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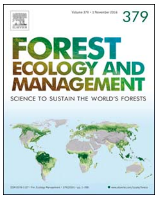

Restoration of oak woodlands and savannas in Tennessee using canopy-disturbance, fire-season, and herbicides

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ABSTRACT

Establishing herbaceous groundcover is essential for oak woodland and savanna restoration. In the Appalachian region, woody vegetation in the understory can persist through many fires and interfere with achieving this goal. Herbicide applications could reduce such vegetation and interact with canopy-disturbance and fire to accelerate restoration. In stands thinned to woodland ($16\ m^2\ ha^{-1}$, 75% canopy closure) or savanna ($5\ m^2\ ha^{-1}$, 24% canopy closure) conditions and burned biennially in the fall (October) or spring (March), we economically applied triclopyr (Garlon® 3A) to understory woody plants using foliar and cut-surface techniques in the fall between fires. From 2011 to 2013, only minor differences in vegetation were observed between areas managed with canopy-disturbance and fire (CF) and areas where herbicides were also used (CFH). Small-sapling (≥ 1.4 m tall, < 7.6 cm DBH) density in CF was 2,566 stems ha^{-1} greater than CFH in 2012. This difference was (1) the only woody control CFH attained beyond CF, (2) only lasted a single growing-season because it was mostly fire-sensitive species top-killed by subsequent fire, and (3) only led to increased herbaceous groundcover in savannas burned in the fall. This included the greatest reported increase in herbaceous groundcover (graminoid +18.2%, forb +8.0%) to be associated with herbicide applications under partial oak canopies in the Appalachian region. Expanding herbicide target constraints, completely removing undesirable seed-sources, increasing triclopyr concentration, exploring tank-mixes, and alternative application timing (*e.g.*, prior to canopy disturbance) could improve effectiveness; however, fire suppression throughout the Appalachian region has increased the dominance of fire-sensitive woody species. Our results demonstrate how such composition can reduce the utility of herbicides relative to fire during oak woodland and savanna restoration.

1. Introduction

Oak (*Quercus* spp.) woodlands and savannas occupy a fraction of their pre-settlement extent (Nuzzo, 1986; Fralish et al., 2000; Hanberry et al., 2014) and are among the most threatened communities in North America (Noss et al., 1995). Only small, isolated remnants persist in the Appalachian region (as defined in Harper et al., 2016) where they were once prevalent (Noss, 2013). A robust and diverse herbaceous groundlayer (DeSelm, 1994) and relatively sparse overstory of oaks distinguishes woodlands (30–80% canopy cover) and savannas (10–30% canopy cover) along the continuum from forest to prairie (Nelson, 2010). In the absence of fire, succession has transformed these communities into closed-canopy forests (Nowacki and Abrams, 2008). This has drastically reduced herbaceous groundcover and diversity by facilitating canopy closure, eliminating understory resource gradients (Brudvig and Asbjornsen, 2009), and increasing competition from woody vegetation (Barrioz et al., 2013). Such structural homogenization of vegetation across landscapes threatens a diverse assemblage of wildlife (Cox et al., 2016; Vander Yacht et al., 2016; Harper et al., 2016), and reduced biodiversity could threaten overall ecosystem productivity, sustainability, and function (Tilman et al., 1996).

Fortunately, the disturbances responsible for creating and maintaining oak woodlands and savannas can also be used to address their decline (McPherson, 1997). Canopy disturbance can shift overstory composition toward desirable species and increase the light available for herbaceous germination and growth (Nielsen et al., 2003; Brewer, 2016). Restoration is then advanced and maintained using a long-term regimen of repeated fire (Dey et al., 2015). Biennial fire maximizes community heterogeneity and herbaceous species richness in the understory by suppressing woody vegetation (Peterson et al., 2007;

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Peterson and Reich, 2008). Increases in understory light can promote a dense layer of woody saplings and shrubs (McCord et al., 2014) which can limit herbaceous layer development (Lashley et al., 2011; Barrioz et al., 2013). Although expensive, the mechanical removal of this vegetation can restore gradients in light, moisture, and nutrients that encourage increases in herbaceous cover and diversity (Brudvig and Asbjornsen, 2009). Fire historically limited woody vegetation dominance in the understory of woodlands and savannas, and remains a cheap and effective tool for restoration efforts (Ryan et al., 2013). However, coupling midstory thinning with fire can result in a greater and more immediate herbaceous response than fire alone (Lettow et al., 2014).

In the Appalachian region, most prescribed fires are conducted in the dormant-season and are followed by prolific resprouting of woody vegetation (Knapp et al., 2009). Suppressing hardwoods with such fire, therefore, requires frequent burning (every 1–2 years) for many years (Hutchinson et al., 2012; Arthur et al., 2015; Knapp et al., 2015). Growing-season fire can result in less resprouting of woody plants and a greater herbaceous response than dormant-season fire (Waldrop et al., 1992; Gruchy et al., 2009; Robertson and Hmielowski, 2014). However, growing-season fire may have been uncommon in the Appalachian region, and its repeated use may be a departure from historical fire regimes (Guyette et al., 2012). Furthermore, studies examining herbaceous response to burn season are limited for hardwood ecosystems (Knapp et al., 2009). Regionally specific experiments that validate the effects of growing-season fire are needed (Gilliam and Roberts, 2003), but so are additional options of understory woody vegetation control.

Herbicide applications that target woody-vegetation in the understory could accelerate restoration without negatively affecting desirable herbaceous species (Ansley and Castellano, 2006; Engle et al., 2006). Such management may also be the most cost-efficient option among methods that reduce or eliminate resprouting potential (Bailey et al., 2011). Using herbicides to control woody vegetation can increase herbaceous groundcover and diversity (Gruchy et al., 2009) by increasing light infiltration (McCord et al., 2014), and the technique has been effective in managing pine savannas (Freeman and Jose, 2009). Most research related to oak woodland and savanna restoration has occurred in the Midwest. Comparatively, the Appalachian region is wetter and has a longer history of fire suppression. Such conditions increase the threat that understory woody growth can pose to restoration, and this could elevate the importance and utility of herbicides as a management tool. However, regionally-specific evaluations of herbicides have narrowly focused on wildlife response to woodland restoration (*e.g.* Lashley et al., 2011; McCord et al., 2014; Greenberg et al., 2016), regeneration of woody species (*e.g.* Schweitzer and Dey, 2011), or utilized soil-active herbicides in the absence of a residual overstory (Nanney, 2016). Also, the influence of canopy-disturbance and fire-season on herbicide treatment efficacy is uncertain. Combining growing-season fire with herbicides warrants further investigation for its potential to efficiently restore open-oak communities.

We conducted an experiment that documented the response of vegetation to understory herbicide treatments within the context of interactions with canopy disturbance and prescribed fire. Specifically, we assessed the ability of herbicide treatments to increase herbaceous groundcover and diversity through decreasing the density of woody and semi-woody vegetation in the understory. We also evaluated how herbicide treatment effects varied across canopy disturbance level (thinning to 16 $m^2 ha^{-1}$ residual basal area and 75% canopy closure, or 5 $m^2 ha^{-1}$ residual basal area and 24% canopy closure) and season of prescribed fire (October or March). We explored relationships between vegetation affected by herbicide treatments and site covariates (aspect, slope, slope position, and canopy closure) to inform herbicide use within the context of such variation. Our goal was to determine if herbicide applications could enhance oak woodland and savanna restoration in the Appalachian region.

2. Methods

2.1. Study area

Our research occurred at Catoosa Wildlife Management Area (36° 07′ 51.71″ N, 84° 87′ 12.49″ W), a 32,374 ha property managed by the Tennessee Wildlife Resources Agency (TWRA) and located in the Cumberland Plateau and Mountains physiographic region (DeSelm, 1994). Site elevation ranged from 437 to 521 m, and soils were mesic typic Hapladults over weathered sandstone conglomerate. Annual mean precipitation and temperature were 140 cm and 13 °C, respectively, for nearby Crossville, TN from 1981 to 2010 (Vander Yacht et al., 2017). Forests were established in the 1920s following logging and agricultural abandonment and are currently oak-dominated, mixed pine-hardwood stands. Shortleaf pine (*Pinus echinata*) was a major overstory component prior to a pine bark beetle (*Dendroctonus frontalis*) outbreak in 1999–2000. Salvage cutting began in 2002, and TWRA began an oak savanna restoration project using prescribed fire. Evidence of historical woodland and savanna conditions included the rapid development of prairie and savanna flora and historical accounts (*i.e.*, pasturing cattle and frequent fire until 1945, Barrioz et al., 2013).

Prior to canopy disturbance (2008), white (*Quercus alba*), southern red (*Q. falcata*), black (*Q. velutina*), and scarlet (*Q. coccinea*) oaks as well as red maple (*Acer rubrum*), sourwood (*Oxydendrum arboreum*), and hickories (*Carya spp.*) all comprised > 1.0 $m^2 ha^{-1}$ of total basal area (17.8 $m^2 ha^{-1}$ ± 1.6 SE) and canopy closure was ≥85%. Snags were common because of beetle-killed pines (3.9 $m^2 ha^{-1}$). The density of understory woody stems (> 1.37 m tall, < 12.7 cm diameter at breast height [DBH]) was 1,936 stems ha^{-1}, and dominant species included blackgum (*Nyssa sylvatica*), downy serviceberry (*Amelanchier arborea*), red maple, sourwood, and sassafras (*Sassafras albidum*). Blueberry (*Vaccinium spp*.), seedlings, and litter dominated the ground-layer. Herbaceous plants were rare (4.4% cover, Vander Yacht et al., 2017).

2.2. Experimental design

We established 8, 20-ha stands that included 2 replicates of 4 randomly assigned treatments: spring fire and woodland residual basal area (SpW: 15.3 $m^2 ha^{-1}$ ± 1.6 SE and 70.9% canopy closure ± 5.6 SE), fall fire and woodland residual basal area (FaW: 16.2 $m^2 ha^{-1}$ ± 1.3 SE and 79.4% canopy closure ± 4.4 SE), spring fire and savanna residual basal area (SpS: 2.6 $m^2 ha^{-1}$ ± 0.6 SE and 14.2% canopy closure ± 3.5 SE), and fall fire and savanna residual basal area (FaS: 7.3 $m^2 ha^{-1}$ ± 0.8 SE and 32.7% canopy closure ± 4.2 SE). Overstory reductions were accomplished in winter 2008–2009 via commercial logging (Vander Yacht et al., 2017). Following canopy disturbance, 76% of total basal area was southern red, white, scarlet, post, and black oak. Remaining basal area was largely red maple, sourwood, and blackgum. We conducted fall fires (11 October 2010) prior to leaf abscission, and spring fires (22 March 2011) prior to leaf emergence. Fall burns were low to moderate in intensity, whereas spring burns were comparatively more intense. Canopy disturbance and 2010–2011 fire treatment details can be found in Vander Yacht et al. (2017).

Following fire (2011), paired plots (16 × 22 m) were installed at 5 random locations within the core (50-m buffer) of each stand (Fig. 1A). We randomly assigned herbicide application within paired plots (n = 40, Fig. 1B, C) that were separated by a 5-m buffer. This created plots managed with only canopy-disturbance and fire (CF) adjacent to plots managed with canopy-disturbance, fire, and herbicides (CFH). Herbicide was applied 2–14 September 2011 when no indications of drought were apparent. We selected triclopyr (Garlon® 3 A; triclopyr amine; [(3,5,6-Trichloro-2-pyridinyl)oxy]acetic acid; Dow Chemical Company, Midland, MI) based on its broad-spectrum control, lack of residual soil activity, and minimal effect on grasses (Dow AgroSciences LLC, 2005). Using backpack sprayers, we applied a 2% Garlon® 3 A and

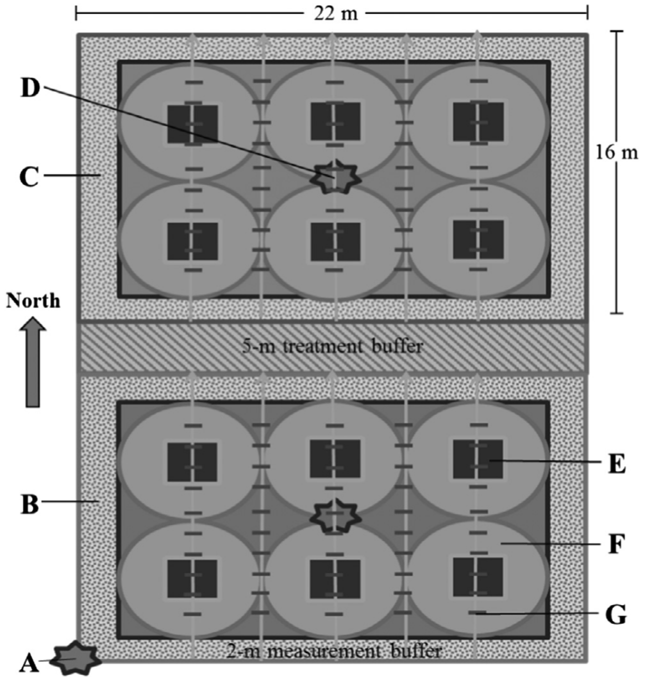

Fig. 1. Arrangement of paired herbicide plots and sampling sub-plots within an oak woodland and savanna restoration experiment (2011–2013) in Cumberland County, TN. (A) random plot location; (B) CF plot; (C) CFH plot; (D) plot center; (E) 1-m^2 shrubby vegetation and seedling (> 30.48 cm tall, < 1.37 m tall) sub-plots; (F) 3-m radius sapling (> 1.37 m tall, < 12.7 cm DBH) sub-plots; (G) point-intercept transects.

1% non-ionic surfactant solution to the foliage of all woody vegetation ≥1.37 m but < 2.44 m tall until thoroughly wetted (not dripping). Stems < 1.37 m tall but with multiple sprouts collectively > 2.54 cm in root-collar diameter were also treated. Stems ≥2.44 m tall but < 12.70 cm DBH were girdled with a hand saw and the cut treated with a 1:1 solution of water and Garlon® 3A (hack-and-squirt). We left ≤5 stems of desirable, fire-tolerant species (*e.g.*, oaks, hickories, and shortleaf pine) in each plot untreated that otherwise met these criteria. These residual stems increased age structure balance and structural diversity important to wildlife. Smaller stems were not treated because of presumed control through burning. Complete removal of understory woody vegetation was not our goal; rather, we desired to test an economical approach to herbicide application.

Stands were burned again based on assigned fire-season (fall: 24 October 2012, spring: 15 March 2013). Leaf abscission was < 5% during fall burns, and spring burns preceded bud-break. A combination of flanking and heading fires burned herbicide plots (Vander Yacht et al., 2017). Rate of spread ($t \leq 2.4$, $p \geq 0.050$, 2.2 m min^{-1}) and flame length ($t \leq 1.6$, $p \geq 0.161$, 0.9 m ± 0.2 SE) were similar across fire types and burn seasons. Ceramic tiles painted with Tempilaq® liquids (fall: n = 34, spring: n = 29) indicated fires burned hotter ($t = 5.6$, $p < 0.001$) in fall (255 °C ± 10 SE) than in spring (162 °C ± 13 SE). Overall, fire intensity was more similar between fire-seasons than it had been during initial fires (Vander Yacht et al., 2017).

2.3. Data collection

We collected data in July-August before (2011) and after (2012–2013) herbicide applications. Only the core (2-m buffer) of each herbicide plot was sampled to reduce edge-effects. From each plot center (Fig. 1D), we recorded aspect, percent slope, slope position (alluvial, cove, toe-slope, mid-slope, shoulder, and ridge; recorded as 1–6, respectively), and canopy closure (mean of four spherical densiometer readings taken in each cardinal direction). We categorized woody vines, shrubs, and semi-woody species (*e.g.*, blackberries [*Rubus* spp.] and greenbriers [*Smilax* spp.]) as shrubby vegetation and tallied stems in 6 systematically located, 1-m^2 sub-plots within each plot (Fig. 1E). We counted all tree seedlings (≥30.5 cm tall, < 1.4 m tall) by species within the same sub-plots. We counted saplings (≥1.4 m tall) in 6 concentric, 3-m radius sub-plots (Fig. 1F). Sapling stems were tallied by species and size class (small, < 7.6 cm DBH; large, ≥7.6 but < 12.7 cm DBH). We used the point-intercept method to characterize herbaceous groundcover at 1-m intervals (n = 50) along 5 parallel transects in each plot (Fig. 1G). All intersecting herbaceous vegetation below 1.4 m was identified to species and classed as graminoid or forb.

3. Data analysis

We calculated annual (2011–2013) plot means for woody stem density (stems ha^{-1}) by category (shrubby vegetation, seedling, small-sapling, and large-sapling), graminoid and forb groundcover, herbaceous richness, and herbaceous diversity (Shannon-Wiener's Diversity Index [H′]). We calculated groundcover by dividing the intercepts where a category was present by the total potential intercepts (50). We tested each dependent variable for normality using Shapiro-Wilk's test (W > 0.90), used square-root transformations when necessary, and graphically assessed equality of variance assumptions.

Separate ANCOVA models for each dependent variable were developed using a completely randomized design with split-plot treatments. We adjusted degrees of freedom using Kenward-Roger, but dropped repeated measures correlation among annual data if residual log likelihood difference between inclusion and omission was less than 5 (Littell et al., 2006). Models included fixed- (whole- [canopy and fire] and sub-plot [herbicide] treatments, year, covariates, all two- and three-way interactions) and random- (replication of whole- and split-plot treatments, and herbicide treatment pairs) effects. Year was a fixed-effect because treatments were applied over time. Orthogonal contrasts also tested if the difference between CF and CFH was similar (α = 0.05) across canopy-disturbance (woodland vs. savanna) and fire-season (spring vs. fall) treatments. We also analyzed the density of the 5 most abundant woody species within each size category. Covariates were not included in these models. Although we included whole-plot effects in all models, we focus on herbicide effects and related interactions. Canopy disturbance and fire-season are discussed specifically in Vander Yacht et al. (2017).

We selected covariates (aspect, slope, slope position, and canopy closure) *a priori* and retained them in models when significant (α = 0.05). We transformed aspect using Beers et al. (1966) to yield a continuous variable between 0.00 (southwest) and 2.00 (northeast). All dependent variables and covariates relationships were reasonably linear, and homogeneity of covariate slopes across treatments and years was determined using model interaction terms. We explored relationships between significant covariates and dependent variables further using polynomial regression. We evaluated polynomial model fit on data collected from all 240 herbicide plots (3 years × 40 pairs × 2 plots per pair). We included second- and third-order models to identify potential thresholds. We sequentially dropped order terms, proceeding from third- to second- and then first-order models based on significance (α = 0.05).

We isolated fire-season effects by identifying variation associated with fire intensity. We used one year post-fire data (2011, 2013) and conducted linear regression on stand-level pairs of fire temperature and dependent variables. Only shrubby vegetation density exhibited a significant relationship with fire temperature ($F_{1,\ 14} = 6.23$, $p = 0.026$, $r^2 = 0.308$). Prior to ANCOVA analysis, we used the relationship derived from this regression (slope = 0.078 ± 0.031 SE, intercept = 24.338 ± 5.340 SE) to adjust post-fire means (2011, 2013) of shrubby vegetation density to values predicted at overall mean fire temperature. This relationship was not significant for all other dependent variables ($F_{1,\ 14} \leq 2.40$, $p \geq 0.144$). We performed all mean

Table 1
ANCOVA results for the density of understory woody vegetation and herbaceous ground-layer variables during (2011–2013) an oak woodland and savanna restoration experiment involving canopy disturbance, fire-season, and herbicide treatments at Catoosa Wildlife Management Area, Cumberland County, TN. Bold font indicates significant effects ($\alpha = 0.05$).

	Fixed effects related to herbicide treatments[b]										
	Herbicide (df = 1, 36)		Herb × Trt (df = 3, 36)		Herb × Yr (df = 2, 144)		Herb × Trt × Yr (df = 6, 144)				
Dependent variables[a]	F	p	F	p	F	p	F	p	Covariates[c]	F	p
Woody density (stems ha^{-1})											
Shrubby vegetation	1.48	0.232	1.24	0.309	0.28	0.754	0.73	0.627	Canopy closure	39.35	< **0.001**
Seedling	0.05	0.820	0.75	0.530	1.88	0.156	0.43	0.857	Slope position	9.43	**0.003**
Small-sapling	14.07	**0.001**	1.58	0.211	15.29	< **0.001**	0.58	0.750	Canopy closure	23.12	< **0.001**
Large-sapling	2.09	0.157	0.04	0.987	0.53	0.593	0.33	0.919	Canopy closure	55.30	< **0.001**
Herbaceous ground-layer											
Graminoid groundcover (%)	1.79	0.190	6.35	**0.001**	0.37	0.689	0.84	0.539	Slope position	13.46	< **0.001**
									Canopy closure	25.61	< **0.001**
Forb groundcover (%)	0.21	0.652	3.16	**0.036**	0.86	0.423	0.82	0.555	Canopy closure	27.74	< **0.001**
Richness (n plot^{-1})	0.55	0.463	0.52	0.669	0.50	0.608	0.43	0.856	Slope position	10.72	**0.001**
									Canopy closure	25.82	< **0.001**
Diversity (Shannon-Wiener H′)	0.54	0.467	0.65	0.590	0.30	0.739	0.47	0.831	Slope position	7.74	**0.006**
									Canopy closure	33.09	< **0.001**

[a] 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.
[b] Fixed effects related to applications of Garlon 3 A® (Herb, n = 40), including interactions with canopy-disturbance and fire-season (Trt, n = 20) and/or time (Yr, 2011–2013, n = 80). Subtract 1 *df* from *ddf* of Herb × Yr and Herb × Trt × Yr for each covariate included in models.
[c] Tested covariates were retained when significant ($\alpha = 0.05$) and included aspect, percent slope, slope position, and canopy closure.

separation using Fisher's Least Significant Difference test ($p < 0.05$), and all analyses were conducted in SAS 9.4 using PROC MIXED (SAS Ins., Cary, N.C., USA).

4. Results

4.1. Understory woody vegetation response

Herbicide applications had no effect on the total density of shrubby vegetation (37,280 stems ha^{-1} ± 1,925 SE) or seedlings (33,041 stems ha^{-1} ± 3,444 SE, Table 1). Herbicide effects on such vegetation were also similar across variation in canopy-disturbance ($F_{1,36} \leq 2.05$, $p \geq 0.161$) and fire-season ($F_{1,36} \leq 1.09$, $p \geq 0.303$). The top 5 shrubby species accounted for 89.4% (± 3.5 SE) of total shrubby density. Blueberry (*Vaccinium* spp.) and southern blackberry (*Rubus argutus*) were especially abundant; mean density for both species exceeded 13,000 stems ha^{-1} (Table 2). Southern blackberry density was similar in CF and CFH for all but SpS, where density in CFH (25,307 stems ha^{-1} ± 5,482 SE) was nearly twice ($F_{3,\ 36} = 2.86$, $p = 0.050$) that of CF (14,169 stems ha^{-1} ± 4,095 SE). No other dominant shrubby species was affected by herbicide treatment ($F \leq 2.44$, $p \geq 0.127$). Seedling density was dominated by red maple and sassafras, and the top 5 species constituted 86.0% (± 4.1 SE) of this category (Table 2). Herbicides did not affect seedling density for any dominant species ($F \leq 2.71$, $p \geq 0.070$).

Small-sapling density in CF was nearly 1,000 stems ha^{-1} greater than CFH. However, an interaction indicated this difference was not constant over time (Table 1). From pre- to post-herbicide application (2011–2012), small-sapling density was constant in CFH but increased 3-fold in CF (Fig. 2). Consequently, density in CF was more than double (+2,566 stems ha^{-1} ± 352 SE) that observed in CFH in 2012. Small-sapling density did not differ between CFH and CF in 2013. Density only declined in CF following the second fire (2012–2013, Fig. 2). Herbicide effects on small-sapling density did not vary across canopy-disturbance levels ($F_{1,36} = 0.01$, $p = 0.908$). The difference in small-sapling density between CF and CFH plots was 1,050 stems ha^{-1} (± 489 SE) greater in fall relative to spring burned plots. In other words, herbicide treatments associated with fall burning were > 3X as

Table 2
Mean (SE) stem density (stems ha^{-1}) of dominant shrubby and seedling species by treatment during (2011–2013) an oak woodland and savanna restoration experiment at Catoosa Wildlife Management Area, Cumberland County, TN.

	Canopy Disturbance and Fire (CF)[b]			Canopy Disturbance, Fire, and Herbicides (CFH)[b]		
Species[a]	2011	2012	2013	2011	2012	2013
Shrubby vegetation						
Blueberry (*Vaccinium* spp.)	14,875 (2,468)	15,667 (2,169)	14,619 (3,270)	14,125 (2,215)	16,083 (2,124)	18,565 (4,845)
Southern blackberry (*Rubus argutus*)	6,917 (1,884)	9,792 (2,247)	18,333 (4,514)	13,458 (3,469)	16,042 (4,189)	13,657 (2,667)
Cat greenbrier (*Smilax glauca*)	2,125 (443)	3,292 (610)	2,095 (517)	3,125 (678)	3,458 (558)	2,176 (372)
Northern dewberry (*Rubus flagellaris*)	958 (421)	3,292 (2,540)	1,000 (528)	1,542 (525)	1,375 (446)	556 (315)
Muscadine vine (*Vitis rotundifolia*)	167 (80)	250 (112)	190 (140)	667 (352)	792 (343)	1,296 (904)
Seedling (≥30.5 cm, < 1.4 m tall)						
Red maple (*Acer rubrum*)	11,417 (1,786)	15,750 (2,243)	15,381 (2,272)	10,542 (1,404)	15,375 (1,927)	17,963 (2,044)
Sassafras (*Sassafras albidum*)	12,167 (2,317)	9,917 (1,825)	8,143 (1,567)	11,708 (2,136)	8,708 (1,813)	9,722 (2,113)
Black oak (*Quercus velutina*)	708 (245)	1,208 (623)	1,762 (474)	625 (320)	1,042 (336)	1,759 (362)
Sourwood (*Oxydendrum arboreum*)	833 (239)	1,458 (419)	857 (274)	458 (119)	875 (348)	2,130 (668)
Blackgum (*Nyssa sylvatica*)	1,250 (336)	2,625 (556)	1,476 (318)	1,417 (340)	1,750 (405)	1,250 (364)

[a] The top 5 species within each category are presented in descending order of overall mean density.
[b] Herbicide treatments were foliar and hack-and-squirt applications of Garlon 3 A®, but did not target most of the vegetation in this table. For each column n = 40 0.04-ha plots. Stem density for all presented species was not responsive to main-effects involving herbicide treatments ($F \leq 2.86$, $p \geq 0.050$).

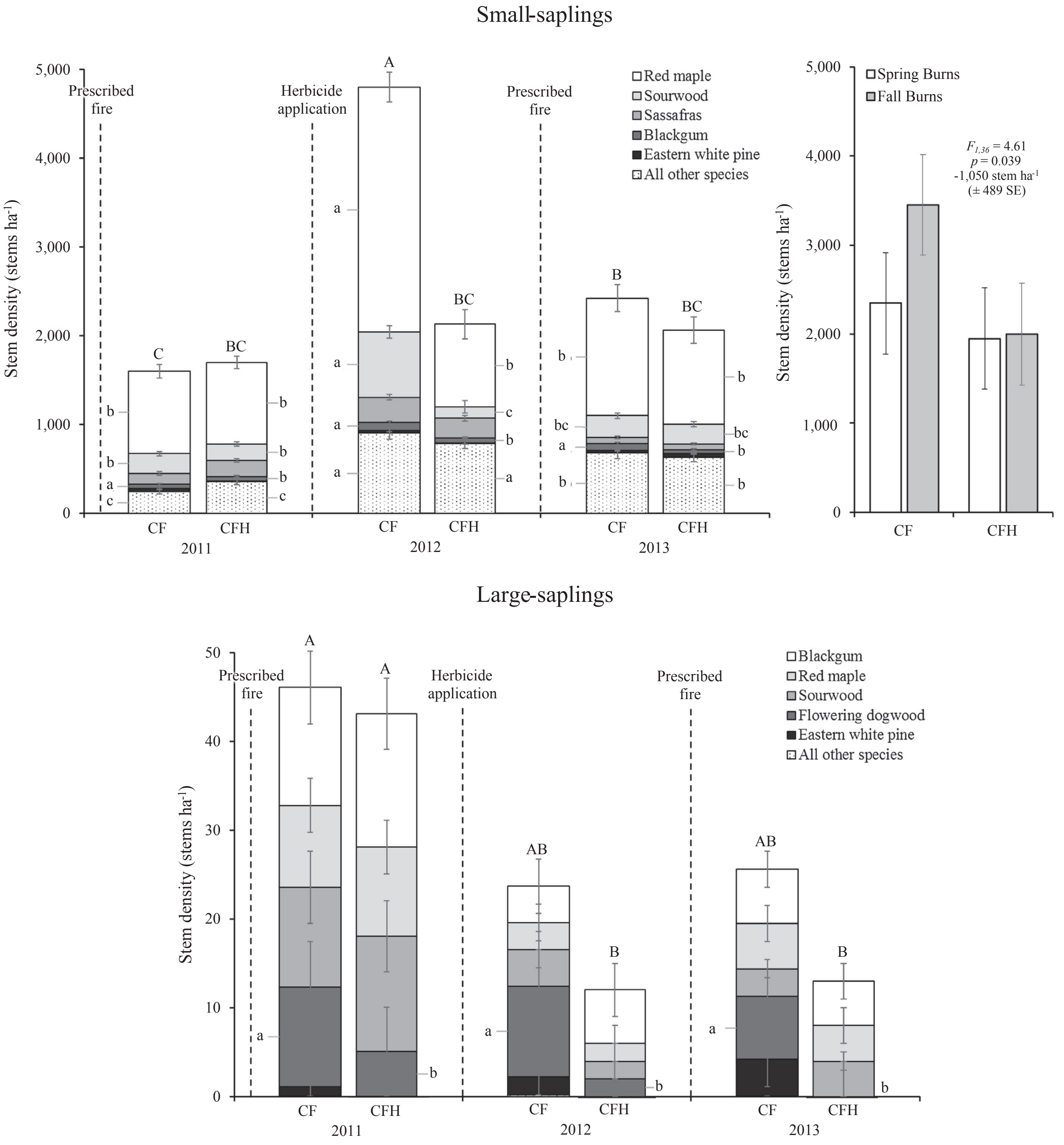

Fig. 2. Herbicide effects on sapling density (stems ha^{-1}) during (2011–2013) an oak woodland and savanna restoration experiment at Catoosa Wildlife Management Area, Cumberland County, TN. Garlon 3A® was not (CF) or was (CFH) applied to plots thinned and burned in the spring (March) or fall (October). An herbicide by year interaction was significant for small-saplings ($p < 0.001$, ≥1.4 m tall, < 7.6 cm DBH) but not for large-saplings ($p = 0.593$, ≥1.4 m tall, ≥7.6 but < 12.7 cm DBH). Small-sapling response also differed by burn treatment (contrast test). The top 5 species are presented. Letters represent LSD differences ($\alpha = 0.05$), with uppercase and lowercase corresponding to total and species-specific densities, respectfully. No letters are presented for species unaffected by herbicides. For each year and treatment, n = 40, 0.04-ha plots.

effective in reducing small-sapling density relative to the same treatment associated with spring burning (Fig. 2).

Dynamics in small-sapling density were primarily driven by the response of red maple, sourwood, and blackgum to herbicide treatments (Fig. 2). Red maple accounted for 53.2% (± 5.1 SE), and sourwood 11.2% (± 3.3 SE), of small-sapling density. Red maple ($F = 10.47$, $p < 0.001$) and sourwood ($F = 21.18$, $p < 0.001$) density nearly tripled in CF by 2012, but returned to 2011 levels by 2013 following fire. Over the same period in CFH, the density of these species was either constant or reduced only immediately following herbicide application (2012). The density of blackgum small-saplings was greater in CF than CFH ($F_{1,\ 36} = 5.33$, $p = 0.027$). Sassafras and eastern white pine (*Pinus strobus*) small-sapling density was similar in CF and CFH ($F \leq 1.10$, $p \geq 0.363$). Together, these 5 species comprised 79.1% (± 5.7 SE) of small-sapling density. Remaining small-sapling density was largely oaks (71 stems ha^{-1} ± 10 SE), hickories, flowering

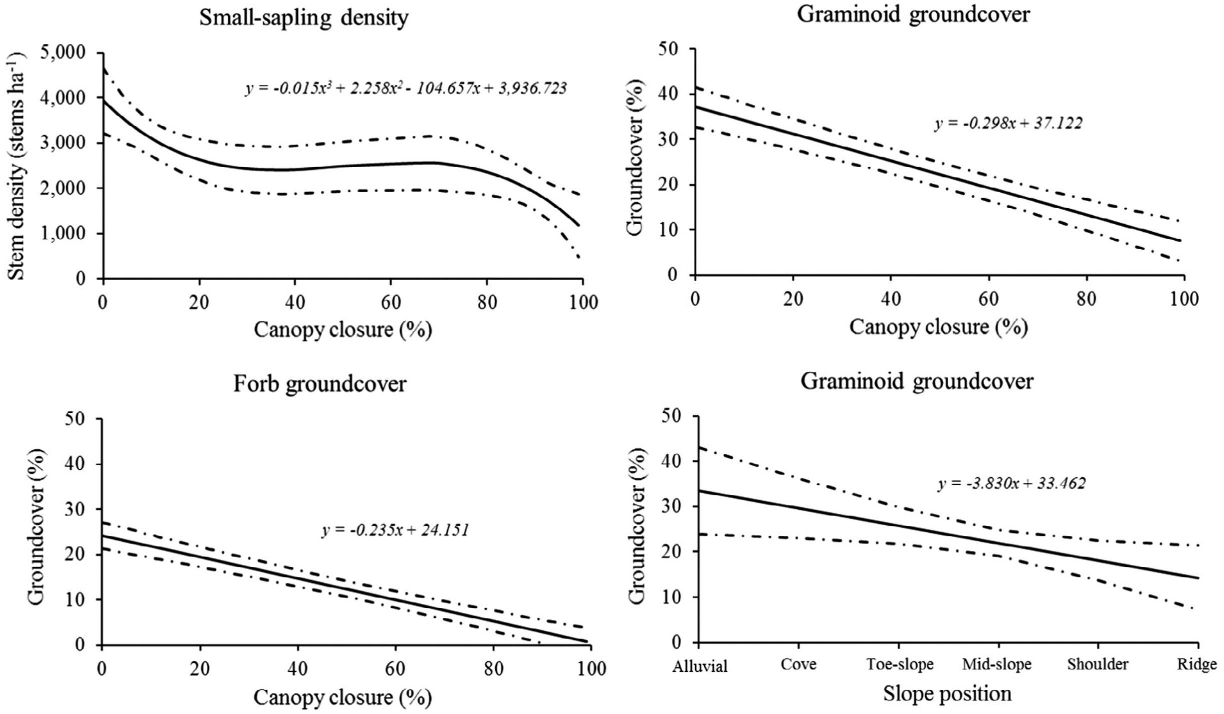

Fig. 3. Relationships between dependent variables affected by herbicide treatments (graminoid groundcover [%], forb groundcover [%], and small-sapling density [stems ha^{-1}]) and significant ANCOVA model covariates (canopy closure or slope position) as determined by polynomial-regression during (2011–2013) an oak woodland and savanna restoration experiment at Catoosa Wildlife Management Area, Cumberland County, TN. Dotted lines indicate upper and lower 95% confidence limits.

dogwood (*Cornus florida*), and black cherry (*Prunus serotina*). Collectively, this density was dynamic over time but never differed between CF and CFH.

Large-sapling density did not differ between CF and CFH (Table 1). From 2011 to 2012, such density declined by 73% (−31.6 stems ha^{-1} ± 10.6 SE) in CFH, but also declined by 50% in CF (−21.8 stems ha^{-1} ± 12.4 SE, Fig. 2). However, only in CFH was large-sapling density less than pre-treatment (2011) levels in 2012 and 2013 (Fig. 2). Herbicide effects on large-sapling density were similar across variation in canopy disturbance ($F_{1,36} = 0.03$, $p = 0.861$) and fire-season ($F_{1,36} = 0.10$, $p = 0.756$). The density of large-sapling flowering dogwood was greater in CF than CFH ($F_{1,36} = 9.99$, $p = 0.003$, Fig. 2), but herbicide effects did not exceed canopy disturbance and fire effects for all other dominant species in the large-sapling size class ($F \leq 3.54$, $p \geq 0.068$). Together, these species constituted 80.0% (±6.2 SE) of large-sapling density.

Tree-of-heaven (*Ailanthus altissima*) was the only non-native and invasive woody plant documented in this study. A seedling was observed in two CF plots in 2011, but the species was not observed again. Aspect and percent slope were not influential on woody vegetation (Table 1). Seedling density increased with slope position (+4,326 stems ha^{-1} ± 1,409 SE), and was greatest along ridges. Canopy closure influenced shrubby (−367 stems ha^{-1} ± 59 SE), small-sapling (−19 stems ha^{-1} ± 4 SE), and large sapling (+0.08 stems ha^{-1} ± 0.01 SE) density (Table 1). A cubic canopy closure model explained 50.3% of the variation in small-sapling density ($F_{1,\ 239} = 11.2$, $p < 0.001$; inflection point, 50.2%; Fig. 3).

4.2. Herbaceous layer response

Herbicide treatments promoted increases in herbaceous groundcover only when associated with heavy canopy disturbance (5.0 $m^2\ ha^{-1}$ residual basal area ± 0.7 SE, 23.5% canopy closure ± 3.9 SE) and fall fire (Table 1, Fig. 4). This included 18.2% (±7.1 SE) and 8.0% (±3.6 SE) increases in graminoid and forb groundcover, respectively. Herbicide treatment effects were consistent across variation in canopy disturbance for graminoid ($F_{1,36} = 1.22$, $p = 0.276$) and forb ($F_{1,36} = 0.00$, $p = 0.949$) groundcover. We documented 83 species of herbaceous plants before herbicide application (2011). After application (2012), we documented 93 species. Despite this moderate increase in richness, herbicide treatments did not affect herbaceous richness or diversity beyond whole-plot effects (Table 1). Herbicide effects on herbaceous richness and diversity also did not differ across variation in canopy-disturbance ($F_{1,36} \leq 0.06$, $p \geq 0.802$) or fire-season ($F_{1,36} \leq 1.24$, $p \geq 0.272$).

Herbaceous groundcover in 2013 was dominated by native cool-season grasses (Table 3). Variable panicgrass (*Dichanthelium commutatum*) was consistently the most abundant species by groundcover across treatments. Povertygrass (*Danthonia* spp.), needlegrass (*Piptochaetium avenaceum*), slender woodoats (*Chasmanthium laxum*), and additional species of deertongue grasses (*Dichanthelium* spp.) also contributed substantially to graminoid groundcover. Only two C_4 grass species (*Andropogon virginicus* and *Schizachyrium scoparium*) had ≥1% groundcover in any one treatment. Rabbit tobacco (*Pseudognaphalium obtusifolium*) and American burnweed (*Erechtites hieraciifolius*) dominated forb response. These species and horseweed (*Conyza canadensis*) were even more abundant immediately following fire. Declines in these forbs were offset by increases in less ruderal forbs, including sweet-scented goldenrod (*Solidago odora*), whorled coreopsis (*Coreopsis major*), and whorled loosestrife (*Lysimachia quadrifolia*). Legume species only exceeded 1% groundcover in savanna treatments. In general, the groundcover of most species was greater in savannas than woodlands and separation between CF and CFH only occurred in FaS (Table 3).

We documented two non-native and invasive herbaceous species: Nepalese browntop (*Microstegium vimineum*) and sericea lespedeza (*Lespedeza cuneata*). Groundcover of these species in any one stand never exceeded 1%, and the number of plots where these species were present declined from 2011 to 2013 (Nepalese browntop: 5, 3, 0; sericea lespedeza: 2, 0, 0).

Slope position and canopy closure routinely influenced the

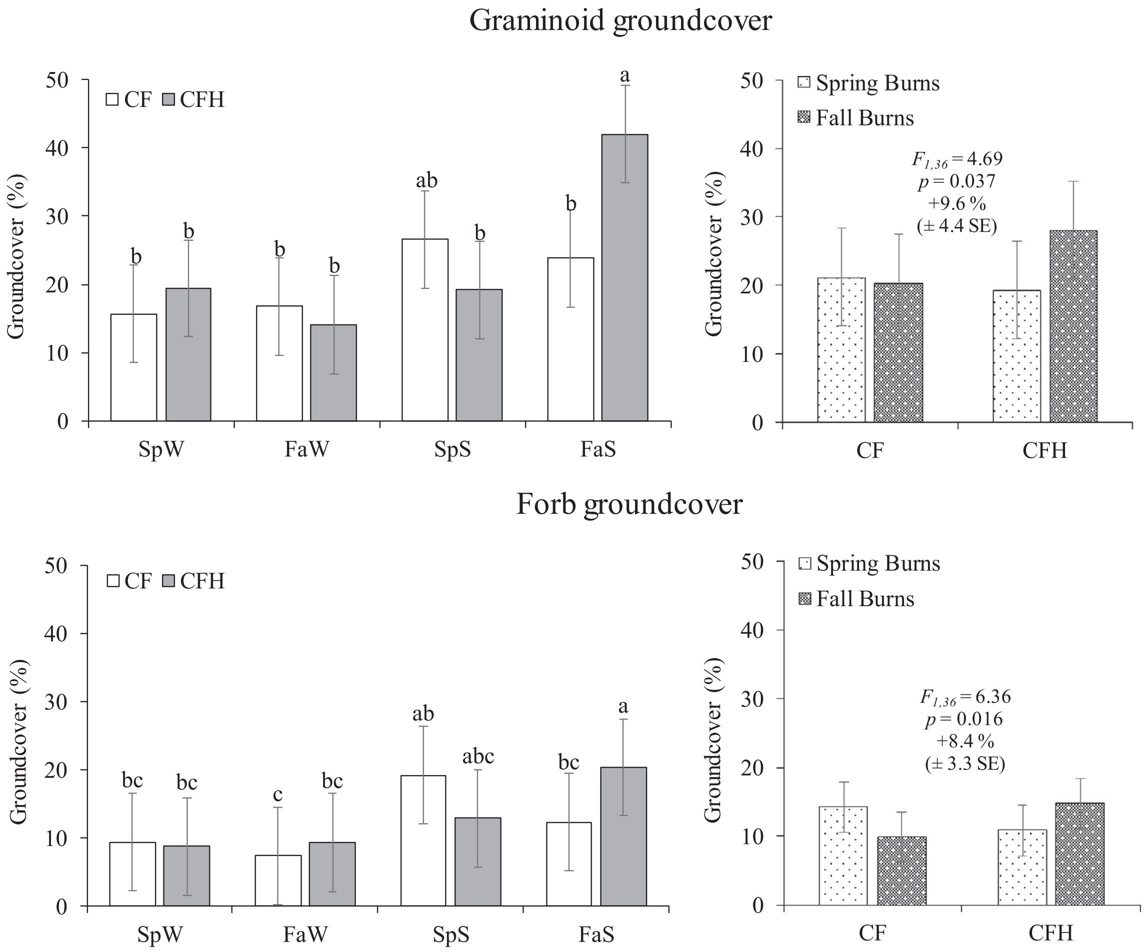

Fig. 4. Herbicide effects on graminoid and forb groundcover during (2011–2013) an oak woodland and savanna restoration experiment at Catoosa Wildlife Management Area, Cumberland County, TN. Garlon 3 A® was not (CF) or was (CFH) applied to stands reduced to woodland (W, 16 $m^2 ha^{-1}$, 75% canopy closure) or savanna (S, 7 $m^2 ha^{-1}$, 24% canopy closure) overstory and burned in the spring (Sp, March) or fall (Fa, October). Graminoid and forb groundcover response also differed by burn treatment (significant contrast). Lowercase letters represent LSD differences ($\alpha = 0.05$). For each year and herbicide treatment, n = 40, 0.04-ha plots.

herbaceous ground-layer (Table 1). Herbaceous richness and diversity were negatively related to slope position (−1.04 species $plot^{-1}$ ± 0.32 SE, −0.14 H′ ± 0.05 SE) and canopy closure (−0.04 species $plot^{-1}$ ± 0.01 SE, −0.01 H′ ± $0.13e^{-2}$ SE), but neither were affected by herbicide treatments. Graminoid ($F_{1,\ 239} = 72.4$, $p < 0.001$, $r^2 = 0.67$) and forb ($F_{1,\ 239} = 104.1$, $p < 0.001$, $r^2 = 0.75$) groundcover declined linearly as canopy closure increased (Fig. 3). Graminoid groundcover also decreased toward ridges and was greatest at alluvial slope positions ($F_{1,\ 239} = 6.6, p = 0.011, r^2 = 0.75$).

5. Discussion

5.1. Understory woody vegetation response

Similar to other research (Outcalt and Brockway, 2010; McCord et al., 2014), the high-light environments of woodlands and savannas encouraged the establishment and vigorous growth of seedlings and shrubs. Seedling density exceeded 30,000 stems ha^{-1}, even after 2 fires. Woody encroachment poses a major threat to restoration (Briggs et al., 2005), but little evidence directly connects dense seedling layers to negative effects on herbaceous layer development. The uniformity of such density across our study limited trend detection. Woody stems < 1.37 m tall were treated if they were vigorously sprouting (> 2.54 cm in root-collar diameter), but small stems likely to be top-killed by fire were not treated (Hutchinson et al., 2012). Some untreated stems were sprouts from established roots. Controlling these stems with fire is difficult (Arthur et al., 2015), so relaxing the lower size restrictions held during herbicide application could improve results. The understory can be dominated by seedlings even after effective broadcast application of herbicide (Lashley et al., 2011; McCord et al., 2014). In contrast, Nanney (2016) successfully transitioned a young forest dominated by woody regeneration into an early successional community dominated by herbaceous plants after spot-spraying all woody vegetation three years following a clearcut harvest. Taken together, these results suggest treating all understory woody stems may not benefit herbaceous plants if the overstory remains an abundant source of seeds. In our study, fire-intolerant species with seeds easily dispersed by wind (red maple, sourwood, sweetgum [*Liquidambar styraciflua*], yellow poplar [*Liriodendron tulipifera*]) or wildlife (flowering dogwood, American holly [*Ilex opaca*]) were unintentionally retained in the overstory (< 1 $m^2 ha^{-1}$). These species were 58% of total seedling density, illustrating the importance of their removal from the overstory. Regardless, expanding herbicide control to newly established seedlings and shrubs under partial canopies may not be as economical as fire.

Herbicide applications only temporarily reduced small-sapling density beyond the effects of fire. Red maple, a fire-sensitive species, constituted a large portion of the observed difference in small-sapling density between herbicide treatments. The second fire top-killed many of these stems, eliminating the enhanced woody control that herbicides provided. Large-sapling density was also dominated by fire-sensitive

Table 3
Mean (SE) percent groundcover of dominant herbaceous species in 2013 across canopy disturbance, fire-season, and herbicide treatments within an oak woodland and savanna restoration experiment, Catoosa Wildlife Management Area, Cumberland County, TN.

	Treatment[b]							
	SpW		FaW		SpS		FaS	
Species[a]	CF	CFH	CF	CFH	CF	CFH	CF	CFH
Graminoids								
Variable panicgrass (*Dichanthelium commutatum*)	5.3 (1.6)	5.4 (1.9)	5.9 (3.0)	6.3 (2.8)	8.0 (3.1)	6.9 (2.8)	9.4 (3.3)	12.4 (3.1)
Povertygrass (*Danthonia* spp.)	4.0 (1.5)	6.0 (4.2)	2.3 (1.4)	1.7 (0.9)	4.8 (2.4)	2.9 (1.0)	2.2 (0.8)	7.6 (2.2)
Needlegrass (*Piptochaetium avenaceum*)	1.3 (0.6)	2.1 (1.0)	2.4 (1.0)	2.3 (0.8)	6.6 (2.8)	5.3 (2.8)	4.8 (1.9)	5.2 (1.3)
Cypress panicgrass (*Dichanthelium dichotomum*)	3.3 (1.5)	4.7 (2.1)	0.5 (0.3)	–	1.1 (0.5)	1.9 (0.7)	2.1 (0.9)	8.4 (3.2)
Slender woodoats (*Chasmanthium laxum*)	2.1 (1.5)	0.6 (0.5)	2.7 (1.2)	2.7 (1.1)	1.3 (0.5)	1.9 (0.6)	4.0 (1.8)	2.2 (0.7)
Sedge (*Carex* spp.)	1.9 (0.9)	2.8 (1.4)	2.3 (0.9)	1.8 (0.7)	2.9 (0.9)	1.5 (0.6)	1.1 (0.5)	2.8 (0.8)
Broomsedge (*Andropogon virginicus*)	1.1 (0.6)	1.9 (0.9)	0.5 (0.4)	1.0 (0.8)	2.1 (0.8)	3.3 (2.2)	2.5 (0.7)	3.2 (1.2)
Little bluestem (*Schizachyrium scoparium*)	1.1 (0.7)	0.3 (0.2)	0.6 (0.6)	0.4 (0.3)	2.1 (1.0)	0.9 (0.5)	1.5 (0.8)	4.4 (1.8)
Openflower rosettegrass (*Dichanthelium laxiflorum*)	0.7 (0.4)	0.6 (0.4)	2.3 (0.9)	2.2 (1.0)	2.9 (1.5)	2.7 (1.4)	2.7 (1.2)	1.0 (0.5)
Needleleaf rosettegrass (*Dichanthelium aciculare*)	–	0.6 (0.6)	1.9 (0.8)	1.2 (0.5)	0.5 (0.3)	0.7 (0.5)	0.9 (0.5)	0.2 (0.2)
Many-flowered deertongue (*Dichanthelium polyanthes*)	0.5 (0.4)	–	0.5 (0.4)	0.2 (0.2)	0.3 (0.2)	0.3 (0.2)	1.1 (0.6)	0.4 (0.4)
Forbs								
Rabbit tobacco (*Pseudognaphalium obtusifolium*)	2.1 (0.8)	4.8 (2.6)	2.8 (1.2)	3.7 (2.1)	5.3 (2.8)	5.5 (2.9)	2.3 (1.2)	5.3 (3.3)
American burnweed (*Erechtites hieraciifolius*)	1.5 (0.6)	1.1 (0.2)	1.0 (0.5)	1.3 (0.5)	6.5 (3.2)	1.8 (0.8)	3.7 (1.8)	6.3 (2.9)
Sweet-scented goldenrod (*Solidago odora*)	2.1 (0.8)	1.5 (0.3)	1.3 (0.4)	1.7 (0.6)	0.8 (0.4)	1.7 (0.9)	1.5 (0.7)	2.7 (1.1)
Whorled coreopsis (*Coreopsis major*)	2.1 (1.2)	0.9 (0.6)	1.4 (0.3)	1.4 (0.4)	1.0 (0.4)	1.1 (0.6)	1.1 (0.7)	1.3 (0.4)
Whorled loosestrife (*Lysimachia quadrifolia*)	1.7 (0.6)	0.5 (0.4)	1.0 (0.5)	0.8 (0.2)	2.2 (1.0)	0.6 (0.3)	1.4 (0.8)	1.1 (0.6)
Horseweed (*Conyza canadensis*)	0.8 (0.2)	0.4 (0.2)	0.9 (0.6)	0.6 (0.4)	0.9 (0.3)	0.7 (0.3)	0.9 (0.5)	1.2 (0.7)
Wrinkleleaf goldenrod (*Solidago rugosa*)	0.2 (0.2)	0.6 (0.6)	0.4 (0.2)	0.5 (0.4)	0.8 (0.4)	1.5 (0.7)	1.3 (0.7)	0.3 (0.2)
Smooth creeping bush clover (*Lespedeza repens*)	0.4 (0.2)	0.5 (0.2)	0.4 (0.3)	0.4 (0.4)	1.1 (1.0)	0.9 (0.8)	0.2 (0.2)	0.3 (0.2)
Late-flowering thoroughwort (*Eupatorium serotinum*)	–	0.4 (0.4)	0.6 (0.4)	0.4 (0.2)	1.3 (0.7)	0.6 (0.4)	–	0.5 (0.3)
Tall bush clover (*Lespedeza hirta*)	0.3 (0.3)	0.2 (0.2)	–	0.3 (0.2)	–	–	1.5 (0.6)	0.6 (0.3)
Loomis' mountain mint (*Pycnanthemum loomisii*)	–	0.6 (0.3)	0.2 (0.2)	0.4 (0.3)	1.1 (0.8)	–	0.3 (0.3)	0.6 (0.2)
Dwarf cinquefoil (*Potentilla canadensis*)	0.5 (0.3)	0.4 (0.2)	0.3 (0.3)	0.2 (0.2)	0.3 (0.3)	1.1 (0.4)	0.9 (0.6)	0.7 (0.4)
Small-flowered partrigde pea (*Chamaecrista nictitans*)	0.3 (0.2)	0.2 (0.2)	–	0.2 (0.2)	0.2 (0.2)	–	0.2 (0.2)	1.3 (0.5)
Downy creeping bush clover (*Lespedeza procumbens*)	0.5 (0.5)	0.4 (0.4)	–	–	0.5 (0.3)	0.2 (0.2)	–	1.1 (0.6)

[a] Species with ≥1% groundcover in a treatment presented in descending order of overall groundcover within graminoid and forb groupings.
[b] Foliar and hack-and-squirt applications of Garlon 3 A® did not (CF) or did (CFH) follow reduction to woodland (W, 16 m^2 ha^{-1}, 75% canopy closure) or savanna (S, 5 m^2 ha^{-1}, 24% canopy closure) overstory and either spring (Sp) or fall (Fa) fire. For each column n = 10, 0.04-ha plots.

species, and declined similarly regardless of herbicide treatment. Fire alone either induced mortality or shifted stems into smaller size-classes. Forest understories throughout the Appalachian region are dominated by fire-sensitive woody species as a result of decades of fire-suppression (Nowacki and Abrams, 2008). This renders our results widely applicable, and reduces the utility of herbicides relative to fire in the region. However, herbicides could be used to selectively enhance the competitive position of fire-tolerant woody species (Lorimer et al., 1994) and address concerns related to the sustainability of open-oak communities (Peterson and Reich, 2001). In addition, fire only top-killed many stems and resprouting is likely (Knapp et al., 2009; Hutchinson et al., 2012). Repeated fire decreases sprouting capacity, and ultimately can eliminate some woody stems (Waldrop et al., 1992), but only if applied without gaps ≥ 3 years during which below-ground resources can be replenished (Hutchinson et al., 2012; Arthur et al., 2015). A dense midstory can remain even after burning for > 60 years if fires only occur every 4 years (Knapp et al., 2015). In contrast, herbicides are translocated and kill the entire plant. Long-term monitoring is required to document the implications of using herbicides to remove vigorously sprouting stems from stand development.

Within the size-classes where it was applied, herbicide-induced mortality was apparent (brown foliage, no basal sprouts). However, herbicide-induced mortality could have been < 100%. Increasing triclopyr concentration above the suggested 2% rate (Dow AgroSciences LLC, 2005) could increase treatment effectiveness. Also, alternative application timing (*e.g.*, prior to canopy disturbance) or combinations of herbicides (tank mixes) that provide a broader spectrum of species control should be explored. Soil-active herbicides can provide impressive control of woody plants (Nanney 2016), but potential mortality of overstory hardwoods limits their use during oak woodland and savanna management. Covariate relationships indicated that the efficacy of herbicide treatments could also be improved in savannas by targeting areas where canopy closure is < 30%. Controlling the increases in small-sapling density that occurred below this threshold would benefit herbaceous groundcover where it is poised to respond. For woodlands, herbicide applications should target areas where canopy closure is < 80%. Above this threshold, herbaceous groundcover and small-sapling density were limited by the overstory.

Reductions in small-sapling density associated with herbicide treatments were 3X greater in plots burned in October (prior to leaf abscission) relative to plots burned in March (before bud break). Resprouting can be less vigorous following growing-season fire than dormant-season fire (Gruchy et al., 2009; Robertson and Hmielowski, 2014), but few regional studies have explored if this advantage extends into October (Sparks et al., 1998). Data collected at our site from 2008 to 2012 found no difference in woody control between October and March fires (Vander Yacht et al., 2017), and there was still no difference after herbicide treatments. However, the difference in small-sapling density between untreated and treated plots was 1,050 stems ha^{-1} greater for plots burned in the fall relative to spring. We believe the increased efficacy of herbicides following fall fire resulted from a difference in the below-ground resources of woody plants across the fire-seasons. Top-kill during the growing-season can disrupt carbohydrate translocation to the roots more so than top-kill during dormancy (Huddle and Pallardy, 1999), and translocation to roots can continue well into November (Loescher et al., 1990). Regardless of the mechanism, a subtle, but positive, advantage of October relative to March fire for the control of woody vegetation was apparent in our results. We do not believe this conclusion is confounded by fire intensity because dependent variable and fire temperature relationships were either adjusted for or insignificant.

5.2. Herbaceous layer response

Transitioning understory dominance from woody to herbaceous plants in eastern oak communities may require more than repeated fire (Hutchinson et al., 2012). Herbicides have been effective in restoring oak savannas along the western periphery of their historical range (Ansley and Castellano, 2006; Engle et al., 2006), and the rapid growth of woody vegetation in the wet climate of the Appalachian region may only increase their utility. Herbicide applications in our study did not affect herbaceous richness or diversity, but nearly doubled graminoid and forb groundcover. This is the greatest reported increase in herbaceous groundcover to be associated with herbicide applications under partial oak canopies in the Appalachian region. Without substantial canopy disturbance, the effects of understory herbicide treatments are indistinguishable from unmanaged forests (Schweitzer and Dey, 2011; Greenberg et al., 2016). Although the removal of understory woody vegetation in the absence of canopy disturbance can increase ground-level light (Lorimer et al., 1994), its effects are temporary, minimal (Schweitzer and Dey, 2011), and may not increase herbaceous development (Franklin et al., 2003). Herbicides, canopy reduction, and fire were used in combination within two related studies (Lashley et al., 2011; McCord et al., 2014), but herbaceous groundcover decreased because broadcast applications of triclopyr killed many desirable, broadleaf plants (Dow AgroSciences LLC, 2005). Limited canopy disturbance, broadcast applications, and differences in applied fire may have limited the herbaceous response documented in other research.

Burning alone can require > 60 years to reduce canopy density (Knapp et al., 2015). Canopy disturbance immediately increases ground-level light and heterogeneity in plant resources (Nielsen et al., 2003; Brudvig and Asbjornsen, 2009). In combination, fire and canopy disturbance synergistically increase herbaceous groundcover and diversity (Peterson and Reich, 2008; Kinkead et al., 2013; Lettow et al., 2014; Brewer, 2016). In our study, heavy canopy disturbance (to 5.0 $m^2 ha^{-1}$ residual basal area, 23.5% canopy closure) was required to increase herbaceous groundcover. However, herbaceous response to herbicide treatments did not differ consistently between woodlands and savannas (insignificant contrasts). We believe this occurred because small-sapling density was 2,340 stems ha^{-1} (± 952 SE) greater in SpS than FaS in 2012 ($t = 2.5$, $p = 0.024$). This stresses how woody cover in both the overstory and understory can suppress herbaceous layer development (Barrioz et al., 2013; McCord et al., 2014). In addition, the dominant herbaceous species at our site were shade-tolerant, cool-season grasses. This may be typical of the early stages of restoration from closed-canopy forests (Vander Yacht et al., 2017). The benefits of similar herbicide treatments could be greater where fire suppression is more recent and shade-intolerant herbaceous species are more common.

As fire-frequency increases, groundcover of woody plants decreases and herbaceous groundcover increases (Waldrop et al., 1992; Peterson et al., 2007). In our study, herbicide treatments reduced understory woody density relative to burning alone in the second growing-season following fire. If this specific difference continues to exist over multiple burn intervals, herbaceous groundcover could expand during each iteration through a biennial burn cycle. In other words, the restoration progress attributable to a single herbicide application could increase over time because herbicide treatments eliminated woody stems in comparison to the top-kill and subsequent resprouting associated with fire. Freeman and Jose (2009) reported herbicide effects on woody vegetation dissipated after the fourth year, but benefits for herbaceous species continued even after the woody vegetation rebounded. Increases in herbaceous groundcover can also contribute fine-fuels that enhance the ability of future fires to control woody vegetation (Peterson and Reich, 2001; Nielsen et al., 2003). Without long-term monitoring, our results suggest the use of herbicides may only be justifiable under open-canopies and following fall fire. Such a conclusion is heavily influenced by the dominance of fire-sensitive woody species at our site.

Herbicide applications increased herbaceous groundcover only when paired with fall fire. Direct fire effects on perennial herbaceous plants are minimal because most sprout from rhizomes buried beneath insulating layers of soil (Holcomb et al., 2014). Indirectly, community composition can be altered over time if fires consistently occur near seasonal peaks in seed production or growth of specific species (Knapp et al., 2009). Our fall burns were ideal for promoting the abundant species of cool-season grasses present at our site, and our spring burns may have been early enough to have similar effects (Harper, 2007). Fire more generally promotes herbaceous species by releasing nutrients for growth (Scharenbroch et al., 2012), removing layers of leaf-litter that inhibit germination, and reducing competition from woody plants (Lashley et al., 2011; Knapp et al., 2015). We believe observed differences in woody control across fire seasons caused the differential response in herbaceous groundcover.

5.3. Conclusions and management implications

In our study, herbicide applications provided the greatest benefit to oak woodland and savanna restoration when associated with heavy canopy disturbance (5 $m^2 ha^{-1}$ residual basal area, 24% canopy closure) and late growing-season fire. Limiting new seedling cohorts by removing seed-sources from the overstory, increasing triclopyr concentration (*e.g.*, 5%), exploring tank-mixes with a broader spectrum of control, and alternative application timing (*e.g.*, prior to canopy disturbance) could further improve treatment efficacy. Target constraints during herbicide applications were intended to limit costs, but treating all woody sprouts following fire should be explored. Treatment efficacy was not limited by topography (slope, aspect, slope position), but would benefit from targeting sites where canopy closure is < 80 or 30% within woodlands and savannas, respectively. Only 3 invasive species were observed in our study, and encounters with each declined over time. Invasive species can pose a greater threat to restoration success at sites with a more recent history of agricultural disturbance (Brewer et al., 2015), but herbicide use presents an opportunity for additional control.

In the Appalachian region, herbicides may be less economical than fire during oak woodland and savanna restoration. Herbicide applications reduced the understory density of woody plants, led to increases in herbaceous groundcover, and did not reduce herbaceous diversity. However, repeated fire eventually matched these benefits. Herbicides reduced small-sapling density beyond the effects of fire, but only for a single growing-season. This was because fire-sensitive woody species dominated the understory of our site and limited herbicide management effects relative to fire. The composition of woody understories throughout the Appalachian region can be similarly characterized thanks to decades of fire suppression. Our results demonstrate how such composition can limit the utility of herbicides relative to fire for restoring oak woodlands and savannas. Long-term research over multiple burn cycles is needed to determine if the resprouting of woody vegetation following fire-alone allows a single herbicide application to relatively accumulate restoration benefits.

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