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Vegetation response to canopy disturbance and season of burn during oak woodland and savanna restoration in Tennessee

Andrew L. Vander Yacht [a,*], Seth A. Barrioz [b], Patrick D. Keyser [a], Craig A. Harper [a], David S. Buckley [a], David A. Buehler [a], Roger D. Applegate [a,c]

[a] Department of Forestry, Wildlife, and Fisheries, University of Tennessee, 274 Ellington Plant Sciences Building, Knoxville, TN 37996, USA
[b] Missouri Department of Conservation, 2901 W. Truman Blvd., Jefferson City, MO 65102, USA
[c] Tennessee Wildlife Resources Agency, PO Box 40747, Nashville, TN 37204, USA

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ABSTRACT

The removal of fire's influence on plant community succession has resulted in the near disappearance of oak (*Quercus* spp.) woodlands and savannas from the Appalachian region. Negative trends in associated plant and wildlife species could be reversed if these communities are restored, but management has been limited by inadequate canopy disturbance, resprouting of woody plants, and a lack of empirical research. To address these issues, we evaluated herbaceous and woody vegetation response (2008–2012) on the Cumberland Plateau in Tennessee to 5 replicated treatments involving canopy reduction (14 m^2 ha^{-1} [woodland] or 7 m^2 ha^{-1} [savanna] residual basal area) and fire-season (mid-March [spring] or early October [fall]) combinations and unmanaged controls. All categories of woody vegetation except large-saplings ($\geqslant$1.4 m tall and $\geqslant$7.6 but <12.7 cm diameter at breast height [DBH]), increased in density as canopy disturbance increased. Fire temporarily reduced small-sapling ($\geqslant$1.4 m tall and <7.6 cm DBH) density, but resprouting resulted in densities equal to or exceeding pre-fire levels. Herbaceous richness increased from 22 to 167 species following canopy disturbance and fire (2008–2012). Native cool-season grasses dominated herbaceous response in treated sites. Herbaceous groundcover, richness, and diversity increased as canopy disturbance increased, and the rate of increase accelerated once basal area was reduced below 15 m^2 ha^{-1} or 30% canopy closure. Following fire, canopy disturbance remained influential as indicated by greater herbaceous response in savannas than woodlands. Graminoid and forb groundcover, herbaceous richness, and herbaceous diversity were 24X, 11X, 9X, and 8X greater, respectively, in treatments than controls by 2012. Invasive species were rare and increased minimally with increasing disturbance. Our results demonstrate the utility of canopy disturbance in conjunction with fire for restoring oak woodlands and savannas from closed-canopy forest conditions. Basal area reduction to 15 and 7 m^2 ha^{-1} respectively approximated woodland and savanna canopy conditions, and increased herbaceous-layer development. The less intense October fire had similar effects on vegetation as the more intense March fire, but greater differences could become apparent following repeated burning. Long-term research documenting the response of vegetation to repeated fire is needed to promote successful oak woodland and savanna restoration throughout the Appalachian region.

1. Introduction

Oak (*Quercus* spp.) woodlands and savannas are among the most threatened communities in North America (Noss et al., 1995). More than 99% of Midwestern oak savannas have vanished since European settlement (Nuzzo, 1986), and declines further east are similar (Delcourt et al., 1998; Brewer, 2001). Early explorers described scattered trees, ground-layers dominated by native warm-season grasses and forbs, and herds of large herbivores (Michaux, 1805; Ramsey, 1853; Van Lear and Waldrop, 1989) across much of the Central Hardwoods and Central and Southern Appalachian regions (hereafter Appalachian, Harper et al., 2016). A sparse oak overstory distinguished savannas (10–30% canopy cover) and woodlands (30–80% canopy cover) from prairies and forests (Faber-Langendoen, 2001; Nelson, 2010) and allowed light to reach a key characteristic of both; a robust ground-layer of

* Corresponding author.
E-mail addresses: avandery@vols.utk.edu (A.L. Vander Yacht), Seth.Barrioz@mdc.mo.gov (S.A. Barrioz), pkeyser@utk.edu (P.D. Keyser), charper@utk.edu (C.A. Harper), dbuckley@utk.edu (D.S. Buckley), dbuehler@utk.edu (D.A. Buehler), Roger.Applegate@tn.gov (R.D. Applegate).

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herbaceous vegetation (Taft, 1997). Sparse overstories also created understory gradients in plant resources (Peterson et al., 2007) that promoted levels of herbaceous diversity that exceeded both prairies and forests (DeSelm, 1994; Leach and Givnish, 1999). These unique associations between sparse oak overstories and herbaceous dominated ground-layers (Faber-Langendoen et al., 2012) are rapidly disappearing as a result of succession in the absence of disturbance (Nowacki and Abrams, 2008).

Although the decline of oak woodlands and savannas involves many factors (Heikens and Robertson, 1994), the removal of fire from its historical role in shaping community development is most frequently implicated (Abrams, 1992; McPherson, 1997; Nowacki and Abrams, 2015). Fire suppression and exclusion decreases herbaceous groundcover and diversity (Breshears, 2006) by facilitating canopy closure, increasing woody encroachment (Briggs et al., 2005), and eliminating understory plant resource gradients (Brudvig and Asbjornsen, 2009). Invading woody growth often is dominated by fire-sensitive, mesophytic species (Abrams, 1992, 1998) that promote dark, moist, and cool micro-environments, decrease fuel-bed flammability (Nowacki and Abrams, 2008; Kreye et al., 2013), and reduce or preclude herbaceous vegetation (Hutchinson et al., 2005; Barrioz et al., 2013; McCord et al., 2014). Decreasing biodiversity increases oak ecosystem susceptibility to invasive species and disease (Knops et al., 1999) and may decrease sustainability and productivity (Tilman et al., 1996; Liang et al., 2016). The diverse array of niches present within oak woodlands and savannas result in an equally diverse wildlife community, increasing the conservation value of such communities in an era marked by widespread habitat loss and fragmentation (Cox et al., 2016; Vander Yacht et al., 2016).

Another critical form of disturbance, canopy reduction, produces desirable and immediate shifts in overstory species composition and structure (Nielsen et al., 2003) which promotes herbaceous response through increasing the amount of light reaching the forest floor (Leach and Givnish, 1999; Brudvig and Asbjornsen, 2009). Thus, canopy reduction accelerates restoration while possibly generating timber revenue to offset costs. On the other hand, the increased availability of understory light also results in the vigorous growth of woody seedlings and sprouts (McCord et al., 2014). The ability of repeated fire to transition understory dominance from woody to herbaceous species makes it an essential tool for community restoration and maintenance (McPherson, 1997; Peterson and Reich, 2001). However, using low- to moderately-intense fire is often insufficient because it is slow to alter overstory characteristics (Knapp et al., 2015). Fires of greater intensity can damage or kill overstory trees, but this is generally undesirable during woodland and savanna restoration where retained trees define the target community (Peterson and Reich, 2001). Restoration goals are best achieved when both canopy disturbance and fire are used in conjunction (Peterson et al., 2007; Lettow et al., 2014).

Most restoration has occurred along the western edge of the historical range of oak woodlands and savannas, where drier conditions and a more recent history of fire suppression and exclusion have allowed such structure to persist. The longer absence of fire and wetter climate within the Appalachian region necessitates restoration proceed from closed-canopy forests. Attempts to restore oak woodlands (Jackson et al., 2006; McCord et al., 2014; Brewer et al., 2015) and savannas (Barrioz et al., 2013) in this region are rare and characterized by the persistence of woody undergrowth. Such growth is usually controlled with dormant-season fire, but woody plants often resprout prolifically (Blankenship and Arthur, 2006; Knapp et al., 2009) and are only eliminated if such fire is applied repeatedly (Arthur et al., 2015). Research has demonstrated that a single late growing-season fire can result in comparatively greater woody plant mortality and herbaceous layer gains than a single dormant-season fire (Keyser et al., 1996; Brose and Van Lear, 1998; Gruchy et al., 2009). Thus, a transition to late growing-season burning could reduce the number of fires required to achieve similar restoration progress. However, the effects fire-season on Appalachian plant communities is poorly understood (Gilliam and Roberts, 2003; Hutchinson et al., 2005; Harper et al., 2016) because very few burning-season studies have occurred in the region (Knapp et al., 2009). In addition, effect interpretation is often complicated by seasonal differences in fire intensity (Brose et al., 2014).

We applied restoration treatments to closed-canopy oak forests in Tennessee to assess their relative effectiveness for restoring oak woodlands and savannas. Our objective was to assess the effects of canopy reduction (woodland vs. savanna) and season of burn (fall vs. spring) on key measures of oak woodland and savanna restoration success including (1) decreased ground-layer dominance of woody and semi-woody vegetation, especially pyrophobic species, (2) establishment of a dominant and diverse herbaceous ground-layer, and (3) control of nonnative and invasive species. We predicted herbaceous groundcover, richness, and diversity would increase with increasing canopy disturbance, but richness and diversity would peak at intermediate levels of overstory density. We similarly expected woody density in the understory to increase with increasing canopy disturbance. We expected fire applied prior to leaf abscission (fall) would result in greater control of woody density, and, therefore, greater increases in herbaceous metrics, than fires occurring just before bud-break (spring).

2. Methods

2.1. Study area

We conducted our research at Catoosa Wildlife Management Area (CWMA), 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 (Soil Survey Staff Natural Resources Conservation Service, 2014) over weathered sandstone and conglomerate (Nicholson et al., 2005). Annual mean precipitation and temperature were 140 cm and 13 °C, respectively, for nearby Crossville, TN (National Climatic Data Center, 2014). Forests were established in the 1920s following logging and agricultural abandonment and are currently oak-dominated, mixed pine-hardwood stands. Shortleaf pine (*Pinus echinata* Mill.) was a major overstory component prior to a pine bark beetle (*Dendroctonus frontalis* Zimmerman) outbreak in 1999–2000. Salvage cutting began in 2002, and subsequently, TWRA implemented an oak savanna restoration project using prescribed fire. The rapid development of common prairie and savanna flora and historical accounts (i.e., pasturing cattle and frequent fire until ca. 1945) provided evidence of previous woodland and savanna conditions at our site (Coffey, 2012; Barrioz et al., 2013).

At our site (36° 07′ 51.71″ N, 84° 87′ 12.49″ W) prior to treatment (2008), white (*Quercus alba* L.), southern red (*Q. falcata* Michx.), black (*Q. velutina* Lam.), and scarlet (*Q. coccinea* Muench.) oaks, as well as red maple (*Acer rubrum* L.), sourwood (*Oxydendrum arboreum* L.), and hickories (*Carya* spp.) were all >1.0 m^2 ha^{-1} of total basal area (17.8 m^2 ha^{-1}) and canopy closure was >85%. Snags were common as a result of beetle-killed pines (3.9 m^2 ha^{-1}). Mid-story vegetation (>1.37 m tall, <12.7 cm diameter at breast height [DBH]) was dense (1936 stems ha^{-1}), and dominant species included blackgum (*Nyssa sylvatica* Marsh.), downy serviceberry (*Amelanchier arborea* (Michx. F.) Fern.), red maple, sourwood, and sassafras (*Sassafras albidum* (Nutt.) Nees.). Blueberry (*Vaccinium*

spp.), seedlings, and litter dominated ground-layers containing little herbaceous vegetation (4.4% cover, Vander Yacht, 2013).

2.2. Experimental and sampling design

We delineated ten, 20-ha experimental units (stands) within a 300-ha area in 2008. Boundaries were configured to maximize core area. Using a completely randomized design with two replicates, we assigned 1 of 5 treatments to each stand: spring fire and woodland residual basal area (14 m^2 ha^{-1}, SpW), fall fire and woodland residual basal area (FaW), spring fire and savanna residual basal area (7 m^2 ha^{-1}, SpS), fall fire and savanna residual basal area (FaS), and unmanaged controls (Control). Commercial logging (winter 2008–2009) removed fire-intolerant species like maples (*Acer* spp.), yellow poplar (*Liriodendron tulipifera* L.), and sweetgum (*Liquidambar styraciflua* L.) and, where possible, oaks, hickories, and shortleaf pine were retained (Fig. 1). Canopy disturbance shifted overstory composition toward oak dominance (58.7% ± 3.0 SE in 2008 to 75.4% ± 2.6 SE in 2012). Post thinning, basal area of southern red oak, white oak, scarlet oak, red maple, sourwood, post oak, and black oak was all $\geqslant$1.0 m^2 ha^{-1}.

We collected pre-treatment (May–June of 2008), post-canopy disturbance (May–August of 2009 and 2010), and post-fire (May–August of 2011 and 2012) data. To reduce the influence of edges, all sampling occurred in the core (50-m buffer) of each 20-ha stand. We sampled 15 plots per stand per year: 11 located along a 70 × 70 m grid (Avery and Burkhart, 2002) and at 4 point-count locations associated with concurrent avian research (Vander Yacht et al., 2016). We recorded slope (%), aspect (°), and slope position from each plot center. Each plot was assigned a numerical code 1–6 that corresponded to alluvial, cove, toe-slope, mid-slope, shoulder, and ridge slope positions, respectively. We determined canopy closure from four spherical densiometer readings taken in each cardinal direction from plot center. We sampled overstory trees within an 11.3-m radius around plot center by identifying to species all trees >12.7 cm in DBH and tallying stems within 5.1-cm interval DBH size classes. Basal area (m^2 ha^{-1}) for each plot was calculated using the midpoint DBH of each size class and associated stem counts.

2.3. Prescribed fires

Fall fires were conducted by TWRA 11 October 2010 prior to leaf abscission, and spring fires 22 March 2011 prior to leaf emergence. Ring and strip-head firing was used as dictated by vegetation density and associated safety concerns. Backing-fires rarely burned into stand cores, which were burned by heading (70%) and flanking (30%) fire. Before ignition, we collected 10, 0.25-m^2 fine-fuel samples (litter and 1-h fuels) at 3 random locations in each stand. We weighed samples in the field and again after oven drying (5 days at 116 °C) to determine moisture content. We also used 10-h fuel-moisture sticks placed at each random location 3 days in advance of each burn. At 30-min intervals during fires, we used a Kestrel© weather meter (Nielsen-Kellerman, Boothwyn, PA) to record ambient temperature (°C), relative humidity (%), wind speed (m s^{-1}), and wind direction (°). We determined rate of spread (m min^{-1}) and mean flame length (m) by fire type (flanking or heading) at systematically established sampling points. We sampled fire temperature at vegetation plots using foil-wrapped ceramic tiles painted with Tempilaq® indicating liquids (79, 107, 135, 163, 191, 218, 246, 274, 343, 371, 399, and 427 °C). We measured scorch height on all overstory stems tallied within sub-plots the following summer.

A two-sample *t*-test assuming unequal variance compared variables describing fires. Both fires occurred during similar ($p > 0.125$) cloud cover (clear), ambient temperature (25.8 °C ± 2.3 SE), and relative humidity (36.9% ± 5.8 SE). Spring fires were characterized by mean wind speeds (3.9 m s^{-1} ± 0.8 SE) that were more than triple ($p < 0.001$) that observed in the fall (1.2 m s^{-1} ± 1.2 SE) and sustained gusts of up to 6.2 m s^{-1}. Winds were out of the northwest (307.0° ± 39.3 SE) in the fall, and out of the southwest (247.1° ± 14.8 SE) during the spring ($p = 0.002$). Moisture content of 10-h fuels did not differ by season ($p < 0.950$, 11.3% ± 0.5 SE), but fine-fuel moisture was greater ($p = 0.001$) in the fall (14.3% ± 3.5 SE) than in the spring (10.2% ± 3.0 SE). Flanking fires did not differ by season in rate of spread (0.7 m min^{-1} ± 0.2 SE, $p = 0.802$) or flame length (0.8 m ± 0.5 SE, $p = 0.489$). Heading fires spread nearly twice as fast ($p < 0.001$) in the spring (2.7 m min^{-1} ± 0.5 SE) relative to fall (1.4 m min^{-1} ± 0.5 SE). Flame lengths during spring burns (1.6 m ± 0.2 SE) were more than triple that observed in the fall (0.5 m ± 0.2 SE, $p < 0.001$). Spring fires also resulted in greater ($p \leqslant 0.008$) scorch height (2.1 m ± 0.2 SE) and burn temperatures (158.0 °C ± 9.1 SE) than fall fires (1.2 m ± 0.2 SE, 75.5 °C ± 11.0 SE).

2.4. Vegetation response data collection

We sampled woody vegetation using fixed-area sub-plots located systematically within each plot (Cox et al., 2016). We located five 1-m^2 sub-plots at 12.5-m intervals along a 50-m transect running perpendicular to slope through plot center. An additional two 1-m^2 sub-plots were located 12.5 m from plot center

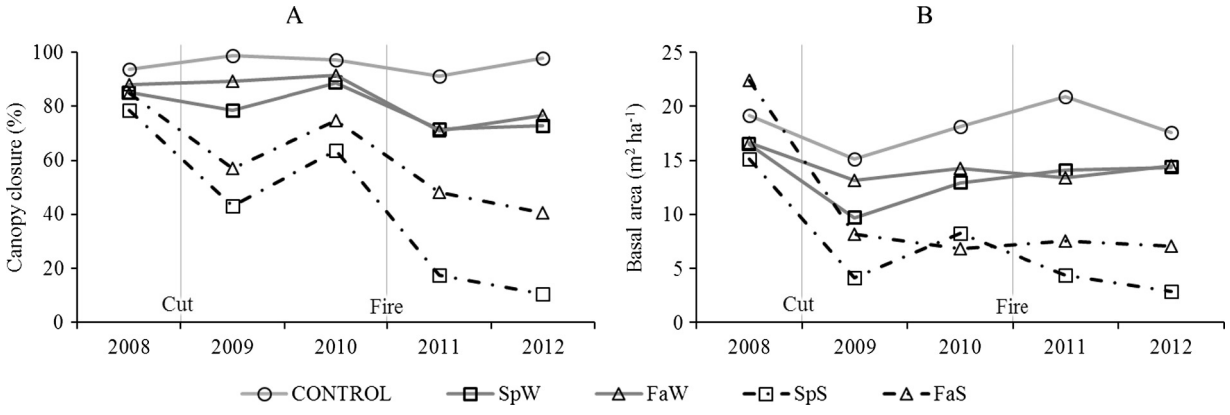

Fig. 1. Mean canopy closure (%, A) and basal area (m^2 ha^{-1}, B) during an oak woodland and savanna restoration experiment (2008–2012) at Catoosa Wildlife Management Area, Cumberland County, TN. Control, unmanaged stands; SpW, spring fire and woodland residual basal area (14 m^2 ha^{-1}); FaW, fall fire and woodland residual basal area; SpS, spring fire and savanna residual basal area (7 m^2 ha^{-1}); and FaS, fall fire and savanna residual basal area. For each treatment and year n = 2, 20-ha stands.

in the up- and down-slope directions. We constructed a 3-m radius sub-plot around each 1-m^2 sub-plot location. Within the seven 1-m^2 sub-plots, we tallied all seedling and shrubby vegetation stems by species. Stems of tree species (typically reaching ⩾4 m in height) that were ⩾30.5 cm tall but <1.4 m tall were considered seedlings. Stems of woody and semi-woody species that were typically multi-stemmed and rarely >4 m tall were considered shrubby vegetation. Blueberries, woody vines (largely *Vitis* spp.), brambles (*Rubus* spp.), and greenbriers (*Smilax* spp.) composed the majority of this group. We tallied sapling stems by size-class and species within the seven 3-m radius sub-plots. Size-classes included small- (⩾1.4 m tall and <7.6 cm DBH) and large- (⩾1.4 m tall and ⩾7.6 but <12.7 cm DBH) saplings. Stems, and not individual plants, were counted to capture sprouting response to treatments. In 2008, plots included one 1-m^2 and one 3-m radius sub-plot. In 2009, plots included three 1-m^2 and three 3-m radius sub-plots. Seven sub-plots of each kind were monitored at each plot starting in 2010; the addition of sub-plots over time helped to reduce sampling variation.

We determined stem density by size-class for 2 groups of tree species based on pyrogenicity: pyrophobic (fire-sensitive) and pyrophyllic (fire-adapted). This allowed us to differentiate effects between species potentially sensitive to fire (largely red maple, sourwood, eastern white pine [*Pinus strobus* L.], and flowering dogwood [*Cornus florida* L.]) and fire-tolerant species (largely sassafras, blackgum, oaks, and hickories). We determined pyrogenicity for each tree species using the Fire Effects Information System (U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Missoula Fire Sciences Laboratory, www.feis-crs.org/feis/), designations within Nowacki and Abrams (2015), and published accounts of species' response to fire. Where disagreement between sources occurred, we relied on author knowledge to influence final group designation (Appendix Table A1).

We characterized herbaceous groundcover along the 50-m transect at 1-m intervals using the point-intercept method (Bonham, 1989). At each interval, we identified all intersecting herbaceous vegetation below a height of 1.37 m to species and categorized each as graminoid, legume, other forb, or fern. We calculated percent groundcover for each category as the number of intercepts where a category was present divided by the total number of intercepts (50). We used these data to determine plot-level herbaceous richness and diversity using Shannon-Wiener's Index (H′) (Magurran, 1988).

3. Data analysis

For each year of data collection (2008–2012), we calculated stand-level means of dependent variables including the density of woody stems by size class (shrubby vegetation, seedlings, small-saplings, and large-saplings) and pyrogenicity (pyrophobic and pyrophyllic) groups, percent groundcover by category (graminoid, legume, and other forb), herbaceous richness, and herbaceous diversity. We developed separate ANCOVA/ANOVA models for each dependent variable and included repeated measures, covariates, mixed-effects. Prior to modeling, we tested each dependent variable for normality (Wilk's test, $W > 0.90$), transformed using a square root function when necessary, and graphically observed equality of variance. Fixed-effects included covariates, treatment, year, and treatment × year interactions. Year was a fixed-effect because treatments were applied over time. Random-effects included replicate × treatment and year × replicate × treatment interactions. We used Kenward-Roger degree of freedom method but dropped autoregressive correlation between annual data because treatments were applied over time and differences in model fit were small (<5, −2 residual log likelihood per covariance parameter) between inclusion and omission (Littell et al., 2006). We conducted all analysis in SAS 9.4 using PROC MIXED (SAS Ins., Cary, N.C., USA).

Basal area and canopy closure covariates were included to address variation inherent in applying treatments across operational scales. Landscape covariates (aspect, slope, and slope position) were also included. We transformed aspect following Beers et al. (1966) to yield a continuous variable between 0.00 (southwest) and 2.00 (northeast). In groundcover and seedling models, we included the density of large-saplings as a covariate. Such vegetation pre-existed management and could affect lower strata development (Barrioz et al., 2013). Woody stems <7.6 cm DBH can be easily top-killed by fire (Hutchinson et al., 2012; Brose et al., 2014), and, therefore, were not included within the midstory covariate to avoid confounding fire effects.

We isolated fire-season effects by accounting for variation associated with fire intensity. A linear regression between fire temperature (independent variable) and scorch height (dependent variable) revealed a positive relationship ($F_{1,41} = 10.25$, $p = 0.003$, slope = 11.8 °C m^{-1} ± 3.7 SE). We concluded scorch height was an acceptable surrogate for fire temperature and representative of fire intensity. This was useful because all plots had associated scorch-height means, but only a subset of plots had reliable pyrometer readings. We then used linear regression to determine the relationship between scorch height and post-fire (2011 and 2012) dependent variables. When a relationship was significant ($\alpha = 0.05$), we adjusted post-fire means of dependent variables to predicted values at mean scorch height prior to running models.

We did not observe evidence of non-linearity when dependent variable and covariate relationships were plotted. When a covariate effect was significant, we added a fixed-effect covariate × treatment interaction. Such interactions were never significant, so they were dropped from models and homogeneity of covariate slopes across treatments was concluded. A similar method determined homogeneity of covariate slopes across years. Although the partial r^2 of some covariates was small (<0.10), their inclusion improved model fit (decreased Akaike's Information Criterion for small sample-size by ⩾2) and reduced residual error variance (⩾6.7%).

We expected results would often involve difficult to interpret treatment × year interactions because treatments were applied over time. Therefore, we used orthogonal contrasts to test specific, *a priori* hypotheses: woodland vs. savanna post-harvest (2009 and 2010), spring vs. fall fire post-burning (2011 and 2012), and differences in 2012 between woodlands vs. savannas, spring vs. fall fire, and controls vs. all other treatments (hereafter, treatments). In addition, we compared controls vs. treatments and woodlands vs. savannas over all year intervals (2008–2009, 2009–2010, 2010–2011, and 2011–2012), and spring vs. fall fire over post-burning intervals (2010–2011, 2011–2012). We limit discussion of insignificant ($\alpha > 0.05$) contrasts to those of interest. We used LSD mean separation ($p < 0.05$) when model results indicated significant main effects without an interaction. We also individually analyzed stem density of dominant (⩾80% of total) woody species within size class and pyrogenicity groups.

We used polynomial regression to explore relationships between overstory (canopy closure and basal area) and herbaceous layer (cover, richness, and diversity) variables. We included data from all 730 plots. We calculated mean herbaceous groundcover (sum of graminoid, legume, and other forbs), richness, and diversity for 31 basal area (0–30 m^2 ha^{-1}, 1 m^2 ha^{-1} interval) and 34 canopy closure (0–99%, 3% intervals) classifications. This improved our ability to detect trends that may have otherwise been obscured by plot level variation. We did not include basal area classifications >30 m^2 ha^{-1} based on limited observations. We explored second- and third-order polynomials to identify potentially important thresholds in herbaceous response. We sequentially dropped order

terms, proceeding from third- to second- and then first-order models based on significance ($\alpha = 0.05$).

4. Results

4.1. Understory woody vegetation

We observed an interaction between treatment and year effects on shrubby vegetation density (Table 1). After correcting for relationships with slope (-1202 stems ha^{-1} ± 496 SE %$^{-1}$ increase) and scorch height (+11,566 stems ha^{-1} ± 3256 SE m^{-1} increase in scorch height), shrubby vegetation density was greater in treatments than controls in 2012, and increased more in savannas than woodlands from 2010 (pre-fire) to 2011 (post-fire, Fig. 2). Lowbush blueberry (*Vaccinium pallidum* Aiton) density was substantial across all treatments and controls (Table 2, Fig. 3). Differences in the density of shrubby vegetation between treatments and controls in 2012 was largely the result of southern blackberry's (*Rubus argutus* Link) positive response of to fire and increasing canopy disturbance (Table 2, Fig. 3).

A similar interaction between treatment and year affected pyrophyllic seedling density (Table 1). Changes from the first growing-season post canopy disturbance (2009) to the second (2010) differed between controls and treatments, and by canopy disturbance level (Fig. 2). After correcting for the influence of scorch height (+4177 stems ha^{-1} ± 1903 SE m^{-1} increase in scorch height), pyrophyllic seedling density in 2012 was nearly 4X greater in treatments than controls and was greater in savannas than woodlands (Fig. 2). The positive response of sassafras, blackgum, and black oak to canopy disturbance and fire (Table 2) contributed greatly to observed differences in pyrophyllic seedling density between controls and treatments (Fig. 3).

In contrast, pyrophobic seedling density only differed by year (Table 1) after adjusting for the influence of canopy closure (+154 stems ha^{-1} ± 73 SE %$^{-1}$ increase) and large-sapling density (-30 stems ha^{-1} ± 12 SE [stems ha^{-1}]$^{-1}$ increase). Savannas did contain less pyrophobic seedling density than woodlands in the years following canopy disturbance (2009–2010, Fig. 2), but this difference was eliminated by increases in both treatments and controls over time (Fig. 4). Resulting pyrophobic seedling density in 2012 was 4X that observed in 2008. Differences in pyrophobic seedling density between controls and treatments in 2012 were largely the result of differences in two species; sourwood and eastern white pine (Table 2, Fig. 3). Red maple was ⩾78% of each treatment's total pyrophobic seedling density in 2012 (Fig. 3), and mean density (17,351 stems ha^{-1} ± 1791 SE) was nearly twice that of the next most common seedling species (sassafras, 8735 stems ha^{-1} ± 2221 SE).

Treatment and year effects on pyrophyllic small-sapling density interacted (Table 1). Changes in density from year to year most often differed between controls and treatments, although at times such changes also differed between woodlands and savannas (Fig. 5). In general, the density of pyrophyllic small-saplings increased over time in treatments where canopy disturbance occurred relative to stable density in controls. In addition, the density of pyrophyllic small-saplings declined by 85% immediately following fire. Subsequent time intervals involved increases in density that were greater in treatments than controls (Fig. 5). Resulting (2012) density in treatments was >3X that observed in controls (Fig. 5). The positive response of sassafras and white oak to disturbance was largely responsible for the observed increases pyrophyllic small-sapling density (Table 2, Fig. 3).

Likewise, treatment and year effects on pyrophobic small-sapling density interacted (Table 1). Changes in such density from one year to the next only ever differed between treatments and controls (Fig. 5). In general, pyrophobic small-sapling density in controls remained constant relative to treatments where such density increased following canopy disturbance, decreased following fire, and then increased by the second growing-season post-fire (2012, Fig. 5). Total pyrophobic small-sapling density in 2012 was similar between treatments and controls (Fig. 5); however, small-sapling density in treatments included substantially more red maple stems, and substantially less eastern white pine stems, than controls (Table 2, Fig. 3). In 2012, red maple constituted ⩾73% of the total pyrophobic small-sapling density in every treatment except for controls (32%) where eastern white pine was dominant (62%; Fig. 3).

Both pyrophyllic and pyrophobic large-sapling stem density did not differ by tested effects (Table 1) after adjusting for relation-

Table 1
ANCOVA/ANOVA model results for woody stem density and herbaceous groundcover variables during an oak woodland and savanna restoration experiment, 2008–2012, at Catoosa Wildlife Management Area, Cumberland County, TN.

Dependent variables[a]		Treatment[b]		Year[b]		Treatment × Year[b]		Model covariates[b]				
		F	*p*	*F*	*p*	*F*	*p*	Variable	*F*	*p*	Partial r^2	Δ AICc
Shrubby vegetation (stems ha^{-1})	Total	1.81	0.265	57.08	<0.001	2.95	**0.013**	Slope	5.88	**0.026**	0.02	20.7
								Scorch height[c]	12.62	**0.003**	0.47	19.1
Seedlings (stems ha^{-1})	Pyrophyllic	16.64	<0.001	34.51	<0.001	2.39	**0.025**	Scorch height[c]	4.82	**0.046**	0.26	18.0
	Pyrophobic	1.87	0.246	20.11	**<0.001**	1.73	0.128	Canopy closure	4.50	**0.046**	0.02	15.0
								Large-sapling	6.39	**0.023**	0.01	12.6
Small-saplings (stems ha^{-1})	Pyrophyllic	6.76	0.001	17.14	<0.001	2.67	**0.014**	None	–	–	–	–
	Pyrophobic	0.48	0.753	45.42	<0.001	2.77	**0.017**	None	–	–	–	–
Large-saplings (stems ha^{-1})	Pyrophyllic	1.57	0.312	0.77	0.557	0.81	0.663	Scorch height[c]	9.28	**0.009**	0.40	8.3
	Pyrophobic	1.76	0.274	0.94	0.462	1.68	0.135	Scorch height[c]	13.42	**0.003**	0.49	8.2
Groundcover (%)	Graminoid	6.14	0.036	38.49	<0.001	3.26	**0.007**	None	–	–	–	–
	Legume	1.10	0.381	6.80	**0.001**	1.79	0.097	Slope position	4.47	**0.045**	0.09	2.2
	Other forb	4.01	0.080	22.50	**<0.001**	1.80	0.106	None	–	–	–	–
	Richness	4.92	0.055	39.13	<0.001	3.39	**0.006**	None	–	–	–	–
	Diversity	5.38	0.047	43.15	<0.001	3.33	**0.006**	None	–	–	–	–

[a] See Table A1 for species in each group. Size classes were seedlings (⩾30.5 cm, <1.4 m tall), small-saplings (⩾1.4 m tall, <7.6 cm DBH), and large-saplings (⩾1.4 m tall, ⩾7.6 but <12.7 cm DBH). Richness and diversity (Shannon-Wiener Index) refer to herbaceous community.

[b] Bold indicates significant ($\alpha = 0.05$) and interpretable effects. Model *df* calculated using Kenward Rogers adjustment. Covariates included landscape (slope position, slope, aspect), treatment application (canopy closure, basal area, large-sapling density), and scorch height variation. The change in model fit (Δ AICc) is the difference between covariate omission and inclusion.

[c] Linear regression determined relationships between scorch height and dependent variables post fire (n = 16). If significant, post-fire data (2011–2012) was adjusted to values expected at mean scorch height prior to analysis. *F* and *p* are from this regression model (*df* = 1, 14).

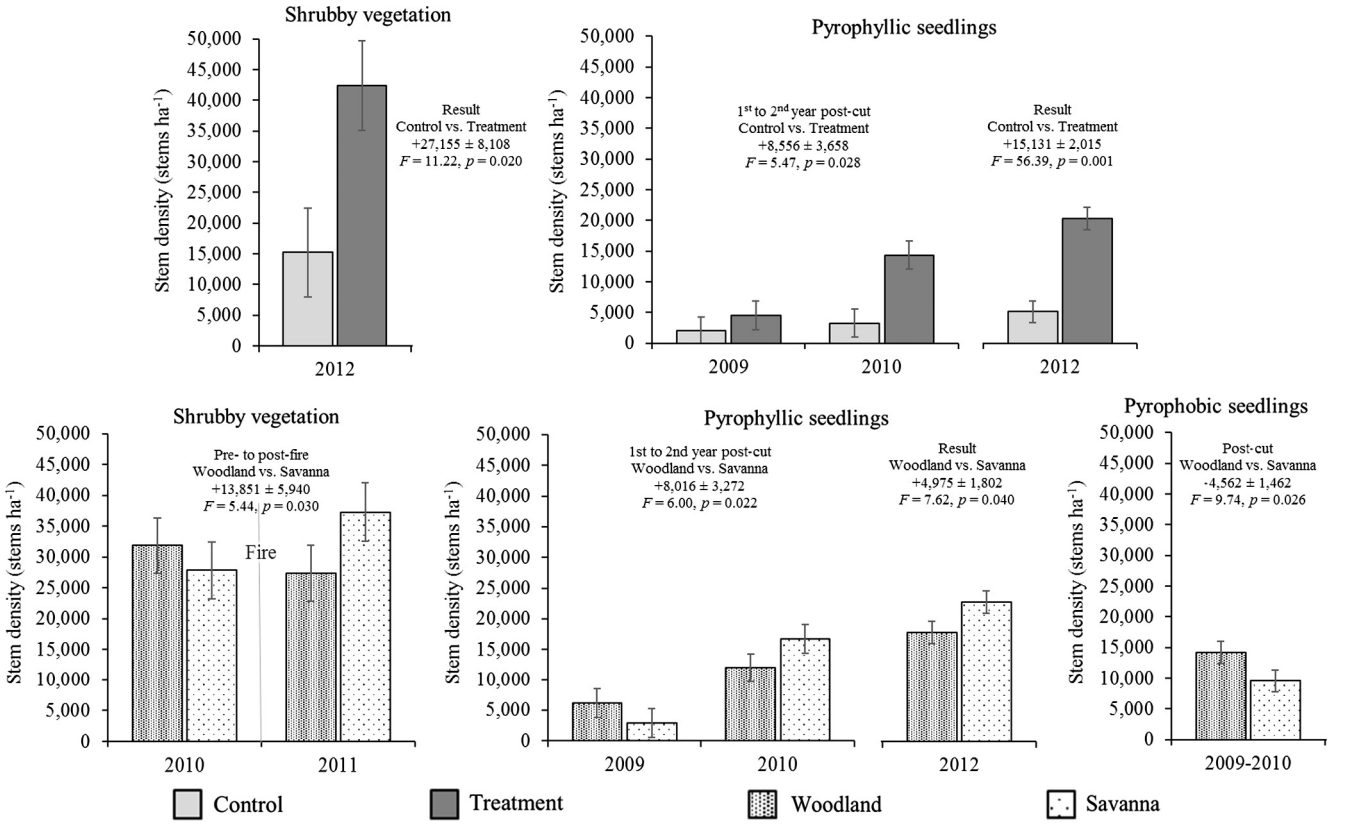

Fig. 2. All significant ($\alpha = 0.05$) contrasts for shrubby vegetation and seedling stem density (stems ha^{-1}) during an oak woodland and savanna restoration experiment (2008–2012) at Catoosa Wildlife Management Area, Cumberland County, TN. Treatment contrasts included Woodland (14 m^2 ha^{-1} residual basal area) vs. Savanna (7 m^2 ha^{-1} residual basal area) post-cut (2009 and 2010), Spring vs. Fall burns post-fire (2011 and 2012), and end result (2012); Control (unmanaged stands) vs. Treatment (all managed stands), Woodland vs. Savanna, and Spring vs. Fall fire. Interaction contrasts included Control vs. Treatment and Woodland vs. Savanna over all year intervals (2008–2012) and Spring vs. Fall fire over post-fire intervals (2010–2012). See Table A1 for species composing each group. Seedlings were ⩾30.5 cm but <1.4 m tall.

ships with scorch height (pyrophyllic: −1.6 stems ha^{-1} ± 0.5 SE m^{-1} increase in scorch height, pyrophobic: −1.0 stems ha^{-1} ± 0.3 SE m^{-1} increase in scorch height). However, significant contrasts indicated the decline of pyrophobic large-sapling density within treatments relative to controls from pre- (2010) to post-fire (2011, Fig. 5). In addition, pyrophobic large-sapling density in 2012 was more that 7X greater in controls than treatments (Fig. 5). This outcome appeared to be the result of decreased red maple and eastern white pine density in treatments relative to controls, (Table 2, Fig. 3).

We encountered 3 nonnative and invasive woody and semi-woody species during our study, including tree-of-heaven (*Ailanthus altissima* [Mill.] Swingle), Japanese honeysuckle (*Lonicera japonica* Thunb), and multiflora rose (*Rosa multiflora* Thunb). Tree-of-heaven saplings occurred almost exclusively in a single stand (FaS replicate 1). Within this stand, tree-of-heaven small-sapling density increased from no encounters (2008 and 2009) to 40 stems ha^{-1} (±29 SE) in 2010, decreased to 30 stems ha^{-1} (±18 SE) following fire (2011), and then returned to 40 stems ha^{-1} (±31 SE) in 2012. A single overstory tree-of-heaven was observed in this stand prior to treatment (2008). The other species occurred more frequently along roads and firebreaks, but were relatively rare within stand cores (⩽6 stems observed year^{-1}).

4.2. Herbaceous ground-layer

We documented 22 herbaceous species across all stands prior to treatment in 2008. By 2012 we had cumulatively documented 167 herbaceous species (Vander Yacht, 2013). Herbaceous plants were rare in controls relative to treatments. When present in both, the groundcover of herbaceous species was generally greater in woodlands than controls, and greater still in savannas. There was little differentiation in groundcover between fire seasons (Table 3). Fern groundcover was minor (0.3% ± 0.2 SE) and was not included in further analysis.

Graminoid groundcover was affected by an interaction between treatment and year (Table 1). Native cool-season grasses dominated herbaceous groundcover in 2012 (Table 3). This included needlegrass (*Piptochaetium avenaceum* [L.] Parodi), the most common herbaceous species in all stands by groundcover, and the common genera *Dichanthelium* and *Danthonia*. Broomsedge (*Andropogon virginicus* L.) was the only native C_4 grass to exceed 1% groundcover in a treatment. Sedges (*Carex* spp.) were also common (Vander Yacht, 2013). The groundcover of graminoids was greater in savannas than woodlands following canopy disturbance (2009 and 2010, Fig. 6). In addition, it increased more in treatments than controls from the first (2011) to the second (2012) growing-season post-fire (Fig. 6). Graminoid groundcover in 2012 was <2% in controls, exceeded 30% in treatments, and was greater in savannas than woodlands (Fig. 6).

We observed a year effect on legume groundcover (Table 1) after adjusting for slope position (−0.5% ± 0.2 SE position^{-1} increase). The genus *Lespedeza* was common, and many legume species increased in groundcover as canopy disturbance of treatments increased (Table 3). Although never >1%, legume groundcover increased over time until it was 8X pre-treatment levels (2008) in the second growing-season following fire (2012). Differences in such increases between controls and treatments were not detected by the overall ANCOVA, but legume groundcover in 2012 was greater in savannas than woodlands (Fig. 6).

Table 2
Contrast tests on the stem density (stems ha^{-1}) of dominant woody species (composing ⩾80% of group stem density) by size class, growth-form, and pyrogenicity groups in 2012 following oak woodland and savanna restoration treatments at Catoosa Wildlife Management Area, Cumberland County, TN.

Category[a]	Species	Control vs. Treatment[b] (*df* = 1, 5)			Woodland vs. Savanna[b] (df = 1, 5)			Spring vs. Fall[b] (df = 1, 5)		
		F	*P*	Estimate (SE)	*F*	*P*	Estimate (SE)	*F*	*P*	Estimate (SE)
Shrubby vegetation	*Vaccinium pallidum*	3.67	0.114	–	1.35	0.298	–	3.97	0.103	–
	Rubus argutus	14.05	**0.013**	+13,524 (5454)	12.96	**0.016**	+13,905 (4878)	0.98	0.367	–
	Smilax glauca	12.72	**0.016**	+1821 (750)	0.00	0.970	–	1.69	0.250	–
Pyrophillic seedlings	*Sassafras albidum*	36.96	**0.002**	+9798 (2332)	0.47	0.524	–	0.95	0.374	–
	Nyssa sylvatica	10.94	**0.021**	+1964 (685)	1.22	0.319	–	0.41	0.550	–
	Quercus alba	0.22	0.657	–	3.87	0.106	–	2.96	0.146	–
	Quercus velutina	7.99	**0.037**	+1179 (508)	0.28	0.620	–	2.77	0.157	–
Pyrophobic seedlings	*Acer rubrum*	0.77	0.421	–	0.12	0.740	–	0.01	0.927	–
	Oxydendrum arboreum	7.60	**0.040**	+1905 (823)	2.46	0.178	–	1.14	0.334	–
	Cornus florida	0.12	0.740	–	0.00	0.988	–	0.27	0.624	–
	Pinus strobus	9.76	**0.026**	−1560 (596)	0.01	0.927	–	0.01	0.927	–
Pyrophillic small-saplings	*Sassafras albidum*	21.00	**0.006**	+343 (112)	0.02	0.887	–	0.00	0.958	–
	Nyssa sylvatica	2.10	0.207	–	0.05	0.825	–	0.03	0.872	–
	Quercus alba	1.97	0.219	–	9.08	**0.030**	+107 (18)	4.79	0.080	–
Pyrophobic small-saplings	*Acer rubrum*	28.61	**0.003**	+2221 (509)	0.00	0.952	–	0.53	0.498	–
	Oxydendrum arboreum	15.92	**0.010**	+637 (194)	0.60	0.473	–	1.05	0.353	–
	Pinus strobus	66.41	**<0.001**	−2329 (121)	0.63	0.462	–	0.63	0.462	–
Pyrophillic large-saplings	*Nyssa sylvatica*	0.79	0.416	–	1.60	0.261	–	2.55	0.171	–
	Quercus alba	0.11	0.751	–	0.35	0.582	–	0.96	0.372	–
	Quercus velutina	0.09	0.775	–	2.31	0.189	–	0.46	0.530	–
Pyrophobic large-saplings	*Acer rubrum*	7.03	**0.045**	−60 (19)	0.29	0.612	–	0.02	0.887	–
	Pinus strobus	7.45	**0.041**	−104 (45)	0.05	0.833	–	0.05	0.833	–
	Cornus florida	4.08	0.100	–	1.76	0.242	–	0.11	0.758	–

[a] Shrubby vegetation was multi-stemmed species <4 m tall. Pyrogenicity determined using the Fire Effects Information System (www.feis-crs.org/feis/), Nowacki and Abrams (2015), and other published accounts. Size classes were: seedlings (>30.5 cm tall, <1.4 m tall), small-saplings (⩾1.4 m tall, <7.6 cm DBH), and large-saplings (⩾1.4 m tall, ⩾7.6 but <12.7 cm DBH).
[b] Contrasts tested for stem density differences between Control vs. Treatment, Woodland vs. Savanna, and Spring vs. Fall in 2012. Bold indicates significant effects ($\alpha = 0.05$).

We similarly observed a year effect on the groundcover of other forbs (Table 1), which was intermediate between that of graminoids and legumes. Rabbit tobacco (*Pseudognaphalium obtusifolium* [L.] Hilliard & B.L. Burtt), horseweed (*Conyza canadensis* [L.] Cronquist), and American burnweed (*Erechtites hieraciifolia* [L.] Raf. ex DC.) were abundant following fire (2011) but declined by the second year post-fire (2012). Increases in the groundcover of less ruderal species (Table 3) compensated for this loss. Significant increases in the groundcover of other forbs from pre-treatment levels (2008: 0.2% ± 0.2 SE) occurred by the second growing season following both canopy disturbance (2010: 2.4% ± 0.3 SE) and fire (2012: 4.6% ± 0.8 SE). The overall ANCOVA did not detect differences in such increases between controls and treatments, but contrasts revealed increases were greater in treatments than controls, and greater in savannas than woodlands, over the interval that fires occurred (2010–2011, Fig. 6). In addition, other forb groundcover in treatments was >11X greater than controls in 2012 (Fig. 6).

Changes in herbaceous richness and diversity were very similar (Table 1, Fig. 7). Both metrics were greater in savannas than woodlands following canopy disturbance (2009–2010). From the first growing-season post-fire (2011) to the second (2012), richness more than doubled and diversity increased by 60% in treatments relative to no change in controls (Fig. 7). In 2012, herbaceous richness and diversity in treatments was >8X that observed in controls (Fig. 7).

We documented 3 nonnative and invasive herbaceous species during our experiment, including sericea lespedeza (*Lespedeza cuneata* [Dum. Cours.] G. Don.), Japanese stiltgrass (*Microstegium vimineum* [Trin.] A. Camus), and miniature beefsteakplant (*Mosla dianthera* [Buch.-Ham. ex Roxb.] Maxim.). The maximum groundcover in a treatment by any of these species was 0.5% ± 0.3 SE (Japanese stiltgrass, SpS 2012). Japanese stiltgrass was encountered every year of monitoring, whereas miniature beefsteakplant and sericea lespedeza were encountered in 2010–2012. Greater cover and additional herbaceous species of nonnative and invasive plants occurred along access roads and within the outer edges of our stands.

4.3. Overstory metrics and herbaceous ground-layer relationships

A quadratic basal area model explained 88.2% of the variation in herbaceous groundcover ($F_{2,28} = 104.8$, $p < 0.001$). Herbaceous groundcover increased exponentially with decreasing basal area, but was functionally constant near 5% until residual basal area fell below 15 m^2 ha^{-1} (Fig. 8A). In comparison, a cubic canopy closure model explained 76.5% of the variation in herbaceous groundcover ($F_{3,30} = 32.5$, $p < 0.001$). Within this relationship, herbaceous groundcover increased as canopy closure declined to 80%, remained constant at 20% groundcover until canopy closure declined below 30%, and then increased with further declines in canopy closure (inflection point: 59.8%, Fig. 8B). A quadratic basal area model explained 90.1% of the observed variation in herbaceous species richness ($F_{2,28} = 126.9$, $p < 0.001$). The rate of increase in herbaceous species richness was greater once basal area was reduced below 15 m^2 ha^{-1} (Fig. 8C). The relationship between species richness and canopy closure was linear ($F_{1,32} = 38.4$, $p < 0.001$) and weaker ($r^2 = 0.55$, Fig. 8D). A quadratic model showed herbaceous species diversity to increase at a greater rate once basal area declined below 15 m^2 ha^{-1} ($F_{1,29} = 75.7$, $p < 0.001$, Fig. 8E). Diversity increased linearly as canopy closure decreased ($F_{1,32} = 42.7$, $p < 0.001$, Fig. 8F). Relationships between diversity and basal area were stronger ($r^2 = 0.84$) than diversity and canopy closure relationships ($r^2 = 0.56$).

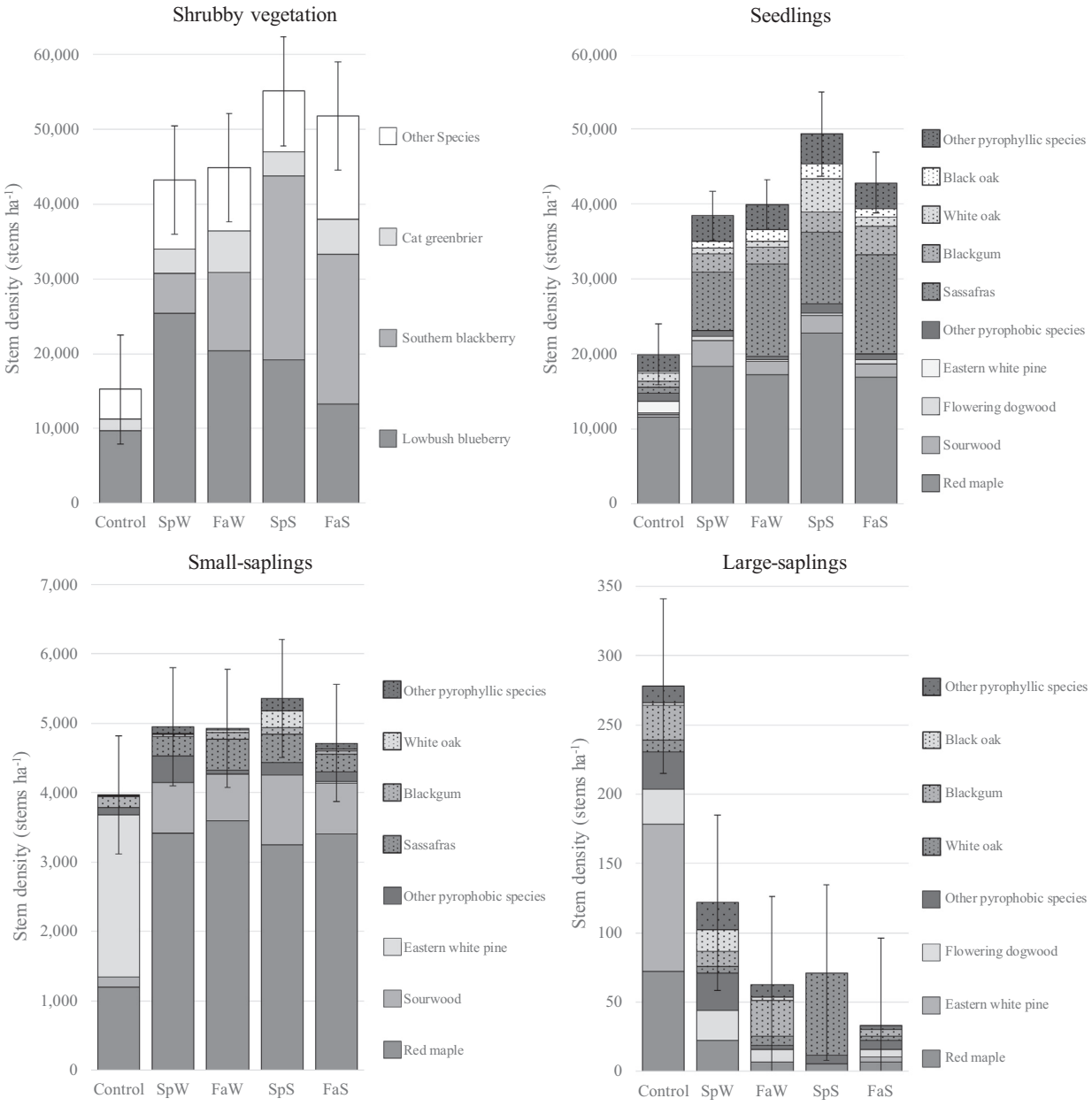

Fig. 3. Composition of woody stem density (stems ha^{-1}) by treatment and size class in 2012 following oak woodland and savanna restoration at Catoosa Wildlife Management Area, Cumberland County, TN. Control, unmanaged stands; Sp, spring fire; Fa, fall fire; W, woodland residual basal area (14 m^2 ha^{-1}); and S, savanna residual basal area (7 m^2 ha^{-1}). For each treatment, n = 2, 20-ha stands. Presented species compose ⩾80% of category stem density (See Table A1 for other species). Shrubby vegetation was multi-stemmed species <4 m tall, and tree size classes were: seedlings (>30.5 cm tall, <1.4 m tall), small-saplings (⩾1.4 m tall, <7.6 cm DBH), and large-saplings (⩾1.4 m tall, ⩾7.6 but <12.7 cm DBH). Pyrogenicity determined using the Fire Effects Information System (www.feis-crs.org/feis/), Nowacki and Abrams (2015), and other published accounts.

5. Discussion

Our results demonstrate the utility of canopy disturbance and fire for restoring oak woodlands and savannas from closed-canopy forests in the Appalachian region. Such insight allows management to compensate for the reduced prevalence of fire, effects of climate change, the loss of large herbivores, and a host of other alterations to a disturbance regime that once maintained oak woodlands and savannas (Heikens and Robertson, 1994; Anderson et al., 1999). Similar to results in the Midwest (Nielsen et al., 2003; Brudvig and Asbjornsen, 2009; Lettow et al., 2014), canopy disturbance immediately shifted overstory conditions toward accepted community definitions (Faber-Langendoen, 2001). Increased graminoid, legume, and other forb groundcover (2-, 3-, and 12-fold, respectively) as well as 2-fold increases in herbaceous richness and diversity were directly attributable to increasing canopy disturbance, but so were increases in shrubby, seedling, and small-sapling stem density. Fire reduced dominance of woody plants in the understory, but its effects were temporary and followed by prolific resprouting. Despite minimal woody control, fire enhanced the positive trends in herbaceous response initiated by canopy disturbance. Treatment vs. control comparisons in 2012 showed increased graminoid (24-fold) and other forb (11-fold) groundcover, and increased herbaceous richness (9-fold) and diversity (8-fold). Few differences in vegetation were directly attributable to fire-season after a single burn, but the lack of

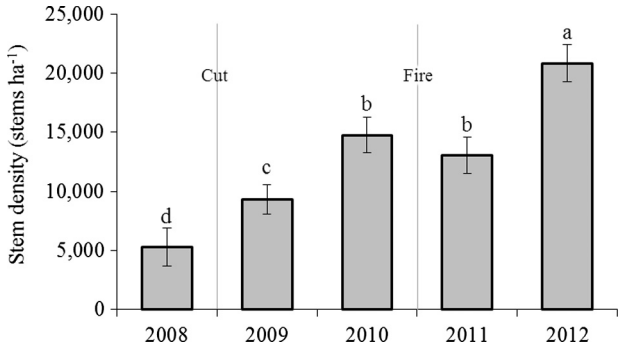

Fig. 4. Year effect ($p < 0.001$) on pyrophobic seedling (⩾30.48 cm, <1.4 m tall) density (stems ha^{-1}) during an oak woodland and savanna restoration experiment, 2008–2012, at Catoosa Wildlife Management Area, Cumberland County, TN. See Table A1 for species within the pyrophobic group. For each year n = 10, 20-ha stands. Lower-case letters represent significant differences by LSD ($p < 0.05$).

relationships between several key variables and scorch height suggests that less intense October fire achieved similar results as the more intense March fire.

5.1. Understory woody vegetation

The influence of canopy disturbance on woody vegetation density varied by size-class and pyrogenicity group. Shrubby vegetation, especially southern blackberry, was promoted by increasing canopy disturbance. In Central Appalachia, Walter et al. (2016) concluded *Rubus* spp. responded positively to increases in nitrogen and canopy openness. Likewise, increases in pyrophyllic seedling and small-sapling density following canopy disturbance were likely the result of increased availability of nitrogen (Reich et al., 2001) and light (Larsen and Johnson, 1998), with sprouting from cut stumps also contributing. In contrast, pyrophobic seedling and small-sapling density was either less responsive to canopy disturbance or decreased as canopy openness increased. This likely occurred because most pyrophyllics were shade-intolerant whereas most pyrophobics were shade-tolerant (Burns and Honkala, 1990a, 1990b). In addition, the removal of pyrophobic seed sources and soil disturbance from logging likely promoted pyrophyllic tree species. This is desirable for long-term community maintenance, but how gaps in fire recurrence influence recruitment (Knapp et al., 2015) and the negative effects woody vegetation can have on herbaceous-layer development (Barrioz et al., 2013; McCord et al., 2014) are important considerations before shifting management focus from understory woody control to overstory maintenance.

Successful restoration requires reducing understory woody competition with herbaceous species (Brudvig and Asbjornsen, 2009; Barrioz et al., 2013). Fire can be economical and effective in accomplishing this objective (Peterson and Reich, 2001), but our single fire stimulated southern blackberry, did not affect seedling density, and only temporarily reduced small-sapling density. Prodigious fruiting following canopy disturbance (Greenberg et al., 2007), widespread dispersal by vertebrates, and long-term seed viability (Cain and Shelton, 2003) can lead to heavy blackberry stocking within seedbanks (Keyser et al., 2012). This allows *Rubus* spp. to respond quickly following fire (Iglay et al., 2010). Although fire-induced mortality of seedlings and small-saplings was observed, vigorous growth from established rootstocks quickly recruited stems into these smaller size-classes. Many woody species persist following fire through basal sprouting (Blankenship and Arthur, 2006; Ward, 2015). Long-term studies in Eastern oak

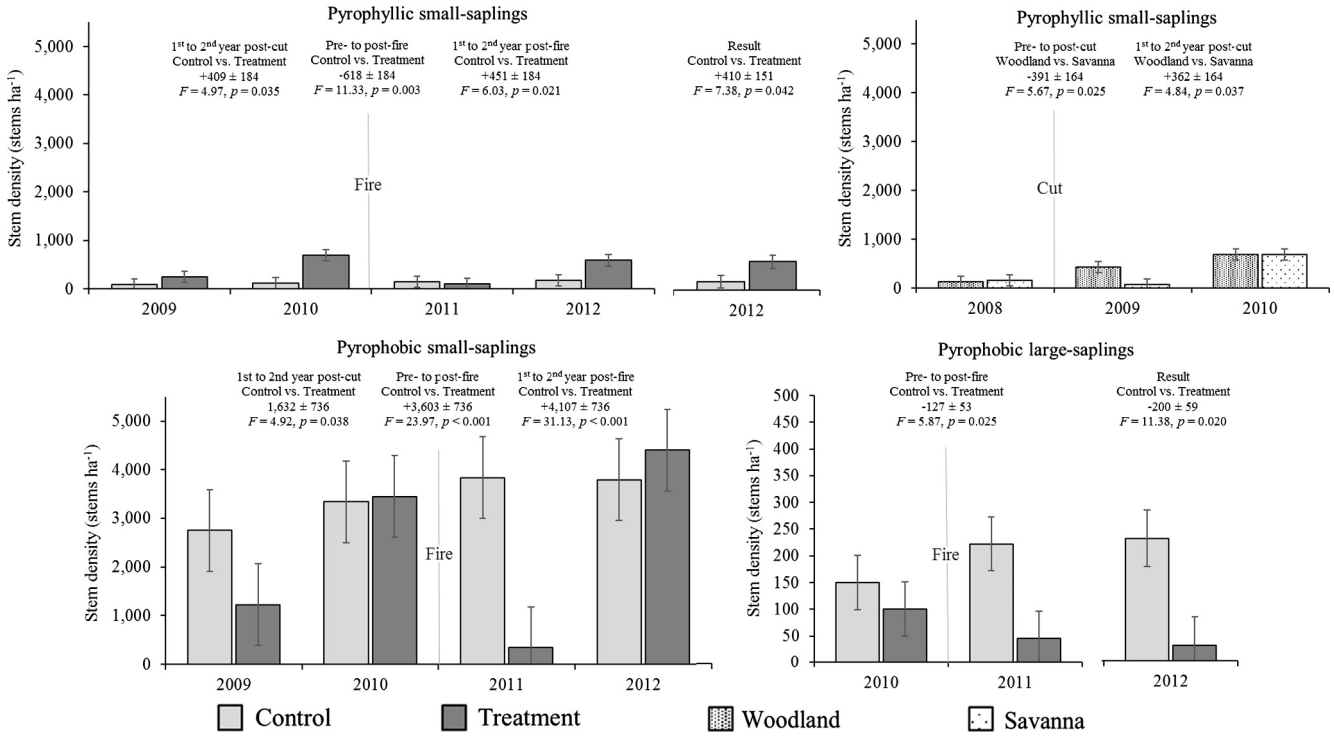

Fig. 5. All significant ($\alpha = 0.05$) contrasts for sapling stem density (stems ha^{-1}) during an oak woodland and savanna restoration experiment (2008–2012) at Catoosa Wildlife Management Area, Cumberland County, TN. Treatment contrasts included Woodland (14 m^2 ha^{-1} residual basal area) vs. Savanna (7 m^2 ha^{-1} residual basal area) post cut (2009 and 2010), Spring vs. Fall burns post fire (2011 and 2012), and end result (2012); Control (unmanaged stands) vs. Treatment (all managed stands), Woodland vs. Savanna, and Spring vs. Fall fire. Interaction contrasts included Control vs. Treatment and Woodland vs. Savanna over all year intervals (2008–2012) and Spring vs. Fall fire over post fire intervals (2010–2012). See Table A1 for species composing each group. Small-saplings were ⩾1.4 m tall but <7.6 cm DBH, and large-saplings were ⩾1.4 m tall and ⩾7.6 but <12.7 cm DBH.

Table 3
Mean (SE) percent groundcover of dominant[a] herbaceous species in 2012 by category and treatment for an oak woodland and savanna restoration experiment at Catoosa Wildlife Management Area, Cumberland County, TN.

Category	Common name	Scientific name	Treatment[b]				
			Control	SpW	FaW	SpS	FaS
Graminoids	Needlegrass	*Piptochaetium avenaceum*	0.7 (0.3)	6.2 (1.7)	9.1 (2.0)	23.3 (3.7)	20.5 (3.7)
	Variable panicgrass	*Dichanthelium commutatum*	0.3 (0.2)	4.0 (1.4)	2.9 (0.9)	9.0 (1.3)	7.7 (1.5)
	Cypress panicgrass	*Dichanthelium dichotomum*	–	3.1 (0.6)	2.0 (0.7)	5.1 (1.0)	3.6 (1.0)
	Povertygrass	*Danthonia* spp.	–	3.5 (1.2)	2.1 (0.8)	3.3 (0.9)	3.3 (1.0)
	Needleleaf rosettegrass	*Dichanthelium aciculare*	–	1.1 (0.3)	1.6 (0.6)	4.7 (1.1)	3.9 (1.0)
	Openflower rosettegrass	*Dichanthelium laxiflorum*	–	2.2 (0.8)	1.5 (0.8)	2.5 (0.8)	1.7 (0.7)
	Broomsedge	*Andropogon virginicus*	–	1.3 (1.0)	0.1 (0.1)	1.1 (0.4)	7.1 (2.0)
	Slender woodoats	*Chasmanthium laxum*	–	1.3 (0.4)	2.5 (1.0)	1.8 (0.9)	3.1 (1.3)
	Swan's sedge	*Carex swanii*	–	0.9 (0.6)	0.4 (0.3)	1.3 (0.7)	1.7 (0.7)
Legumes	Smooth creeping bushclover	*Lespedeza repens*	–	0.5 (0.3)	0.3 (0.1)	0.9 (0.3)	0.9 (0.4)
	Small-flowered partrigde pea	*Chamaecrista nictitans*	–	–	–	0.3 (0.2)	0.9 (0.4)
	Nakedflower tick-trefoil	*Desmodium nudiflorum*	0.3 (0.1)	0.1 (0.1)	–	0.2 (0.1)	0.2 (0.1)
	Hairy bushclover	*Lespedeza hirta*	–	–	0.1 (0.1)	–	0.3 (0.1)
	Downy creeping bushclover	*Lespedeza procumbens*	–	0.1 (0.1)	–	0.1 (0.1)	0.1 (0.1)
Other forbs	Horseweed	*Conyza canadensis*	–	0.1 (0.1)	–	1.1 (0.3)	3.3 (1.0)
	Whorled loosestrife	*Lysimachia quadrifolia*	–	0.5 (0.2)	1.0 (0.3)	0.7 (0.2)	0.7 (0.3)
	Sweet-scented goldenrod	*Solidago odora*	–	0.1 (0.1)	0.3 (0.2)	1.3 (0.4)	0.9 (0.3)
	Rabbit tobacco	*Pseudognaphalium obtusifolium*	–	3.5 (1.2)	0.3 (0.2)	0.7 (0.4)	0.9 (0.3)
	American burnweed	*Erechtites hieraciifolia*	0.1 (0.1)	1.0 (0.5)	0.1 (0.1)	0.9 (0.4)	0.5 (0.3)
	Whorled coreopsis	*Coreopsis major*	–	0.1 (0.1)	0.4 (0.2)	0.5 (0.2)	1.1 (0.3)

[a] The top 5 species by groundcover and additional species with ⩾1% cover in any treatment are presented for each species group.
[b] Control, unmanaged stands; SpW, spring fire and woodland residual basal area (14 m^2 ha^{-1}); FaW, fall fire and woodland residual basal area; SpS, spring fire and savanna residual basal area (7 m^2 ha^{-1}); and FaS, fall fire and savanna residual basal area. For each treatment n = 2, 20-ha stands.

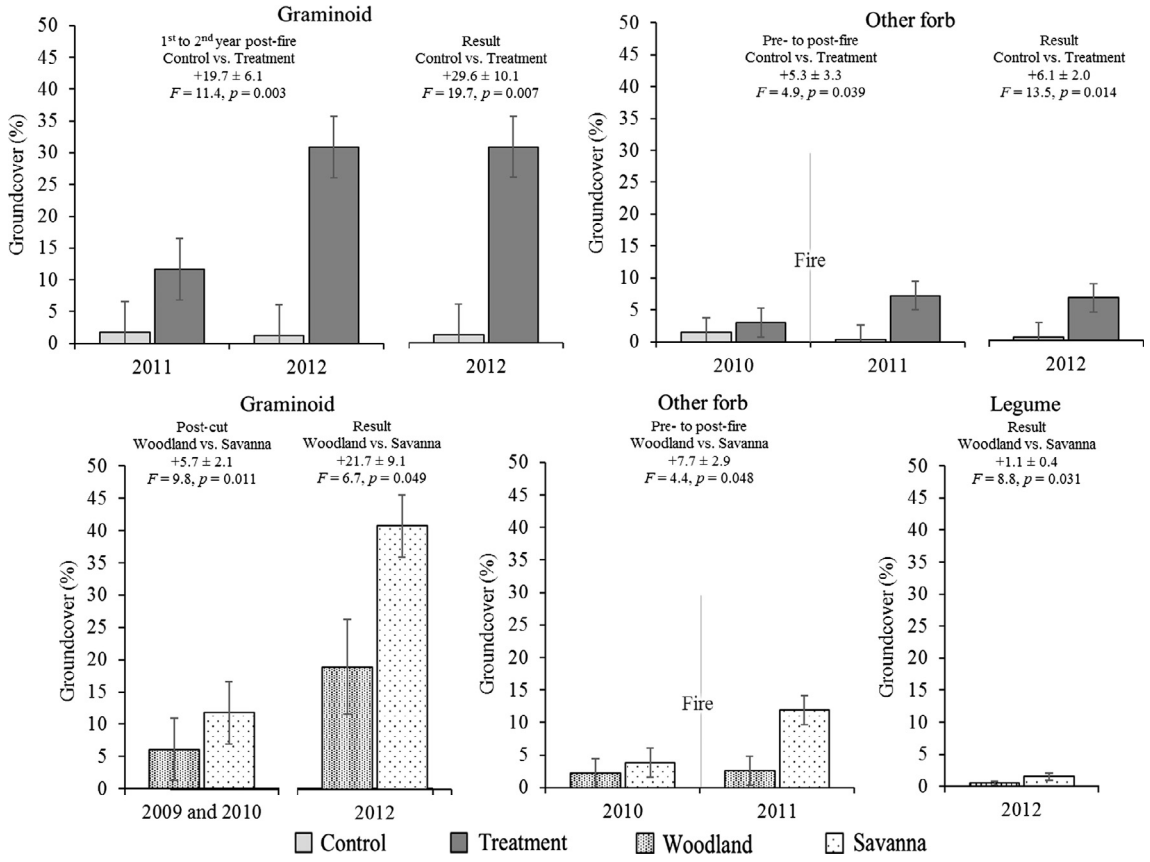

Fig. 6. All significant (α = 0.05) contrasts for herbaceous groundcover (%) categories during an oak woodland and savanna restoration experiment (2008–2012) at Catoosa Wildlife Management Area, Cumberland County, TN. Treatment contrasts included Woodland (14 m^2 ha^{-1} residual basal area) vs. Savanna (7 m^2 ha^{-1} residual basal area) post-cut (2009 and 2010), Spring vs. Fall burns post-fire (2011 and 2012), and end result (2012) comparisons; Control (unmanaged stands) vs. Treatment (all managed stands), Woodland vs. Savanna, and Spring vs. Fall fire. Interaction contrasts compared Control vs. Treatment and Woodland vs. Savanna over all year intervals (2008–2012) and Spring vs. Fall fire over post-fire intervals (2010–2012). See Vander Yacht (2013) for documented species within each group.

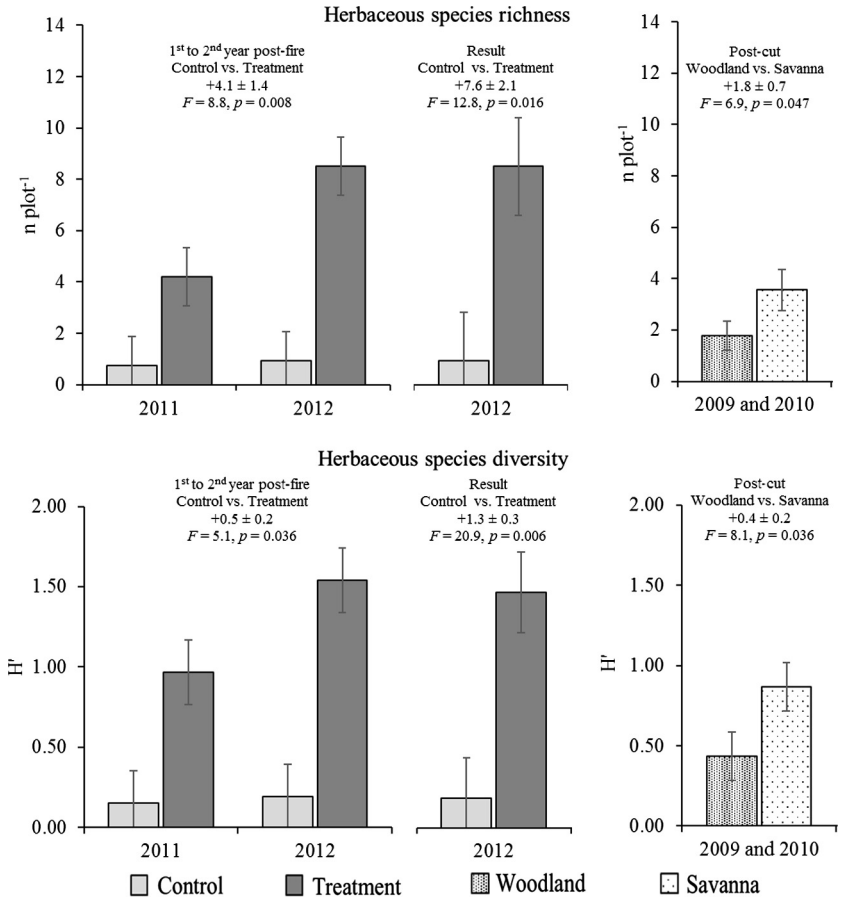

Fig. 7. All significant ($\alpha = 0.05$) contrasts for herbaceous species richness (n plot^{-1}) and diversity (Shannon-Wiener Index, H′) during an oak woodland and savanna restoration experiment (2008–2012) at Catoosa Wildlife Management Area, Cumberland County, TN. Treatment contrasts included Woodland (14 m^2 ha^{-1} residual basal area) vs. Savanna (7 m^2 ha^{-1} residual basal area) post-cut (2009 and 2010), Spring vs. Fall burns post-fire (2011 and 2012), and end result (2012) comparisons; Control (unmanaged stands) vs. Treatment (all managed stands), Woodland vs. Savanna, and Spring vs. Fall fire. Interaction contrasts compared Control vs. Treatment and Woodland vs. Savanna over all year intervals (2008–2012) and Spring vs. Fall fire over post fire intervals (2010–2012).

forests show multiple fires force saplings to repeatedly resprout under low-light conditions, with each fire decreasing sprouting capacity, but only if applied without gaps ⩾3 years during which below-ground resources can be replenished (Hutchinson et al., 2012; Arthur et al., 2015). For instance, Knapp et al. (2015) observed a dense midstory within plots burned every 4 years for >60 years, but virtually no seedlings and saplings in plots burned annually. Sparse overstory structure increases understory plant resources (e.g., light) and may reduce sapling recovery time following fire. Reducing woody density in such conditions may require at least three biennial burns (Outcalt and Brockway, 2010; Brewer, 2014), but definitive determination requires long-term, regionally specific research under sparse oak canopies.

The response of woody vegetation to fire differed little across pyrogenicity groups, especially within smaller size-classes. Detecting a differential response to fire among species often requires multiple fires, even if comparisons involve species varying widely in fire tolerance (Waldrop and Lloyd, 1991; Arthur et al., 2015). In our study, pyrophobic stems were 7.5X more abundant than pyrophyllic stems and constituted 88%, on average, of the total small-sapling density (largely red maple) following canopy disturbance and fire (2012). Understories dominated by fire-intolerant species are not unique to our study. The lack of disturbance (Nowacki and Abrams, 2008) have made such conditions common in eastern forests (Abrams, 1998). Our results and others (Arthur et al., 2015) suggest multiple burns or other management (e.g., herbicides, mechanical removal; Hutchinson et al., 2012) will be required to reduce this substantial and less fire-tolerant component of the midstory. In contrast, a single fire reduced pyrophobic but not pyrophyllic large-sapling density. Bark thickness provides thermal insulation and increases faster in pyrophyllic than pyrophobic species as size increases (Hammond et al., 2015). Reducing the dark, moist, and cool micro-environments that pyrophobic species promote in proportion to their size (Nowacki and Abrams, 2008), and the survival of advanced pyrophyllic regeneration, represents considerable restoration progress.

Although models adjusted for observed effects, fire intensity was greater in March than October in congruence with the findings of Sparks et al. (1999). Large-sapling density declined as scorch height increased. Top-killing large (>10 cm in DBH) midstory stems may require relatively intense fire (Ward, 2015), but such fire can injure or even kill overstory oaks (Peterson and Reich, 2001). Fire intensity targets within oak woodland and savanna restoration must reflect this balance. The increasing density of shrubs and pyrophyllic seedlings as scorch height increased was probably the result of concomitant decreases in competition from large-saplings. Also, the more-intense March fires spread faster than the less-intense October fires, and sprouting by stems exposed briefly to intense fire could have been greater than stems exposed to less intense fire for a longer period of time (Michaletz and Johnson, 2007). Perhaps of greatest interest, the density of pyrophobic seedlings and both pyrogenicity classes of small-saplings

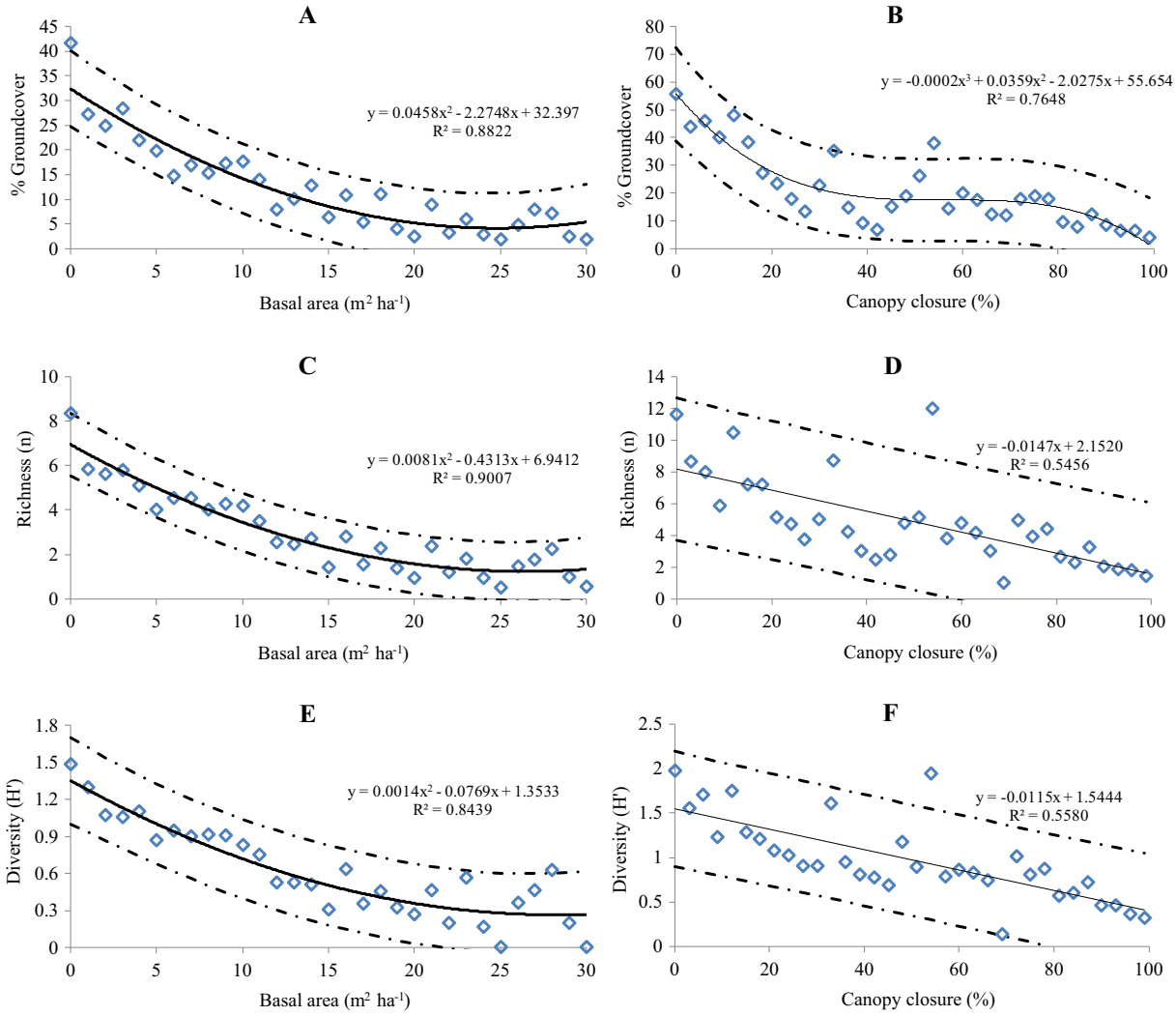

Fig. 8. Polynomial-regression determined relationships between herbaceous layer development and overstory measures during an oak woodland and savanna restoration experiment, 2008–2012, at Catoosa Wildlife Management Area, Cumberland County, TN. (A) Basal area (m^2 ha^{-1}) versus total herbaceous groundcover (sum of graminoid, legume, and other forbs); (B) canopy closure (%) versus total herbaceous groundcover; (C) basal area versus herbaceous species richness (n $plot^{-1}$); (D) canopy closure versus herbaceous species richness; (E) basal area versus herbaceous species diversity (Shannon-Wiener Index, H′); (F) canopy closure versus herbaceous species diversity. Broken lines present 95% confidence intervals.

was unaffected by scorch height or season. Thus, within these categories, the less intense October fire had effects similar to those of the more intense March fire. In other words, both fires achieved the minimum intensity required to elicit the observed response. The comparable effects on woody vegetation in combination with reduced risk associated with a less-intense fire provides an argument for the increased use of late growing-season fire during restoration.

Scorch height, though positively related to fire temperature, may have failed to capture all forms of energy release during a fire (Keeley, 2009). If this was the case, the timing of fire in relation to plant phenology, such as seasonal variation in root carbohydrate reserves (Loescher et al., 1990; Landhausser and Lieffers, 2002), may have compensated for unaccounted differences in intensity. Such an influence seems reasonable given other studies documenting growing-season fire as more effective than dormant-season fire in reducing understory woody density (Brose and Van Lear, 1998; Gruchy et al., 2009; Robertson and Hmielowski, 2014). It must also be recognized that our results were likely influenced by the composition and density of woody vegetation at our site prior to treatment.

5.2. Herbaceous ground-layer

Successful oak woodland and savanna restoration requires developing a robust herbaceous ground-layer containing a diversity of C_4 grasses, legumes, and other forbs (DeSelm, 1994). Although we observed 5 C_4 grasses, C_3 grasses dominated herbaceous response. The recent history of dormant-season fire under closed canopies at our site would have encouraged cool-season grasses (Harper, 2007) and increased their representation in the seedbank. Legumes, important because of their ability to fix nitrogen, promote invertebrate diversity, and provide wildlife food resources, were rare in our study plots. Multiple fires are often required to elicit a positive legume response (Sparks et al., 1998; Knapp et al., 2015), and we did observe greater legume cover and diversity in nearby areas subjected to multiple fires. Nielsen et al. (2003) attributed a weak legume response even after multiple fires to seedbank depletion following canopy closure. Leaf-litter dominance also promotes acidic soils which can limit legume establishment and growth (Ferguson et al., 2013). In our study, groundcover of forbs was less than graminoids, but forbs can respond slowly and with only small increases in cover after multi-

ple fires (Hutchinson et al., 2005). Herbaceous groundcover did not exceed 55% in any treatment, reflecting the limited restoration progress achieved by a single fire. However, the presence of prairie and savanna flora at all is remarkable when considering canopy closure and cessation of regular burning occurred >65 years ago.

Reducing canopy density using fire alone may require 60 years or more of repeated burning (Burton et al., 2011; Knapp et al., 2015). Mechanical overstory disturbance instantly increases the amount of light available for herbaceous germination and growth (Scholes and Archer, 1997; Peterson et al., 2007; McCord et al., 2014). This was demonstrated within previous work at our site (Barrioz et al., 2013) and in the current study as herbaceous cover, richness, and diversity were negatively related to basal area and canopy closure. The stabilization of herbaceous groundcover near 20% as canopy closure decreased to near 80% provides a target to exceed for woodland restoration efforts. Additional increases once canopy closure declined below 30% provides a similar target for savannas. The routine inclusion of 80% and 30% upper canopy closure thresholds within traditional community definitions (Faber-Langendoen, 2001; Nelson, 2010) and previous research (Barrioz et al., 2013) supports these figures. Trends in herbaceous layer metrics as related to basal area indicated increases were near linear as soon as overstory reductions exceeded 15 m^2 ha^{-1}. Basal area models also were more precise and provided greater predictive power for herbaceous layer response.

Canopy disturbance, especially when conducted irregularly, restores understory heterogeneity in plant resources and encourages herbaceous diversity (Jackson et al., 2006; Peterson and Reich, 2008; Brudvig and Asbjornsen, 2009). We attribute the lack of peaks in herbaceous metrics at intermediate levels of overstory to the effects of thick, woody understories (Scholes and Archer, 1997; Barrioz et al., 2013). Although large-sapling density did not influence herbaceous metrics in our study, seedling and small-sapling density was great and likely had a negative effect on herbaceous development. In addition, most dominant herbaceous species at our site were shade-tolerant, cool-season grasses (e.g., needlegrass). This may be typical of herbaceous response within the early stages of restoration. Negative effects of midstory subcanopies may become more evident as shade-intolerant herbaceous species become more common. Topographical variation can encourage herbaceous diversity (Leach and Givnish, 1999; Peterson and Reich, 2001). In our study, legume groundcover increased as slope position approached drains and swales, but aspect and slope percentage did not influence herbaceous groundcover. Our site was generally level in topography, but oak woodlands and savannas were historically more frequent on xeric, southwesterly aspects (DeSelm, 1994).

Increased herbaceous development following fire occurs as a result of release from woody competition, reductions in litter (Lashley et al., 2011), and increases in soil nutrient availability (Scharenbroch et al., 2012). In our study, fire increased herbaceous cover, richness, and diversity. This provides regionally specific evidence of the elsewhere well-established link between fire and open-oak community restoration (Peterson et al., 2007). Herbaceous response following a single fire was similar between October and March burns. The effects of seasonal variation in fire on herbaceous communities often become more apparent after multiple fires (Knapp et al., 2009). This includes altering the relative abundance of C_4 grasses (Holcomb et al., 2014), legumes, and other forbs (Gruchy et al., 2009; Howe, 2011). Annual to biennial fire also maximizes understory species richness within oak ecosystems (Peterson and Reich, 2008; Burton et al., 2011). However, the effects of fire on herbaceous communities is minimal without canopy disturbance (Hutchinson et al., 2005). Our contrasts indicated fire induced increases in graminoid and other forb groundcover were even greater as canopy disturbance increased.

Keyser et al. (2004) reported growing-season fires increased the dominance of herbaceous species more so than less intense dormant-season fires. In contrast, Sparks et al. (1998) and our work showed that herbaceous response following dormant- and growing-season fire was similar when dormant-season fires were more intense. Thus, growing-season fire appears to accomplish similar increases in herbaceous dominance when less intense, and greater increases when more intense, relative to dormant-season fire. This suggests an advantage of growing-season fire for oak woodland and savanna restoration. Herbaceous community development increases with increasing fire intensity (Van Lear and Waldrop, 1989; McMurry et al., 2007), but so does overstory mortality (Peterson and Reich, 2001). This limits the use of high-intensity fire within oak woodland and savanna management.

5.3. Non-native invasive species

Disturbance can increase the abundance of non-native and invasive species (Mack et al., 2000) which threaten restoration success (Brewer et al., 2015). During five growing seasons, over which two major disturbances (cutting and burning) occurred, we identified 6 nonnative and invasive species within our stand cores. Similar to findings of Barrioz et al. (2013), these species were restricted to areas near stand peripheries, skid trails, log landings, and roads. Although generally rare, the cover and density of these species did increase over time. All species had been previously reported in Cumberland County, TN except for *A. altissima* and *M. dianthera* which were reported in adjacent counties (University of Tennessee Herbarium). Given the rarity and exceptional conservation value of open-oak communities, taking some risk of limited invasion seems acceptable if otherwise functional woodlands and savannas are achieved. Continued monitoring is warranted, but the limited abundance of nonnative and invasive species we observed suggests that maintaining community integrity during restoration can be feasible. Control of known populations prior to restoration initiation may be the best approach.

5.4. Management implications and conclusions

Our work adds substantially to knowledge concerning oak woodland and savanna restoration within the understudied Appalachian region. To achieve similar results, managers must recognize the complexities of eastern forests and target xeric sites where oaks and pines are dominant. Canopy disturbance to a basal area of 7 m^2 ha^{-1} resulted in progress toward oak savanna restoration, and 15 m^2 ha^{-1} resulted in limited woodland restoration progress. These targets allow for some loss to occur as fuels accumulated during the absence of fire may increase fire-intensity initially. Both canopy disturbance and fire were important for promoting increases in herbaceous cover, richness, and diversity. Repeated burning will be required to maintain, and further promote, the increases in herbaceous groundcover and reductions in midstory density observed after a single fire. Because resprouting returned small-sapling density to pre-fire levels by the second growing-season following fire, we recommend an initial 2-year fire return interval. This will maximize woody control while allowing fine-fuel loads to recharge. We documented a similar vegetation response to October and March fires even though October fires were less intense. The safety implications of this observation and research that suggests late growing-season fire is more effective in controlling hardwoods should cause managers to explore burning outside of the traditional dormant-season. Restoration feasibility is generally enhanced on ridges and southwesterly aspects. However, our results were generally consistent across landscape variation, and herbaceous diversity actually benefitted from including drains and swales within management sites.

Treating known populations prior to initiation, minimizing the movement of heavy equipment through site interiors, and increasing area-to-perimeter ratios of stands can reduce the spread of invasive species during restoration. Long-term research documenting the response of vegetation to successively applied fires is needed to advance oak woodland and savanna restoration throughout the Appalachian region.

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Appendix A

Table A1
Common and scientific names of all woody and semi-woody species encountered during an oak woodland and savanna restoration experiment, 2008–2012, at Catoosa Wildlife Management Area, Cumberland County, TN.

Common Name	Scientific Name
Pyrophobic Trees[a]	
Red maple	*Acer rubrum*
Sugar maple	*Acer saccharum*
Downy serviceberry	*Amelanchier arborea*
Pawpaw	*Asimina triloba*
Black birch	*Betula lenta*
American hornbeam	*Carpinus caroliniana*
Eastern redbud	*Cercis canadensis*
Flowering dogwood	*Cornus florida*
Common persimmon	*Diospyros virginiana*
American beech	*Fagus grandifolia*
White ash	*Fraxinus americana*
Green ash	*Fraxinus pennsylvanica*
American holly	*Ilex opaca*
Butternut	*Juglans cinerea*
Eastern red cedar	*Juniperus virginiana*
Sweetgum	*Liquidambar styraciflua*
Yellow poplar	*Liriodendron tulipifera*
Cucumber magnolia	*Magnolia acuminata*
Fraser magnolia	*Magnolia fraseri*
Bigleaf magnolia	*Magnolia macrophylla*
Umbrella magnolia	*Magnolia tripetala*
Eastern hophornbeam	*Ostrya virginiana*
Sourwood	*Oxydendrum arboreum*
Eastern white pine	*Pinus strobus*
Virginia pine	*Pinus virginiana*
Black cherry	*Prunus serotina*
American basswood	*Tilia americana*
Eastern hemlock	*Tsuga canadensis*
Winged elm	*Ulmus alata*
Pyrophillic Trees[a]	
Tree-of-heaven	*Ailanthus altissima*[c]
Bitternut hickory	*Carya cordiformis*
Pignut hickory	*Carya glabra*
Shellbark hickory	*Carya laciniosa*
Shagbark hickory	*Carya ovata*
Hickory	*Carya* spp.
Mockernut hickory	*Carya tomentosa*
American chestnut	*Castanea dentata*
Black walnut	*Juglans nigra*
Blackgum	*Nyssa sylvatica*
Shortleaf pine	*Pinus echinata*
Loblolly pine	*Pinus taeda*
Bigtooth aspen	*Populus grandidentata*
White oak	*Quercus alba*
Scarlet oak	*Quercus coccinea*
Southern red oak	*Quercus falcata*
Blackjack oak	*Quercus marilandica*
Chestnut oak	*Quercus montana*
Chinkapin oak	*Quercus muehlenbergii*
Northern red oak	*Quercus rubra*
Post oak	*Quercus stellata*
Black oak	*Quercus velutina*
Black locust	*Robinia pseudoacacia*
Sassafras	*Sassafras albidum*
Shrubby Vegetation[b]	
Devils walking stick	*Aralia spinosa*
Crossvine	*Bignonia capreolata*
Allegheny chinkapin	*Castanea pumila*
American bittersweet	*Celastrus scandens*
Dotted hawthorn	*Crataegous punctata*
Hawthorne	*Crataegus* spp.
Dodder	*Cuscuta* spp.
Strawberry bush	*Euonymus americanus*
Eastern wahoo	*Euonymus atropurpureus*
Carolina silverbell	*Halesia tetraptera*
Mountain holly	*Ilex ambigua*
Wild potato vine	*Ipomoea pandurata*
Mountain laurel	*Kalmia latifolia*
Spicebush	*Lindera benzoin*
Japanese honeysuckle	*Lonicera japonica*[c]
Virginia creeper	*Parthenocissus quinquefolia*
Flame azalea	*Rhododendron* spp.
Winged sumac	*Rhus copallinum*
Multiflora rose	*Rosa multiflora*[c]
Southern blackberry	*Rubus argutus*
Northern dewberry	*Rubus flagellaris*
Swamp dewberry	*Rubus hispidus*
Black raspberry	*Rubus occidentalis*
Elderberry	*Sambucus canadensis*
Cat greenbrier	*Smilax glauca*
Roundleaf greenbrier	*Smilax rotundifolia*
Bristly greenbrier	*Smilax tamnoides*
Mountain camellia	*Stewartia ovata*
Poison ivy	*Toxicodendron radicans*
Lowbush blueberry	*Vaccinium pallidum*
Deerberry	*Vaccinium stamineum*
Farkleberry	*Vaccinium arboreum*
Arrow wood	*Viburnum dentatum*
Mapleleaf viburnum	*Viburnum acerifolium*
Muscadine vine	*Vitis rotundifolia*
Summer grape	*Vitis aestivalis*

[a] Pyrogenicity of species was designated using Nowacki and Abrams (2015). For species not found within this work, we used author knowledge and the 'Silvics of North America' (Burns and Honkala, 1990a, 1990b).
[b] Species typically multi-stemmed and rarely reaching >4 m in height.
[c] Non-native, invasive species.

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