fire intervals. At LBL, 5 seedling species were indicators of controls and 12, including all six treatment-associated oak species, indicated management. Most seedling species at LBL indicated post-cut, rather than the post-fire, periods. At GRGL, sassafras seedlings were savanna indicators, but all other associated seedling species indicated woodlands.

Sapling oaks were never associated with unmanaged controls (Appendix SIII3.3). At CWMA, Eastern white pine, American beech (*Fagus grandifolia* Ehrh.), and American holly (*Ilex opaca* Aiton) saplings indicated the absence of management. More sapling species at CWMA were associated with management than controls, and specifically, savanna and spring burns relative to woodlands and fall burns. All but four period-associated sapling species at CWMA indicated post-fire periods. Nine species at LBL were indicators of the absence of management while 14 species, half of which were oaks, indicated managed stands. Nearly all sapling species at LBL were associated with the post-cut period. Red maple and sourwood saplings were strong indicators (index ≥ 0.64) of management at GRGL. Most sapling species at GRGL were indicators of woodlands and post-fire periods.

Indicator analysis results were supported by univariate trends in woody density across treatments and periods (Fig. III2-III3, Appendices SIII4-SIII5). Shrubby density at CWMA was greater in managed than control treatments. Specifically, southern blackberry density was more than 1,000X greater in savannas than controls, and *Vaccinium* spp. density was greater than controls in all treatments except for FaS. After initial increases following canopy disturbance, fire appeared to decrease *Smilax* spp. density. Likewise at LBL, canopy disturbance promoted

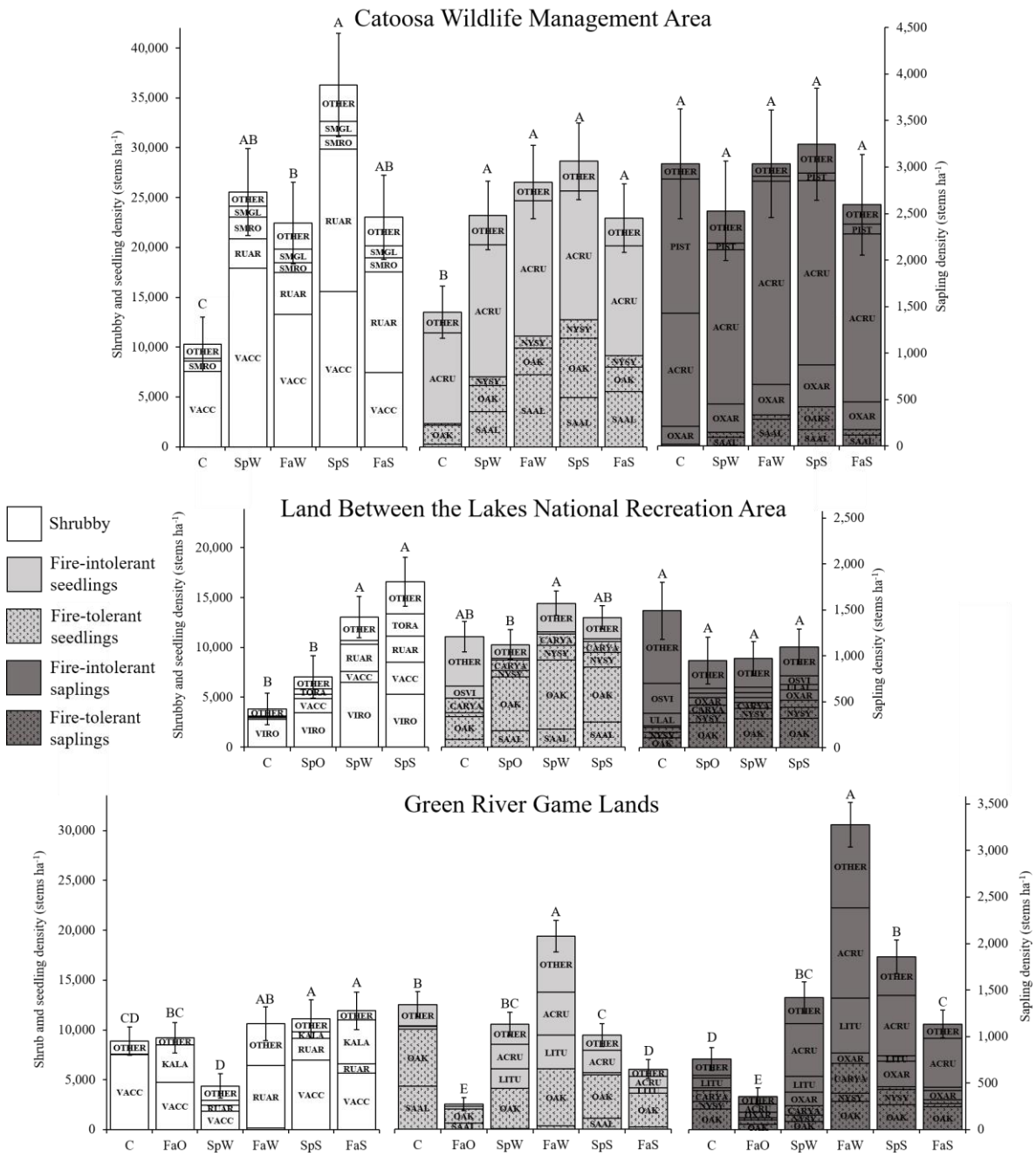


Fig. III2. Differences in shrub, seedling, and sapling communities by treatment at three sites as determined by mixed-effect ANOVA. Treatments were unmanaged (Control), burned only in the spring (SpO) or fall (FaO), and combinations of spring and fall fire with woodland (14 m^2 ha^{-1}) or savanna (7 m^2 ha^{-1}) residual basal area. Individual species accounting for ≥ 5% of the total stem density within any one treatment are presented and coded to the first two letters of genus and species. Shrubby vegetation included multi-stemmed woody and semi-woody (e.g., *Smilax* and *Rubus* spp.) species rarely >4 m tall and lianas. Seedlings are tree species (≥4 m in height at maturity) ≥30.5 cm tall but <1.4 m tall. Saplings are tree species ≥1.4 m tall and <7.6 cm diameter at breast height. All *Carya* spp. (CARYA), Quercus spp. (OAKS), and *Vaccinium* spp. (VACC) except *Vaccinium arboreum* were aggregated.

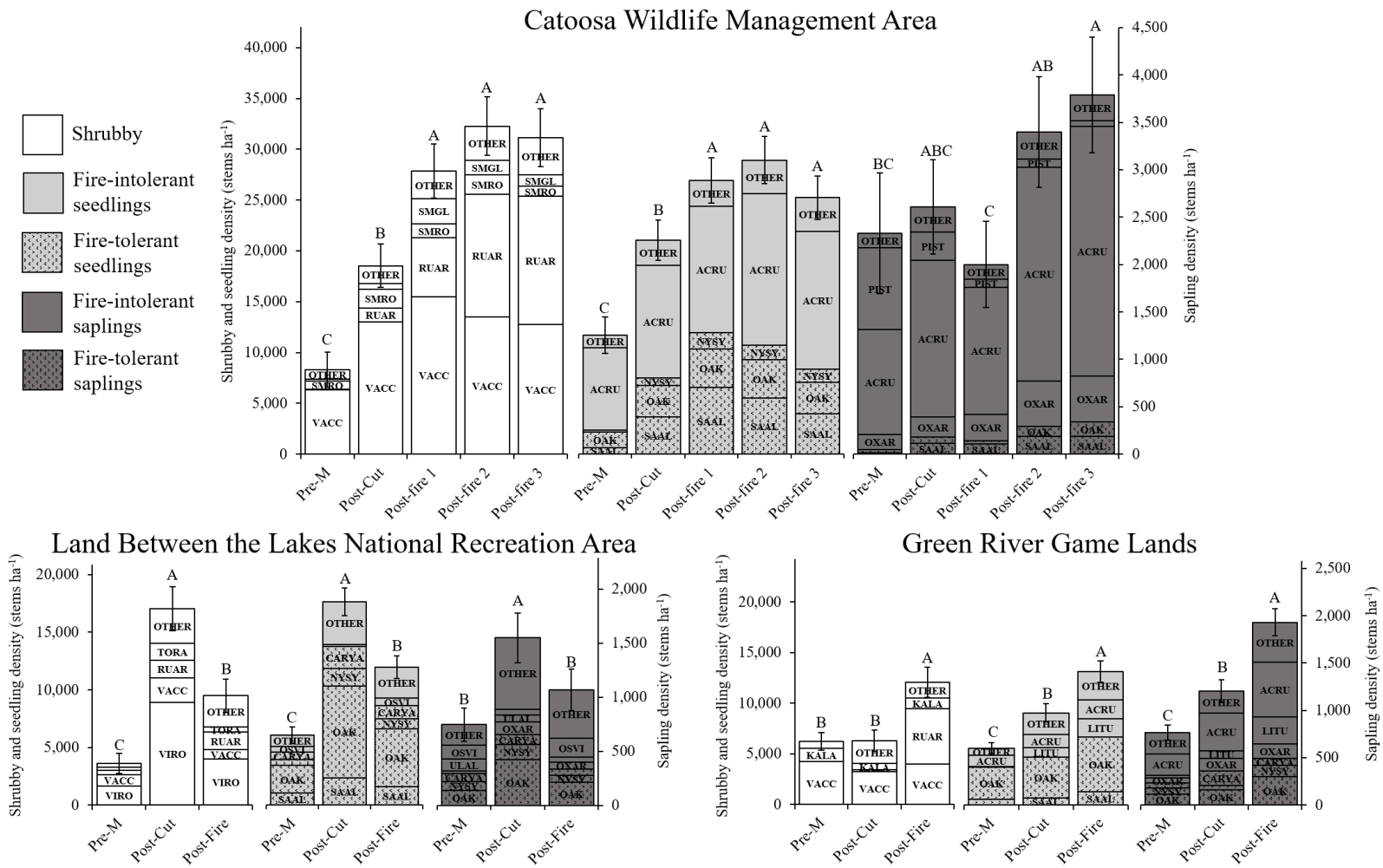


Fig. III3. Differences in shrub, seedling, and sapling communities across management periods at three sites as determined by mixed-effect ANOVA. Periods were pre-management (Pre-M), post canopy disturbance (Post-Cut), and post prescribed fire (Post-Fire, multiple at CWMA). Individual species accounting for ≥ 5% of the total stem density within any one treatment are presented and coded to the first two letters of genus and species. Shrubby vegetation included multi-stemmed woody and semi-woody (e.g., *Smilax* and *Rubus* spp.) species rarely >4 m tall and lianas. Seedlings are tree species (≥4 m in height at maturity) ≥30.5 cm tall but <1.4 m tall. Saplings are tree species ≥1.4 m tall and <7.6 cm diameter at breast height. All *Carya* spp. (CARYA), Quercus spp. (OAKS), and *Vaccinium* spp. (VACC) except *Vaccinium arboreum* were aggregated.

increases in the density of shrubby species prior to fire-induced reductions. Total shrubby density at GRGL did not increase following canopy disturbance and was greatest following fire.

Seedling density was greater in all managed treatments than controls at CWMA, largely a result of increased blackgum (*Nyssa sylvatica* Marshall) and sassafras density. Oak seedling density was only greater than controls in SpS, but did increase overall from pre- to post-management. Red maple dominated seedling composition at CWMA across treatments (≥ 43%), increasing in density following canopy disturbance and again after fire. In managed treatments relative to controls at LBL, seedling density of sassafras, blackgum, and oaks was greater, and eastern hophornbeam (*Ostrya virginiana* [Mill.] K. Koch) was 5X less. Total seedling density at LBL increased following canopy disturbance and declined following fire, driven by trends in sassafras, blackgum, hickories, and oaks. Total seedling density at GRGL was variable across treatments and increased from pre-management to post-fire. Trends over periods were largely related to increasing red maple, yellow poplar, sassafras, and oak seedling density.

Thinning and burning decreased eastern white pine sapling density >18-fold relative to controls at CWMA. Sassafras sapling density was greater in all managed treatments relative to controls, but sourwood and oak sapling density was only greater than controls in SpS. From pre-management to after the third fire at CWMA, increases in sourwood (>3X), sassafras (>10X), and oak (5X) sapling density were observed while eastern white pine declined (>13X). Over this same period, red maple sapling density more than doubled and dominated (≥ 56%) the total sapling density of managed treatments. We did not observe a difference in total sapling density, or a difference in any of the sapling species tested, across treatments at LBL. Total sapling density at LBL increased following canopy disturbance and decreased to pre-management levels after fire, a trend largely driven by oaks. At GRGL, variation across treatments in total sapling

density was similar to that observed for total seedling density at the site. Total sapling density also increased over time, largely driven by increases in red maple, yellow poplar, and oaks.

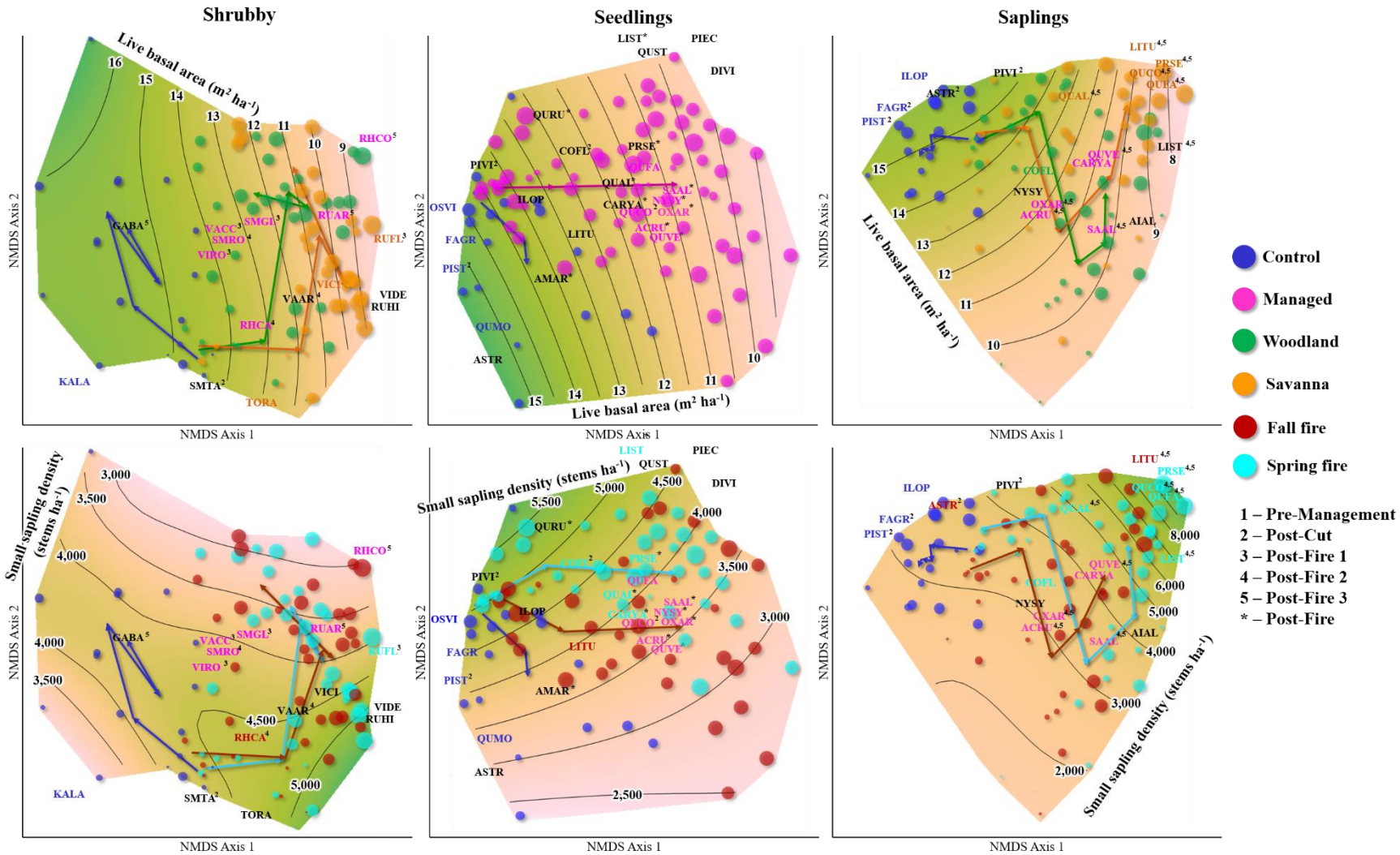
Ordination and Relationships with Density Gradients

Final NMDS solutions for shrubby (stress = 0.17), seedling (stress = 0.19), and sapling (stress = 0.15) communities at CWMA respectively explained 97.2%, 96.4%, and 97.7% (non-metric R^2) of the variation between ordinated distances and observed dissimilarity in treatment stands (Fig. III4). Ordinations were consistently related to live basal area and small sapling density (Appendix SIII6). Including tensor product terms of shrubby, seedling, or sapling NMDS axes improved, or did not affect (shrubby and live basal area), top STAR models predicting live basal area and small sapling density. Shrubby community NMDS axes did, however, explain 57% of the variation in live basal area. Performance of STAR models predicting large sapling density was reduced (decline in AIC) when tensor product terms of shrubby or sapling NMDS axes were included. Live basal area was consistently related to year, slope, and random stand effects. Small sapling density was consistently related to year, live basal area, slope, and random stand effects.

Ordinations visually supported PERMANOVA, indicator analysis, and univariate tests (Fig. III4). Woody communities in control and managed treatments were distinct. Although less apparent, differences between woodlands and savannas, and fall and spring burning, were also depicted. Canopy disturbance shifted savannas into a region defined by less overstory and greater understory density relative to woodlands. Post-fire movement in shrubby and seedling communities was towards regions defined by reduced understory density, whereas movement of sapling communities post-fire was initially negatively and then positively associated with dense understories. More species were ordinated with spring fire, which appeared characterized by

Fig. III4. NMDS ordinations of woody communities at Catoosa Wildlife Management Area during a mesophication reversal experiment involving variation in canopy disturbance (Woodland: 14 m^2 ha^{-1}, Savanna: 7 m^2 ha^{-1}) and prescribed fire-season (Fall, October or Spring, March). Replicate 20-ha stands (n = 10) within a year (2008 to 2016) are colored based on PERMANOVA determined differences ($\alpha = 0.05$) and size-scaled to density (stems ha^{-1}). Species labels depict indicator analysis associations with treatments (colored) and periods (super-scripts). Arrows depict changes across pre-management to post-fire periods. Rows depict differences in canopy disturbance (top) and fire-season (bottom) treatments. Contour surfaces are predicted live basal area and small sapling density from structured additive regression, and are significantly related to the ordinations they underlie. Ordinated species position is coded to the first two letters of genus and species, and only species that were ≥1% of total density at ≥10% of stands within a year were included.

Fig. III4. Continued.



greater understory density than fall fire. Species associated with management were ordinated along interfaces between specific treatments, whereas species associated with specific treatments were ordinated among clustered observations of those treatments.

DISCUSSION

There is increasing recognition that a lack of disturbance has greatly altered woody regeneration dynamics in oak forests of the Mid-South (Dey 2014; Keyser et al. 2016). The strong separation we observed between unmanaged and managed stands supports this assertion. Management began to reverse mesophication effects on understory woody communities at sites throughout the region. Thinning and fire increased variation by promoting shade-intolerant and fire-tolerant species formerly suppressed under closed-canopy conditions. This included the positive response of many lianas, semi-woody species, and shrubs. Averaged across sites, oak seedling density from pre- to post-management nearly doubled (+2,256 stems ha^{-1} ± 434 SE). Similar trends were observed for other disturbance-dependent seedlings. Effects on saplings were less dramatic; however, indicator analysis almost always associated oaks and other disturbance-dependent saplings were with managed treatments. Shade-tolerant, mesophytic species were associated with unmanaged forests. Paradoxically, red maple was often an exception, and perhaps limited the response of oaks and other xerophytic species in managed stands. Fire-season effects were not observed univariately, but multivariate results suggested spring burning was associated with more woody species and a greater understory density than fall burning.

Canopy disturbance had strong effects on woody vegetation. Increases in light (Larsen and Johnson 1998) and nitrogen (Reich et al. 2001) availability following canopy disturbance likely promoted overall increases in woody vegetation density. However, most species increasing in density or associated with disturbed-canopies were shade-intolerant (Burns and Honkala

1990a; Burns and Honkala 1990b). Reducing overstory and midstory density can increase understory light for several years and have positive effects on the regeneration of species like oaks (Brudvig and Asbjornsen 2009; Lorimer et al. 1994). Logging also disturbed soils, removed overstory seed-sources of shade-intolerant competition, and shifted overstory composition toward disturbance-adapted species – probably leading to increased dominance of seed-rain (Brudvig and Asbjornsen 2008). Together, such effects transitioned understory composition towards precisely the species threatened by mesophication associated canopy-closures (Dey et al. 2008; Johnson et al. 2009; South and Harper 2016). The often robust response of shade-tolerant red maple following canopy disturbance was an exception. Extended time under closed-canopies probably promoted the pre-management dominance of red maple, which sprouted vigorously from well-established rootstocks during our study. This illustrates the positive feedback nature of mesophication and how the effort required to achieve reversal can increase over time in the absence of disturbance. Alternatively, the disturbance adapted tree species that thinning promotes can exhibit positive feedbacks of their own, including a highly flammable fuel-bed that maintains sparse woodland and savanna structure (Mitchell et al. 2009; Varner et al. 2016).

Repeated fire reduces the density of understory woody vegetation and promotes fire-adapted species (Peterson and Reich 2001). In our study, fire maintained or enhanced the positive effects of canopy disturbance on such species, including commonly promoting increases in oak seedling and sapling density. However, nearly all woody species increased in density over post-fire periods. Prodigious fruiting after canopy disturbance (Greenberg et al. 2007), widespread dispersal by wildlife, and long-term seed viability (Cain and Shelton 2003) can increase blackberry presence in seedbanks (Keyser et al. 2012) and support a robust post-fire response (Iglay et al. 2010). Like others, we observed vigorous resprouting and growth from

rootstocks after top-kill by fire (Blankenship and Arthur 2006; Ward 2015). Repeated fire decreases sprouting capacity if applied without gaps ≥3 years during which below-ground resources can be replenished (Arthur et al. 2015; Hutchinson et al. 2012). To illustrate, stands burned for >60 years had dense midstories if fires occurred every 4 years, but virtually no midstory if fires occurred annually (Knapp et al. 2015). Eventually, maintaining overstories dominated by disturbance adapted trees will require an increased understanding of how pauses in fire recurrence influence recruitment.

Sparse overstory structure increases understory plant resources (e.g., light) and may reduce sapling recovery time following fire. Our results indicate reducing woody density under such conditions could require more than three biennial burns, but results will also vary by site. Nowacki and Abrams (2008) predicted differences in the rate of community state transitions between xeric and mesic uplands. Comparing our results at LBL to more mesic sites supports this prediction. The relatively shallower soils, warmer temperatures, and drier climate of LBL could explain how a single fire decreased woody density and quickly established the understory dominance of fire-tolerant species. Light intensity in the understory of xeric sites often can support oak survival, growth, and the accumulation of advanced regeneration (Blizzard et al. 2013; Johnson et al. 2009). A substantial lack of mesophytic competitors (*e.g.*, red maple and yellow-poplar) also distinguished LBL from other sites. Under such conditions, promoting shade-intolerant and fire-tolerant species may only require canopy disturbance.

Fire intensity was consistently greater in March than October, but this difference did not result in a consistent effect on woody vegetation. Woody plant mortality increases with increasing fire temperature and duration of exposure (Michaletz and Johnson 2007). Perhaps the slower-spread of October fires compensated for lower burning temperatures relative to March

fires. The timing of fire in relation to plant phenology, such as seasonal variation in root carbohydrate reserves (Landhausser and Lieffers 2002; Loescher et al. 1990), may have also compensated for observed differences in intensity. This is reasonable given that growing-season fire can be more effective than dormant-season fire in inducing woody plant mortality (Gruchy et al. 2009; Robertson and Hmielowski 2014). Even for adapted species like oaks, not all fire is equally beneficial (Arthur et al. 2012). The negative effects of burning shortly after acorn drop (Greenberg et al. 2012) and when dormancy is not protecting meristematic tissues (Hengst and Dawson 1994) could explain the reduced density of oak seedlings and saplings in FaS relative to SpS at CWMA. Perhaps such a difference would eventually occur at GRGL after repeated burning, but it is also possible that the site lacked the effect because fire outside of tree dormancy had greater negative effects on oak competitors than oaks (Brose and Van Lear 1998). Regardless, October fires were less intense and achieved similar effects as March burning. This may represent an advantage over more traditionally used dormant-season burning (Knapp et al. 2009), but fire intensities great enough to induce desired effects will still need to be targeted. In Arkansas, fires in September and October were less intense and less effective in reducing larger (>1 m tall) midstory stems than fires in March and April (Sparks et al. 1999).

Thinning and burning had consistently negative effects on some shade-tolerant and fire-intolerant species (*e.g.*, eastern white pine, eastern hophornbeam, and American beech), but others responded positively to canopy disturbance and resprouted prolifically after fire (*e.g.*, yellow poplar and red maple). This second group perhaps limited any gains in the competitive position of fire-tolerant species in our study and elsewhere (Arthur et al. 2015; Iverson et al. 2017). Canopy disturbance equivalent to our woodland treatments has been suggested to maintain fine-fuel loads (*i.e.*, leaf litter) and increase understory light while minimizing the

growth of shade-intolerant competition (Brose and Van Lear 1998). During our study, the density of such competition (*i.e.*, yellow poplar and red maple) was equal or greater in woodlands relative to savannas. This suggests the shelterwood technique for promoting oaks may be more effective when greater canopy disturbance (to 7 m^2 ha^{-1} residual basal area) is utilized.

The ability of oak competitors to resprout, even after multiple fires (Blankenship and Arthur 2006), warrants research into seasonal variations of fire that will favor oak dominance. After repeated burning, indicator analysis associated more oak species with spring relative to fall burning; however, oak competitors were equally associated with both seasons of fire. This, and limited differences in density across fire-seasons, does not clearly demonstrate the advantage of growing-season fire in selecting for fire-tolerant species that others have observed (Brose et al. 2013; Brose and Van Lear 1998). Perhaps October is too late regionally to gain such an advantage (Pallardy 2010). Understories dominated by fire-intolerant species are not unique to our study. Altered disturbance regimes have made such conditions common in eastern forests (Abrams 1998; Nowacki and Abrams 2008). Our results and others (Arthur et al. 2015) suggest multiple burns or other management (e.g., herbicides; Vander Yacht et al. 2017b) may be required to reduce this substantial and less fire-tolerant component of understory woody communities. Otherwise, applied disturbances may simply accelerate succession into forests dominated by mesophytic species (Abrams and Nowacki 1992).

CONCLUSIONS

Fire suppression has altered the understory woody composition of eastern oak (*Quercus* spp.) ecosystems. Across the Mid-South, we used disturbance to increase the density of shade-intolerant and fire-tolerant species that had been suppressed prior to management. Shifts in

shrubby, seedling, and sapling communities were directly related to canopy disturbance and fire effects on overstory and understory density, respectively. Replicating historical savanna conditions (7 m^2 ha^{-1}) increased the understory density of oaks and other disturbance-dependent species, and did not promote shade-intolerant competitors more so than woodland conditions (14 m^2 ha^{-1}). Thus, heavy canopy disturbance may be an under-utilized tool for reversing mesophication effects in the eastern U.S. We also demonstrated that disturbance-adapted woody species were more readily promoted on xeric sites where mesophytic competitors were less abundant. Avoiding disturbance-mediated acceleration of succession on more mesic sites could require a timing of fire that preferentially selects for desired woody species. In this regard, we did not document strong differential effects between October and March fires on understory woody composition. Further evaluation of alternative fire-seasons, specifically earlier (August-September), late growing-season fire, may be warranted. Our results demonstrate how disturbance can be used to promote the understory dominance of disturbance-dependent woody species, but research exploring how gaps in fire recurrence dictate recruitment into the overstory is still needed. Regardless, active management now should prime eastern oak ecosystems with the woody regeneration diversity capable of enabling forest resiliency in the face of forecasted climatic and environmental changes.

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APPENDICES

Appendix SIII1. Seasonal comparison of weather, fuel moisture, and fire behavior for prescribed fires during mesophication reversal experiments at Catoosa Wildlife Management Area (CWMA), Green River Game Lands (GRGL), and Land Between the Lakes (LBL). Statistics based on a two-sample t-test assuming unequal variance.

		Fire season				
Variable	Units	Fall	Spring	*t*	*df*	*p*
Ambient temperature	˚C	24.6 ± 0.5	17.6 ± 0.6	8.80	101	< **0.001**
Relative humidity	%	39.0 ± 1.2	38.6 ± 1.5	0.17	110	0.867
Wind speed	m s^{-1}	1.6 ± 0.2	3.5 ± 0.2	6.86	102	< **0.001**
Wind direction	˚	214.8 ± 15.8	204.5 ± 14.4	0.48	94	0.631
Fine-fuel moisture	%	12.5 ± 0.8	17.0 ± 1.5	2.67	90	**0.009**
10-hour fuel moisture	%	9.2 ± 0.9	10.1 ± 0.6	0.78	22	0.446
Flanking fire rate-of-spread	m min^{-1}	0.6 ± 0.1	1.1 ± 0.3	1.45	25	0.159
Flanking fire flame-length	m	0.4 ± 0.1	0.6 ± 0.1	1.55	44	0.127
Heading fire rate-of-spread	m min^{-1}	1.6 ± 0.1	2.9 ± 0.4	3.03	30	**0.005**
Heading fire flame-length	m	0.7 ± 0.1	1.3 ± 0.1	3.61	37	< **0.001**
Fire temperature	˚C	170.6 ± 7.7	210.2 ± 15.3	2.32	122	**0.022**

[1]Fall burns at CWMA: 11 Oct 2010, 24 Oct 2012, and 24 Oct 2014. Spring burns at CWMA: 22 Mar 2011, 15 Mar 2013, and 18 Mar 2015. Fall burn at GRGL: 27 Oct 2014. Spring burn at GRGL: 18 March 2015. Buffalo Trace spring burn at LBL: 29 Mar 2016. Cemetery Ridge spring burn at LBL: 22 Apr 2015.

Appendix SIII2. Common and scientific name, and four-letter codes, for all woody and semi-woody species documented during (2008 to 2016) mesophication reversal experiments at Catoosa Wildlife Management Area (Cumberland County, TN), Land Between the Lakes National Recreation Area (Stewart County, TN), and Green River Game Lands (Polk County, NC).

Shrubs, vines, and semi-woody species[1]		
Common Name	Scientific Name	Species Code
Indian hemp	*Apocynum cannabinum* L.	APCA
Devils walking stick	*Aralia spinosa* L.	ARSP
Black chokeberry	*Aronia melanocarpa* (Michx.) Elliott	ARME
Crossvine	*Bignonia capreolata* L.	BICA
Carolina allspice	*Calycanthus floridus* L.	CAFL
Allegheny chinkapin	*Castanea pumila* (L.) Mill.	CAPU
American bittersweet	*Celastrus scandens* L.	CESC
Oriental bittersweet	*Celastrus orbiculatus* Thunb. **	CEOR
Devil's darning needles	*Clematis virginiana* L.	CLVI
Alternateleaf dogwood	*Cornus alternifolia* L. f.	COAL
American hazelnut	*Corylus americana* Walter	COAM
Dotted hawthorn	*Crataegus punctata* Jacq.	CRPU
Wild yam	*Dioscorea villosa* L.	DIVI2
Autumn olive	*Elaeagnus umbellata* Thunb. **	ELUM
Redtwig doghobble	*Eubotrys recurvus* (Buckley) Britton	EURE
Strawberry bush	*Euonymus americanus* L.	EUAM
Eastern wahoo	*Euonymus atropurpureus* Jacq.	EUAT
Black huckleberry	*Gaylussacia baccata* (Wangenh.) K. Koch	GABA
Carolina silverbell	*Halesia tetraptera* Ellis	HATE
Ashy hydrangea	*Hydrangea cinerea* Small	HYCI
Mountain holly	*Ilex ambigua* (Michx.) Torr.	ILAM
Possumhaw	*Ilex decidua* Walter	ILDE
Wild potato vine	*Ipomoea pandurata* (L.) G. Mey.	IPPA
Mountain laurel	*Kalmia latifolia* L.	KALA
Dog hobble	*Leucothoe fontanesiana* (Steud.) Sleumer	LEFO
Spicebush	*Lindera benzoin* (L.) Blume	LIBE
Japanese honeysuckle	*Lonicera japonica* Thunb. **	LOJA
Amur honeysuckle	*Lonicera maackii* (Rupr.) Herder **	LOMA
Maleberry	*Lyonia ligustrina* (L.) DC.	LYLI
Southern crab apple	*Malus angustifolia* (Aiton) Michx.	MAAN
Maroon Carolina milkvine	*Matelea carolinensis* (Jacq.) Woodson	MACA
Climbing hempvine	*Mikania scandens* (L.) Willd.	MISC
Virginia creeper	*Parthenocissus quinquefolia* (L.) Planch.	PAQU

Purple passionflower	*Passiflora incarnata* L.	PAIN
Yellow passionflower	*Passiflora lutea* L.	PALU
American plum	*Prunus americana* Marshall	PRAM
Southern pinxter azalea	*Rhododendron canescens* (Michx.) Sweet	RHCA
Cumberland azalea	*Rhododendron cumberlandense* E.L.Braun	RHCU
Rosebay rhododendron	*Rhododendron maximum* L.	RHMA
Winged sumac	*Rhus copallinum* L.	RHCO
Smooth sumac	*Rhus glabra* L.	RHGL
Bristly locust	*Robinia hispida* L.	ROHI
Multiflora rose	*Rosa multiflora* Thunb. **	ROMU
Southern blackberry	*Rubus argutus* Link	RUAR
Northern dewberry	*Rubus flagellaris* Willd.	RUFL
Swamp dewberry	*Rubus hispidus* L.	RUHI
Black raspberry	*Rubus occidentalis* L.	RUOC
Southern dewberry	*Rubus trivialis* Michx.	RUTR
Elderberry	*Sambucus canadensis* L.	SACA
Biltmore's carrionflower	*Smilax biltmoreana* (Small) J.B.S. Norton ex Pennell	SMBI
Saw greenbrier	*Smilax bona-nox* L.	SMBO
Cat greenbrier	*Smilax glauca* Walter	SMGL
Roundleaf greenbrier	*Smilax rotundifolia* L.	SMRO
Bristly greenbrier	*Smilax tamnoides* L.	SMTA
Mountain camellia	*Stewartia ovata* (Cav.) Weath.	STOV
American snowbell	*Styrax americanus* Lam.	STAM
Coralberry	*Symphoricarpos orbiculatus* Moench	SYOR
Poison oak	*Toxicodendron pubescens* Mill.	TOPU
Poison ivy	*Toxicodendron radicans* (L.) Kuntze	TORA
Highbush blueberry	*Vaccinium corymbosum* L.	VACO
Lowbush blueberry	*Vaccinium pallidum* Aiton	VAPA
Deerberry	*Vaccinium stamineum* L.	VAST
Farkleberry	*Vaccinium arboreum* Marshall	VAAR
Arrow wood	*Viburnum dentatum* L.	VIDE
Mapleleaf viburnum	*Viburnum acerifolium* L.	VIAC
Muscadine vine	*Vitis rotundifolia* Michx.	VIRO
Summer grape	*Vitis aestivalis* Michx.	VIAE

Tree species (seedlings and saplings)[2]

Common Name	Scientific Name	Species Code
Red maple	*Acer rubrum* L.	ACRU
Silver maple	*Acer saccharinum* L.	ACSA
Sugar maple	*Acer saccharum* Marshall	ACSA2

Tree-of-heaven	*Ailanthus altissima* (Mill.) Swingle **	AIAL
Downy serviceberry	*Amelanchier arborea* (Michx. f.) Fernald	AMAR
Smooth serviceberry	*Amelanchier laevis* Wiegand	AMLA
Pawpaw	*Asimina triloba* (L.) Dunal	ASTR
Yellow birch	*Betula alleghaniensis* Britton	BEAL
Sweet birch	*Betula lenta* L.	BELE
River birch	*Betula nigra* L.	BENI
American hornbeam	*Carpinus caroliniana* Walter	CACA
Pignut hickory	*Carya glabra* (Mill.) Sweet	CAGL
Bitternut hickory	*Carya cordiformis* (Wangenh.) K. Koch	CACO
Shellbark hickory	*Carya laciniosa* (Michx. f.) G. Don	CALA
Shagbark hickory	*Carya ovata* (Mill.) K. Koch	CAOV
Mockernut hickory	*Carya tomentosa* (Lam.) Nutt.	CATO
American chestnut	*Castanea dentata* (Marshall) Borkh.	CADE
Northern hackberry	*Celtis occidentalis* L.	CEOC
Eastern redbud	*Cercis canadensis* L.	CECA
Flowering dogwood	*Cornus florida* L.	COFL
Common persimmon	*Diospyros virginiana* L.	DIVI
American beech	*Fagus grandifolia* Ehrh.	FAGR
White ash	*Fraxinus americana* L.	FRAM
Green ash	*Fraxinus pennsylvanica* Marshall	FRPE
Honeylocust	*Gleditsia triacanthos* L.	GLTR
American witch hazel	*Hamamelis virginiana* L.	HAVI
American holly	*Ilex opaca* Aiton	ILOP
Butternut	*Juglans cinerea* L.	JUCI
Black walnut	*Juglans nigra* L.	JUNI
Eastern red cedar	*Juniperus virginiana* L.	JUVI
Sweetgum	*Liquidambar styraciflua* L.	LIST
Yellow poplar	*Liriodendron tulipifera* L.	LITU
Cucumber magnolia	*Magnolia acuminata* (L.) L.	MAAC
Fraser magnolia	*Magnolia fraseri* Walter	MAFR
Bigleaf magnolia	*Magnolia macrophylla* Michx.	MAMA
Umbrella magnolia	*Magnolia tripetala* (L.) L.	MATR
White mulberry	*Morus alba* L.**	MOAL
Red mulberry	*Morus rubra* L.	MORU
Water tupelo	*Nyssa aquatica* L.	NYAQ
Blackgum	*Nyssa sylvatica* Marshall	NYSY
Eastern hophornbeam	*Ostrya virginiana* (Mill.) K. Koch	OSVI
Sourwood	*Oxydendrum arboreum* (L.) DC.	OXAR

Princess tree	*Paulownia tomentosa* (Thunb.) Siebold & Zucc. ex Steud. **	PATO
Eastern white pine	*Pinus strobus* L.	PIST
Shortleaf pine	*Pinus echinata* Mill.	PIEC
Pitch pine	*Pinus rigida* Mill.	PIRI
Loblolly pine	*Pinus taeda* L.	PITA
Virginia pine	*Pinus virginiana* Mill.	PIVI
American sycamore	*Platanus occidentalis* L.	PLOC
Bigtooth aspen	*Populus grandidentata* Michx.	POGR
Black cherry	*Prunus serotina* Ehrh.	PRSE
White oak	*Quercus alba* L.	QUAL
Scarlet oak	*Quercus coccinea* Münchh.	QUCO
Southern red oak	*Quercus falcata* Michx.	QUFA
Chestnut oak	*Quercus montana* Willd.	QUMO
Cherrybark oak	*Quercus pagoda* Raf.	QUPA
Northern red oak	*Quercus rubra* L.	QURU
Post oak	*Quercus stellata* Wangenh.	QUST
Black oak	*Quercus velutina* Lam.	QUVE
Blackjack oak	*Quercus marilandica* Münchh.	QUMA
Chinkapin oak	*Quercus muehlenbergii* Engelm.	QUMU
Black locust	*Robinia pseudoacacia* L.	ROPS
Black willow	*Salix nigra* Marshall	SANI
Sassafras	*Sassafras albidum* (Nutt.) Nees	SAAL
Bigleaf snowbell	*Styrax grandifolius* Aiton	STGR
American basswood	*Tilia americana* L.	TIAM
Eastern hemlock	*Tsuga canadensis* (L.) Carrière	TSCA
Winged elm	*Ulmus alata* Michx.	ULAL
Slippery elm	*Ulmus rubra* Muhl.	ULRU

** Non-native Invasive Species. [1]Shrubby vegetation included multi-stemmed woody and semi-woody (e.g., *Smilax* and *Rubus* spp.) species rarely >4 m tall and lianas. [2]Tree species were woody plants typically ≥4 m in height at maturity. All *Carya* spp. (CARYA) and *Vaccinium* spp. (VACC) except *Vaccinium arboreum* were aggregated in presented analyses.

Appendix SIII3.1. Shrubby vegetation significantly indicative of treatments and periods within management. Treatments were unmanaged oak forests (C), savanna residual basal area (7 m^2 ha^{-1}, S), woodland residual basal area (14 m^2 ha^{-1}, W), spring burned stands (Sp), fall burned stands (Fa), or thinned and/or burned stands (M). Period associations were pre-management (PM), post-cut (PC), or post-fire (PF, multiple at Catoosa). Specificity (A), sensitivity (B), indicator value (IndVal), and *p*-values (4,999 permutations) are presented.

Treatment																	
Catoosa Wildlife Management Area						Land Between the Lakes National Recreation Area						Green River Game Lands					
Species	Trt	*A*	*B*	Ind Val	*p*	Species	Trt	*A*	*B*	Ind Val	*p*	Species	Trt	*A*	*B*	Ind Val	*p*
KALA	C	0.96	0.09	0.08	0.003	VIRO	W	0.48	0.64	0.31	0.001	PAQU	W	0.99	0.16	0.16	0.001
						RUAR	W	0.47	0.44	0.21	0.011	SMRO	W	0.77	0.26	0.19	0.001
RUFL	S	0.81	0.20	0.16	< 0.001	VAAR	W	0.51	0.16	0.08	0.025	TORA	W	0.97	0.09	0.09	0.013
TORA	S	0.68	0.05	0.04	0.002	ARSP	W	0.88	0.19	0.17	< 0.001	VIRO	W	0.73	0.21	0.16	0.012
VICI	S	0.79	0.05	0.04	< 0.001	LOJA	W	0.57	0.08	0.05	0.009	VICI	W	0.89	0.17	0.15	< 0.001
RUFL	Sp	0.60	0.14	0.08	0.004	VACC	S	0.68	0.44	0.30	< 0.001	VACC	S	0.81	0.7	0.56	< 0.001
						TORA	S	0.76	0.34	0.26	< 0.001	KALA	S	0.82	0.5	0.41	0.001
RHCA	Fa	0.66	0.06	0.04	0.007	RHCO	S	0.56	0.31	0.18	0.003	RHMA	S	0.75	0.11	0.08	0.013
						SMGL	S	0.50	0.27	0.14	0.014						
VACC	M	0.88	0.76	0.66	< 0.001	PAQU	S	0.65	0.25	0.16	0.001						
RUAR	M	0.99	0.57	0.58	< 0.001	RUFL	S	0.65	0.19	0.12	0.002						
SMRO	M	0.87	0.39	0.34	0.009	VICI	S	0.52	0.17	0.08	0.011						
SMGL	M	0.94	0.45	0.42	0.002												
RHCO	M	0.99	0.18	0.18	< 0.001												
VIRO	M	0.81	0.15	0.10	< 0.001												
Period																	
SMTA	PC	0.93	0.06	0.06	< 0.001	VIRO	PC	0.64	0.80	0.50	< 0.001	RHMA	PC	0.93	0.22	0.20	< 0.001
						VACC	PC	0.54	0.47	0.26	< 0.001	SMRO	PC	0.45	0.25	0.12	0.042
VACC	PF1	0.26	0.89	0.23	0.002	RUAR	PC	0.48	0.45	0.21	0.020	RHCA	PC	0.82	0.07	0.05	0.003
SMGL	PF1	0.43	0.67	0.29	< 0.001	TORA	PC	0.72	0.37	0.26	0.001						
VIRO	PF1	0.28	0.19	0.05	0.045	SMRO	PC	0.56	0.33	0.18	< 0.001	RUAR	PF	0.89	0.52	0.46	0.001
RUFL	PF1	0.47	0.20	0.10	0.001	PAQU	PC	0.62	0.30	0.18	< 0.001	SMGL	PF	0.51	0.28	0.14	0.026
						VAAR	PC	0.65	0.18	0.12	0.012	VIRO	PF	0.52	0.19	0.10	0.016
SMRO	PF2	0.28	0.50	0.14	0.001	RUFL	PC	0.52	0.20	0.10	0.015	RUFL	PF	0.94	0.11	0.10	0.004
VAAR	PF2	0.76	0.08	0.06	< 0.001	SYOR	PC	0.54	0.13	0.07	0.008						
RHCA	PF2	0.40	0.10	0.04	0.002	VICI	PC	0.79	0.20	0.16	< 0.001						
						ARSP	PC	0.64	0.19	0.12	0.039						
RUAR	PF3	0.38	0.66	0.25	< 0.001												
RHCO	PF3	0.54	0.29	0.16	< 0.001	RHCO	PF	0.73	0.35	0.26	0.001						
GABA	PF3	0.99	0.11	0.11	< 0.001												

[1]Shrubby vegetation included multi-stemmed woody and semi-woody (e.g., *Smilax* and *Rubus* spp.) species rarely >4 m tall and lianas. Species codes are the first two letters of genus and species. All *Vaccinium* spp. except *Vaccinium arboreum* were aggregated (VACC). All species ≥1% of total density at ≥10% of stands within a year were tested. Species not indicative of a treatment ($p > 0.05$) included: SMRO and SYOR at LBL, and RUAR, SMGL, RUFL, and COAM at GRGL. Species not indicative of any period ($p > 0.05$) included: VICI at CWMA, SMGL and LOJA at LBL, and VACC, KALA, PAQU, CAFL, and VICI at GRGL. Within treatments and periods, species are in descending order of overall mean density (stems ha^{-1}).

Appendix SIII3.2. Seedling species determined to be significant indicators of treatments and periods within management. Treatments were unmanaged oak forests (C), savanna residual basal area (7 m^2 ha^{-1}, S), woodland residual basal area (14 m^2 ha^{-1}, W), spring burned stands (Sp), fall burned stands (Fa), or thinned and/or burned stands (M). Period associations were pre-management (PM), post-cut (PC), or post-fire (PF, multiple at Catoosa). Specificity (A), sensitivity (B), indicator value (IndVal), and *p*-values (4,999 permutations) are presented.

Catoosa Wildlife Management Area						Land Between the Lakes National Recreation Area						Green River Game Lands					
						Treatment											
Species	Trt	*A*	*B*	Ind Val	*p*	Species	Trt	*A*	*B*	Ind Val	*p*	Species	Trt	*A*	*B*	Ind Val	*p*
PIST	C	0.81	0.26	0.21	< 0.001	FRPE	C	0.80	0.29	0.23	0.002	ACRU	W	0.64	0.77	0.50	0.002
QUMO	C	0.52	0.07	0.04	0.025	OSVI	C	0.84	0.40	0.34	< 0.001	LITU	W	0.81	0.52	0.42	< 0.001
OSVI	C	0.84	0.05	0.04	0.005	ASTR	C	0.85	0.11	0.10	0.030	QUAL	W	0.72	0.50	0.36	0.002
FAGR	C	0.85	0.08	0.07	< 0.001	ULAM	C	0.87	0.13	0.12	0.031	QURU	W	0.64	0.35	0.22	0.019
						FAGR	C	0.88	0.15	0.13	< 0.001	CARYA	W	0.82	0.38	0.31	0.001
QUAL	Sp	0.54	0.32	0.18	0.015							PRSE	W	0.92	0.28	0.25	< 0.001
CARYA	Sp	0.43	0.26	0.12	0.003	QUAL	M	0.75	0.49	0.37	< 0.001	MAAC	W	0.94	0.12	0.12	0.011
COFL	Sp	0.56	0.13	0.07	< 0.001	NYSY	M	0.81	0.40	0.32	< 0.001	COFL	W	0.84	0.12	0.10	0.013
LIST	Sp	0.91	0.10	0.09	< 0.001	QUCO	M	0.83	0.21	0.17	0.001	HACA	W	0.89	0.06	0.05	0.028
PRSE	Sp	0.68	0.09	0.06	< 0.001	SAAL	M	0.73	0.48	0.35	< 0.001						
						QUST	M	0.99	0.11	0.11	0.001	SAAL	S	0.66	0.41	0.27	0.039
LITU	Fa	0.82	0.09	0.07	0.005	QUFA	M	0.84	0.16	0.14	0.003						
						QUMO	M	0.92	0.31	0.29	0.002						
ACRU	M	0.85	0.86	0.72	0.007	PRSE	M	0.90	0.28	0.25	< 0.001						
SAAL	M	0.99	0.70	0.69	< 0.001	QUVE	M	0.67	0.39	0.26	0.002						
NYSY	M	0.96	0.40	0.38	< 0.001	LITU	M	0.89	0.10	0.09	0.044						
OXAR	M	0.97	0.32	0.31	< 0.001	DIVI	M	0.99	0.09	0.10	0.008						
QUCO	M	0.90	0.31	0.28	0.001	LIST	M	0.91	0.11	0.10	0.006						
QUVE	M	0.91	0.29	0.26	< 0.001												
QUFA	M	0.95	0.16	0.15	< 0.001												
						Period											
QUCO	PC	0.47	0.30	0.14	0.033	FRAM	PM	0.8	0.09	0.08	0.044	QUVE	PC	0.43	0.33	0.14	0.046
COFL	PC	0.52	0.13	0.07	0.044							MAFR	PC	0.71	0.08	0.06	0.026
PIVI	PC	0.79	0.06	0.05	0.002	QUAL	PC	0.52	0.64	0.32	< 0.001						
						NYSY	PC	0.52	0.54	0.28	< 0.001	ACRU	PF	0.41	0.81	0.34	0.023
ACRU	PF	0.45	0.93	0.42	< 0.001	ULAL	PC	0.39	0.35	0.14	0.018	LITU	PF	0.55	0.68	0.37	0.016
SAAL	PF	0.54	0.69	0.37	< 0.001	SAAL	PC	0.46	0.61	0.28	< 0.001	QUAL	PF	0.47	0.57	0.26	0.005
NYSY	PF	0.65	0.43	0.28	< 0.001	QUST	PC	0.55	0.2	0.11	0.007	QUCO	PF	0.45	0.51	0.23	0.006
QUAL	PF	0.55	0.32	0.18	< 0.001	QUFA	PC	0.59	0.25	0.14	0.014	QURU	PF	0.48	0.42	0.20	0.007
OXAR	PF	0.77	0.35	0.27	< 0.001	CARYA	PC	0.52	0.65	0.34	< 0.001	NYSY	PF	0.63	0.49	0.30	0.004
QUVE	PF	0.48	0.30	0.14	0.004	QUMO	PC	0.63	0.44	0.27	< 0.001	OXAR	PF	0.58	0.30	0.18	0.008
CARYA	PF	0.58	0.29	0.17	< 0.001	PRSE	PC	0.57	0.42	0.24	< 0.001	ROPS	PF	0.61	0.33	0.20	0.009
LIST	PF	0.78	0.06	0.05	0.002	ACRU	PC	0.66	0.19	0.12	< 0.001	PRSE	PF	0.44	0.21	0.09	0.021
AMAR	PF	0.48	0.08	0.04	0.028	QUVE	PC	0.49	0.58	0.28	< 0.001	AIAL	PF	0.60	0.32	0.19	0.040
PRSE	PF	0.63	0.07	0.04	0.002	LITU	PC	0.58	0.14	0.08	< 0.001						
QURU	PF	0.79	0.09	0.07	0.001	AMAR	PC	0.52	0.23	0.12	< 0.001						
						DIVI	PC	0.56	0.17	0.10	0.019						
						QURU	PC	0.51	0.21	0.11	0.005						
						OXAR	PC	0.6	0.25	0.15	< 0.001						
						LIST	PC	0.52	0.19	0.10	0.004						
						ULAM	PC	0.89	0.16	0.14	< 0.001						
						FAGR	PC	0.5	0.06	0.03	0.007						
						CECA	PC	0.55	0.07	0.04	0.026						
						COFL	PF	0.63	0.11	0.07	0.020						
						FRPE	PF	0.54	0.27	0.14	0.028						
						OSVI	PF	0.57	0.31	0.18	0.001						

[1]Seedlings defined as tree species (≥4 m in height at maturity) ≥30.5 cm tall but <1.4 m tall. Species codes are the first two letters of genus and species. All hickories were aggregated (CARYA). All species ≥1% of total density at ≥10% of stands within a year were tested. Species not indicative of any treatment ($p > 0.05$) included: AMAR and QURU at CWMA, ULAL, CARYA, FRAM, ACRU, COFL, AMAR, QURU, QUMA, OXAR, and CECA at LBL, and QUVE, NYSY, OXAR, AIAL, MAFR, QUCO, and ROPS at GRGL. Species not indicative of a period ($p > 0.05$) included: PIST, QUFA, and LITU at CWMA, QUCO, QUMA, and ASTR at LBL, and MAAC, SAAL, QUMO, CARYA, and COFL at GRGL. Within treatments and periods, species in descending order of overall mean density (stems ha^{-1}).

Appendix SIII3.3. Sapling species determined to be significant indicators of treatments and periods within management. Treatments were unmanaged oak forests (C), savanna residual basal area (7 m^2 ha^{-1}, S), woodland residual basal area (14 m^2 ha^{-1}, W), spring burned stands (Sp), fall burned stands (Fa), or thinned and/or burned stands (M). Period associations were pre-management (PM), post-cut (PC), or post-fire (PF, multiple at Catoosa). Specificity (A), sensitivity (B), indicator value (IndVal), and *p*-values (4,999 permutations) are presented.

Catoosa Wildlife Management Area						Land Between the Lakes National Recreation Area						Green River Game Lands					
						Treatment											
Species	Trt	*A*	*B*	Ind Val	*p*	Species	Trt	*A*	*B*	Ind Val	*p*	Species	Trt	*A*	*B*	Ind Val	*p*
PIST	C	0.88	0.92	0.81	< 0.001	OSVI	C	0.77	0.59	0.45	< 0.001	CADE	C	0.59	0.24	0.14	0.007
FAGR	C	0.58	0.23	0.13	< 0.001	ULAL	C	0.71	0.47	0.34	0.023						
ILOP	C	0.43	0.18	0.08	0.002	FAGR	C	0.92	0.67	0.61	< 0.001	LITU	W	0.71	0.67	0.48	< 0.001
						ASTR	C	0.83	0.14	0.12	0.004	CARYA	W	0.64	0.26	0.17	0.018
COFL	W	0.60	0.34	0.20	0.006	ACSA	C	0.95	0.53	0.50	< 0.001	PRSE	W	0.89	0.45	0.40	< 0.001
						ULAM	C	0.89	0.19	0.17	0.040	QUAL	W	0.63	0.43	0.27	< 0.001
LITU	S	0.93	0.10	0.10	< 0.001	FRPE	C	0.75	0.28	0.21	0.010	QURU	W	0.53	0.37	0.19	0.008
QUAL	S	0.83	0.28	0.23	< 0.001	COFL	C	0.68	0.28	0.19	0.027	AIAL	W	0.79	0.20	0.16	0.014
PRSE	S	0.89	0.17	0.14	< 0.001	ACRU	C	0.81	0.24	0.19	0.034	MAAC	W	0.68	0.30	0.21	0.008
QUCO	S	0.81	0.30	0.24	< 0.001							PIST	W	0.71	0.40	0.28	< 0.001
QUFA	S	0.63	0.18	0.12	< 0.001	QUMO	M	0.95	0.38	0.36	< 0.001	HACA	W	0.87	0.17	0.14	0.002
						NYSY	M	0.76	0.56	0.42	< 0.001	HAVI	W	0.54	0.07	0.04	0.036
LITU	Fa	0.93	0.10	0.10	< 0.001	OXAR	M	0.78	0.41	0.31	0.001						
ASTR	Fa	0.74	0.05	0.04	< 0.001	CARYA	M	0.67	0.49	0.32	0.007	QUMO	S	0.59	0.60	0.35	0.001
						QUVE	M	0.66	0.48	0.31	0.007	QUCO	S	0.54	0.36	0.19	0.004
QUAL	Sp	0.81	0.24	0.19	0.002	SAAL	M	0.85	0.43	0.37	< 0.001	TSCA	S	0.54	0.06	0.03	0.035
PRSE	Sp	0.85	0.16	0.13	< 0.001	QUAL	M	0.69	0.42	0.29	0.002						
LIST	Sp	0.96	0.20	0.19	< 0.001	PRSE	M	0.83	0.43	0.36	< 0.001	ACRU	M	0.98	0.87	0.85	< 0.001
QUCO	Sp	0.77	0.26	0.20	< 0.001	QUCO	M	0.94	0.30	0.28	< 0.001	OXAR	M	0.94	0.67	0.64	0.001
QUFA	Sp	0.76	0.21	0.16	< 0.001	AMAR	M	0.71	0.24	0.17	0.019	ROPS	M	0.93	0.26	0.24	0.002
COFL	Sp	0.66	0.38	0.25	< 0.001	QUFA	M	0.97	0.20	0.19	0.001						
						QURU	M	0.63	0.21	0.13	0.032						
ACRU	M	0.87	0.89	0.77	0.006	QUST	M	0.91	0.18	0.17	0.001						
OXAR	M	0.90	0.72	0.64	0.007	DIVI	M	0.96	0.12	0.11	0.008						
SAAL	M	0.99	0.51	0.50	< 0.001												
CARYA	M	0.94	0.21	0.19	0.002												
QUVE	M	0.97	0.24	0.23	< 0.001												
						Period											
PIST	PC	0.34	0.44	0.15	0.018	FRAM	PM	0.85	0.11	0.10	0.003	PIST	PM	0.64	0.28	0.18	0.014
FAGR	PC	0.59	0.12	0.07	0.004							COFL	PM	0.46	0.34	0.16	0.011
ASTR	PC	0.70	0.06	0.04	0.009	QUMO	PC	0.59	0.46	0.27	0.001	TSCA	PM	0.72	0.06	0.04	0.002
PIVI	PC	0.57	0.07	0.04	0.012	NYSY	PC	0.41	0.68	0.27	0.022						
						OXAR	PC	0.49	0.53	0.26	0.001	CARYA	PC	0.46	0.37	0.17	0.023
ACRU	PF2-3	0.55	0.96	0.53	< 0.001	CARYA	PC	0.42	0.63	0.26	0.010	MAFR	PC	0.49	0.23	0.12	0.040
OXAR	PF2-3	0.61	0.86	0.52	< 0.001	QUVE	PC	0.50	0.64	0.32	0.001						
SAAL	PF2-3	0.60	0.54	0.32	< 0.001	SAAL	PC	0.46	0.51	0.24	0.015	ACRU	PF	0.47	0.82	0.38	0.037
LITU	PF2-3	0.88	0.09	0.08	0.015	QUAL	PC	0.53	0.54	0.28	0.001	LITU	PF	0.58	0.64	0.37	0.002
QUAL	PF2-3	0.73	0.25	0.18	0.001	PRSE	PC	0.57	0.58	0.34	< 0.001	NYSY	PF	0.54	0.66	0.36	0.025
QUVE	PF2-3	0.52	0.24	0.12	0.013	LIST	PC	0.51	0.35	0.18	0.008	QUMO	PF	0.53	0.57	0.30	0.005
PRSE	PF2-3	0.79	0.13	0.10	0.004	ULAM	PC	0.81	0.26	0.20	0.001	SAAL	PF	0.60	0.57	0.34	0.001
LIST	PF2-3	0.73	0.15	0.11	0.002	QUCO	PC	0.63	0.37	0.23	0.011	PRSE	PF	0.71	0.33	0.24	0.010
QUCO	PF2-3	0.84	0.27	0.23	< 0.001	AMAR	PC	0.41	0.31	0.12	0.039	QUCO	PF	0.63	0.40	0.25	0.005
QUFA	PF2-3	0.77	0.19	0.14	< 0.001	ACRU	PC	0.6	0.26	0.15	0.006	QUAL	PF	0.45	0.34	0.15	0.017
						QUST	PC	0.61	0.27	0.17	0.005	ROPS	PF	0.76	0.47	0.36	0.001
						DIVI	PC	0.74	0.18	0.13	0.024	QURU	PF	0.55	0.42	0.23	0.002
						CECA	PC	0.56	0.17	0.10	0.022	AIAL	PF	0.73	0.23	0.17	0.031
						OSVI	PF	0.53	0.5	0.26	0.022						

[1]Saplings defined as tree species (≥4 m in height at maturity) ≥1.4 m tall and <7.6 cm diameter at breast height. Species codes are the first two letters of genus and species. All hickories were aggregated (CARYA). All species ≥1% of total density at ≥10% of stands within a year were tested. Species not indicative of a treatment ($p > 0.05$) included: NYSY and LIST at CWMA, FRAM, JUVI, LITU, LIST, and CECA at LBL, and FRPE, NYSY, SAAL, QUVE, COFL, MAMA, and MAFR at GRGL. Species not indicative of a period ($p > 0.05$) included: ILOP, NYSY, CARYA, and COFL at CWMA, QUMA, ULRU, ULAL, COFL, QUFA, QURU, JUVI, LITU, FAGR, ASTR, and ACSA at LBL, and HACA, CADE, MAMA, OXAR, QUVE, FRPE, and MAAC at GRGL. Within treatments and periods, species in descending order of overall mean density (stems ha^{-1}).

Appendix SIII4. Differences in the density (stems ha^{-1}) of woody and semi-woody species across treatments during mesophication reversal experiments at Catoosa Wildlife Management Area (CWMA), Land Between the Lakes National Recreation Area (LBL), and Green River Game Lands (GRGL). Treatments included unmanaged (Control), burned only in the spring (SpO) or fall (FaO), and combinations of spring and fall fire with woodland (14 m^2 ha^{-1}) or savanna (7 m^2 ha^{-1}) residual basal area. Only species ≥ 5% of the total stem density within a vegetation category and exhibiting a difference across treatments (α = 0.05) are presented. Lowercase letters depict these differences (Fisher's Least Significant Difference tests).

			Treatments					
Site	Vegetation	Species	Control	SpW	FaW	SpS	FaS	
CWMA	Shrubby	VACC	7,574 (1,079) c	17,907 (1,659) a	13,300 (1,429) b	15,553 (1,546) ab	7,432 (1,069) c	
		RUAR	12 (111) d	2,986 (1,718) c	4,173 (2,031) bc	14,287 (3,758) a	10,127 (3,164) ab	
		SMGL	244 (116) b	1,109 (248) a	1,396 (278) a	1,411 (279) a	1,241 (262) a	
	Seedlings	SAAL	224 (190) c	3,496 (751) b	7,241 (1,080) a	4,909 (889) ab	5,513 (943) ab	
		NYSY	201 (92) c	837 (188) b	1,208 (225) ab	1,830 (277) a	1,100 (215) b	
		OAKS	1,901 (548) b	2,659 (648) b	2,625 (644) b	5,983 (972) a	2,493 (628) b	
	Saplings	PIST	1,446 (670) a	71 (148) b	53 (128) b	81 (159) b	107 (182) b	
		SAAL	3 (6) c	93 (31) b	287 (55) a	178 (43) ab	117 (35) b	
		SAAL	3 (6) c	93 (31) b	287 (55) a	178 (43) ab	117 (35) b	
		OAKS	18 (19) b	57 (34) b	49 (31) b	247 (70) a	61 (35) b	
			Control	SpO	SpW	SpS		
LBL	Shrubby	RUAR	58 (197) c	405 (519) bc	2,713 (949) a	2,610 (931) ab		
	Seedlings	SAAL	784 (280) b	1,649 (406) ab	1,771 (298) a	2,517 (355) a		
		NYSY	390 (246) b	638 (315) ab	1,445 (335) a	1,420 (332) a		
		OSVI	1,221 (382) a	186 (149) b	183 (104) b	310 (136) b		
		OAKS	2,244 (840) b	5,369 (1,299) a	6,970 (1,047) a	5,518 (931) a		
	Saplings	-	-	-	-	-		
			Control	FaO	SpW	FaW	SpS	FaS
GRGL	Shrubby	VACC	7,537 (1,017) a	4,761 (809) b	1,836 (502) c	175 (155) d	6,991 (980) ab	5,679 (883) ab
		RUAR	0 (5) d	0 (0) d	635 (180) c	6,244 (564) a	2,185 (334) b	893 (213) c
		KALA	64 (71) c	3,761 (545) a	488 (196) b	6 (22) c	629 (223) b	4,443 (592) a
	Seedlings	ACRU	34 (37) e	261 (104) d	2,466 (319) b	4,322 (423) a	2,224 (303) b	1,156 (219) c
		LITU	273 (109) c	1 (6) d	1,995 (294) b	3,373 (382) a	205 (94) c	543 (153) c
		SAAL	4,305 (399) a	599 (149) c	90 (58) e	358 (115) cd	1,129 (204) b	219 (90) de
		OAKS	5,747 (623) a	1,453 (313) c	3,992 (519) b	5,686 (619) a	4,343 (541) ab	3,407 (479) b
	Saplings	ACRU	31 (13) d	88 (22) c	565 (56) b	970 (73) a	653 (60) b	523 (54) b
		CARYA	118 (39) b	28 (19) c	104 (37) bc	319 (64) a	32 (20) c	44 (24) bc
		LITU	103 (22) bc	0 (1) e	171 (29) b	589 (54) a	58 (17) cd	38 (14) d
		OXAR	33 (11) d	57 (14) cd	144 (23) b	115 (20) b	273 (31) a	97 (19) bc
		NYSY	80 (13) b	47 (10) cd	68 (12) bc	88 (14) b	162 (19) a	30 (8) d
		OAKS	222 (26) b	55 (13) c	88 (17) c	304 (31) a	267 (29) ab	247 (28) ab

*Shrubby vegetation included multi-stemmed woody and semi-woody (e.g., *Smilax* and *Rubus* spp.) species rarely >4 m tall and lianas. Seedlings: tree species (≥4 m in height at maturity) ≥30.5 cm tall but <1.4 m tall. Saplings: tree species ≥1.4 m tall and <7.6 cm diameter at breast height. Species codes are the first two letters of genus and species. All *Carya* spp. (CARYA), Quercus spp. (OAKS), and *Vaccinium* spp. (VACC) except *Vaccinium arboreum* were aggregated. Standard error presented parenthetically.

Appendix SIII5. Differences in the density (stems ha^{-1}) of woody and semi-woody species across periods during mesophication reversal experiments at Catoosa Wildlife Management Area (CWMA), Land Between the Lakes National Recreation Area (LBL), and Green River Game Lands (GRGL). Periods included observations prior to management (pre-M), after canopy disturbance (post-cut), and following prescribed fire (post-fire, multiple at CWMA). Only species ≥ 5% of the total stem density within a vegetation category and exhibiting a difference across treatments (α = 0.05) are presented. Lowercase letters depict these differences (Fisher's Least Significant Difference tests).

			Period				
Site	Vegetation	Species	Pre-M	Post-cut	Post-fire 1	Post-fire 2	Post-fire 3
CWMA	Shrubby	VACC	6,303 (1,000) b	13,037 (1059) a	15,497 (1,154) a	13,496 (1,077) a	12,736 (1,046) a
		RUAR	65 (154) d	1346 (601) c	5,772 (1,244) b	12,068 (1,799) a	12,617 (1,840) a
		SMRO	833 (256) b	1821 (295) a	1,390 (257) ab	1,900 (301) a	1,007 (219) b
		SMGL	204 (91) d	564 (116) c	2,469 (242) a	1,465 (187) b	1,095 (161) b
	Seedlings	ACRU	8,147 (1,510) c	11,091 (1562) b	12,449 (1,655) ab	14,892 (1,810) a	13,551 (1,726) a
		SAAL	640 (263) c	3,655 (487) b	6,531 (652) a	5,486 (597) a	3,955 (507) b
		NYSY	162 (83) c	728 (130) b	1,588 (192) a	1,458 (184) a	1,301 (174) a
		OAKS	1,541 (355) b	3,088 (406) a	3,803 (450) a	3,768 (448) a	3,114 (407) a
	Saplings	ACRU	1,107 (368) c	1,652 (320) abc	1,340 (288) bc	2,254 (374) ab	2,637 (404) a
		OXAR	156 (66) b	214 (55) b	278 (63) ab	479 (82) a	483 (82) a
		PIST	862 (242) a	297 (139) b	86 (75) c	86 (74) c	62 (63) c
		SAAL	18 (18) b	117 (32) a	106 (30) a	185 (40) a	186 (40) a
		OAKS	31 (22) c	61 (24) bc	37 (18) c	109 (31) ab	153 (37) a
			Pre-M	Post-cut	Post-fire		
LBL	Shrubby	VIRO	1,684 (569) c	8,920 (1,310) a	3,988 (876) b		
		VACC	958 (500) b	2,130 (745) a	829 (465) b		
		RUAR	400 (257) b	1,536 (504) a	1,521 (501) a		
		TORA	231 (251) b	1,473 (634) a	440 (347) b		
	Seedlings	OSVI	505 (147) a	143 (78) b	643 (166) a		
		SAAL	1,043 (172) c	2,335 (258) a	1,603 (214) b		
		NYSY	499 (140) c	1,489 (242) a	877 (185) b		
		CARYA	656 (159) c	1,953 (274) a	1,120 (207) b		
		OAKS	2,373 (447) c	7,982 (819) a	5,006 (649) b		
	Saplings	OSVI	128 (52) ab	54 (34) b	171 (60) a		
		NYSY	84 (16) b	137 (21) a	69 (15) b		
		OXAR	24 (13) c	116 (29) a	61 (21) b		
		ULAL	109 (23) a	64 (18) ab	49 (16) b		
		CARYA	71 (15) ab	92 (17) a	56 (13) b		
		OAKS	138 (45) b	424 (78) a	211 (55) b		
			Pre-M	Post-cut	Post-fire		
GRGL	Shrubby	RUAR	7 (12) c	199 (75) b	5,469 (396) a		
		KALA	1,277 (194) a	607 (164) b	1,052 (216) ab		
	Seedlings	ACRU	1,005 (125) b	1,235 (170) b	1,802 (205) a		
		LITU	68 (33) c	874 (146) b	1,687 (203) a		
		SAAL	544 (87) b	625 (114) b	1,234 (160) a		
		OAKS	3,006 (276) b	3,844 (382) b	5,121 (441) a		
	Saplings	ACRU	230 (47) c	394 (31) b	580 (53) a		
		CARYA	50 (16) b	156 (34) a	76 (23) b		
		LITU	26 (7) c	81 (15) b	281 (28) a		
		OXAR	53 (8) b	133 (16) a	152 (18) a		
		NYSY	70 (8) b	41 (7) c	121 (12) a		
		OAKS	111 (11) c	163 (17) b	299 (23) a		

*Shrubby vegetation included multi-stemmed woody and semi-woody (e.g., *Smilax* and *Rubus* spp.) species rarely >4 m tall and lianas. Seedlings: tree species (≥4 m in height at maturity) ≥30.5 cm tall but <1.4 m tall. Saplings: tree species ≥1.4 m tall and <7.6 cm diameter at breast height. Species codes are the first two letters of genus and species. All *Carya* spp. (CARYA), Quercus spp. (OAKS), and *Vaccinium* spp. (VACC) except *Vaccinium arboreum* were aggregated. Standard error presented parenthetically.

Appendix SIII6. Modeled relationships between overstory (live basal area, LBA) or midstory (small and large sapling) density and the ordinated position (non-metric multidimensional scaling) of 20-ha stands by year (2008 to 2016) in shrubby, seedling, and sapling compositional and relative abundance explanatory space during management at Catoosa Wildlife Management Area. The best structured additive regression (STAR) model, determined by a stepwise procedure, are presented for each density metric. Potential effects of treatment (TRT), year (YR), slope, slope position, or aspect were added to the tensor product of the 2 ordination axes and random stand effects (reSTAND). Potential canopy closure (CC), LBA, and dead basal area (DBA) effects were also included in sapling models. Smoothing functions (sx) were selected if trends were non-linear.

			Multiple regression[3] (df = 2, 87)		
Vegetation	Final STAR models[1]	ΔAIC[2]	F	p	R^2
Shrubs	LBA ~ NMS(Shrubby)+YR+sx(slope)+reSTAND	0.04	59.7	< **0.001**	0.57
	Large sapling density ~ NMS(Shrubby)+TRT+sx(DBA)+CC+aspect+sx(slope position)+reSTAND	-6.62	23.2	< **0.001**	0.33
	Small sapling density ~ NMS(Shrubby)+YR+sx(LBA)+sx(slope)+reSTAND	4.56*	2.6	0.082	0.03
Seedlings	LBA ~ NMS(Seedlings)+YR+sx(slope)+reSTAND	2.37*	36.0	< **0.001**	0.44
	Large sapling density ~ NMS(Seedlings)+TRT+sx(DBA)+CC+aspect+sx(slope position)+reSTAND	15.26*	15.4	< **0.001**	0.24
	Small sapling density ~ NMS(Seedlings)+YR+sx(LBA)+sx(slope)+reSTAND	3.03*	4.1	**0.019**	0.07
Saplings	LBA ~ NMS(Saplings)+YR+sx(slope)+reSTAND	11.43*	34.9	< **0.001**	0.43
	Large sapling density ~ NMS(Saplings)+TRT+sx(DBA)+CC+aspect+sx(slope position)+reSTAND	-7.88	18.5	< **0.001**	0.28
	Small sapling density ~ NMS(Saplings)+YR+sx(LBA)+sx(slope)+reSTAND	41.98*	34.7	< **0.001**	0.43

[1]Modeled sapling (tree species ≥4 m in height at maturity) size classes included small (≥1.4 m tall and <7.6 cm diameter at breast height [DBH]) and large (≥1.4 m tall and ≥7.6 but <12.7 cm DBH). [2]Change in Akaike's information criterion after dropping the tensor term (ΔAIC). *Denotes ΔAIC >2.0, or relationship between tensor and density terms. [3]Determined by modeling density metrics as a function of both NMS axis scores.

CHAPTER IV
DISTURBANCE MEDIATED PROMOTION OF HERBACEOUS GROUND-LAYERS IN MID-SOUTHERN OAK FORESTS

This chapter is original work by Andrew L. Vander Yacht with contributions from co-authors Patrick D. Keyser, Seth A. Barrioz, Charles Kwit, Mike C. Stambaugh, Wayne K. Clatterbuck, and Dean M. Simon. It has not yet been published, but the authors intend on submitting it to "*Ecological Applications*".

ABSTRACT

Fire suppression and subsequent woody encroachment has degraded the herbaceous components of oak-dominated communities throughout the Mid-South. Efficient restoration could involve combining canopy disturbance with growing-season fire. We monitored groundcover response to replicated combinations of thinning (none, 7, and 14 m^2 ha^{-1} residual basal area) and seasonal fire (none, March [prior to leaf expansion], and October [prior to leaf abscission]) from 2008 to 2016 at three sites in the Mid-South. We observed 5.1 to 12.7-fold increases in site-specific herbaceous richness from pre to post treatment. At all sites, Shannon-Wiener's diversity index was greater in treatments than controls during the final biennial interval of monitoring (2015 and 2016). Preceding gains in herbaceous groundcover and diversity were greatest in heavily thinned and burned stands. Averaged across 2015 and 2016, heavily thinned (to 7 m^2 ha^{-1} residual basal area) and burned stands relative to unmanaged controls had greater graminoid (6.8X) and forb (6.2X) groundcover, and contained greater herbaceous richness (4.3X) and diversity (4.1X). Increasing woody groundcover in all but closed-canopy treatments suggested the mechanism behind fire's promotion of herbaceous ground-layers was more associated with leaf-litter removal and related increases in bare ground than woody competition control. Fire-season effects were more subtle and inconsistent across sites. Overall, our results conflict with warnings concerning the potential negative effects of fire on diversity east of the prairie-woodland transition zone. We conclude canopy disturbance and prescribed fire

contributed positively to the restoration of herbaceous ground-layers in oak ecosystems throughout the Mid-South.

Keywords: herbaceous groundcover; fire-season; canopy disturbance; restoration; Tennessee; North Carolina; woody encroachment; savanna; woodland.

INTRODUCTION

Oak woodlands (30-80% canopy cover) and savannas (10-30% canopy cover, Nelson 2010) once covered substantial portions of the Appalachian and Central Hardwood regions of eastern North America (hereafter, Mid-South, Nuzzo 1986; DeSelm 1994). Sparse overstories dominated by oaks (*Quercus* spp.) and other disturbance-adapted trees were created and maintained by frequent fire throughout the region (Fralish et al. 2000, Guyette et al. 2006, Lafon et al. 2017). Such overstory structure distinguished woodlands and savannas from prairies and forests (Faber-Langendoen 2001), and allowed light to reach and promote another defining characteristic – robust and diverse herbaceous ground-layers (Taft 1997). Early European explorations of the Mid-South described herds of large herbivores grazing on an abundance of native warm-season grasses, legumes, and other forbs species (Michaux 1805, Ramsey 1853). Understory gradients in plant resources likely radiated outward from the boles of scattered trees (Peterson et al. 2007), promoting levels of herbaceous diversity that exceeded both prairies and forests (DeSelm 1994, Leach and Givnish 1999). Herbaceous ground-layers were well-adapted to post-fire environments, but also created self-reinforcing feedbacks that maintained such conditions by providing a continuous, well-ventilated, and easily ignited fuel-bed (Mitchell et al. 2009, Maynard and Brewer 2013).

Presently, these unique associations between herbaceous ground-layers and sparse oak overstories have been nearly eliminated from the Mid-South. More than 99% of Midwestern oak

savannas have vanished since European settlement (Nuzzo 1986, Noss et al. 1995), and declines further east are similar (Delcourt et al. 1998, Brewer 2001). Although there are many contributing factors (Heikens and Robertson 1994), the suppression and exclusion of fire is most frequently implicated (Abrams 1992, McPherson 1997, Nowacki and Abrams 2015). Fire's absence has facilitated succession, leading to increasing canopy closure and woody encroachment (Briggs et al. 2005) and related reductions in herbaceous groundcover and plant resource gradients that sustain herbaceous diversity (Breshears 2006, Brudvig and Asbjornsen 2009). Dark, moist, and cool micro-environments now dominate forest understories (Nowacki and Abrams 2008) and preclude herbaceous layers (Hutchinson et al. 2005, Barrioz et al. 2013). Shifts in the physical and chemical properties of leaf-litter that have accompanied regional increases in the dominance of fire-intolerant woody species have reduced fuel-bed flammability (Kreye et al. 2013, Alexander and Arthur 2014) and thus, fire's ability to control woody growth. The near elimination of herbaceous ground-layers from eastern oak ecosystems may have increased their susceptibility to invasive species (Knops et al. 1999), encouraged regional declines in pollinators (Hanula et al. 2015) and disturbance-dependent wildlife (Harper et al. 2016, Vander Yacht et al. 2016), and compromised the restoration potential of imperiled oak woodlands and savannas (Noss et al. 1995, Maynard and Brewer 2013).

The exponential increase in the costs and effort required to reverse such effects within eastern oak ecosystems creates an urgent need for management intervention. Fortunately, the disturbances responsible for creating and maintaining these communities can also be used to address their degradation (McPherson 1997). Prescribed fire stimulates herbaceous plants by making nutrients available for growth (Scharenbroch et al. 2012) and removing layers of leaf-litter that inhibit herbaceous germination (Lashley et al. 2011). Fire is essential for oak woodland

and savanna restoration (Peterson and Reich 2001), but safety constraints typically result in low to moderately intense fires that are slow to alter overstory characteristics (Knapp et al. 2015). Mechanical canopy disturbance can quickly increase the light available for herbaceous germination and growth (Nielsen et al. 2003, Brewer 2016), but increases in light also stimulate woody vegetation (McCord et al. 2014) that can limit herbaceous layer development (Lashley et al. 2011, Barrioz et al. 2013). Suppressing woody understory growth with a long-term regimen of biennial fire can maximize herbaceous groundcover and richness (Peterson et al. 2007, Peterson and Reich 2008). Thus, restoring herbaceously dominated ground-layers is best accomplished when canopy disturbance and fire are used in conjunction (Lettow et al. 2014).

Techniques for restoring the ground-layer characteristics of oak woodlands and savannas have been well developed along the western edge of their historical range, but the applicability of such work in the Mid-South is limited by differences in climate, length of active fire-suppression, and near-absence of degraded remnants. Documented attempts to restore oak woodlands (Jackson et al. 2006, McCord et al. 2014, Brewer et al. 2015) and savannas (Barrioz et al. 2013) in the Mid-South are rare, typically proceed from closed-canopy forests, and are characterized by persistent woody undergrowth. Woody plants often resprout prolifically after fire (Blankenship and Arthur 2006, Vander Yacht et al. 2017a), and eliminating such vegetation requires a long-term commitment to prescribed burning (Hutchinson et al. 2012, Arthur et al. 2015). Growing-season fire can result in comparatively greater woody plant mortality and herbaceous layer gains than dormant-season fire (Waldrop et al. 1992, Gruchy et al. 2009, Robertson and Hmielowski 2014), and this effect could be explained by seasonal differences in fire behavior (Vander Yacht et al. 2017a) or root carbohydrate reserves (Huddle and Pallardy 1999). Combining growing-season fire with canopy disturbance could accelerate restoration

relative to the traditional use of dormant-season fire (Knapp et al. 2009). However, experimental evaluation is needed in the Mid-South where the seasonal effects of fire on herbaceous communities is poorly understood (Gilliam and Roberts 2003) and where growing-season fire may be a departure from historical regimes (Guyette et al. 2006).

We implemented a replicated experiment at three sites located across the Mid-South, and monitored groundcover response from 2008 to 2016 across combinations of canopy disturbance (none, and to 7 or 14 m^2 ha^{-1} residual basal area) and season of prescribed fire (none, March [prior to leaf expansion], and October [prior to leaf abscission]). We hypothesized that canopy disturbance and fire-season would interact such that heavy thinning and late growing-season fire would result in the greatest promotion of herbaceous groundcover and diversity. Our goal was to elucidate management capable of efficiently increasing herbaceous groundcover and diversity in oak communities throughout the Mid-South.

METHODS

Study Areas

Our first site was Catoosa Wildlife Management Area (CWMA), a 32,374-ha property managed by the Tennessee Wildlife Resources Agency (TWRA) on the Cumberland Plateau in the Southwestern Appalachians ecoregion (all ecoregions: Level III, U.S. EPA 2013). Broad ridges and dissecting ravines ranged from 437-521 m in elevation. Soils are Mesic Typic Hapludults (Soil Survey Staff NRCS 2014) over weathered sandstone and conglomerate (Nicholson et al. 2005). Annual precipitation and temperature averaged 140 cm and 13 °C, respectively, from 1981 to 2010 (National Climatic Data Center 2014). Forests were established following agricultural abandonment (1920's) and were dominated by oaks at study initiation, including white (*Q. alba* L.), southern red (*Q. falcata* Michx.), black (*Q. veluntina* Lam.), and

scarlet (*Q. coccinea* Münchh.). Red maple (*Acer rubrum* L.), sourwood (*Oxydendrum arboreum* L.), and hickories were also abundant. Shortleaf pine became a minimal overstory component after the southern pine bark beetle (*Dendroctonus frontalis* Zimmermann) outbreak of 1999-2000. In response, TWRA began managing for oak woodlands and savannas using salvage cutting and prescribed fire. The site's floral (Barrioz et al. 2013, Vander Yacht et al. 2017a) and faunal (Cox et al. 2016, Vander Yacht et al. 2016) response indicated restoration progress.

Our second site was Green River Game Lands (GRGL), a 5,726 ha North Carolina Wildlife Resources Commission (NCWRC) property situated at the interface between the Blue Ridge and Piedmont ecoregions. Narrow ridges and steep ravines ranged from 366 – 640 m in elevation. Soils are deep (>1 m), well-drained, and mostly in the Evard series (fine loamy, oxidic, Mesic Typic Hapludults, Keenan 1998) over gneiss, schist, and phyllite rock (Clark 2008). Annual precipitation and temperature averaged 139 cm and 14 °C, respectively, from 1981 to 2010 (National Climatic Data Center 2014). Forests were 80-120 years old with no recent disturbance history. Forest canopies were also dominated by oaks at our study's outset, but chestnut oak (*Q. montana* Willd.), northern red oak (*Q. rubra* L.), and yellow poplar (*Liriodendron tulipifera* L.) were more common relative to other sites. A dense ericaceous understory (*i.e.*, mountain laurel [*Kalmia latifolia* L.] and rosebay rhododendron [*Rhododendron maximum* L.]) occurred throughout the site.

Our third site was Land Between the Lakes (LBL), a 68,797 ha National Recreation Area in western Kentucky and Tennessee managed by the U.S. Forest Service and situated in the Western Highland Rim of the Interior Plateau. Rolling topography, with elevations of 122–198 m, is underlain by limestone bedrock. Soil series are Bodine, Baxter and Hammock with loess caps on ridgetops and mid-slopes (Franklin et al. 2003). Mean precipitation and temperature

from 1981 to 2010 was 134 cm and 14 ˚C, respectively. Relative to other sites, forest composition lacked a significant pine component and was more heavily dominated by white oak, chestnut oak, hickories, and post oak (*Quercus stellata* Wangenh.).

Experimental Design and Restoration Treatments

We treated sites as independent experiments because of differences in species composition, the timing and type of treatments, and discontinuity of data collection. At each site, 20-ha forested stands were configured to maximize core area and assigned a treatment using a completely randomized design. Treatments included: 1) unmanaged (Control), 2) thinned to woodland residual basal area (14 m^2 ha^{-1}) and spring burned (SpW), 3) thinned to woodland residual basal area and fall burned (FaW), 4) thinned to savanna residual basal area (7 m^2 ha^{-1}) and spring burned (SpS), and 5) thinned to savanna residual basal area and fall burned (FaS). All fires at LBL were conducted in spring (no FaS, FaW), including a 6) burn-only during the spring (SpO) treatment. Target residual basal area for savannas was greater (9 m^2 ha^{-1}) at LBL than other sites due to administrative constraints. At GRGL, we also included 7) burn-only in the fall (FaO, in place of SpO). Treatments were replicated twice at CWMA, four times at LBL (except for only 2 replicates of SpO and Control), and once at GRGL. Prior to treatments, canopy closure averaged 90.7 % (± 2.5 SE) and live basal area was 20.1 m^2 ha^{-1} (± 2.0 SE). Midstory density (stems >1.4 m tall, < 12.7 cm diameter at breast height [DBH]) descended from east to west (GRGL: 2,423 stems ha^{-1} ± 391 SE, CWMA: 1,936 stems ha^{-1} ± 182 SE, LBL: 985 stems ha^{-1} ± 219 SE). Herbaceous groundcover was consistently minimal (5.7 % ± 2.0 SE), and ericaceous shrubs, woody regeneration, and litter dominated understories (Vander Yacht et al. 2017a).

Canopy reductions were completed commercially during the dormant season (Fig. IV1). Where possible, oaks, hickories, and shortleaf pine were retained while fire-intolerant species

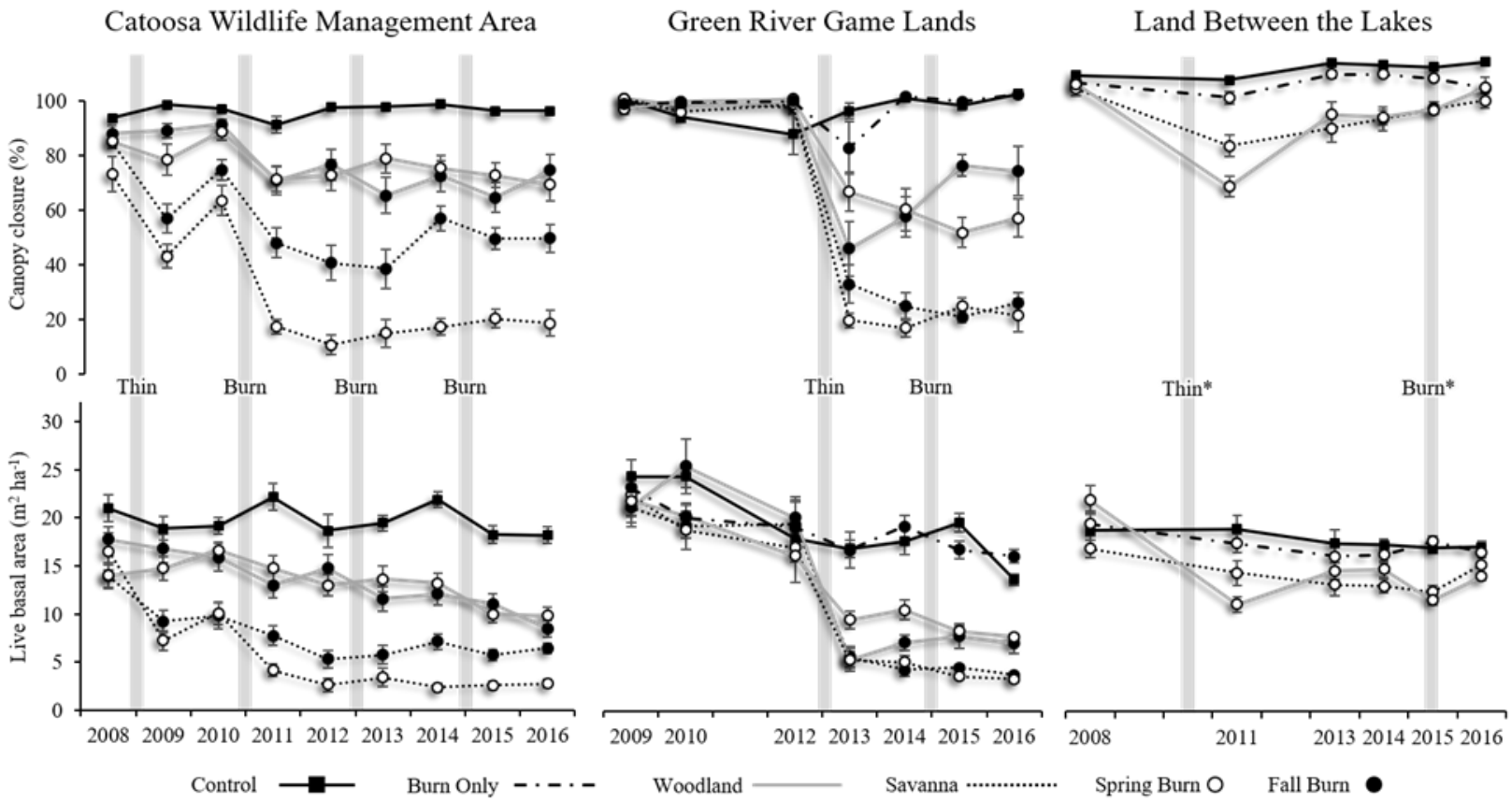

Fig. IV1. Depiction of treatment implementation effects on canopy closure (%) and live tree basal area (m^2 ha^{-1}) during (2008 to 2016) oak woodland and savanna restoration experiments at 3 sites located across the Mid-South. Treatments included canopy disturbance (THIN) and prescribed fire in the fall (Fa) or spring (Sp).

including maples (*Acer* spp.), yellow poplar, and sweetgum (*Liquidambar styraciflua* L.) were removed. After thinning, but before burning, residual basal area and canopy closure was comparable across sites within control and burn-only stands (21.4 m^2 ha^{-1} ± 1.1 SE, 97.6 % ± 0.4 SE), woodlands (14.6 m^2 ha^{-1} ± 1.5 SE, 77.7 % ± 4.6 SE), and savannas (9.3 m^2 ha^{-1} ± 1.6 SE, 53.7 % ± 4.2 SE). Site managers conducted all prescribed fires (Fig. IV1). Ring firing was used at CWMA to burn FaW and FaS 3 times in mid-October prior to bud-break (2010, 2012, and 2014), and SpW and SpS 3 times in mid-March prior to leaf abscission (2011, 2013, and 2015). Similar seasonal timing of fire (October 2015 and March 2016) was applied once using strip-head firing at GRGL. At LBL, half of both SpW and SpS replicates and all SpO replicates were burned using strip-head firing in late April, 2015. Remaining SpW and SpS replicates were burned in late March, 2016 using aerial ignition from a helicopter.

Burning conditions and fire behavior were monitored at all sites following (Vander Yacht et al. 2017a). Fuel samples were oven dried to determine moisture content, weather was recorded on-site, and fire spread and flame lengths were systematically measured. We sampled fire temperature using foil-wrapped ceramic tiles (n = 181) placed at fuel sampling points (70 × 70 m grid) and painted with Tempilaq® indicating liquids. Burning conditions and fire behavior were generally consistent by season across sites, and we present means across all sites by season for simplicity (Appendix 1). Conditions were warmer (+7˚ C) and less windy (-1.9 m s^{-1}), and fine-fuels (litter and 1-hour twigs) were nearly 5% drier, during fall relative to spring burns. However, heading fires in spring had nearly double the rate-of-spread and flame length of those in fall. Spring fires also burned nearly 40 ˚C hotter, on average, than fall fires.

Sampling Design and Data Collection

We collected data from 2008-2016 in late May though early August, and this included sampling within all treatment intervals at all sites (Fig. IV1). We systematically located permanent plots (n = 15 stand^{-1}) along a 70 X 70 m grid within the core (50-m buffer) of each stand. Understory woody vegetation was surveyed in seven nested 1-m^2 and 3-m radius sub-plots at each plot. Five sub-plots were located at 12.5-m intervals along a 50-m transect running through plot center and perpendicular to landscape slope. Two additional sub-plots were placed 12.5 m up- and down-slope from plot center. Within 1-m^2 sub-plots, stems of all seedling and shrubby vegetation were tallied. Seedlings were tree species (typically ≥4 m in height at maturity) ≥30.5 cm tall but <1.4 m tall. Shrubby vegetation included woody, semi-woody (largely *Smilax* and *Rubus* spp.) and liana species that were typically multi-stemmed and rarely >4 m tall. We tallied small (<7.6 cm DBH) and large (≥7.6, <12.7 cm DBH) sapling stems (tree species ≥1.4 m tall) within 3-m radius sub-plots. At the ends and center of each 50-m transect, we measured live and dead tree basal area (2-factor metric prism), canopy closure (convex spherical densiometer), percent slope (clinometer), aspect, and slope position. Each location within a plot was assigned a numerical slope position (1-6: alluvial, cove, toe-slope, mid-slope, shoulder, or ridge).

We characterized groundcover along the 50-m transect at 1-m intervals using the point-intercept method (Bonham 1989). At each interval, cover below a height of 1.37 m was categorized as either woody (tree and shrub species), litter, debris (down woody material >7.6 cm in diameter), bare, graminoid, forb, or fern. All intersected herbaceous vegetation was identified to species. We calculated percent groundcover for each category as the number of intercepts where a category was present divided by the total number of intercepts (50). These

data determined plot-level herbaceous richness, and diversity was calculated using Shannon-Wiener's Index (H′, Magurran 1988).

Data Analysis

We conducted all analysis in SAS 9.4 using PROC MIXED (SAS Ins., Cary, N.C., USA). Stand-level means by site and year (2008-2016) for woody, litter, debris, bare, graminoid, and forb groundcover (%), herbaceous richness, and herbaceous diversity were calculated. Fern groundcover was never substantial (overall mean = 1.8% ± 0.2 SE) and was not individually analyzed. Prior to modeling, we tested each dependent variable for normality (Wilk's test, W > 0.90), transformed using a square root function when necessary, and graphically observed equality of variance. We then developed separate ANCOVA/ANOVA models for each dependent variable, and included repeated measures, covariates, and mixed-effects. Fixed-effects included covariates, treatment, year, and treatment × year interactions. Year was a fixed-effect because treatments were applied over time. Random-effects included replicate × treatment interactions. We used Kenward-Roger degree of freedom method but dropped autoregressive correlation between annual data because differences in model fit between inclusion and omission were small (<5, -2 residual log likelihood per covariance parameter, Littell et al. 2006).

An *a priori* set of covariates were included to address variation inherent in applying our treatments across operational scales (20 ha). Covariates were only retained when a significant ($\alpha = 0.05$) relationship with dependent variables was observed. We included aspect, slope, and slope position covariates to correct for landscape-induced variation. We transformed aspect following (Beers et al. 1966) to yield a continuous variable between 0.00 (southwest) and 2.00 (northeast). Within-stand variation in the overstory was captured by live and dead tree basal area (m^2 ha^{-1}) and canopy closure (%) covariates. Large-sapling density ($stems^{-1}$ ha) was also

included as a covariate because it pre-existed implementation of our treatments and could affect lower strata development (Barrioz et al. 2013). To reduce the within-treatment variation in herbaceous response associated with low-lying woody growth, we included woody groundcover, and shrub, seedling, and small-sapling density (stems^{-1} ha), covariates. These variables were not included in models of woody groundcover. To avoid collinearity, only the most significant covariate within a correlated ($r > 0.6$) grouping (overstory, landscape, low-lying woody growth) was retained in final models. Plots of dependent variable and covariate relationships provided evidence of linearity. When a covariate was significant, we tested covariate × treatment interactions. Such effects were never significant, supporting homogeneity of covariate slopes across treatments, and were therefore dropped from models. We used a similar method to determine homogeneity of covariate slopes across years. Although some covariates had small partial r^2 (≥ 0.15), their inclusion decreased Akaike's Information Criterion for small sample-size by ≥ 2 and reduced residual error variance ($\geq 8.2\%$).

We expected difficult to interpret treatment × year interactions because treatments were applied over time. Therefore, we used orthogonal contrasts to test specific, *a priori* hypotheses. Differences of interest were controls vs. burn-only treatments, controls vs. thinned and burned treatments, woodlands vs. savannas, and fall vs. spring burns. These comparisons were evaluated in two separate ways by site: 1) treatment contrasts that evaluated groundcover differences across treatments in 2015 and 2016, and 2) interaction contrasts that evaluated differential changes in groundcover between treatment groupings across specific, annual intervals. The pooled 2015 and 2016 data that treatment contrasts analyzed represented the restoration progress achieved by treatments while recognizing the variation inherent in a biennial fire regime. Specific contrasts were only tested at applicable sites (*e.g.*, no burn-only treatment at CWMA).

For interaction contrasts, control vs. treatment comparisons were always tested but others followed the implementation of referred to treatments. All significant ($\alpha = 0.05$) contrasts are presented in Appendix 2, and those of interest are highlighted.

RESULTS

Graminoid Groundcover

Prior to implementing treatments, we encountered 10, 3, and 9 species of graminoids at CWMA, GRGL, and LBL, respectively. Across all sites, pre-treatment graminoid groundcover was dominated by the genera *Dichanthelium* and *Carex*. By the conclusion of monitoring, we cumulatively documented 74 (CWMA), 49 (GRGL), and 58 (LBL) graminoid species (Appendix 3). Needlegrass (*Piptochaetium avenaceum* [L.] Parodi) was the most frequently encountered graminoid at CWMA, where it was encountered nearly 4X as often as the next most common graminoid (*Dichanthelium dichotomum* [L.] Gould), and was the 9th (GRGL) and 5th (LBL) most frequently encountered graminoid at other sites. By the conclusion of monitoring, we documented 26 *Carex* and 13 *Dichanthelium* species. These genera, and *Chasmanthium* and *Danthonia*, were often among the most commonly encountered across all sites. Broomsedge (*Andropogon virginicus* L.) was also common, and other documented native warm-season grasses included little bluestem (*Schizachyrium scoparium* [Michx.] Nash), big bluestem (*Andropogon gerardii* Vitman), indiangrass (*Sorghastrum nutans* [L.] Nash), and side-oats grama (*Bouteloua curtipendula* [Michx.] Torr.). We documented two invasive grasses; Nepalese browntop (*Microstegium vimineum* [Trin.] A. Camus) was common at all sites and Chinese silvergrass (*Miscanthus sinensis* Anderss.) was common at GRGL.

We observed an interaction between treatment and year for graminoid groundcover at all sites (Table IV1). This primarily involved greater increases over time in treatments relative to

Table IV1. ANCOVA/ANOVA model results for percent groundcover variables during (2008 to 2016) point intercept monitoring of oak woodland and savanna restoration experiments at Catoosa Wildlife Management Area (Cumberland County, TN), Green River Game Lands (Polk County, NC), and Land Between the Lakes National Recreation Area (Stewart County, TN).

Site	Groundcover variable	Treatment *F*	Treatment *p*	Year *F*	Year *p*	Treatment × Year *F*	Treatment × Year *p*
Catoosa Wildlife Management Area	Graminoid	2.2	0.203	25.6	< 0.001	6.8	**< 0.001**
	Forb	4.4	0.062	34.4	< 0.001	6.3	**< 0.001**
	Richness	3.1	0.120	22.9	< 0.001	6.6	**< 0.001**
	Diversity	3.8	0.086	24.5	< 0.001	5.0	**< 0.001**
	Woody	17.6	0.002	132.4	< 0.001	8.9	**< 0.001**
	Litter	30.9	0.001	15.7	< 0.001	3.3	**< 0.001**
	Debris	0.3	0.879	26.8	< 0.001	4.1	**< 0.001**
	Bare	11.5	0.007	13.4	< 0.001	4.5	**< 0.001**
Green River Game Lands	Graminoid	31.2	< 0.001	67.6	< 0.001	14.3	**< 0.001**
	Forb	10.0	< 0.001	21.8	< 0.001	4.2	**< 0.001**
	Richness	20.5	< 0.001	45.3	< 0.001	7.2	**< 0.001**
	Diversity	30.3	< 0.001	50.8	< 0.001	8.7	**< 0.001**
	Woody	21.4	< 0.001	9.0	< 0.001	8.6	**< 0.001**
	Litter	28.4	< 0.001	60.6	< 0.001	8.5	**< 0.001**
	Debris	7.1	< 0.001	12.4	< 0.001	3.7	**< 0.001**
	Bare	17.6	< 0.001	57.0	< 0.001	6.8	**< 0.001**
Land Between the Lakes	Graminoid	7.4	0.011	10.2	< 0.001	5.2	**< 0.001**
	Forb	0.6	0.612	17.3	< 0.001	2.7	**0.001**
	Richness	2.6	0.123	20.0	< 0.001	5.4	**< 0.001**
	Diversity	2.8	0.109	19.9	< 0.001	4.8	**< 0.001**
	Woody	5.8	0.020	68.3	< 0.001	5.7	**< 0.001**
	Litter	41.0	< 0.001	10.9	< 0.001	5.4	**< 0.001**
	Debris	12.7	0.003	12.6	**< 0.001**	1.6	0.069
	Bare	6.3	0.016	31.3	< 0.001	3.9	**< 0.001**

Richness and diversity (Shannon-Wiener Index) refer to the herbaceous community. Bold indicates significant ($\alpha = 0.05$) and interpretable effects. Model *df* calculated using Kenward Rogers adjustment.

controls (Fig. IV2, Appendix 2). At CWMA, a biennial cycle of increasing graminoid groundcover after disturbance followed by decreases after fire was more apparent relative to other sites. Increases within this cycle were greater in treatments than controls, and greater in savannas than woodlands, from the first to second year following canopy disturbance (2009 to 2010: $F > 6.4$, $p < 0.012$) and from the first to second year following the first (2011 to 2012: $F > 4.9$, $p < 0.027$) and second (2013 to 2014: $F > 6.2$, $p < 0.013$) prescribed fires. Gains in graminoid groundcover appeared to stabilize after the third fire; increases in treatments from 2015 to 2016 did not differ from trends within controls ($F = 1.6$, $p = 0.206$). Increases in graminoid groundcover over this final interval were 7.1 % (± 3.4 SE) greater in savannas relative to woodlands ($F = 4.3$, $p = 0.038$), and 8.0 % (± 3.4 SE) greater in fall relative to spring burns ($F = 5.5$, $p = 0.019$). Reductions in graminoid groundcover within the observed cycle were 9.2 % (± 3.6 SE) greater, on average, in savannas than woodlands after the second and third fires ($F > 5.4$, $p < 0.021$). Resulting (2015 and 2016) graminoid groundcover at CWMA was 19.0 % (± 6.8 SE) greater in savannas relative to woodlands ($F = 7.9$, $p = 0.035$), but collectively treatments did not differ from controls ($F = 2.4$, $p = 0.171$).

At GRGL, substantial changes in graminoid groundcover occurred following fire (Fig. IV2). Graminoid groundcover increased more in savannas than woodlands from pre (2014) to post (2015) fire ($F = 6.5$, $p = 0.011$), but this difference was largely driven by the single SpS replicate. Increases in graminoid groundcover during this interval were 10.0 % (± 2.5 SE) greater in spring relative to fall burns ($F = 11.7$, $p = 0.001$), but this effect was also largely dependent on the single SpS replicate. Increases in graminoid groundcover from 2015 to 2016 were 18.4 % (± 3.1 SE) greater in treatments relative to controls ($F = 17.1$, $p < 0.001$). Graminoid groundcover

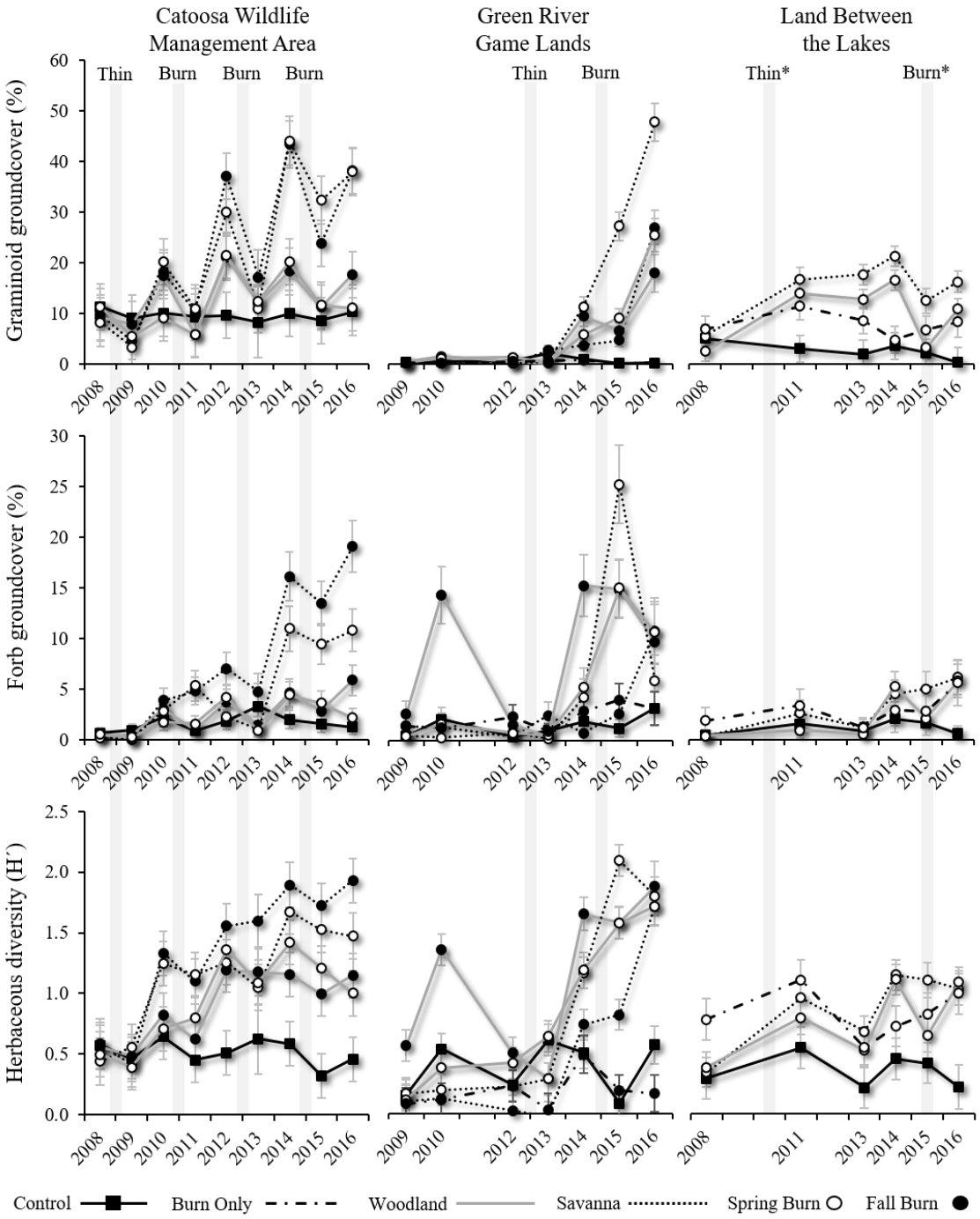

Fig. IV2. Graminoid and forb groundcover, and herbaceous diversity (Shannon-Wiener Index), during (2008 to 2016) oak woodland and savanna restoration experiments at 3 sites located across the Mid-South. Treatments included unmanaged oak forests (Control), burn only in spring or fall, and savanna (7 m^2 ha^{-1}, S) or woodland (14 m^2 ha^{-1}, W) residual basal area paired with spring or fall fire. Please consult Appendix 2 for a list of significant (α = 0.05) treatment and interaction contrasts.

in 2015 and 2016 at GRGL was 22.9 % (± 2.7 SE) greater in treatments relative to controls (F = 153.8, $p < 0.001$), 10.5 % (± 2.4 SE) greater in savannas relative to woodlands (F = 17.4, $p < 0.001$), and 13.0 % (± 2.4 SE) greater in spring relative to fall burns (F = 35.0, $p < 0.001$).

At LBL, graminoid groundcover increased in treatments more than controls from 2008 to 2013 (+11.8 % ± 2.2 SE, F = 29.6, $p < 0.001$) and from 2013 to 2014 (+4.8 % ± 2.2 SE, F = 4.8, p = 0.028). These were the only significant contrasts, and graminoid groundcover at LBL in 2015 and 2016 was comparable across all treatments ($F < 3.4$, $p > 0.103$). Within-treatment effects on graminoid groundcover of landscape, overstory density, and understory density were corrected for at all sites (Appendix 4).

Forb Groundcover

Pre-treatment, we encountered 6, 22, and 30 species of forbs at CWMA, GRGL, and LBL, respectively. Few of these species were encountered more than 4 times (1 at CWMA: *Desmodium nudiflorum* [L.] DC., 2 at GRGL: *Galax urceolata* [Poir.] Brummitt and *Viola pubescens* Aiton, and 3 at LBL: *Actaea racemosa* L., *Desmodium nudiflorum* [L.] DC., and *Pycnanthemum pycanthemoides* [Leavenworth] Fernald). By 2016, we cumulatively documented 181 (CWMA), 145 (GRGL), and 146 (LBL) forb species (Appendix 3). American burnweed (*Erechtites hieraciifolia* [L.] Raf. ex DC.) was the most, or second most, commonly encountered forb at all three sites. Across sites, *Eupatorium* (9 species), *Solidago* (15 species), and *Viola* (10 species) genera accounted for substantial portions of forb diversity. Herbaceous composition was quite similar at CWMA and GRGL, but more distinct at LBL; six of the top ten most frequently encountered forbs at LBL were legumes. Across all sites, the genera *Lespedeza* (7 species) and *Desmodium* (9 species) accounted for many of the commonly encountered legumes.

We observed an interaction between treatment and year for forb groundcover at all sites (Table IV1). Generally, increases over time were greater in treatments relative to controls (Fig. IV2, Appendix 2). Increases in forb groundcover at CWMA were greater in savannas relative to other treatments, and most of this increase occurred from the first to second year post second fire (2013 to 2014). Over this interval, increases in forb groundcover were 8.1 % (± 4.0 SE) greater in treatments relative to controls (F = 9.1, p = 0.003) and 6.6 % (± 2.3 SE) greater in savannas relative to woodlands (F = 7.8, p = 0.005). Increases in forb groundcover over the intervals following the first (2011-2012) and third (2015-2016) fire were, on average, 4.4 % (± 2.0 SE) greater in Fa relative to Sp treatments ($F > 4.8$, $p < 0.029$). Forb groundcover did not end up significantly greater in Fa relative to Sp treatments, however, and the only significant contrast in 2015 and 2016 indicated savannas contained 6.8 % (± 2.9 SE) more forb groundcover than woodlands (F = 8.1, p = 0.033). Changes in forb groundcover at GRGL were more erratic, but were similarly 4-fold greater in treatments relative to controls (F = 6.1, p = 0.015) by 2015 and 2016. Forb groundcover at LBL rarely exceeded 5%, and treatments did not differ from controls in 2015 and 2016 (F = 1.8, p = 0.215). Across all sites, forb groundcover was negatively related to canopy closure, and positively related to woody understory covariates (Appendix 4).

Herbaceous Richness and Diversity

We encountered 46 unique herbaceous species across all sites prior to treatments. By the conclusion of monitoring (2016), we had cumulatively documented 370 herbaceous species (Appendix 3). Similar site-specific figures indicated 12.7-fold (CWMA, 21 to 266 species), 7.3-fold (GRGL, 28 to 203 species), and 5.1-fold (LBL, 43 to 218 species) increases in total species richness. After thinning and 3 fires at CWMA, nearly 5 additional herbaceous species were encountered per 50-m transect in treatments relative to controls, and in savannas relative to

woodlands (Fig. IV3, Appendix 2). Herbaceous diversity also increased in treatments more so than in controls (Table IV1, Fig. IV2), and was greater in treatments than controls at all sites in 2015 and 2016 (Fig. 3, $F > 5.3$, $p < 0.049$). Treatments ranged from 3.5 (CWMA) to 5.0 (GRGL) times as herbaceously diverse as controls. In 2015 and 2016 at GRGL, herbaceous diversity and richness were also greater in Sp relative to Fa treatments (Fig. IV3). At LBL, resulting (2015 and 2016) herbaceous richness in treatments did not differ significantly from controls but herbaceous diversity was greater in thinned and burned treatments (Fig. IV3). Herbaceous richness and diversity were related to numerous covariates (Appendix 4). Typically, such metrics increased with increasing seedling density and woody groundcover and decreased with increasing large-sapling and overstory density. Herbaceous richness and diversity was also greater in alluvial slope-positions and on southeasterly facing slopes.

Additional Groundcover Measures

The remainder of groundcover was primarily woody and litter (Fig. IV4). In treatments relative to controls, woody groundcover increased whereas litter groundcover decreased. Debris groundcover initially decreased or remained stable, and then increased following prescribed fire. Bare ground at CWMA and GRGL oscillated between greater groundcover years immediately following disturbance (either thinning or burning) and less groundcover in the second year following disturbance. Bare ground at LBL increased at rate that was almost exponential in all but control treatments. Generally, canopy disturbance and fire reduced litter and increased woody, debris, bare, forb, and graminoid groundcover relative to controls (Fig. IV5); however, patterns in resulting (2015 and 2016) groundcover across treatments varied by site. At CWMA, woodlands and savannas differed in debris, forb, and grass cover but groundcover in fall and spring treatments was similar. At GRGL, woodlands and savannas only differed in graminoid

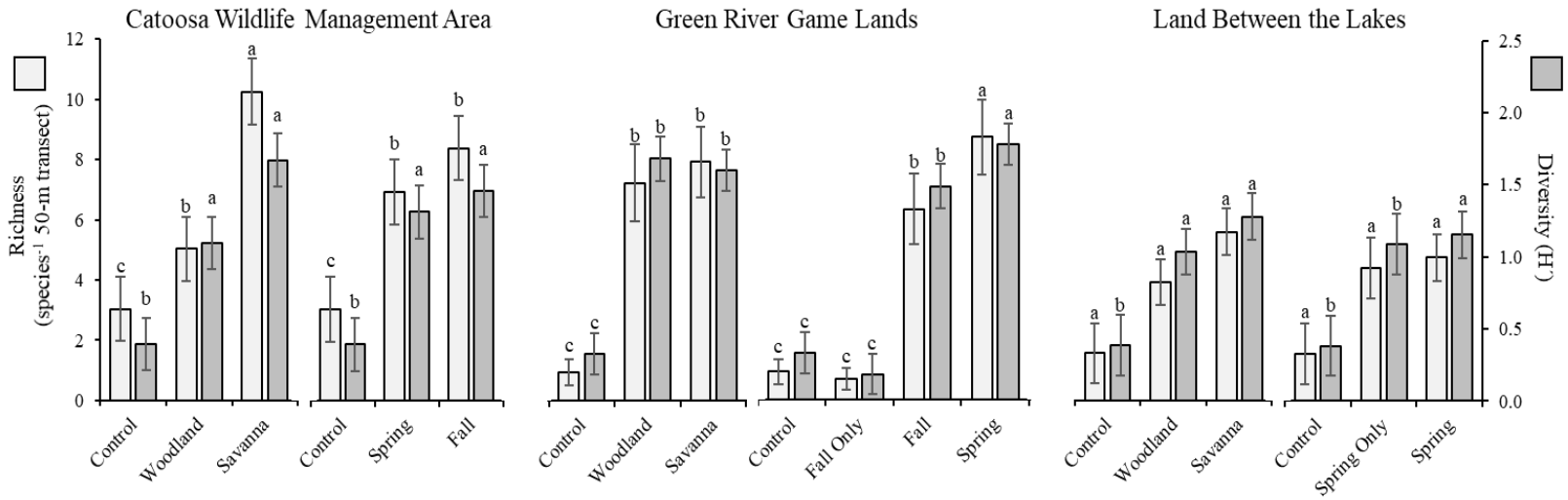

Fig. IV3. Differences in herbaceous richness and diversity (Shannon-Wiener Index) in the final two years of monitoring (2015 and 2016) oak woodland and savanna restoration experiments at 3 sites located across the Mid-South. Treatments included unmanaged oak forests (Control), burn only in spring or fall, and savanna (7 m^2 ha^{-1}, S) or woodland (14 m^2 ha^{-1}, W) residual basal area paired with spring or fall fire. Lowercase letters represent significant ($\alpha = 0.05$) differences by orthogonal contrast tests (Appendix 2).

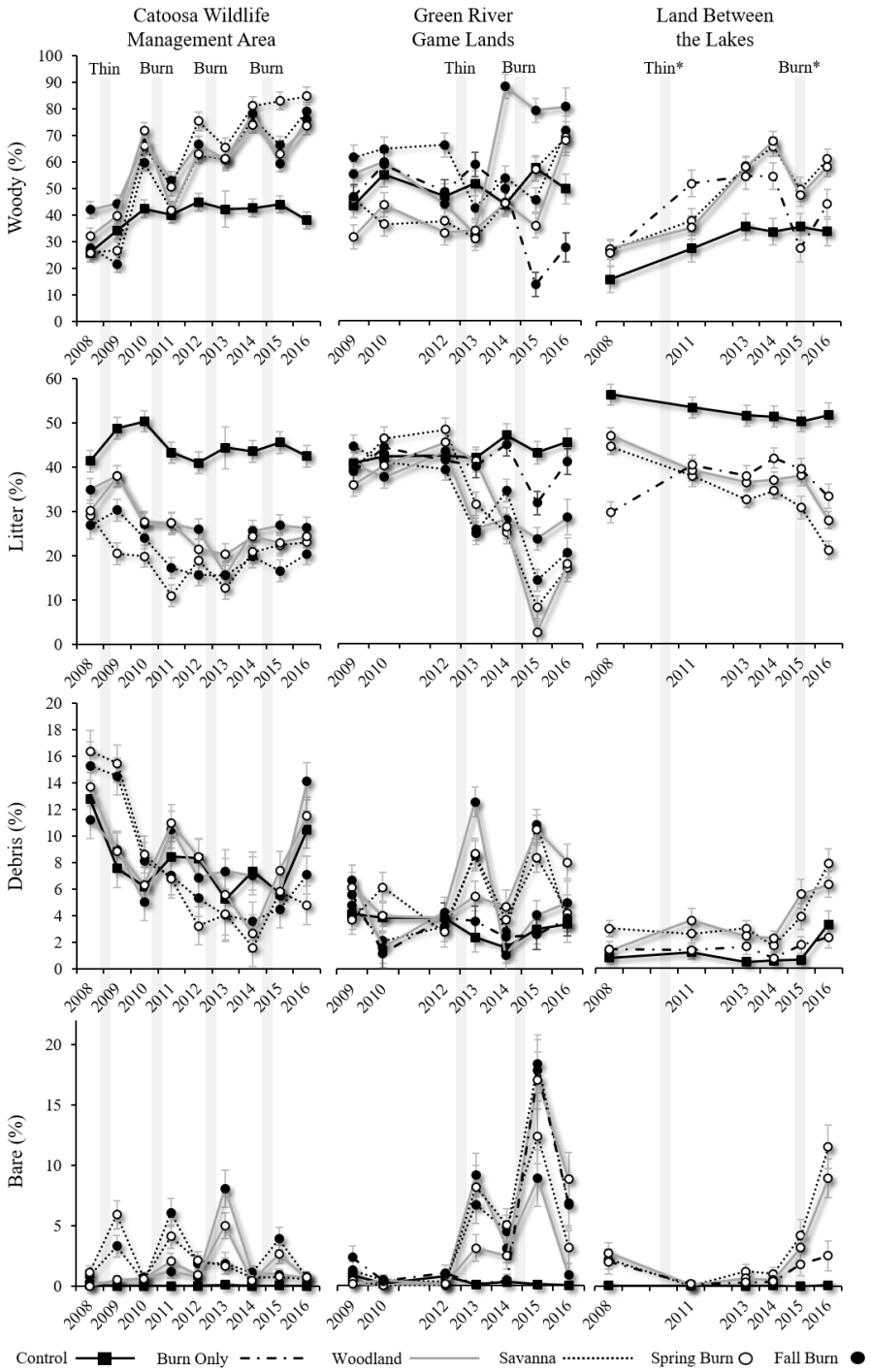

Fig. IV4. Woody, litter, debris, and bare groundcover during (2008 to 2016) oak woodland and savanna restoration experiments at 3 sites located across the Mid-South. Treatments included unmanaged oak forests (Control), burn only in spring or fall, and savanna (7 m^2 ha^{-1}, S) or woodland (14 m^2 ha^{-1}, W) residual basal area paired with spring or fall fire. Please consult Appendix 2 for a list of significant ($\alpha = 0.05$) treatment and interaction contrasts.

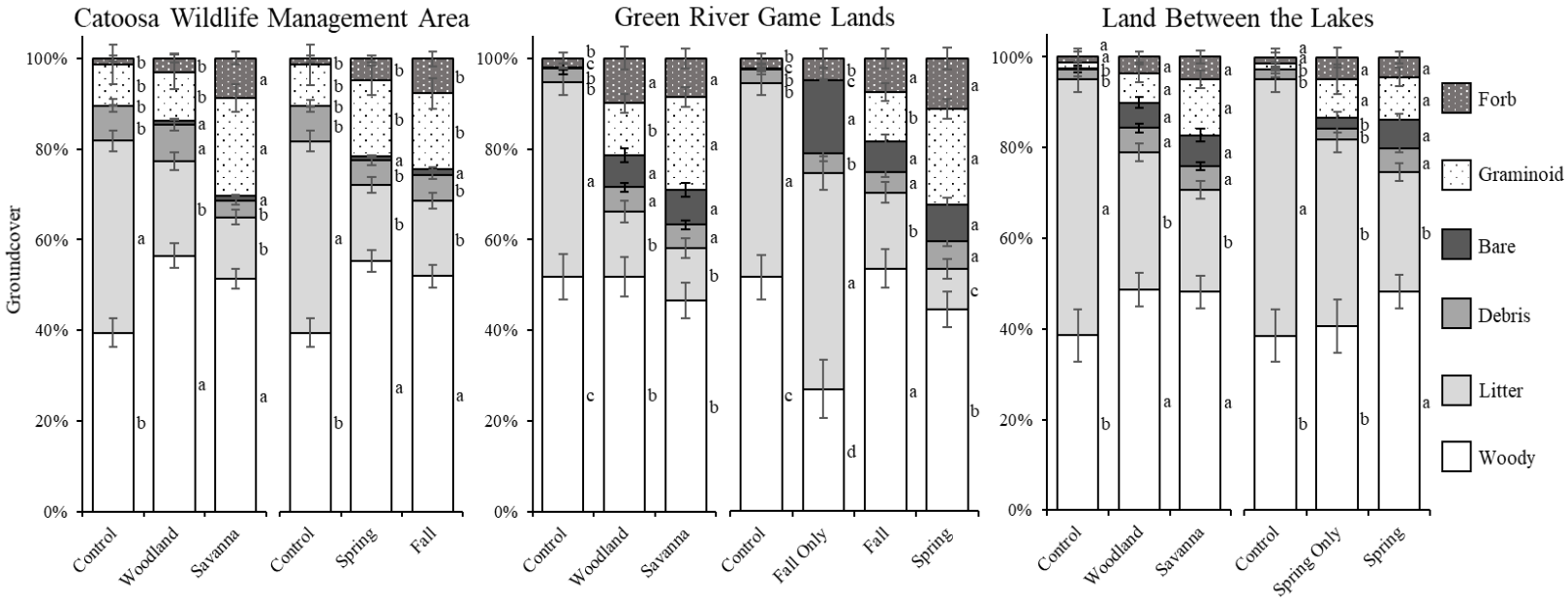

Fig. IV5. Comparisons of final groundcover results (2015 and 2016) within oak woodland and savanna restoration experiments at 3 sites located across the Mid-South. Treatments included unmanaged oak forests (Control), burn only in spring or fall, and savanna (7 m^2 ha^{-1}, S) or woodland (14 m^2 ha^{-1}, W) residual basal area paired with spring or fall fire. Lowercase letter represent significant (α = 0.05) differences as determined by orthogonal contrasts (Appendix 2).

groundcover but fall and spring treatments also differed in woody and litter groundcover. Less substantial thinning in savannas at LBL relative to other sites perhaps contributed to the lack of difference between canopy treatments at the site. Relative to controls, burning alone did result in some groundcover differences but did not increase graminoid or forb groundcover.

DISCUSSION

Our results demonstrate that a combination of canopy disturbance and prescribed fire can contribute to herbaceous ground-layer restoration in oak forests throughout the Mid-South. Similar management has proven effective in the northwestern periphery of the historical range of open-oak communities (Nielsen et al. 2003, Peterson and Reich 2008, Brudvig and Asbjornsen 2009, Lettow et al. 2014), but our results provide regionally specific evidence. Averaged across 2015 and 2016 site observations, heavily thinned (to 7 m^2 ha^{-1} residual basal area) and burned stands relative to unmanaged controls had greater graminoid (6.8X) and forb (6.2X) groundcover, and contained greater herbaceous richness (4.3X) and diversity (4.1X). These increases were directly attributable to increasing canopy disturbance, and fire further enhanced herbaceous response. Fire-season effects were more subtle and inconsistent across sites. Using this information to widely restore the lost herbaceous components of eastern oak ecosystems would address the conservation of imperiled oak woodlands and savannas (Nuzzo 1986, Noss et al. 1995), benefit associated wildlife (Harper et al. 2016, Vander Yacht et al. 2016), and improve forest resiliency in the face of forecasted climatic change (Vose and Elliott 2016).

Herbaceous Response to Canopy Disturbance

Graminoid and forb groundcover, as well as herbaceous richness and diversity, increased at all sites after canopy disturbance and before burning. In addition, subsequent increases in these metrics after burning were often greater in savannas than woodlands. Such observations

highlight the importance of broken canopies and light to herbaceous layer development. Previous work at our site documented that herbaceous cover, richness, and diversity were all negatively related to basal area and canopy closure (Barrioz et al. 2013, Vander Yacht et al. 2017a). More than 60 years of burning alone can be required to reduce canopy density (Burton et al. 2011, Knapp et al. 2015). In comparison, mechanical thinning immediately increases ground-level light and heterogeneity in plant resources, especially when conducted irregularly (Nielsen et al. 2003, Brudvig and Asbjornsen 2009).

Differences in the herbaceous ground-layer between woodlands and savannas were less obvious at GRGL and LBL, and became apparent at CWMA only after multiple fires. Savanna treatments at LBL only targeted 9 m^2 ha^{-1} residual basal area (7 m^2 ha^{-1} at other sites), and tree harvests were often restricted to narrow, flat ridges within stands. This resulted in overall stand basal area that differed little from woodland treatments (Fig. 1), and resulting (2015 and 2016) herbaceous ground-layer metrics across canopy treatments at LBL did not differ. At GRGL, and in the early stages of restoration at CWMA, many of the dominant herbaceous species were light-seeded, ruderal forbs (*e.g.*, American burnweed) and shade-tolerant, cool-season grasses (*e.g.*, needlegrass, Appendix 3). This early herbaceous response, which may be typical in oak forests where canopies have been closed for decades (Vander Yacht et al. 2017a), perhaps initially reduced the importance of canopy cover until the more shade-intolerant components of the herbaceous layer were stimulated (*e.g.*, C_4 grasses). Final (2015 and 2016) treatment contrasts at CWMA and GRGL support this conclusion; herbaceous layer differences at GRGL principally involved control versus treatment comparisons, whereas differences between woodlands and savannas were more common at CWMA where restoration was more advanced.

Increasing canopy disturbance also increased the density of woody vegetation in the understory. Herbaceous metrics were often positively associated with woody groundcover (Appendix 4), but this probably indicated the early stages of restoration and regions dominated by seedlings. Conversely, sapling density often negatively affected herbaceous metrics. We suspect this often-described relationship of competition between woody and herbaceous vegetation (Briggs et al. 2005, Peterson et al. 2007, Barrioz et al. 2013) will become more apparent as restoration progresses. Repeated fire transitions herbaceous composition towards more conservative and shade-intolerant species (Brewer and Menzel 2009, Brewer 2016) that could be more sensitive to dense, woody understories. However, the effects of fire on herbaceous communities is minimal without canopy disturbance (Hutchinson et al. 2005). In addition, our results demonstrate that greater canopy disturbance can enhance fire-related increases in herbaceous groundcover, richness, and diversity.

Herbaceous Response to Fire

Our results add to an understanding of fire effects on herbaceous layers in eastern deciduous forests (Gilliam and Roberts 2003). Herbaceous metrics increased with increasing canopy disturbance, but additional increases following fire suggest burning also had positive effects. Fires constrained by prescription to moderate intensity rarely alter overstory characteristics (Fig. 1, Burton et al. 2011), but can promote herbaceous development by reducing woody competition in the understory (Knapp et al. 2015), consuming germination-inhibiting leaf litter (Lashley et al. 2011), increasing soil nutrient availability (Scharenbroch et al. 2012), and improving seed germination rates (Emery et al. 2011). We suggest any fire-related increases in herbaceous metrics during our study were more related to the former three of these listed effects because woody groundcover increased in all thinned treatments. Glasgow and Matlack (2007)

suggested fire's effects on litter and soil nutrients were more important than canopy openness in directing herbaceous response, but admitted the small size of canopy gaps within their study may have failed to alter understory microclimates. Given adequate canopy disturbance, we propose fire's effects on leaf litter, soil nutrients, and seed germination are important mechanisms behind the promotion of herbaceous ground-layers throughout restoration, but the effects of woody competition reduction may be restricted to advanced stages. Suppressing woody competition can require decades of frequent (every 1-2 years) burning (Hutchinson et al. 2012, Arthur et al. 2015). Initial mechanisms behind increases in herbaceous vegetation could then be disproportionately important based on the positive feedbacks associated with early fine-fuel contributions that enhance the ability of future fires to control woody vegetation (Peterson and Reich 2001, Nielsen et al. 2003).

Annual to biennial fire maximizes understory species richness within oak ecosystems (Peterson and Reich 2008, Burton et al. 2011). In our study, such a fire regime maintained a 22 % reduction in litter, biennially increased bare ground, and likely precluded greater increases in woody competition. These effects increased herbaceous cover, richness and diversity; an observation that directly conflicts with assertions that fire could reduce diversity east of the prairie-woodland transition zone (Matlack 2013, 2015). While fire effects could certainly have negative effects in more mesic and fire-intolerant forest communities, our results demonstrate positive effects on herbaceous ground-layers in upland oak forests throughout the Mid-South (Stambaugh et al. 2015). Although we did not focus our analyses on trends in individual herbaceous species, we note most increased and few noticeably declined during our study. Forbs responded less vigorously than graminoids, but are known to increase slowly over multiple fires (Hutchinson et al. 2005). Nielsen et al. (2003) attributed a weak forb response after multiple fires

to seedbank depletion following canopy closure. Leaf-litter dominance also promotes acidic soils which can limit forb establishment and growth (Ferguson et al. 2013). Recent, pre-treatment site histories were characterized by dormant-season fire under closed canopies. This would increase the seedbank presence of cool-season grasses (Harper 2007), which dominated herbaceous response across our sites.

Few studies have evaluated the effects of seasonal variation in fire on herbaceous understories of eastern hardwood ecosystems (Knapp et al. 2009). Direct effects on perennial herbaceous plants are minimal because most sprout from rhizomes buried beneath insulating layers of soil. Indirectly, community composition can be altered over time if fires consistently occur near seasonal peaks in seed production or growth of specific species. In our study, seasonal fire effects were not strong. Many differences we observed were interactions involving greater change in one fire-season treatment over a time interval followed by greater change in the other over a subsequent interval. As a result, few final (2015 and 2016) differences in the herbaceous layer were directly attributable to fire season. An exception was GRGL, but the greater herbaceous response after spring burns was largely the result of a single replicate stand. Also, the effects of fire-season were difficult to isolate from fire intensity effects in our study. Throughout, spring fires were more intense (Appendix 1). This was particularly true at GRGL where spring fires spread nearly three times as fast, had flame heights that were more than double, and temperatures nearly double, those observed during fall burns. Herbaceous development can increase with increasing fire intensity (McMurry et al. 2007), and we conclude differences in fire intensity between seasons probably contributed to observed herbaceous-layer differences.

As a corollary, it is also true that less intense October fires had similar herbaceous layer effects as the more intense March fires at CWMA. At times (2011 to 2012, 2015 to 2016), fall

fires at CWMA increased grass and forb groundcover more than spring fires. The effects of seasonal variation in fire on herbaceous communities often becomes more apparent after repeated burning (Knapp et al. 2009) like that conducted at CWMA. Late growing-season fire at this site appeared to induce similar or greater increases in herbaceous dominance than more intense dormant-season fire. This advantage could be related to differential effects on woody sapling density, which was negatively related to herbaceous development metrics at CWMA. Woody stem mortality increases with increasing fire temperature and duration of exposure (Michaletz and Johnson 2007), so perhaps the slower-spread of October fires compensated for lower burning temperatures relative to March fires. It is also possible that the timing of fire in relation to plant phenology, such as seasonal variation in root carbohydrate reserves (Loescher et al. 1990), may have compensated for observed differences in intensity. Evidence suggesting that growing-season fire is more effective than dormant-season fire in inducing woody plant mortality (Brose and Van Lear 1998, Gruchy et al. 2009, Robertson and Hmielowski 2014) renders both explanations plausible. October may also have been too late at our latitude/altitude to gain a benefit related to woody plant phenology (Huddle and Pallardy 1999). Research that isolates the effects of fire-season from seasonal differences in intensity is needed for a more complete understanding of herbaceous layer response. Transitioning understory dominance from woody to herbaceous plants in eastern oak communities may require more than repeated, dormant-season fire (Hutchinson et al. 2012). Growing-season fire could meet restoration objectives more efficiently than more labor intensive and costly alternatives (e.g., herbicides; Vander Yacht et al. 2017b).

CONCLUSIONS AND MANAGEMENT APPLICATIONS

Our work details how canopy disturbance and prescribed fire interact to promote herbaceous ground-layers in oak communities throughout the Mid-South. After such management, herbaceous groundcover and diversity increased by greater than 4-fold, demonstrating the resiliency of herbaceous components after decades of fire exclusion and suppression. Reducing basal area to 7 m^2 ha^{-1} mimicked historical oak savanna structure and greatly enhanced herbaceous layer development. Thinning to 15 m^2 ha^{-1} achieved oak woodland structure, but herbaceous response was at times more limited. Restoring herbaceous dominance under denser, woodland canopies may require greater reduction of understory woody competition than achieved by three biennial fires. In fact, fire seemed to contribute to herbaceous promotion through reducing leaf-litter and did not substantially reduce low-lying woody competition. This suggests continuing a regimen of repeated fire may further increase herbaceous metrics through reductions in the understory density of woody vegetation. Monitoring through this stage of restoration could be important in detecting an effect of fire-season, which was only subtle and contradictory in our study. However, the less-intense October fires were as good or better at promoting herbaceous groundcover and diversity relative to more-intense March fires where burning occurred repeatedly (CWMA). We conclude longer-term research, or controlled experiments that better isolate phenological effects, are needed to fully understand fire-season effects in oak-dominated communities of the Mid-South. Regardless, the return of woody groundcover to pre-burn levels within two growing-seasons suggests the use of no less than biennial fire. Model covariates commonly indicated herbaceous response was greater on reduced slopes and southwesterly aspects, and by including drains and swales within

restoration. Using our results to restore the lost herbaceous components of oak communities across the Mid-South could substantially increase their economic and ecological value.

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APPENDICES

Appendix SIV1. Seasonal comparison of weather, fuel moisture, and fire behavior for prescribed fires during an oak woodland and savanna restoration experiment at Catoosa Wildlife Management Area (CWMA), Green River Game Lands (GRGL), and Land Between the Lakes (LBL). Statistics based on a two-sample t-test assuming unequal variance.

		Fire season				
Variable	Units	Fall	Spring	*t*	*df*	*p*
Ambient temperature	˚C	24.6 ± 0.5	17.6 ± 0.6	8.80	101	**< 0.001**
Relative humidity	%	39.0 ± 1.2	38.6 ± 1.5	0.17	110	0.867
Wind speed	m s^{-1}	1.6 ± 0.2	3.5 ± 0.2	6.86	102	**< 0.001**
Wind direction	˚	214.8 ± 15.8	204.5 ± 14.4	0.48	94	0.631
Fine-fuel moisture	%	12.5 ± 0.8	17.0 ± 1.5	2.67	90	**0.009**
10-hour fuel moisture	%	9.2 ± 0.9	10.1 ± 0.6	0.78	22	0.446
Flanking fire rate-of-spread	m min^{-1}	0.6 ± 0.1	1.1 ± 0.3	1.45	25	0.159
Flanking fire flame-length	m	0.4 ± 0.1	0.6 ± 0.1	1.55	44	0.127
Heading fire rate-of-spread	m min^{-1}	1.6 ± 0.1	2.9 ± 0.4	3.03	30	**0.005**
Heading fire flame-length	m	0.7 ± 0.1	1.3 ± 0.1	3.61	37	**< 0.001**
Fire temperature	˚C	170.6 ± 7.7	210.2 ± 15.3	2.32	122	**0.022**

[1]Fall burns at CWMA: 11 Oct 2010, 24 Oct 2012, and 24 Oct 2014. Spring burns at CWMA: 22 Mar 2011, 15 Mar 2013, and 18 Mar 2015. Fall burn at GRGL: 27 Oct 2014. Spring burn at GRGL: 18 March 2015. Buffalo Trace spring burn at LBL: 29 Mar 2016. Cemetery Ridge spring burn at LBL: 22 Apr 2015.

Appendix SIV2. Significant (α = 0.05) orthogonal treatment and interaction contrasts for percent groundcover variables during (2008 to 2016) point intercept monitoring of oak woodland and savanna restoration experiments at Catoosa Wildlife Management Area (CWMA, Cumberland County, TN), Green River Game Lands (GRGL, Polk County, NC), and Land Between the Lakes National Recreation Area (LBL, Stewart County, TN).

Site	Ground cover	Annual Interval	Management Interval	Contrast	*F*	*p*	Estimate	SE
CWMA	Graminoid	2009-2010	Post-cut to post-cut	C vs. T	6.0	0.015	4.1	2.3
				W vs. S	8.5	0.004	-3.4	2.0
		2011-2012	Post-fire 1 to post-fire 1	C vs. T	24.6	< 0.001	18.9	3.8
				W vs. S	4.9	0.027	-7.5	3.4
		2012-2013	Post-fire 1 to post-fire 2	W vs. S	7.7	0.006	10.5	3.8
		2013-2014	Post-fire 2 to post-fire 2	C vs. T	6.2	0.013	16.6	6.7
				W vs. S	34.9	< 0.001	-22.7	3.8
		2014-2015	Post-fire 2 to post-fire 3	C vs. T	7.5	0.006	-10.4	3.8
				W vs. S	5.4	0.021	7.9	3.4
		2015-2016	Post-fire 3 to post-fire 3	W vs. S	4.3	0.038	-7.1	3.4
				Fa vs. Sp	5.5	0.019	-8.0	3.4
		2015 & 2016	Result	W vs. S	7.9	0.035	19.0	6.8
	Forb	2009-2010	Post-cut to post-cut	C vs. T	6.0	0.015	4.1	2.3
				W vs. S	8.5	0.004	-3.4	2.0
		2010-2011	Pre to post-fire 1	W vs. S	6.5	0.011	-5.9	2.0
		2011-2012	Post-fire 1 to post-fire 1	W vs. S	10.1	0.002	6.2	2.0
				Fa vs. Sp	4.8	0.029	-4.3	2.0
		2013-2014	Post-fire 2 to post-fire 2	C vs. T	9.1	0.003	8.1	4.0
				W vs. S	7.8	0.005	-6.6	2.3
		2015-2016	Post-fire 3 to post-fire 3	Fa vs. Sp	6.4	0.012	-4.5	2.0
		2015 & 2016	Result	W vs. S	8.1	0.033	6.8	2.9
	Richness	2009-2010	Post-cut to post-cut	C vs. T	6.1	0.014	2.5	1.0
				W vs. S	8.9	0.003	-2.7	0.9
		2011-2012	Post-fire 1 to post-fire 1	C vs. T	8.8	0.003	3.0	1.0
		2013-2014	Post-fire 2 to post-fire 2	W vs. S	22.7	< 0.001	-4.9	1.0
				Fa vs. Sp	4.7	0.030	2.2	1.0
		2015-2016	Post-fire 3 to post-fire 3	W vs. S	4.0	0.046	-1.8	0.9
				Fa vs. Sp	10.1	0.002	-2.9	0.9
		2015 & 2016	Result	C vs. T	6.1	0.043	4.5	1.8
				W vs. S	8.6	0.029	4.5	1.5
	Diversity	2009-2010	Post-cut to post-cut	C vs. T	5.9	0.015	0.4	0.2
				W vs. S	11.5	0.001	-0.5	0.1
		2011-2012	Post-fire 1 to post-fire 1	C vs. T	5.5	0.019	0.4	0.2
				W vs. S	4.2	0.040	0.3	0.1
		2013-2014	Post-fire 2 to post-fire 2	Fa vs. Sp	4.7	0.030	0.3	0.2
		2015-2016	Post-fire 3 to post-fire 3	Fa vs. Sp	5.0	0.025	-0.3	0.1
		2015 & 2016	Result	C vs. T	12.0	0.013	1.0	0.3
	Woody	2009-2010	Post-cut to post-cut	C vs. T	34.6	< 0.001	24.9	4.2
				W vs. S	9.3	0.002	-11.6	3.8
		2010-2011	Pre to post-fire 1	C vs. T	16.1	< 0.001	-17.1	4.3
		2011-2012	Post-fire 1 to post-fire 1	C vs. T	13.1	< 0.001	15.3	4.2
		2013-2014	Post-fire 2 to post-fire 2	C vs. T	3.9	0.048	14.8	7.5
		2014-2015	Post-fire 2 to post-fire 3	C vs. T	6.6	0.011	-10.9	4.2
				W vs. S	8.2	0.004	-10.9	3.8
				Fa vs. Sp	6.7	0.010	9.8	3.8

Site	Ground cover	Annual Interval	Management Interval	Contrast	*F*	*p*	Estimate	SE
		2015-2016	Post-fire 3 to post-fire 3	C vs. T	15.2	< 0.001	16.5	4.2
				Fa vs. Sp	5.0	0.025	-8.5	3.8
		2015 & 2016	Result	C vs. T	38.1	< 0.001	20.4	3.3
	Litter	2008-2009	Pre to post-cut	C vs. T	4.2	0.041	-6.0	2.9
				W vs. S	8.6	0.003	8.1	2.8
		2009-2010	Post-cut to post-cut	C vs. T	8.7	0.003	-8.6	2.9
				W vs. S	7.8	0.005	-7.2	2.6
		2010-2011	Pre to post-fire 1	W vs. S	9.2	0.002	7.8	2.6
		2011-2012	Post-fire 1 to post-fire 1	W vs. S	7.0	0.008	-6.8	2.6
		2015 & 2016	Result	C vs. T	78.8	< 0.001	-21.9	2.5
	Debris	2009-2010	Post-cut to post-cut	W vs. S	4.0	0.046	3.4	1.7
		2010-2011	Pre to post-fire 1	W vs. S	14.7	< 0.001	6.5	1.7
		2014-2015	Post-fire 2 to post-fire 3	C vs. T	4.0	0.045	3.8	1.9
				Fa vs. Sp	7.8	0.005	4.8	1.7
		2015-2016	Post-fire 3 to post-fire 3	W vs. S	10.6	0.001	5.6	1.7
				Fa vs. Sp	5.6	0.018	-4.0	1.7
		2015 & 2016	Result	W vs. S	18.8	0.003	-4.7	1.1
	Bare	2008-2009	Pre to post-cut	W vs. S	5.6	0.019	-0.9	1.4
		2009-2010	Post-cut to post-cut	W vs. S	31.4	< 0.001	7.2	1.3
		2010-2011	Pre to post-fire 1	C vs. T	7.2	0.008	2.7	1.5
				W vs. S	15.9	< 0.001	-5.9	1.3
		2012-2013	Post-fire 1 to post-fire 2	W vs. S	28.9	< 0.001	7.8	1.5
		2013-2014	Post-fire 2 to post-fire 2	W vs. S	16.2	< 0.001	-6.3	1.5
		2015 & 2016	Result	C vs. T	15.8	0.001	2.6	0.6
GRGL	Graminoid	2012-2013	Pre to post-cut	W vs. S	12.1	0.001	-4.7	2.5
		2013-2014	Post-cut to post-cut	C vs. T	32.2	< 0.001	8.1	2.2
				W vs. S	4.4	0.037	4.1	2.6
		2014-2015	Post-cut to post-fire	C vs. T	8.2	0.004	4.9	2.8
				W vs. S	6.5	0.011	-8.3	2.5
				Fa vs. Sp	11.7	0.001	10.0	2.5
		2015-2016	Post-fire to post-fire	C vs. T	17.1	< 0.001	18.4	3.1
		2015 & 2016	Result	C vs. T	153.8	< 0.001	22.9	2.7
				W vs. S	17.4	< 0.001	10.5	2.4
				Fa vs. Sp	35.0	< 0.001	13.0	2.4
	Forb	2013-2014	Post-cut to post-cut	W vs. S	13.2	< 0.001	10.4	3.2
		2014-2015	Post-cut to post-fire	C vs. T	7.2	0.008	10.7	3.5
				W vs. S	4.4	0.037	-7.4	3.2
				Fa vs. Sp	13.7	< 0.001	14.5	3.2
		2015-2016	Post-fire to post-fire	Fa vs. Sp	11.6	0.001	-13.6	3.6
		2015 & 2016	Result	C vs. T	6.1	0.015	8.9	4.6
	Richness	2013-2014	Post-cut to post-cut	C vs. T	13.3	< 0.001	2.8	0.9
		2014-2015	Post-cut to post-fire	C vs. T	10.2	0.002	3.8	1.1
				W vs. S	4.0	0.046	-2.8	1.0
				Fa vs. Sp	13.2	< 0.001	5.0	1.0
		2015-2016	Post-fire to post-fire	Fa vs. Sp	9.0	0.003	-5.2	1.1
		2015 & 2016	Result	C vs. T	94.8	< 0.001	7.3	0.9
				Fa vs. Sp	10.0	0.002	2.3	0.8
	Diversity	2013-2014	Post-cut to post-cut	C vs. T	19.1	< 0.001	0.7	0.2
		2014-2015	Post-cut to post-fire	C vs. T	13.8	< 0.001	0.7	0.2
				Fa vs. Sp	12.9	< 0.001	0.6	0.2
		2015-2016	Post-fire to post-fire	Fa vs. Sp	10.4	0.001	-0.7	0.2
		2015 & 2016	Result	C vs. T	87.2	< 0.001	1.3	0.1
				Fa vs. Sp	7.7	0.006	0.3	0.1
	Woody	2012-2013	Pre to post-cut	C vs. T	9.9	0.002	-17.4	5.5
		2013-2014	Post-cut to post-cut	C vs. T	30.7	< 0.001	31.1	5.6
				W vs. S	10.0	0.002	20.5	6.5

Site	Ground cover	Annual Interval	Management Interval	Contrast	*F*	*p*	Estimate	SE
		2014-2015	Post-cut to post-fire	C vs. T	5.7	0.017	-17.1	7.2
				C vs. FaO	29.7	< 0.001	-49.8	9.1
		2015-2016	Post-fire to post-fire	C vs. T	10.1	0.002	25.8	8.1
				C vs. FaO	4.8	0.029	21.9	10.0
		2015 & 2016	Result	C vs. T	15.9	< 0.001	13.7	3.4
				C vs. FaO	51.0	< 0.001	-29.4	4.1
				Fa vs. Sp	10.7	0.001	-9.9	3.0
	Litter	2012-2013	Pre to post-cut	C vs. T	15.9	< 0.001	-12.3	3.1
		2013-2014	Post-cut to post-cut	C vs. T	5.3	0.021	-7.3	3.1
				W vs. S	4.7	0.031	-7.9	3.6
		2014-2015	Post-cut to post-fire	C vs. T	9.8	0.002	-12.4	4.0
				Fa vs. Sp	5.0	0.026	-8.0	3.6
		2015 & 2016	Result	C vs. T	176.0	< 0.001	-30.1	2.4
				Fa vs. Sp	15.0	< 0.001	-8.2	2.1
	Debris	2012-2013	Pre to post-cut	C vs. T	19.9	< 0.001	6.1	1.4
		2013-2014	Post-cut to post-cut	C vs. T	11.7	0.001	-4.7	1.4
		2014-2015	Post-cut to post-fire	C vs. T	5.0	0.027	4.0	1.8
		2015-2016	Post-fire to post-fire	W vs. S	7.4	0.007	5.1	1.9
		2015 & 2016	Result	C vs. T	10.1	0.002	3.6	1.1
	Bare	2012-2013	Pre to post-cut	C vs. T	59.3	< 0.001	11.9	2.0
		2013-2014	Post-cut to post-cut	C vs. T	5.5	0.019	-4.6	2.1
		2014-2015	Post-cut to post-fire	C vs. T	17.5	< 0.001	9.4	2.6
				C vs. FaO	35.3	< 0.001	20.4	3.4
		2015-2016	Post-fire to post-fire	C vs. T	7.7	0.006	-7.7	2.9
				C vs. FaO	5.0	0.026	-13.3	3.6
		2015 & 2016	Result	C vs. T	71.1	< 0.001	11.8	2.1
				C vs. FaO	44.4	< 0.001	12.2	2.8
LBL	Graminoid	2008-2013	Pre to post-cut	C vs. T	29.6	< 0.001	11.8	2.2
		2013-2014	Post-cut to post-cut	C vs. T	4.8	0.028	4.5	2.2
	Forb	2013-2014	Post-cut to post-cut	C vs. T	5.8	0.017	3.7	1.4
		2014-2016	Pre to post-fire	C vs. T	4.5	0.035	2.6	2.0
				C vs. SpO	6.1	0.014	4.2	2.5
	Richness	2008-2013	Pre to post-cut	C vs. T	8.5	0.004	1.8	0.6
		2013-2014	Post-cut to post-cut	C vs. T	20.1	< 0.001	2.8	0.6
		2014-2016	Pre to post-fire	C vs. SpO	6.7	0.010	3.2	0.7
	Diversity	2008-2013	Pre to post-cut	C vs. T	12.9	< 0.001	0.5	0.1
		2013-2014	Post-cut to post-cut	C vs. T	8.6	0.004	0.4	0.1
		2014-2016	Pre to post-fire	C vs. SpO	7.0	0.008	0.6	0.2
		2015 & 2016	Result	C vs. T	5.3	0.049	0.6	0.3
	Woody	2013-2014	Post-cut to post-cut	C vs. T	6.0	0.015	9.5	3.9
		2015 & 2016	Result	C vs. T	5.7	0.045	18.6	7.8
	Litter	2008-2013	Pre to post-cut	C vs. T	23.2	< 0.001	-13.0	2.7
		2014-2016	Pre to post-fire	C vs. T	9.4	0.002	-11.6	3.8
		2015 & 2016	Result	C vs. T	12.0	0.010	-25.4	7.3
	Debris	2015 & 2016	Result	C vs. T	12.0	0.001	2.8	1.1
	Bare	2014-2016	Pre to post-fire	C vs. T	20.5	< 0.001	9.0	2.1
		2015 & 2016	Result	C vs. T	7.5	0.026	16.6	6.9

Richness and diversity (Shannon-Wiener Index) refer to the herbaceous community. Model *df* calculated using Kenward Rogers adjustment.

Appendix SIV3. Scientific and common and names, and total individual encounters by site, for all herbaceous species documented during (2008 to 2016) oak woodland and savanna restoration experiments at Catoosa Wildlife Management Area (CWMA, Cumberland County, TN), Green River Game Lands (GRGL, Polk County, NC), and Land Between the Lakes National Recreation Area (LBL, Stewart County, TN).

Graminoids				
		Individual encounters		
Scientific Name	Common Name	CWMA	GRGL	LBL
Agrostis scabra Willd.	rough bent grass	4	1	0
Agrostis perennans (Walter) Tuck.	upland bent grass	3	0	0
Andropogon gerardii Vitman	big bluestem	119	6	7
Andropogon virginicus L.	broomsedge	828	338	115
Anthoxanthum odoratum L.	sweet vernal grass	4	0	0
Arrhenatherum elatius (L.) P. Beauv. Ex J. Presl & C. Presl	tall oat grass	6	0	0
Arundinaria appalachiana Triplett, Weakley, & L.G. Clark	appalachian hill cane	0	17	0
Bouteloua curtipendula (Michx.) Torr.	side-oats grama	2	0	0
Bromus arvensis L.	japanese chess	1	0	0
Bromus secalinus L.	rye brome	1	0	0
Carex abscondita Mackenzie	thicket sedge	0	8	0
Carex albicans Willd. ex Spreng.	white tinged sedge	347	36	90
Carex albursina Sheldon	white bear sedge	1	2	27
Carex aureolensis Steud.	broadscale sedge	0	1	0
Carex blanda Dewey	eastern woodland sedge	0	4	9
Carex caroliniana Schwein.	carolina sedge	5	0	0
Carex cephalophora Muhl. ex Willd.	oval leaf sedge	6	0	11
Carex communis L.H. Bailey	fibrous root sedge	14	0	2
Carex debilis Michx.	white edge sedge	54	1	1
Carex digitalis Willd.	slender woodland sedge	4	1	0
Carex gracilescens Steud.	slender looseflower sedge	0	0	21
Carex gravida L.H. Bailey	heavy sedge	0	0	21
Carex hirsutella Mack.	fuzzy wuzzy sedge	39	0	70
Carex hirtifolia Mack.	pubescent sedge	0	3	0
Carex jamesii Schwein.	james sedge	43	9	78
Carex laxiculmis Schwein.	spreading sedge	0	20	0
Carex laxiflora Lam.	broad looseflower sedge	22	5	80
Carex louisianica L.H. Bailey	louisiana sedge	1	0	2
Carex picta Steud.	bootts sedge	0	0	1
Carex prasina Wahlenb.	drooping sedge	7	0	0
Carex rosea Schkuhr ex Willd.	rosy sedge	1	0	0

Carex sparganioides Muhl. ex Willd.	bur reed sedge	0	0	2
Carex spp.	carex spp	236	5	430
Carex striatula Michx.	lined sedge	2	6	28
Carex swanii (Fernald) Mack.	swans sedge	386	40	327
Carex virescens Muhl. ex Willd.	ribbed sedge	2	79	15
Chasmanthium laxum (L.) Yates	slender wood oats	814	2	180
Chasmanthium sessiliflorum (Poir.) Yates	sessile leaf woodoats	365	1	7
Chasmanthium spp.	chasmanthium spp	1	0	9
Cyperus esculentus L.	yellow nutsedge	0	1	4
Dactylis glomerata L.	orchard grass	0	0	5
Danthonia compressa Austin	flattened oat grass	1	0	1
Danthonia sericea Nutt.	fuzzy poverty grass	187	4	53
Danthonia spicata (L.) P. Beauv. Ex Roem. & Schult	poverty oat grass	417	13	90
Danthonia spp.	danthonia spp	470	14	313
Dichantehlium latifolium (L.) Gould & C.A. Clark	broadleaf deertongue	253	238	279
Dichanthelium aciculare (Desv. ex Poir.) Gould & C.A. Clark	needleleaf rosette grass	564	31	72
Dichanthelium commutatum (Schultes) Gould	variable deertongue	698	324	144
Dichanthelium depauperatum (Muhl.) Gould	starved panic grass	14	0	12
Dichanthelium dichotomum (L.) Gould ssp. Roanokense	forked deertongue	2	1	0
Dichanthelium dichotomum (L.) Gould	cypress panic grass	964	193	471
Dichanthelium laxiflorum (Lam.) Gould	openflower rosette grass	367	2	215
Dichanthelium linearifolium (Scribn. ex Nash) Gould	slimleaf panic grass	24	0	10
Dichanthelium oligosanthes (Schult.) Gould	hellers rosette grass	11	0	0
Dichanthelium polyanthes (Schult.) Mohlenbr.	many flowered deertongue	48	1	14
Dichanthelium scoparium (Lam.) Gould	velvet panicum	11	0	4
Dichanthelium sphaerocarpon (Elliott) Gould	round seeded panic grass	7	0	0
Dichanthelium spp.	dichanthelium spp	848	206	686
Digitaria ischaemum (Schreb.) Schreb. ex Muhl.	smooth crabgrass	2	0	2
Elymus hystrix L.	bottlebrush grass	5	14	14
Elymus virginicus L.	virginia wild rye	1	7	6
Juncus coriaceus Mack.	leathery rush	1	0	0
Juncus effusus L.	common rush	6	0	0
Juncus marginatus Rostk.	grassleaf rush	2	0	0
Juncus spp.	juncus spp	10	0	0
Juncus tenuis Willd.	path rush	13	3	8
Leersia virginica Willd.	white grass	10	1	0
Microstegium vimineum (Trin.) A. Camus	nepalese browntop	42	35	10

Miscanthus sinensis Anderss.	chinese silvergrass	0	16	0
Muhlenbergia tenuiflora (Willd.) Britt.	slender muhly	4	19	22
Panicum anceps Michx.	beaked panicum	6	1	11
Panicum rigidulum Bosc ex Nees	red top panic grass	1	0	1
Piptochaetium avenaceum (L.) Parodi	needlegrass	3844	38	327
Rhynchospora capitellata (Michx.) Vahl	brownish beakrush	8	0	1
Rhynchospora spp.	rhynchospora spp	3	0	3
Saccharum alopecuroides (L.) Nutt.	silver plume grass	1	0	0
Schedonorus arundinaceus (Schreb.) Dumort., nom. cons.	tall fescue	8	0	68
Schizachyrium scoparium (Michx.) Nash	little bluestem	174	18	32
Schoenoplectus tabernaemontani (C.C. Gmel.) Palla	softstem bulrush	1	1	0
Scirpus cyperinus (L.) Kunth	wool grass bulrush	1	1	0
Scirpus pendulus Muhl.	rufous bulrush	1	2	0
Scleria minor W. Stone	slender whip nutrush	110	29	20
Scleria triglomerata Michx.	whip nutrush	67	58	7
Sorghastrum nutans (L.) Nash	indian grass	14	0	5
Sorghum halepense (L.) Pers.	johnson grass	0	0	3
Steinchisma hians (Elliott) Nash	nash gaping grass	5	0	2

Legumes

		Individual encounters		
Scientific Name	Common Name	CWMA	GRGL	LBL
Amphicarpaea bracteata (L.) Fernald	American hog peanut	4	0	100
Baptisia tinctoria (L.) R. Br.	yellow wild indigo	11	2	0
Chamaecrista fasciculata (Michx.) Greene	partridge pea	23	5	2
Chamaecrista nictitans (L.) Moench	wild sensitive plant	114	14	0
Clitoria mariana L.	atlantic pigeonwings	4	0	2
Desmodium cuspidatum (Muhl. ex Willd.) DC. ex D. Don	largebract tick trefoil	0	0	5
Desmodium glabellum (Michx.) DC.	dillenius tick trefoil	2	0	0
Desmodium laevigatum (Nutt.) DC.	smooth tick trefoil	12	1	21
Desmodium marlandicum (L.) DC.	smooth small-leaved tick trefoil	2	2	8
Desmodium nudiflorum (L.) DC.	nakedflower tick trefoil	62	53	77
Desmodium nuttallii (Schindl.) B.G. Schub.	nuttalls trefoil	3	0	4
Desmodium obtusum (Muhl. Ex Willd.) DC.	stiff tick trefoil	1	0	4
Desmodium paniculatum (L.) DC.	panicled tick trefoil	0	1	4
Desmodium rotundifolium DC.	dollar leaf	6	10	78
Desmodium spp.	desmodium spp	5	0	15
Galactia volubilis (L.) Britton	downy milk pea	0	1	9
Lespedeza cuneata (Dum. Cours.) G. Don	sericea lespedeza	16	1	12

Lespedeza hirta (L.) Hornem.	hairy bushclover	73	0	50
Lespedeza intermedia (L.) Pers.	intermediate lespedeza	2	0	0
Lespedeza procumbens Michx.	downy creeping bushclover	64	9	116
Lespedeza repens (L.) W.P.C. Barton	smooth creeping bushclover	259	10	118
Lespedeza spp.	lespedeza spp	27	1	24
Lespedeza violacea (L.) Pers.	violet lespedeza	13	1	0
Lespedeza virginica (L.) Britton	slender lespedeza	1	0	2
Mimosa microphylla Dryand.	sensitive briar	13	0	0
Orbexilum pedunculatum (Mill.) Rydb.	sampsons snakeroot	5	0	1
Strophostyles helvola (L.) Elliott	trailing fuzzy bean	0	0	4
Stylosanthes biflora (L.) Britton, Sterns & Poggenb.	pencil flower	0	0	1
Trifolium campestre Schreb.	yellow hop clover	1	1	0
Trifolium repens L.	white clover	0	0	3

Other Forbs

		Individual encounters		
Scientific Name	Common Name	CWMA	GRGL	LBL
Acalypha virginica L.	virginia threeseed mercury	2	6	15
Achillea millefolium L.	yarrow	0	0	1
Actaea racemosa L.	black cohosh	0	27	67
Agalinis gattingeri (Small) Small	gattingers false foxglove	0	1	0
Agalinis tenuifolia (Vahl) Raf.	slimleaf false foxglove	7	0	1
Ageratina altissima (L.) R.M. King & H. Rob.	white snakeroot	0	16	18
Ageratina aromatica (L.) Spach	small-leaved white snakeroot	0	0	2
Ageratina luciae-brauniae (Fernald) R.M. King & H. Rob.	lucy braun's snakeroot	0	2	0
Agrimonia striata Michx.	woodland agrimony	1	1	0
Agrimonia pubescens Wallr.	downy agrimony	1	9	11
Ambrosia trifida L.	giant ragweed	0	1	0
Ambrosia artemisiifolia L.	common ragweed	7	14	3
Angelica venenosa (Greenway) Fernald	hairy angelica	5	0	2
Antennaria plantaginifolia (L.) Richardson	plantainleaf pussytoes	17	4	6
Aristolochia serpentaria L.	virginia snakeroot	6	2	1
Arnoglossum reniforme (Hook.) H. Rob.	great indian plantain	0	1	0
Asclepias variegata L.	white milkweed	0	2	1
Aster spp.	aster spp	17	1	5
Astilbe biternata (Vent.) Britton	false goatsbeard	0	1	0
Aureolaria virginica (L.) Pennell	downy yellow false foxglove	1	0	2
Aureolaria laevigata (Raf.) Raf.	entireleaf yellow false foxglove	3	0	0
Bidens aristosa (Michx.) Britton	bearded beggarticks	6	0	0
Blephilia ciliata (L.) Benth.	downy wood mint	0	4	1

Blephilia hirsuta (Pursh) Benth.	hairy wood mint	2	0	0
Boehmeria cylindrica (L.) Sw.	false nettle	0	3	0
Bradburia pilosa Nutt.	soft golden aster	2	0	0
Ceanothus americanus L.	new jersey tea	7	0	0
Chamaelirium luteum (L.) A. Gray	fairy wand	1	0	0
Chimaphila maculata (L.) Pursh	pipsissewa	37	3	0
Chrysopsis mariana (L.) Elliott	maryland golden aster	8	0	0
Circaea lutetiana L.	encanters nightshade	11	0	4
Cirsium carolinianum (Walter) Fernald & B.G. Schub.	carolina thistle	3	0	0
Cirsium discolor	field thistle	3	2	2
Cleistes bifaria	upland spreading pogonia	10	1	0
Collinsonia canadensis	wild horse balm	0	1	0
Collinsonia tuberosa	deep woods horse balm	0	1	0
Comandra umbellata (L.) Nutt.	bastard toadflax	3	0	3
Conopholis americana (L.) Wallr.	squaw root	1	1	0
Conyza canadensis	horseweed	167	39	11
Coreopsis major	whorled coreopsis	213	45	24
Cunila origanoides	stone mint	0	21	133
Cuscuta spp.	dodder	3	0	0
Cynoglossum virginianum L.	wild comfrey	0	1	28
Daucus carota L.	queen annes lace	0	1	0
Diodia teres	rough buttonweed	0	0	1
Dioscorea virginiana	wild yam	14	14	27
Doellingeria umbellata	parasol whitetop	2	0	0
Elephantopus carolinianus	carolina elephants foot	15	3	5
Elephantopus tomentosus	devils grandmother	14	3	0
Epigaea repens L.	trailing arbutus	0	1	0
Erechtites hieraciifolia	American burnweed	511	297	212
Erigeron annuus	daisy fleabane	1	0	3
Eryngium yuccifolium	rattlesnake master	1	0	0
Eupatorium album	white thoroughwort	0	3	0
Eupatorium perfoliatum L.	common boneset	1	0	1
Eupatorium pilosum	hairy thoroughwort	8	0	0
Eupatorium purpureum	sweet joe pye	0	19	0
Eupatorium serotinum	late flowering thoroughwort	37	0	4
Eupatorium sessilifolium L.	upland boneset	0	14	0
Eupatorium capillifolium	dog fennel	8	7	12
Eupatorium hyssopifolium	hyssopleaf thoroughwort	3	0	1
Eupatorium rotundifolium	roundleaf thoroughwort	44	0	0
Euphorbia corollata	flowering spurge	3	5	2

Eurybia divaricata (L.) G.L. Nesom	white wood aster	0	1	0
Eurybia hemispherica	southern prairie aster	23	0	0
Eurybia surculosa	creeping aster	33	0	0
Fragaria virginiana	wild strawberry	4	2	0
Frasera caroliniensis Walter	American columbo	0	0	4
Galax urceolata (Poir.) Brummitt	galax	5	315	15
Galearis spectabilis (L.) Raf.	showy orchid	0	1	0
Galium aparine	catchweed bedstraw	2	1	2
Galium circaezans Michx.	licorice bedstraw	23	33	18
Galium pilosum Aiton	hairy bedstraw	2	0	0
Galium triflorum	fragrant bedstraw	3	2	2
Gamochaeta purpurea (L.) Cabrera	purple cudweed	18	3	4
Gentiana decora	showy gentian	1	2	0
Gentiana saponaria L.	harvest bells	2	1	0
Gentiana villosa L.	striped gentian	2	0	0
Gillenia stipulata (Muhl. ex Willd.) Baill.	American ipecac	0	0	6
Gnaphalium obtusifolium	rabbit tobacco	157	0	13
Goodyera pubescens	rattlesnake plantain	0	1	0
Helianthus divaricatus	woodland sunflower	0	3	1
Helianthus hirsutus	stiff haired sunflower	2	0	8
Helianthus spp.	helianthus spp	0	1	0
Helianthus strumosus L.	paleleaf woodland sunflower	0	0	3
Helianthus microcephalus Torr. & Gray	small headed sunflower	1	9	1
Hexastylis arifolia	little brown jug	8	0	0
Hieracium longipilum Torr.	hairy hawkweed	0	0	1
Hieracium venosum	rattlesnake weed	2	6	1
Houstonia caerulea	quaker ladies	3	1	0
Houstonia purpurea	summer bluet	0	26	0
Hypericum denticulatum Walter	coppery st johnswort	0	0	2
Hypericum drummondii	nits and lice	7	0	4
Hypericum nudiflorum	early st johnswort	1	0	0
Hypericum stragulum	reclining st andrews cross	59	7	24
Hypericum mutilum	dwarf saint johnswort	2	2	44
Hypochaeris radicata	cats ear	0	5	0
Hypoxis hirsuta	yellow star grass	0	3	0
Impatiens capensis	orange jewelweed	0	1	0
Impatiens pallida	yellow jewelweed	0	0	1
Ipomoea pandurata	wild potato vine	8	10	4
Iris cristata	dwarf crested iris	15	21	9
Iris verna	upland dwarf violet iris	19	0	1

Krigia biflora	two flowered cynthia	18	2	3
Lactuca canadensis	canada lettuce	16	1	9
Lactuca floridana	woodland blue lettuce	12	4	3
Lechea minor	thymeleaf pinweed	11	0	0
Lechea spp.	lechea spp	4	0	0
Lechea mucronata	hairy pinweed	3	0	0
Liatris aspera	tall blazing star	2	0	3
Ligusticum canadense	lovage	5	0	0
Linum medium	stiff yellow flax	9	0	0
Lobelia spicata	palespike lobelia	1	0	0
Lobelia inflata	indian tobacco	0	3	0
Lobelia puberula	downy lobelia	6	4	7
Ludwigia alternifolia	seedbox	2	0	5
Lycopus americanus Muhl. ex W.P.C. Barton	cutleaf water whorehound	3	0	0
Lycopus virginicus	virginia water horehound	1	1	0
Lysimachia ciliata	fringed loosestrife	3	0	0
Lysimachia quadrifolia	whorled loosestrife	531	67	11
Lysimachia lanceolata	lance leaf loosestrife	9	0	0
Maianthemum racemosum	solomons plume	13	14	5
Medeola virginiana L.	indian cucumber	0	6	1
Mikania scandens (L.) Willd.	climbing hempvine	0	0	1
Mitchella repens	partridge berry	11	0	0
Monarda didyma	scarlet bee balm	0	1	0
Monarda fistulosa	wild bergamot	0	1	44
*Mosla dianthera***	miniature beefsteak plant	2	0	0
Oxalis grandis	yellow wood sorrel	4	14	15
Packera anonyma (Wood) Weber & A. Löve	appalachian groundsel	6	0	2
Panax quinquefolius	American ginseng	0	0	1
Passiflora lutea L.	yellow passion flower	0	6	4
Perilla frutescens (L.) Britton	beefsteak plant	0	0	17
Phlox amoena	hairy phlox	6	0	0
Phryma leptostachya L.	lopseed	0	0	2
Physalis virginiana Mill.	virginia ground cherry	1	0	0
Phytolacca americana	pokeweed	6	43	0
Pityopsis graminifolia (Michx.) Nutt.	grassleaf golden aster	1	0	0
Plantago aristata	large bracted plantain	3	0	3
Plantago major	broadleaf plantain	0	1	0
Podophyllum peltatum	mayapple	0	10	9
Polygala polygama Walter	racemed milkwort	0	1	0
Polygala curtissii	curtis milkwort	32	0	0

Polygonatum biflorum	smooth solomons seal	19	16	5
Polygonatum pubescens (Willd.) Pursh	hairy solomons seal	0	1	0
Polygonum cespitosum Blume, nom. inq.	oriental ladys thumb	2	0	2
Polygonum spp.	smartweed	3	0	0
Porteranthus trifoliatus	bowmans root	10	0	3
Potentilla canadensis	dwarf cinquefoil	182	242	22
Potentilla simplex	common cinquefoil	58	1	49
Prunella vulgaris	heal all	0	3	0
Pycnanthemum loomisii	loomis mountain mint	4	3	0
Pycnanthemum montanum	thinleaf mountain mint	2	10	0
Pycnanthemum pycanthemoides (Leavenworth) Fernald	southern mountain mint	0	9	23
Pycnanthemum tenuifolium Schrad.	narrowleaf mountain mint	0	0	1
Ranunculus recurvatus	hooked buttercup	4	18	7
Ranunculus septentrionalis	northern swamp buttercup	0	1	0
Rhexia mariana	maryland meadow beauty	9	0	0
Rhexia virginica	virginia meadow beauty	7	0	0
Rosa carolina	carolina rose	5	0	9
Rosa setigera Michx.	prairie rose	1	0	0
Rudbeckia hirta L.	black eyed susan	5	0	0
Ruellia humilis Nutt.	hairy ruellia	0	0	3
Rumex acetosella L.	sheep sorrel	8	0	0
Sabatia angularis	rose pink	5	0	2
Salvia lyrata	lyreleaf sage	3	3	3
Sanguinaria canadensis L.	bloodroot	0	8	0
Saururus cernuus L.	lizards tail	1	0	0
Scutellaria incana	hoary skullcap	9	0	0
Scutellaria integrifolia	hyssopleaf skullcap	6	0	0
Scutellaria serrata	showy skullcap	1	0	0
Scutellaria spp.	scutellaria spp	0	1	0
Scutellaria elliptica	hairy skullcap	11	5	2
Sericocarpus linifolius	narrow leaf white top aster	4	0	3
Silene stellata	starry campion	0	4	0
Sisyrinchium albidum	pale blue eyed grass	8	0	0
Sisyrinchium angustifolium	narrowleaf blue-eyed grass	0	1	0
Sisyrinchium mucronatum	needletip blue-eyed grass	0	2	0
Smilax biltmoreana (Small) J.B.S. Norton ex Pennell	biltmores carrion flower	0	4	1
Smilax ecirrhata	upright carrion flower	0	1	0
Solanum carolinense	horse nettle	11	0	0
Solidago altissima	tall goldenrod	3	2	6

Solidago arguta	atlantic goldenrod	2	0	0
Solidago bicolor L.	white goldenrod	0	1	1
Solidago caesia	wreath goldenrod	7	7	8
Solidago curtisii	mountain decumbent goldenrod	4	0	0
Solidago erecta	erect goldenrod	14	0	27
Solidago gigantea Aiton	giant goldenrod	1	1	0
Solidago hispida	hairy goldenrod	0	0	1
Solidago juncea	early flowering goldenrod	2	1	0
Solidago nemoralis Aiton	gray goldenrod	2	0	9
Solidago odora	sweet scented goldenrod	510	2	37
Solidago rugosa	wrinkle leaf goldenrod	124	3	8
Solidago speciosa	showy goldenrod	6	0	0
Solidago sphacelata	autumn goldenrod	0	0	1
Solidago spp.	solidago spp	13	5	1
Solidago ulmnifolia	elmleaved goldenrod	0	0	1
Spiraea tomentosa	steeple bush	3	0	0
Streptopus roseus	rosy twisted stalk	10	0	4
Symphyotrichum patens	late purple aster	0	0	3
Symphyotrichum pilosum (Willd.) G.L. Nesom	white heath aster	98	2	5
Taraxacum officinale F.H. Wigg.	dandelion	1	1	0
Tephrosia virginiana	goats rue	0	0	2
Teucrium canadense	canada germander	3	0	2
Thalictrum pubescens	tall meadow rue	7	0	0
Thalictrum revolutum DC.	waxyleaf meadow rue	5	0	0
Thalictrum thalictroides (L.) Eames & B. Boivin	rue anemone	0	2	1
Torilis arvensis	spreading hedge parsley	0	7	6
Trillium grandiflorum	large flowered trillium	0	0	1
Trillium spp.	trillium spp	0	2	8
Triodanis perfoliata (L.) Nieuwl.	venus looking glass	2	0	0
Uvularia perfoliata L.	perfoliate bellwort	12	5	4
Uvularia sessilifolia L.	sessile bellwort	0	1	2
Verbascum thapsus L.	common mullein	0	1	1
Verbesina occidentalis (L.) Walter	yellow crownbeard	0	27	0
Verbesina alternifolia	wingstem	2	6	4
Vernonia gigantea	tall ironweed	6	3	1
Viola canadensis	canada violet	1	0	0
Viola hastata	halberdleaf yellow violet	1	13	0
Viola lanceolata	lanceleaf violet	13	0	0
Viola primulifolia	primrose-leaved violet	5	0	0

Viola pubescens Aiton	yellow woodland violet	11	44	19
Viola sagittata	arrowleaf violet	38	12	0
Viola spp.	viola spp	2	42	1
Viola triloba Schwein.	three lobed violet	1	8	20
Viola hirsutula	southern woodland violet	6	20	3
Viola rotundifolia	round leaved violet	9	0	0
Viola sororia	common blue violet	7	3	2
Xyris torta	slender yellow eyed grass	0	1	0

Ferns

		Individual encounters		
Scientific Name	Common Name	CWMA	GRGL	LBL
Asplenium bradleyi D.C. Eaton	bradleys spleenwort	0	0	1
Asplenium platyneuron (L.) Britton, Sterns & Poggenb.	ebony spleenwort	0	0	1
Athyrium filix-femina	southern lady fern	255	104	31
Botrychium virginianum (L.) Sw.	rattlesnake fern	0	1	2
Dennstaedtia punctilobula (Michx.) T. Moore	hay scented fern	1	0	1
Dryopteris intermedia	wood fern	22	14	3
Lygodium palmatuma	climbing fern	218	0	1
Osmunda cinnamomea	cinnamon fern	251	23	1
Osmunda regalis	royal fern	50	0	0
Phegopteris hexagonoptera (Michx.) Fée	beech fern	0	3	27
Polystichum acrostichoides	christmas fern	104	40	153
Pteridium aquilinum	bracken fern	121	14	59
Sceptridium biternatum (Sav.) Lyon	sparselobe grape fern	1	0	0
Thelypteris noveboracensis	new york fern	408	94	1
Woodwardia areolata (L.) T. Moore	netted chain fern	0	0	6

** Non-native Invasive Species.

Appendix SIV4. Significant (α = 0.05) covariates within ANCOVA models of groundcover variables during (2008 to 2016) point intercept monitoring of oak woodland and savanna restoration experiments at Catoosa Wildlife Management Area (Cumberland County, TN), Green River Game Lands (Polk County, NC), and Land Between the Lakes National Recreation Area (Stewart County, TN).

	Catoosa Wildlife Management Area				Green River Game Lands				Land Between the Lakes			
Model	Covariates	*F*	*p*	Slope (SE)	Covariates	*F*	*p*	Slope (SE)	Covariates	*F*	*p*	Slope (SE)
Grass	Slope	4.8	0.028	-0.13 (0.06)	Aspect	12.7	< 0.001	-1.40 (0.54)	Slope	14.3	< 0.001	-0.12 (0.03)
	Position	31.3	< 0.001	-2.28 (0.41)	Large-sapling density	4.7	0.031	-2.6E-3 (1.7E-3)	Live basal area	9.9	0.002	-0.18 (0.06)
	Canopy closure	117.1	< 0.001	-0.18 (0.02)	Seedling density	10.8	0.001	7.1E-5 (2.7E-5)	Shrub density	5.6	0.019	-4.0E-5 (1.9E-5)
	Small-sapling density	13.3	< 0.001	-4.5E-4 (1.2E-4)								
	Woody groundcover	20.5	< 0.001	0.12 (0.03)								
Forb	Aspect	12.6	< 0.001	1.21 (0.38)	Canopy closure	4.9	0.028	-0.07 (0.02)	Canopy closure	9.0	0.003	-0.04 (0.02)
	Canopy closure	177.2	< 0.001	-0.13 (0.01)	Woody groundcover	4.2	0.040	0.02 (0.02)	Woody groundcover	7.5	0.006	0.03 (0.01)
	Small-sapling density	11.5	0.001	-2.8E-4 (0.7E-4)								
	Shrub density	12.2	0.001	3.6E-5 (1.0E-5)								
Richness	Position	38.3	< 0.001	-0.68 (0.11)	Aspect	5.1	0.025	-0.58 (0.21)	Live basal area	15.1	< 0.001	-6.2E-2 (1.6E-2)
	Canopy closure	173.2	< 0.001	-6.0E-2 (0.5E-2)	Position	9.0	0.003	-0.26 (0.15)	Woody groundcover	7.1	0.008	1.5E-2 (0.5E-2)
	Woody groundcover	19.1	< 0.001	0.03 (0.01)	Large-sapling density	4.3	0.039	-11.9E-4 (6.8E-4)				
					Seedling density	8.5	0.004	3.2E-5 (1.1E-5)				
Diversity	Aspect	5.0	0.025	0.06 (0.03)	Slope	7.0	0.008	4.2E-3 (1.6E-3)	Slope	4.5	0.034	-4.1E-3 (1.9E-3)
	Position	56.4	< 0.001	-0.13 (0.02)	Aspect	8.6	0.004	-0.11 (0.04)	Live basal area	18.8	< 0.001	-1.5E-2 (0.3E-2)
	Canopy closure	105.0	< 0.001	-7.2E-3 (0.7E-3)	Position	4.7	0.030	-0.06 (0.03)	Woody groundcover	12.6	< 0.001	4.1E-3 (1.2E-3)
	Woody groundcover	28.1	< 0.001	5.4E-3 (1.0E-3)	Large-sapling density	5.9	0.016	-3.0E-4 (1.3E-4)				
					Seedling density	4.7	0.030	4.3E-6 (2.0E-6)				
Woody	Aspect	4.8	0.030	-1.55 (0.71)	Slope	4.7	0.030	-0.12 (0.06)	Slope	5.5	0.019	0.13 (0.06)
	Position	15.0	< 0.001	1.76 (0.45)					Aspect	10.9	0.001	3.09 (0.94)
	Live basal area	14.1	< 0.001	-0.30 (0.08)					Large-sapling density	6.7	0.010	-1.3E-2 (0.5E-2)
	Dead basal area	16.3	< 0.001	0.57 (0.14)								
	Large sapling density	24.8	< 0.001	-1.2E-2 (0.2E-2)								
Litter	Aspect	33.8	< 0.001	2.76 (0.47)	Aspect	7.5	0.007	2.09 (0.76)	Position	6.7	0.010	-1.17 (0.45)
	Position	20.9	< 0.001	1.42 (0.31)	Woody groundcover	642.8	< 0.001	-0.59 (0.02)	Canopy closure	8.2	0.004	0.09 (0.03)
	Large-sapling density	16.3	< 0.001	6.7E-3 (1.7E-3)					Dead basal area	7.2	0.008	-0.73 (0.27)
	Woody groundcover	887.6	< 0.001	-0.57 (0.02)					Woody groundcover	859.4	< 0.001	-0.69 (0.02)
Debris	Aspect	10.3	0.001	-1.0 (0.32)					Live basal area	6.9	0.009	-0.07 (0.03)
	Live basal area	45.8	< 0.001	-0.22 (0.03)					Woody groundcover	24.4	< 0.001	-0.05 (0.01)
Bare	Aspect	4.2	0.041	-0.51 (0.25)	Small-sapling density	7.2	0.008	-3.1E-4 (1.6E-4)	Slope	7.1	0.008	0.07 (0.02)
	Position	14.2	< 0.001	0.58 (0.16)	Woody groundcover	43.7	< 0.001	-0.10 (0.02)	Canopy closure	11.0	0.001	-0.05 (0.02)
	Canopy closure	25.7	< 0.001	-3.6E-2 (0.7E-2)					Dead basal area	7.4	0.007	0.31 (0.15)
	Large-sapling density	12.8	< 0.001	-3.0E-3 (0.9E-3)					Woody groundcover	85.5	< 0.001	-0.12 (0.01)
	Woody groundcover	179.8	< 0.001	-0.13 (0.01)								

CONCLUSIONS

Our work demonstrates how a lack of disturbance has affected vegetation and fuels in oak ecosystems of the Mid-South. Closed-canopy stands, the result of successional advance in the absence of fire, were characterized by: a lack of shortleaf-bluestem community components; plentiful fine woody, but limited herbaceous, fuel; an abundance of shade-tolerant and fire-sensitive woody regeneration; and depauperate herbaceous ground-layers. Our work also demonstrates the positive effects of returning disturbance on woody and herbaceous community diversity. Prescribed fire and canopy thinning promoted the establishment of key shortleaf-bluestem community components, increased density of shade-intolerant and fire-adapted woody regeneration, and increased herbaceous groundcover and diversity. Although we observed reductions in fine-woody fuel-loads, which can disproportionately influence fire behavior relative to other woody fuels, our results suggest similar management may not reduce total fuel-loads. Thinning increased coarse-woody fuel-loads, and increases in herbaceous fuels may eventually off-set reductions in fine-woody fuel-loads. Regardless, our treatments clearly benefitted disturbance-adapted elements of biodiversity. Within our spatially and temporally extensive experiment, disturbance-adapted components of eastern oak ecosystems responded positively to thinning and burning despite decades of fire-suppression. The specifics of this demonstrated resiliency should inform oak and shortleaf community management throughout the Mid-South, and offer managers regionally-appropriate approaches to effectively enhance and preserve ecological function and sustainability under uncertain future conditions.

SHORTLEAF-BLUESTEM COMMUNITY RESTORATION

A cascade of canopy closure, understory thickness, and site-condition effects were associated with the response of keystone shortleaf-bluestem community components. Promoting *P. echinata* and C_4 grasses began with reducing the overstory below 65 % canopy closure, which

was approximately 16 m^2 ha^{-1} basal area in our study. With repeated fire, thresholds in understory conditions were attained, including vertical woody cover in the understory (< 48 %) and woody groundcover (< 85 %). Intense fire can create these conditions; however, moderating intensity with strip-head firing could retain more *P. echinata* than the intense ring-firing used at CWMA. Late growing-season fire may harm *P. echinata* vigor, but this should be weighed against the potential for increased competition control and herbaceous development. Restoration should be most effective along ridges, southwest aspects, and downwind from mature *P. echinata*. Undisturbed forests (controls) had minimal, if any, shortleaf-bluestem community response. Canopy disturbance and fire simultaneously promoted *P. echinata* and C_4 grass, reflecting their historically intimate association. While this demonstrates resiliency, it also suggests that without active management shortleaf-bluestem communities could continue to decline in the eastern US.

EFFECTIVENESS OF RESTORATION ASSOCIATED FUEL-TREATMENTS

Past fire suppression and future climate change threaten to disrupt historical fuel-dynamics in the Mid-South. Oak woodland and savanna restoration require thinning and prescribed fire, and these techniques can reduce fuels and wildfire risk. However, our results clearly demonstrate that returning disturbance after a prolonged absence can increase total fuel loading. Thinning added 20 Mg ha^{-1} of logging slash that remained even after 3 fires in 6 years. Fine-fuels were reduced, but maintaining reductions will require continued burning every 2 to 3 years. Even then, increases in herbaceous fuels could potentially compensate for the loss of leaf litter and twigs within 10 years under open (7 m^2 ha^{-1}) canopies. Where fuel reduction is a priority, applied techniques could be more specifically designed to remove fuels. This could include the complete removal of logging debris or mulching into smaller pieces that would be

more readily consumed by prescribed fire. Greater canopy cover could be retained to preclude increases in herbaceous fuels, but this will limit restoration progress. All fire-sensitive tree species should be removed from the overstory to prevent future fuel inputs as snags deteriorate. Moderately intense fire, capable of consuming fuel while limiting overstory mortality, could make a critical contribution to a long-term reduction in loading of heavier fuels. Our results suggest restoration-associated thinning increases coarse fuel-loads, and reducing such loads with prescribed fire could take decades. Future research is needed to evaluate whether long-term management that shifts fine-fuel composition, and not necessarily amounts, from litter and twigs to herbaceous plants represents a decrease in wildfire severity or risk.

REVERSING MESOPHICATION EFFECTS ON UNDERSTORY WOODY VEGETATION

At sites located across the Mid-South, we used disturbance to increase the density of shade-intolerant and fire-tolerant species that were suppressed prior to management. Shifts in shrubby, seedling, and sapling layers were directly related to the effects of canopy disturbance on overstory density, and the effects of fire on understory density. Managing for historical savanna conditions (7 m^2 ha^{-1}) increased the understory density of oaks and other xerophytic species, and did not promote shade-intolerant competitors (e.g., yellow poplar) more so than woodland conditions (14 m^2 ha^{-1}). Thus, heavy canopy disturbance may be an under-utilized tool for reversing mesophication effects in the eastern U.S. We also demonstrated the greater effectiveness of management in altering woody communities on xeric sites where mesophytic competitors are less abundant. We did not find strong evidence of differences between October and March fires, but further research comparing alternative fire-seasons is warranted. After disturbance adequately promotes oaks and other fire-tolerant species in the understory, gaps in

fire recurrence could be required to recruit such regeneration into the overstory. Priming the woody regeneration pool of eastern oak ecosystems now with active management could prepare managers for action when such strategies are indicated, and increase the resiliency of regional forests to forecasted climatic and environmental changes.

ESTABLISHING ROBUST AND DIVERSE HERBACEOUS GROUNDCOVER

Our work adds substantially to limited knowledge concerning the promotion of herbaceous ground-layers in oak communities of the Mid-South region. The greater than 4-fold increases in herbaceous groundcover and diversity that we observed following thinning and prescribed fire demonstrate the resiliency of this component of oak woodlands and savannas. Canopy disturbance to a basal area of 7 m^2 ha^{-1} resulted in progress toward oak savanna restoration, while 15 m^2 ha^{-1} resulted in more limited woodland restoration progress. Both canopy disturbance and fire were important for promoting increases in herbaceous cover, richness, and diversity. Repeated burning will be required to maintain, and further promote, the increases in herbaceous groundcover and reductions in woody competition. Because resprouting often returned small-sapling density to pre-fire levels by the second growing-season following fire, we recommend an initial 2-year fire return interval. This will maximize woody control while allowing fine-fuel loads to recharge. We documented a similar herbaceous response to October and March fires even though October fires were less intense. Combining the safety implication of fall burning with research that suggests late growing-season fire is more effective in controlling hardwoods should cause managers to explore burning outside of the traditional dormant-season period. Our results were generally consistent across landscape variation and herbaceous diversity benefitted from including drains and swales within management sites.

Long-term research documenting the response of vegetation to successively applied fires is needed to advance oak woodland and savanna restoration throughout the Mid-South region.

VITA

Andrew Vander Yacht is from Port Sheldon, Michigan, where the trout reach sizes Tennesseans can only dream about. He attended Hope College in Holland, Michigan, where he earned a B.S. in Biology with minors in Chemistry and Environmental Science and played four years of Division 3 football. Andy has worked with the U.S. Fish and Wildlife Service in the Florida Keys, on a REU position researching the ecological effects of fungal endophytes in cool season grasses, with the Michigan Department of Natural Resources, and as a watershed monitor with a local West Michigan environmental coalition. He was first exposed to the forestry, wildlife, and fisheries department here at The University of Tennessee through time spent as a technician on the Peabody WMA quail project. That exposure landed him the opportunity to work under Dr. Pat Keyser and earn his M.S. degree in wildlife science. After a short hiatus living on the Caribbean island of St. Kitts monitoring nesting sea turtles and seabird colonies, Andy returned to UT and began his PhD research. He is currently employed by Michigan State University as a Research Specialist in the Forestry Department. He hopes to continue researching disturbance ecology in forests throughout the world.