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ARTICLE

# Landscape- and site-level responses of woody structure and ground flora to repeated prescribed fire in the Missouri Ozarks

Calvin J. Maginel, Benjamin O. Knapp, John M. Kabrick, and Rose-Marie Muzika



**Abstract:** Landscape-scale prescribed burning may be appealing for natural community restoration due to operational efficiency and possible heterogeneity in fire effects across broad spatial scales. We monitored plant community responses for >15 years with variable prescribed fire frequencies applied across a Missouri Ozarks landscape stratified into distinct ecological site types. Through the study period, burning had no effect on the overstory tree density or basal area. Midstory stem densities decreased rapidly in periodically burned units and more gradually with annual fire. Burning increased total ground flora cover and the cover of forbs, grasses, and legumes. The effect of burning on species richness differed among site types, with increased species richness through time on exposed slopes. There was no effect of prescribed burning on species richness on two of three protected slope site types, and annual burning decreased species richness in upland waterways. Among the site types, the upland waterways had the most species associated with pre-burn communities. We conclude that (*i*) burning consistently increased cover of ground layer vegetation across the landscape, while decreasing the midstory stem densities, and (*ii*) site type moderated ground flora richness response, with more pronounced effects of prescribed burning on exposed sites than on protected sites.

*Key words:* ground flora, landscape scale, Ozarks, prescribed fire, woodland restoration.

**Résumé :** À l'échelle du paysage, le brûlage dirigé peut être attrayant pour restaurer les communautés naturelles à cause de l'efficacité opérationnelle et de l'hétérogénéité potentielle des effets du feu sur de vastes étendues. Pendant plus de 15 ans, nous avons suivi les réactions des communautés végétales soumises à des brûlages dirigés effectués à des fréquences variables à travers un paysage stratifié sur la base du type écologique dans les monts Ozark au Missouri. Durant la période à l'étude, le brûlage n'a eu aucun effet sur la densité ou la surface terrière des arbres de l'étage dominant. La densité des tiges de l'étage intermédiaire a diminué rapidement dans les unités brûlées périodiquement et plus graduellement dans le cas des brûlages annuels. Le brûlage a augmenté le couvert végétal total au sol ainsi que celui des plantes herbacées non graminoïdes, des graminées et des légumineuses. L'effet du brûlage sur la richesse en espèces différait selon le type de station et celle-ci augmentait avec le temps sur les pentes exposées. Le brûlage dirigé n'a pas eu d'effet sur la richesse en espèces dans deux des trois types de stations sur des pentes protégées et le brûlage annuel a diminué la richesse en espèces dans les stations propices à l'écoulement des eaux sur les hautes terres. Parmi les types de stations, les stations propices à l'écoulement des eaux sur les hautes terres avaient le plus d'espèces associées aux communautés présentes avant les brûlages. Nous concluons que (*i*) le brûlage a constamment augmenté le couvert de la strate végétale au sol partout dans le paysage tout en diminuant la densité des tiges de l'étage intermédiaire et (*ii*) le type de station a tempéré la réaction de la richesse en espèces de la flore au sol et les effets du brûlage dirigé étaient plus prononcés dans les stations exposées que dans les stations protégées. [Traduit par la Rédaction]

*Mots-clés :* flore au sol, à l'échelle du paysage, monts Ozark, brûlage dirigé, restauration des boisés.

## 1. Introduction

Creating and maintaining open-canopy ecosystems such as woodlands are common management objectives throughout much of the central and eastern United States (US). Woodlands are characterized by open midstories and dense ground flora comprising forbs, grasses, sedges, and relatively low stature woody trees and shrubs (Nelson 1985; Nuzzo 1986). Woodlands were once common in the western Central Hardwoods Region, a prairie–forest transition zone, where historic stem densities have been reported to be up to approximately 2.3 times lower than current levels (Hanberry et al. 2014*b*). Evidence of historically frequent, low-intensity fires (Guyette et al. 2002) suggests that fire maintained the open structure in areas that can support woody vegetation (Abrams 1992; Guyette et al. 2007; Hanberry et al. 2014*a*), and consequently, prescribed fire is currently used for restoring woodlands and associated ground flora communities.

In the western Central Hardwoods Region, there has been increased application of landscape-scale prescribed burning for woodland restoration (Stambaugh and Guyette 2006) due to both operational and ecological considerations. Operationally, large burn units allow greater area to be treated by minimizing labor requirements (e.g., reducing total fire break length and ignition points) per area burned and by allowing critical elements of burn plan prescriptions (e.g., wind speed, relative humidity, etc.) to be met during a single day (Johnson and Miyanishi 1995; Cleaves et al. 2000). From an ecological perspective, landscape-scale burning

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may better emulate historic fire patterns by allowing variability in fire behavior based on the spatial distribution in vegetation types and topo-edaphic characteristics (Stambaugh and Guyette 2008). The resulting patchiness in fire effects may create desirable conditions across the landscape by increasing the heterogeneity of habitat (Swengel 2001; Noss et al. 2006).

Variability in fire effects on ecosystem structure and composition created by landscape-scale burning may be expected due to interactions among fire behavior, topo-edaphic factors, and plant communities. Fire behavior (e.g., fire intensity, rate of spread, flame length) varies based on topo-edaphic characteristics such as slope and aspect (Iverson et al. 2004; Yang et al. 2008). Characteristics of the plant community (e.g., structure, composition, and abundance) can further affect fire behavior by influencing fuel characteristics through the arrangement, chemistry, and moisture content of fuels (Nowacki and Abrams 2008; Ellair and Platt 2013; Kreye et al. 2013). Thus, variability in fire behavior across sites can elicit differential plant community responses (Schwartz et al. 2016). Differences in fire tolerance of constituent species among plant communities across the landscape may also drive response patterns to landscape-scale burning.

There are few reports of fire effects on plant communities across both broad spatial and temporal scales. Several short-term studies demonstrate effects of prescribed fire on plant communities, commonly reducing woody stem abundance and increasing the abundance of herbaceous plants. For example, Barden and Matthews (1980) showed that two fires in eastern Central Hardwood deciduous forests increased grass and forb cover while decreasing shrub cover. In the Ouachita Mountains in Arkansas, consecutive years of prescribed fire promoted herbaceous cover in shortleaf pine (*Pinus echinata* Mill.) stands (Sparks et al. 1998). Long-term studies (>15 years), commonly based on relatively small plots, have consistently shown that repeated burning reduces densities (stems·ha$^{-1}$) of small-diameter stems and results in greater abundance of herbaceous plants in the ground layer (Waldrop et al. 1992; Knapp et al. 2015). In Minnesota oak savannas, Tester (1996) found that repeated prescribed fire over 20 years increased abundance of prairie grasses, forbs, and shrubs, while non-prairie species decreased in abundance.

This nearly two decade study determined vegetative response to landscape-scale fire at different frequencies across sites that varied in topo-edaphic characteristics in the Missouri Ozarks. The specific objectives of this study were to (1) determine the effects of repeated, landscape-scale prescribed burning of two different frequencies on overstory and midstory structure and ground flora abundance and richness, (2) determine differences in woody structure and ground flora responses across the landscape, based on ecological site classifications, and (3) identify species associated with pre- and post-fire plant communities within each site type to generalize broad patterns in species turnover. We hypothesized (H1) that prescribed burning over this time period would show little effect on overstory structure but would decrease midstory stem density and increase abundance of ground flora. We also hypothesized (H2) that the magnitude of the observed fire effects would be associated with ecological site types, with the strongest effects occurring on drier conditions (e.g., south-facing aspect or upper slope positions).

## 2. Methods

### 2.1. Study area

This study was conducted in predominately oak–hickory forests within the Current River Hills ecological subsection in southeastern Missouri (Nigh and Schroeder 2002). Study plots were distributed across the landscape within the Chilton Creek Management Area (CCMA) and the Missouri Ozark Forest Ecosystem Project (MOFEP) (Fig. 1). Elevation of the study area ranges from 150 to 300 m above sea level, with local relief of 50 to 150 m that is characterized by long, narrow ridgetops dissected by equally narrow, sinuous valleys (Meinert et al. 1997). Bedrock formations include the Roubidoux, the Gasconade, and the Eminence–Potosi. In this region, the Roubidoux formation (RO) includes interbedded sandstone, sandy dolostone, quartzose, and chert. The upper half of the Gasconade formation (UG) includes thick beds of coarsely crystalline dolostones interbedded with chert and the lower half (LG) includes finely crystalline dolostone with few chert nodules and a bed of sandstone and quartzose from 1 to 3 m thick at its base. The Eminence–Potosi formation (EM) includes thick beds of coarsely crystalline dolostone. The parent materials and soils reflect the lithology and character inherited from the bedrock formations. Deep, nutrient-poor Ultisols occur in the cherty hillslope sediments and cherty residuum derived from the RO and UG, and Alfisols that have a greater variability in depth and greater nutrient supply occur in the clayey residuum derived from the LG and EM formations (Meinert et al. 1997). These textural, depth, and nutrient-supply differences influence plant composition and richness and are important factors for land classification in this region.

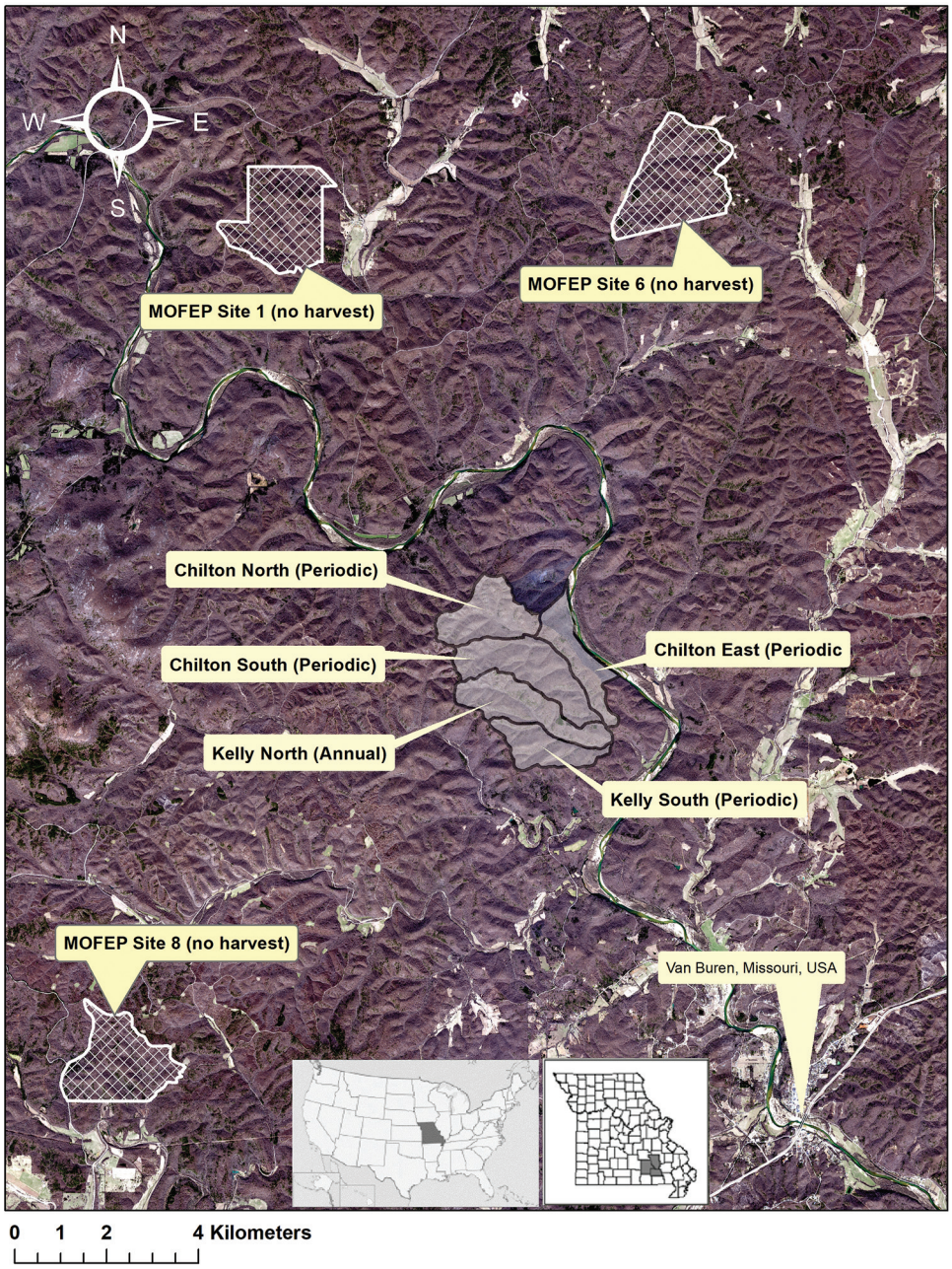
### 2.2. Experimental design

In 1996, five management units (each between 160 and 240 ha) were established at CCMA to determine the effects of landscape-scale burning on plant communities. Since 1998, four of the units were periodically burned, and one unit was burned annually. Periodic units were each burned on independent and random 1- to 4-year fire return intervals. To randomize the burn schedule for each periodic unit, a random interval from 1 to 4 was determined immediately following a burn (similar to rolling a four-sided die), with 1 representing burning as soon as possible, 2 representing burning after the next growing season, and so on. Each unit was thus treated with an independent and random burn schedule, with an overall mean fire return interval of 2.4 years (Table 1). The prescribed burns occurred primarily in March or early April, based on operational considerations and the similarity to post-European invasion fire regimes for the Ozark region (Guyette et al. 2002). Fuels included patchy areas of warm-season grass within the larger matrix of hardwood litter, although fuels varied across the landscape in relation to the plant community structure and composition. Burn units were ignited at the boundaries and with strategic interior strips, causing low- to moderate-intensity fires, and no additional effort was made to achieve 100% blackening (Hartman and Heumann 2003). Burn plans at CCMA call for a range of temperatures from –1 °C to 27 °C (30–80 °F), relative humidity from 25% to 70%, and 6 m (20 foot) wind speeds between 8 and 32 km·h$^{-1}$ (5–20 miles·h$^{-1}$) (2018 Chilton Creek Burn Plan, unpublished).

CCMA and MOFEP sites were separated by <16 km and, although spatially disjunct, were originally designed as paired landscapes for this study. MOFEP is a landscape-scale experiment designed to evaluate the effects of even-aged forest management, uneven-aged forest management, and no forest management on ecosystem responses. The untreated (i.e., no forest management) units in MOFEP were designated as the control units for the CCMA study. The MOFEP control units have received no forest management — prescribed fire or timber harvest — since around 1950 (Shifley and Brookshire 2000; Knapp et al. 2014). Extensive pretreatment data indicated similarity in landscape character and forest structure and composition as justification for the use of the MOFEP sites as control units for the CCMA burn units. Moreover, both studies include pretreatment data that allow comparison of conditions prior to initiation of burning at CCMA. Study units in MOFEP were 312–514 ha, with three units randomly assigned as untreated controls.

The Missouri Department of Conservation's Ecological Classification System (ECS) was developed to describe ecological units based on soils, geology, landform, and vegetation (Nigh et al. 2000).

**Fig. 1.** Map of study site locations. MOFEP is the Missouri Forest Ecosystem Project, and the five units make up the Chilton Creek Management Area. "Periodic" and "Annual" refer to burn treatment frequency. Van Buren, Missouri, is the closest town. [Colour online.]




Ecological land types (ELTs) are fine-scale (1:24 000) designations within the ECS structure and are commonly used to characterize Ozark forest communities based on landform position, aspect, and soils (Meinert et al. 1997). The ELTs occurring within this study area included four lithological formations (RO, UG, LG, EM), five slope positions (shoulders, shoulder ridges, backslopes, benches, and upland waterways), two aspect classes (exposed slopes on south and west aspects, azimuth range 135° to 314°, and protected slopes on north and east aspects, azimuth range 315° to 134°), and soil depth. At both CCMA and MOFEP, management units were stratified into ELTs, and sampling plots were randomly located within each ELT. For this study, we used 245 plots from CCMA and 124 plots from the MOFEP control units that occurred on ELTs that were common to those at CCMA. We hereafter refer to the nine ELTs used to partition the landscape into local sites as "site types" (Table 2).

### 2.3. Data collection

Vegetation inventory used a nested plot design. Circular, 0.2 ha plots were used to record all overstory trees > 11.4 cm diameter at breast height (dbh, 1.37 m). Within each plot at four locations along cardinal directions 17 m from the plot center were circular 0.02 ha subplots for the inventory of large midstory trees (3.8–11.4 cm dbh) (Shifley and Kabrick 2002). Each of the four subplots included four 1 m² quadrats. Each quadrat was located at NE, SE, SW, and NW compass points 6 m from each subplot center. The ground flora was sampled within each of these 16 quadrats per plot, with percent cover of each vascular plant species with vegetation ≤ 1 m in height recorded to the nearest 1%. Tree data were collected during the dormant season (beginning in mid-October) in 1997, 2001, 2007, 2013, and 2017 at CCMA and for the same years at MOFEP, without 1997 and with the addition of 1995 and 1998. Ground flora data were collected between May and September in

**Table 1.** Dates of prescribed burning by unit at CCMA, including total number of burns and mean fire interval (average number of years between fires for each unit), for each year since the study began.

| Year | Chilton East | Chilton North | Chilton South | Kelly North | Kelly South |
|---|---|---|---|---|---|
| 1998 | 2 April | 13 March | 26 March, 23 November | 5 April, 24 November | 6 April |
| 1999 | | | | | |
| 2000 | | | 7 March | 6 March | 6 March |
| 2001 | | | | 10 March | 10 March |
| 2002 | 30 March | 6 March | | 1 April | |
| 2003 | 11 March | | 15 March | 15 March | |
| 2004 | | 27 February | | 17 March | 28 February |
| 2005 | 30 November | | | 3 March | |
| 2006 | | | | 25 March | |
| 2007 | | 6 March | 6 March | 6 March | |
| 2008 | | | | 7 April | 7 April |
| 2009 | 18 March | | 18 March | 26 March | |
| 2010 | | | | 5 March | |
| 2011 | | 13 March | 12 March | 1 March | 1 March |
| 2012 | | | | | |
| 2013 | 28 March | 1 April | 3 April | 3 April | 3 April |
| 2014 | 10 March | | 6 February | 13 March | |
| 2015 | | 16 March | | 30 March | 30 March |
| 2016 | 5 March | | 5 March | 5 March | |
| 2017 | | 9 March | | 16 March | 16 March |
| Total no. of fires (20 years) | 8 | 8 | 10 | 19 | 9 |
| Mean fire interval (years) | 2.6 | 2.6 | 2.1 | 1.1 | 2.3 |

**Table 2.** The number of plots within each site type (ecological land type; see Nigh et al. 2000) found at CCMA and MOFEP in each treatment type.

| Site type | Annual unit | Periodic units | Control units | Total |
|---|---|---|---|---|
| RO/UG shoulders, shoulder ridges, and high benches | 2 | 16 | 13 | 31 |
| Exposed RO/UG backslope | 9 | 27 | 41 | 77 |
| Protected RO/UG backslope | 8 | 39 | 25 | 72 |
| Exposed LG/EM backslope | 4 | 8 | 8 | 20 |
| Protected LG/EM backslope | 4 | 25 | 8 | 37 |
| Exposed variable depth to dolomite | 12 | 14 | 6 | 32 |
| Protected variable depth to dolomite | 5 | 7 | 6 | 18 |
| LG/EM benches or shoulder ridges | 13 | 28 | 10 | 51 |
| Upper and lower reaches and upland waterways | 5 | 19 | 7 | 31 |
| Total | 62 | 183 | 124 | 369 |

**Note:** Bedrock formation and lithology include Roubidoux sandstone (RO), Upper Gasconade dolomite (UG), Lower Gasconade dolomite (LG), and Eminence–Potosi dolomite (EM).

1997, 2001, 2009, and 2013 at CCMA and in 1995, 1999, 2001, 2009, and 2013 at MOFEP. Unknown species were collected from outside quadrats whenever necessary and subsequently identified in the laboratory. Nomenclature follows Ladd and Thomas (2015).

### 2.4. Data analysis

Species were assigned to functional groups based on criteria identified by Ladd and Thomas (2015), with additional separation of forbs into legumes (family Fabaceae) and all other forbs (Peterson et al. 2007), and we grouped ground flora level shrubs and trees into one category. Consequently, we included seven functional groups: ferns, forbs, grasses, legumes, sedges, vines, and trees and shrubs. Functional group percent cover was calculated as the plot-level mean. We calculated total species richness (native + adventive) at the quadrat level (species·m$^{-2}$). Due to the disparity in sample years between CCMA and MOFEP in the 1990s, we averaged data from MOFEP sample years 1995 and 1998 (overstory) and 1995 and 1999 (ground flora) for comparison to CCMA data from 1997.

The experimental design was a repeated measures split plot with burn treatment (fire frequency) as the whole-plot effect and site type as the split-plot effect. The landscape-scale burn units were used as the whole-plot experimental units because it was the level at which the burn treatment (periodic, annual, or no burn) was applied. Within each burn unit, mean values across sampling plots were determined for each site type as the split-plot experimental unit. For objectives 1 and 2, we used generalized linear mixed models to determine the effects of prescribed burning on each response variable using PROC GLMMIX in SAS 9.3 (SAS Institute Inc., Cary, North Carolina). Burn unit was specified as a random effect in the models, and a compound symmetry covariance structure was used for the repeated measures on year. Degrees of freedom were adjusted as per Kenward and Roger (1997), who showed that their method performed well when sample sizes were small and (or) unequal. Significant interactions among site type, burn treatment, and year would indicate that response varied among site types for the treatments (objective 2). In the case of significant interactions among year, site type, and (or) burn treatment, we tested for significant effects of each term within each level of the interacting term. Tukey's honestly significant difference (HSD) test was used to minimize family-wise error during pairwise comparisons. In cases for which significant treatment effects were determined but Tukey's HSD indicated that pairwise comparisons were not significant, we report $p$ values for the main effect ("slice" $p$ value) and otherwise present $p$ values from pairwise comparisons ("Tukey's" $p$ value). An alpha of 0.05 was used as statistical significance for all tests.

**Table 3.** Results from ANOVA of overstory basal area (BA) and trees per hectare (TPH), midstory TPH, and ground flora percent cover.

| | yr | trt | ST | yr×trt | ST×yr | trt×ST | trt×ST×yr |
|---|---|---|---|---|---|---|---|
| Overstory BA | **0.001** (4, 17, 7.3) | 0.175 (2, 4, 2.7) | 0.099 (8, 21, 2.0) | 0.596 (8, 18, 0.8) | 0.615 (32, 84, 0.9) | 0.999 (16, 21, 0.2) | 0.666 (64, 84, 0.9) |
| Overstory TPH | 0.133 (4, 17, 2.0) | 0.734 (2, 4, 0.3) | 0.284 (8, 21, 1.3) | 0.435 (8, 18, 1.1) | 0.232 (32, 84, 1.2) | 0.941 (16, 21, 0.5) | 0.074 (64, 84, 1.4) |
| Midstory TPH | **<0.001** (4, 20, 20.3) | **0.039** (2, 35, 3.6) | **0.007** (8, 24, 3.6) | **0.008** (8, 20, 3.8) | 0.142 (32, 83, 1.4) | 0.507 (16, 24, 1.0) | 0.904 (64, 83, 0.7) |
| Ferns | 0.089 (3, 10, 2.9) | 0.727 (2, 3, 0.4) | 0.068 (8, 21, 2.2) | 0.713 (6, 11, 0.6) | 0.545 (24, 63, 1.0) | 0.978 (16, 21, 0.4) | 0.818 (48, 62, 0.8) |
| Forbs | **<0.001** (3, 11, 17.9) | 0.105 (2, 4, 4.0) | **<0.001** (8, 21, 17.7) | **0.002** (6, 11, 7.7) | 0.405 (24, 63, 1.1) | 0.440 (16, 21, 1.1) | 0.554 (48, 63, 1.0) |
| Grasses | **<0.001** (3, 10, 22.7) | **0.022** (2, 4, 10.3) | **<0.001** (8, 21, 22.6) | **0.004** (6, 11, 6.4) | 0.247 (24, 63, 1.2) | 0.205 (16, 21, 1.5) | 0.125 (48, 62, 1.4) |
| Legumes | **<0.001** (3, 10, 33.3) | 0.156 (2, 3, 3.8) | **<0.001** (8, 21, 7.2) | **<0.001** (6, 11, 11.2) | 0.120 (24, 64, 1.5) | 0.309 (16, 21, 1.3) | 0.188 (48, 63, 1.3) |
| Sedges | **0.001** (3, 8, 14.0) | **0.020** (2, 4, 11.8) | **<0.001** (8, 21, 11.4) | 0.119 (6, 9, 2.4) | 0.540 (24, 61, 1.0) | 0.292 (16, 21, 1.3) | 0.683 (48, 61, 0.9) |
| Woody vines | **0.036** (3, 12, 4.0) | 0.577 (2, 5, 0.6) | **<0.001** (8, 21, 10.5) | 0.258 (6, 12, 1.5) | 0.376 (24, 62, 1.1) | 0.413 (16, 21, 1.1) | 0.873 (48, 62, 0.7) |
| Shrubs and trees | **0.016** (3, 13, 5.1) | 0.366 (2, 4, 1.3) | 0.225 (8, 21, 1.5) | 0.067 (6, 13, 2.7) | 0.699 (24, 65, 0.8) | 0.876 (16, 21, 0.6) | 0.066 (48, 64, 1.5) |
| Total cover | **<0.001** (3, 15, 15.9) | 0.332 (2, 5, 1.4) | **<0.001** (8, 21, 10.5) | **0.001** (6, 15, 6.8) | 0.961 (24, 63, 0.5) | 0.641 (16, 21, 0.8) | 0.894 (48, 63, 0.7) |
| Richness | 0.323 (3, 14, 1.3) | **0.045** (2, 5, 6.3) | **<0.001** (8, 21, 63.4) | 0.476 (6, 14, 1.0) | **<0.001** (24, 63, 5.1) | 0.061 (16, 21, 2.1) | **<0.001** (48, 63, 2.7) |

**Note:** The $p$ values are provided, with degrees of freedom (df) and $F$ statistic included in parentheses as follows: (df numerator, df denominator, $F$). Values in bold indicate statistical significance ($p < 0.05$). Abbreviations: yr, year; ST, site type; trt, treatment.

To address objective 3, we used indicator species analysis to determine species' associations with pretreatment conditions (1997) and with conditions after 16 years of prescribed burning (2013) (McCune and Mefford 2011). Analyses were conducted separately for each site type, using data combined from annual and periodic burn treatments, to determine species associated with pre-burn and post-burn conditions. The species matrix consisted of percent cover values to represent abundance, and species present in fewer than 1% of plots within each site type were removed from analyses. Indicator values (IV) for each group of interest (pre-burn and 16 years post-burn) were calculated from relative abundance and relative frequency (Dufrene and Legendre 1997), and we used the default number of 4999 randomizations for the Monte Carlo test of significance for group association. A $p$ value of <0.05, as reported by the Monte Carlo test, determined which species exhibited both high relative abundance and high relative frequency within a particular group. To report results in each site type, we subtracted the IV for pre-burn (1997) conditions from the IV for post-burn (2013) conditions for each species significantly associated with one of the time periods, so negative values indicate association to pre-burn conditions. Analyses were conducted using PC-ORD software (PC-ORD 6.08; MjM Software Design, Gleneden Beach, Oregon).

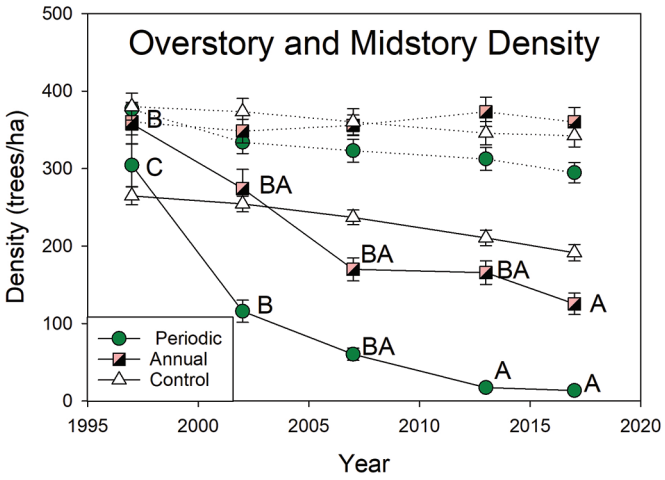
## 3. Results

### 3.1. Woody vegetation structure

Overstory basal area increased 16% over 20 years, regardless of treatment ($p$ = 0.001; Table 3). Basal area (BA) increased significantly between 1997 (16.7 $m^2 \cdot ha^{-1}$) and 2007 (18.5 $m^2 \cdot ha^{-1}$; Tukey's $p$ = 0.025), 2012 (19.2 $m^2 \cdot ha^{-1}$; Tukey's $p$ = 0.003), and 2017 (19.3 $m^2 \cdot ha^{-1}$; Tukey's $p$ = 0.002). Trees per hectare (TPH) in the overstory decreased 14% but without a significant year effect (Fig. 2; Table 3). The three-way interaction of year × site type × treatment had a $p$ value of 0.074 and may become more pronounced through time.

The number of trees in the midstory decreased between 1997 and 2017 by 336% in the periodic burns, by 185% in the annual burn, and by 38% in the control (Fig. 2; Table 3). In the periodic burn, TPH was greater in 1997 than in any other year (Tukey's $p \leq 0.012$). In the annual burn unit, TPH was greater in 1997 than in 2017 (Tukey's $p = 0.043$). Midstory stem density differed among site types (Table 3) in which RO/UG shoulders and exposed RO/UG backslopes had fewer stems than protected variable depth to dolomite (mean TPH 168, 171, and 270, respectively; Tukey's $p \leq 0.021$).

**Fig. 2.** Means (±1 standard error) of overstory (dotted lines) and midstory (solid lines) trees per hectare. Different uppercase letters indicate a significant difference among years within a treatment. [Colour online.]



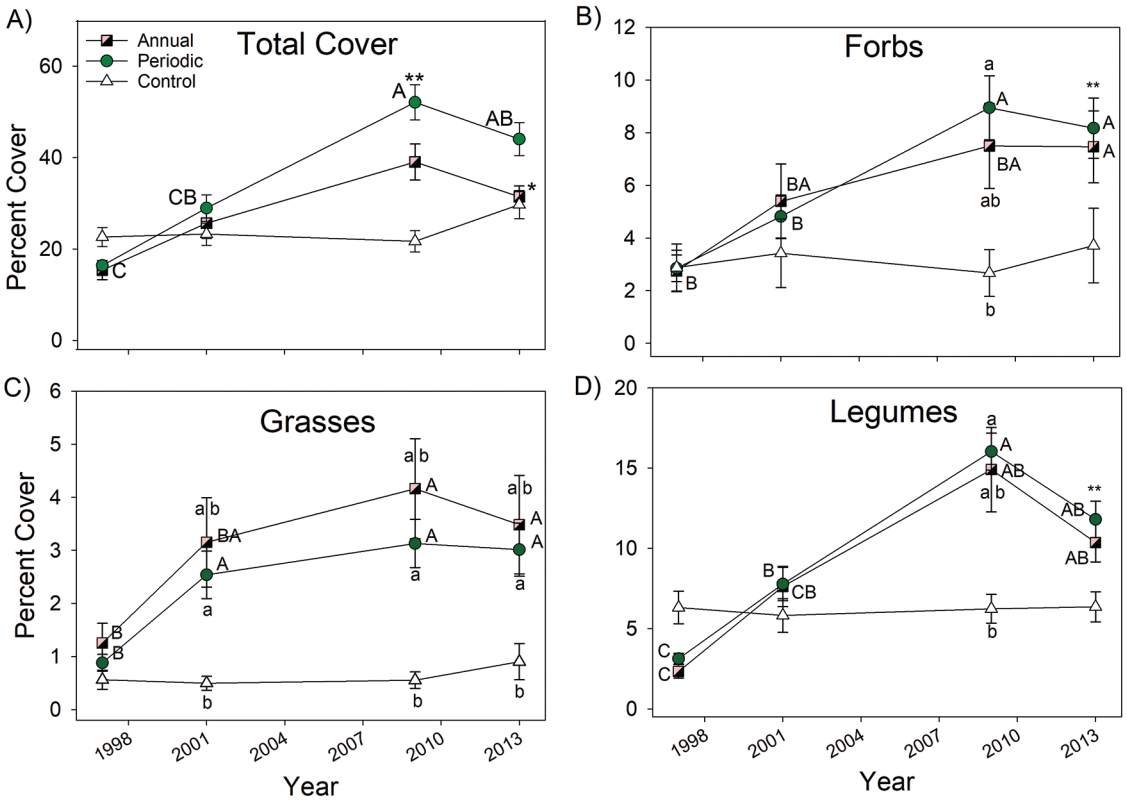

### 3.2. Ground flora percent cover and richness

Throughout the study period, total cover increased 107% on annual and 144% on period treatments while increasing 31% on control treatments (Fig. 3; Table 3). In the two burn treatments, total cover peaked in 2009; in the periodic burn, total cover was greater in 2013 than in 1997 (Tukey's $p < 0.001$) and was greater in 2009 than in 2001 and 1997 (Tukey's $p \leq 0.004$). In the annual burn unit, total cover increased through time (slice $p = 0.032$), although the pairwise comparisons of years were not significant with Tukey's HSD adjustment. There was a significant burn treatment effect in 2009 (slice $p = 0.022$), but no pairwise comparisons were significant with the Tukey adjustment. We found a significant effect of site type on total cover, with the greatest total cover on upper and lower reaches and upland waterways and the least cover on RO/UG shoulders, shoulder ridges, and high benches (Table 3; Supplementary Fig. S1[1]).

Forb, grass, or legume percent cover did not differ between the periodic and annual burn treatments, and cover for both burn frequencies increased through time compared with the control (Fig. 3; Table 3). Between 1997 and 2013, the percent increase in the annual and periodic units for forbs was 154% and 187%, respectively, while grasses increased 119% and 222%, respectively, and legumes increased 369% and 240%, respectively. There was a sig-

[1]Supplementary data are available with the article through the journal Web site at http://nrcresearchpress.com/doi/suppl/10.1139/cjfr-2018-0492.

**Fig. 3.** Means (±1 standard error) of percent cover of (A) total cover, (B) forbs, (C) grasses, and (D) legumes by year and treatment. Different uppercase letters indicate a significant difference among years within a treatment, while different lowercase letters indicate a significant difference between treatments within a year. An asterisk (*) denotes a significant year effect within a treatment but no significant pairwise comparisons using Tukey's adjustment; ** denotes a significant treatment effect within a year but no significant pairwise comparisons using Tukey's adjustment. [Colour online.]



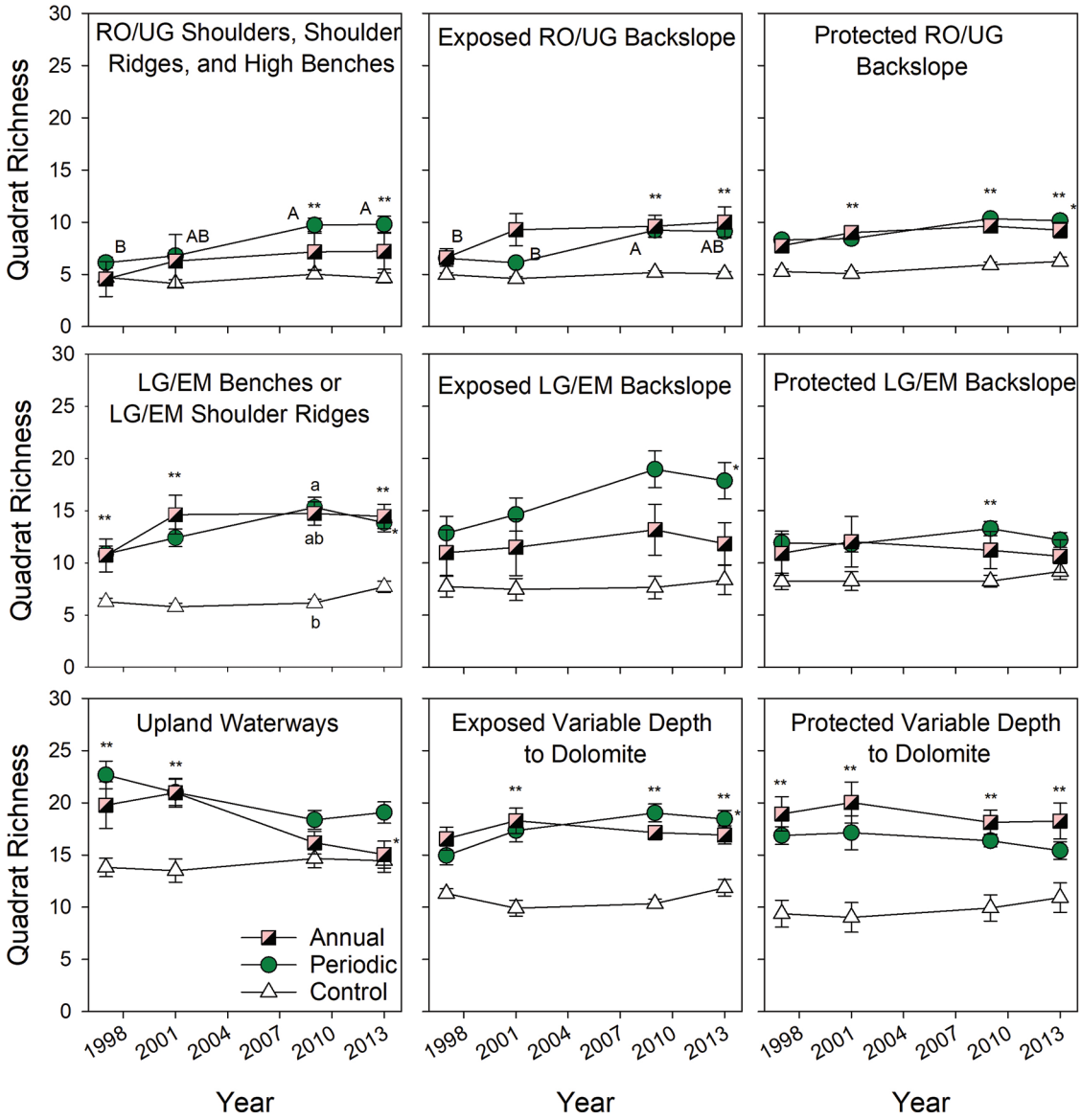

nificant difference in forb cover between the periodic burn and control in 2009 (Tukey's $p = 0.036$), as well as a burn treatment effect in 2013 (slice $p = 0.035$). Both burn frequencies had greater legume cover in 2009 (Tukey's $p \leq 0.002$) and 2013 (Tukey's $p \leq 0.011$) than in 1997. Grass cover in periodic burns was greater in 2001 (Tukey's $p = 0.003$) than in 1997 and was greater in both burn frequencies in 2009 (Tukey's $p \leq 0.017$) and 2013 (Tukey's $p \leq 0.047$) than in 1997. There were also significant differences between the periodic burn and control in 2001 (Tukey's $p = 0.040$), 2009 (Tukey's $p = 0.013$), and 2013 (Tukey's $p = 0.021$). Cover of sedges, woody vines, and shrubs and trees were not affected by interactions between year and burning (Supplementary Table S1[1]). Periodic burns resulted in greater sedge cover than was found on control sites (Tukey's $p = 0.019$). Regardless of burn treatment, cover of sedges, woody vines, and shrubs and trees increased through time. The cover of forbs, grasses, legumes, sedges, and woody vines differed among the site types (Supplementary Table S2[1]).

Species richness increased in the periodic burns in six site types, with increases ranging from 11% to 43%, while exhibiting no change for any control site type (Fig. 4; Table 3). Specifically, richness was significantly greater in 2009 and 2013 than in 1997 on RO/UG shoulders and was also greater in 2009 than in 1997 and 2001 on exposed RO/UG backslopes (Tukey's $p$ values $\leq 0.009$). In addition, there were increases in richness in periodic treatments on protected RO/UG backslopes, exposed LG/EM backslopes, exposed variable depth to dolomite, and LG/EM benches, although no pairwise comparisons were significant with the Tukey's HSD adjustment (slice $p$ values $\leq 0.010$). The only significant year effect within annual treatments was in upland waterways, where richness decreased 32% through time (slice $p$ value = 0.036). Within year and site type combinations, periodic treatments had greater richness than control treatments in 2009 on LG/EM benches (Tukey's $p$ value = 0.014). There were several significant treatment effects that did not have significant pairwise comparisons with the Tukey's HSD adjustment, including those for all years on protected variable depth to dolomite (slice $p$ values $\leq 0.022$), for the years of 2001, 2009, and 2013 on protected RO and UG backslopes and exposed variable depth to dolomite (slice $p$ values $\leq 0.036$), and for the years of 2009 and 2013 on RO/UG shoulders and RO/UG exposed backslopes (slice $p$ values $\leq 0.015$). Upland waterways had significant treatment effects in 1997 and 2001 (slice $p$ values $\leq 0.024$).

### 3.3. Species associated with prescribed burning by site type

Indicator species analysis identified species significantly associated with the pre-and post-burn communities for each of the nine ELTs (Supplementaty Table S3[1]). Two species, *Cornus florida* L. (flowering dogwood) and *Viola sororia* Willd. (common blue violet), were significant indicators of the pre-burn condition on eight and six site types, respectively. Generally, more species were indicators of the post-burn communities than of the pre-burn communities across site types (Fig. 5). Four genera included multiple species with increases in IV across site types: *Carex* (sedge), *Dichanthelium* (grass), *Desmodium* (including *Hylodesmum*, per Ladd and Thomas 2015), and *Lespedeza* (legumes). At least one species from two additional genera, *Rhus* and *Rubus*, were indicators of the post-burn communities on all site types except for protected variable depth to dolomite. Three site types, the upland waterways, protected variable depth to dolomite, and protected LG/EM backslopes, had the lowest ratio of the number of post-burn to pre-burn community indicator species (Fig. 5).

**Fig. 4.** Means (±1 standard error) of richness per 1 m$^2$ by year, treatment, and site type. The same uppercase letter indicates no significant difference among years within treatment and ecological land type (ELT); the same lowercase letter indicates no significant difference among treatments within year and ELT. An asterisk (*) denotes a significant year effect within a treatment and site type but no significant pairwise comparisons using Tukey's adjustment; ** denotes a significant treatment effect within a year and site type but no significant pairwise comparisons using Tukey's adjustment. Site type names include formation and lithology, which are Roubidoux sandstone (RO), Upper Gasconade dolomite (UG), Lower Gasconade dolomite (LG), and Eminence–Potosi dolomite (EM). [Colour online.]



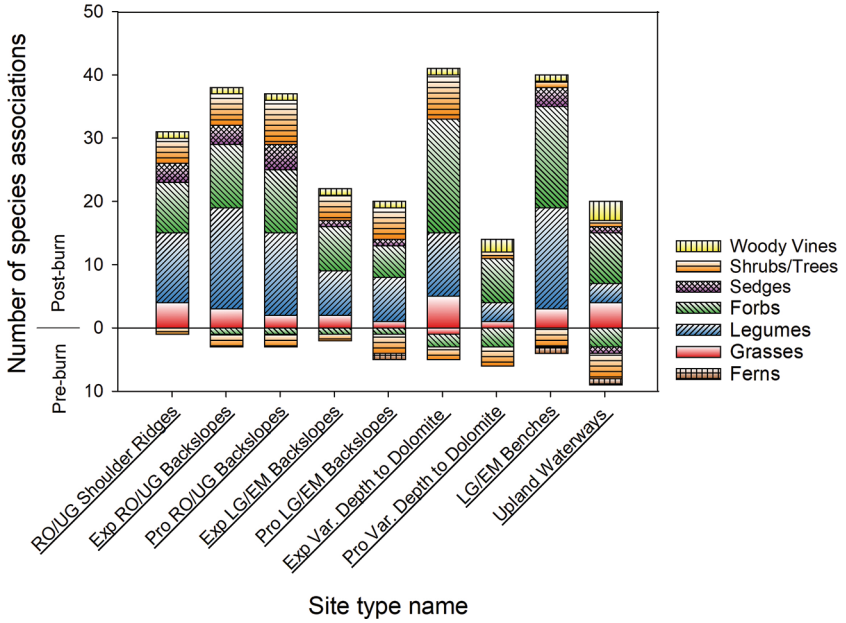

## 4. Discussion

Landscape-scale prescribed burning has increased across the US, with objectives ranging from fuel reduction in the Southeast (Addington et al. 2015) and western US (Knapp et al. 2007) to oak regeneration in the Appalachian Mountains (Royse et al. 2010) and community restoration in Arkansas (Sparks et al. 1998). In Missouri, landscape-scale prescribed fire has been implemented at CCMA and other sites to mimic historic anthropogenic fire regimes and restore the native plant communities (Nature Conservancy 1997; Mark Twain National Forest (MTNF) 2011; Kinkead et al. 2013).

### 4.1. Fire effects on forest structure and ground flora cover

Repeated prescribed fire at low to moderate intensities acts as a bottom-up disturbance that reduces abundance of small-diameter stems but has diminishing effect as tree size increases (Hutchinson et al. 2012; Knapp et al. 2015). Our results corroborate these findings and support hypothesis 1, showing negligible reduction in overstory TPH but significant decreases in midstory TPH with burning. Tree size is an important determinant of "top kill" or mortality following surface fire. Overstory trees in oak–hickory forests commonly have thick bark that protects the stem from mortality due to cambium damage, but bark thickness of midstory trees varies considerably among species (Pausas 2015; Schafer et al. 2015). Previous studies have reported species-specific differences in top kill – mortality rates following prescribed burning (Dey and Hartman 2005; Fan et al. 2012), providing a potential mechanism of filtering species composition; however, long-term studies have also demonstrated complete removal of hardwood stems <12 cm dbh with repeated burning (Knapp et al. 2017). Given the frequent sampling at CCMA, results from this study provide insight into the rate at which midstory stem abundance is reduced with pre-

**Fig. 5.** Count of species with significant indicator values by site type, separated by functional group, with the values above the horizontal line at 0 representing the number of species with significant associations to post-burn communities and the values below the line representing the number of species associated with pre-burn communities. Site type names include aspect, formation and lithology, and soil depth, which are exposed (exp) and protected (pro), Roubidoux sandstone (RO), Upper Gasconade dolomite (UG), Lower Gasconade dolomite (LG), and Eminence–Potosi dolomite (EM), and variable (Var.) depth to dolomite where it is present in the soil.




scribed burning at different frequencies. Moreover, this pattern of midstory reduction was consistent across site types, suggesting that repeated landscape-scale burning can contribute to open vertical structure across a broad spatial extent.

The increase in overstory basal area, regardless of treatment, suggests that the growth of residual overstory trees or recruitment of new overstory trees offset the mortality that occurred. Prescribed burning affects tree growth rates in complex ways, including direct effects through potential tissue damage (Marschall et al. 2014) and indirect effects through changes to soil conditions or nutrient cycling (Certini 2005). Prescribed burning has been reported to increase tree growth by reducing the density of competing stems (Anning and McCarthy 2013), but it also has been found to reduce radial growth of overstory trees compared with thinning alone (Kinkead et al. 2017). Because there was no apparent change in overstory stem density through time at CCMA, the increased basal area indicates that there were growth increases related to landscape-scale burning within the time frame of this study.

As hypothesized in H1, our results demonstrated that total percent cover steadily increased across all site types during the first 10 years of prescribed burning. Repeated, frequent prescribed burning increases the abundance of vegetation in the ground layer, as demonstrated in Illinois oak woodland ecosystems subjected to 13 years of varied fire treatments (Apfelbaum et al. 2000). Brockway and Lewis (1997) documented increases in cover of ground flora in longleaf pine ecosystems after 40 years of annual burning. However, we also observed decreased ground flora cover from 2010 to 2013. This is likely explained by the timing of prescribed burn treatments in the study, as all units were subjected to an early April prescribed burn in 2013. Ground flora cover is commonly reduced during the growing season immediately following fire, with recovery to pre-burn levels in subsequent growing seasons (Biondini et al. 1989; Howe 1994). In addition, the study site was in moderate drought conditions for the months of May and June 2012 and severe drought in July and August 2012 (Dai 2017). It is unclear if drought conditions, fire, or a combination further slowed vegetation recovery; however, the control sites did not have reduced cover during the same period, suggesting that the early April fire probably had a greater effect on the ground flora cover than the drought event.

Effects of prescribed fire on cover differed among the herbaceous functional groups. Similar to White (1983), we observed an increase in cover through time for forbs, grasses, and legumes, with legumes displaying the strongest response. Many forbs and grasses present in the Missouri Ozarks are also present in the tallgrass prairie ecotone (Steyermark 1963) and are adapted to repeated fires and increased sunlight (Packard and Mutel 1997). Similarly, Peterson et al. (2007) showed that legumes respond to prescribed fire with greater increases in cover when the overstory canopy is intact. Among the graminoids encountered, at least one species of *Dichanthelium* (rosette panic-grasses) responded through a significant increase in IV in all site types (Supplementary Table S3[1]). This C3 grass genus has been shown to respond positively to fire, with no canopy treatment, in sandstone barrens in southern Illinois (Taft 2003). Alternatively, we expect that C4 grasses would increase in abundance if overstory density was reduced through mechanical means, higher intensity fire, or other mortality events (Peterson et al. 2007).

The indicator species analysis showed that more genera and species were associated with the post-burn plant communities than with the pre-burn communities. Indicator species for the post-burn communities included both annual (e.g., *Acalypha*) and perennial (e.g., *Dichanthelium*) genera across site types, suggesting that species with a variety of life history strategies responded to increased growing space and changes in competition dynamics following fire. Fire stimulates germination and recruitment of herbaceous species by exposing mineral soil, increasing nutrient availability, and increasing understory light availability due to midstory reduction (Whelan 1995). While it was likely that new plants, particularly annuals, established from newly dispersed seeds following the burns, perennial species may have developed from existing structures belowground or from the seedbank. Among the functional groups, legumes demonstrated the greatest increase in cover with the burn treatments, and many legumes (e.g., *Lespedeza* and *Desmodium*) were identified as indicators of the

post-burn community. Legumes are commonly associated with frequent-fire ecosystems and can persist in the seedbank for many years due to the characteristic hard seed coat of many species in this family (Kaeser and Kirkman 2012).

### 4.2. Consistency of vegetative response by site type

Based on our study, we can generalize some vegetation responses to repeated prescribed burning across the landscape, while other responses varied by site type. For example, repeated burning consistently reduced the abundance of small-diameter woody stems in the midstory and resulted in greater abundance of herbaceous ground flora throughout. However, effects of fire on species richness varied by site type (H2). Reintroducing fire into unburned forest ecosystems has been reported to increase plant species richness (Wilhelm and Masters 1994; Taft 2003). Our results, however, suggest that the response of the plant community varies by site, with generally stronger effects for communities on drier sites. In fact, the wettest of the site types, upland waterways, indicated reduced species richness with burning. In a study from the southern Appalachian region, fire also had varying effects on species richness and diversity based on slope position, with significant increases in richness on ridge tops, no change in valley positions, and significant decreases in richness and diversity on middle slopes (Elliott et al. 1999). Thus, specific characteristics of the ecological community may result in variable effects of repeated fire on species richness.

Variation in ground flora response across site types may be related to variation in topo-edaphic conditions that affect fire behavior (Iverson et al. 2004). Exposed sites commonly receive greater solar radiation than protected sites (Meinert et al. 1997), which accelerates fuel drying and increases ground temperatures (Pyne et al. 1984). Moisture levels of forest litter, an important fuel source for prescribed fire in the Missouri Ozarks, vary based on aspect (Stambaugh et al. 2006). Differences in fire intensity among site types may account for the variation in ground flora response, but no data were available to describe fire behavior across plots at CCMA. Future research that details fire behavior associated with landscape-scale burning would further elucidate drivers for the ground flora response observed in our study.

It is possible that fire behavior–intensity was similar across all site types and the different patterns in ground flora richness observed were due to differences in the plant communities associated with each site type. Many plant species associated with exposed sites are considered to be adapted to fire and (or) xeric conditions (Nigh and Schroeder 2002). Species that may be indicators of fire-treated sites based on our data include *Galactia regularis* (L.) Britton, Sterns & Poggenb. (eastern milkpea) and *Helianthus hirsutus* Raf. (hairy sunflower). Fire-sensitive species are generally more common on mesic sites, and studies have shown that prescribed burning can reduce the abundance of fire-sensitive tree species (Hutchinson 2004; Nowacki and Abrams 2008). Fewer studies have quantified fire effects on mesic ground flora species. One herbaceous species, *Viola sororia* Willd. (common blue violet), decreased in six out of nine site types and may be an indicator of communities not adapted to fire. Additional research is warranted to determine patterns of species turnover with repeated burning across different site types.

### 4.3. Management implications

Frequent fire is commonly prescribed for woodland restoration and management, with interest in reducing stand density in accordance with desired woodland characteristics (Hanberry et al. 2014*b*). Prescribed burn plans often include objectives to open the vertical structure by reducing the midstory layer without extensive loss of overstory trees, although woodland ecosystems can vary greatly in overstory tree density (Nelson 1985). Our results show that nearly two decades of repeated prescribed burning consistently reduced the abundance of midstory vegetation, resulting in open vertical structure across site types. Because overstory density remained high (i.e., at the level commonly associated with closed woodlands or forests), light interception by the canopy also remained relatively high (Blizzard et al. 2013). Ground flora species differ in light requirements (Peterson et al. 2007), and additional reductions to canopy density could result in an enhanced response of light-demanding species. Management objectives that include the reduction of stand density or increased light levels in the short term would likely necessitate targeted tree removal in addition to prescribed burning.

The use of prescribed burning at the landscape scale may be motivated by interest in creating heterogeneous fire effects across the landscape. Although we observed consistency in fire effects on vegetation structure for all site types, effects on species richness of the ground flora varied. Species richness increased with fire on exposed site types, but responded variably on protected site types and decreased in annually burned upland waterways. These results provide some support for previous findings that landscape-scale prescribed burning may homogenize plant communities by reducing the presence of fire-sensitive species from the species pool (Sasseen and Muzika 2004; Myers et al. 2015). Future research into fire effects on community composition would additionally inform patterns in landscape-scale heterogeneity associated with prescribed burning.

Management decisions on prescribed fire regimes (including fire frequency, extent, intensity, and seasonality) are generally informed by expected outcomes relative to management objectives. Although our study included different fire frequencies, the range of fire return intervals was narrow and limits interpretation of differences between the annual and periodic burn treatments. The historic mean fire interval of the Current River Hills has been shown to be greater than the range of 1.1–2.7 years at CCMA, with a dendrochronological fire history from MOFEP indicating an MFI of 4.4 years and a fire return range of 1–17 years from 1604 to 1996 (Guyette and Stambaugh 2004). The short fire return interval at CCMA within our study may result in fire effects that would differ from longer fire return intervals or intervals with greater variability through time.

Our study demonstrates distinct, yet complex, effects of frequent prescribed burning at the landscape scale on ground flora in the Missouri Ozarks. In the control units, forest density increased while ground flora was generally unresponsive. In burned sites, the overstory was left intact while periodic burning drastically decreased midstory density and annual burning gradually decreased midstory density. Total ground flora cover more than doubled with prescribed burning, with three functional groups — forbs, grasses, and legumes — responding with increased cover in prescribed burned units. Richness increased in burned site types with exposed slopes, shoulders, ridges, or higher elevation protected backslopes while exhibiting no significant response in lower elevation protected site types and decreasing somewhat in upland waterways. Managers implementing landscape-scale prescribed fire can use the results of this study to inform long-term restoration decisions, as we conclude that (*i*) vegetation structure is strongly affected by repeated prescribed fire, regardless of site type, (*ii*) ground flora species richness response to prescribed burning varies by site type, and (*iii*) the variation that we have documented is important for understanding whether landscape-scale burning will meet management objectives.

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