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Oak savanna management strategies and their differential effects on vegetative structure, understory light, and flowering forbs

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ABSTRACT

High quality oak savanna communities were once abundant in the North American Midwest, but have become exceedingly rare. Where remnant savannas remain, fire suppression and resulting woody encroachment have dramatically altered vegetative structure, resulting in reduced understory light levels and precipitating declines in herbaceous understory diversity. Restoration of fire suppressed oak savannas generally involves the reintroduction of fire, but questions remain regarding the necessity and impact of mechanical woody vegetation reduction in addition to fire. We report here on initial short-term results of a long-term experiment in a remnant fire-suppressed oak savanna in Southern Michigan to compare a gradient of oak savanna management intensities including; (1) unmanaged reference plots, (2) burning alone (low management intensity), and (3) progressive mechanical thinning combined with burning (high management intensity). We measured several metrics of restoration success: understory, shrub, and canopy cover, understory light levels, understory floral resources, and flowering forb diversity, in the first two growing seasons after initiation of restoration treatments. We found that increasing management intensity largely corresponded with increased understory light availability, abundance of floral resources (i.e. forb bloom abundance and diversity), and with decreased shrub and canopy cover. Low management intensity did not increase light availability, or decrease vegetative or canopy cover relative to unmanaged references, while high management intensity achieved both management goals. Both burning alone and thinning + burning generally increased diversity of flowering forbs, where the effect was greatest with high intensity management. These increases were most pronounced in the second growing season after burning, when we saw sharp increases in richness and abundance of flowering forbs. In restored plots, the flowering forb community consisted of pre-existing shade tolerant species, native and exotic ruderals, as well as savanna indicator species. In sum, low-intensity management can achieve some restoration objectives over the short-term; however, we show a clear initial advantage of coupling thinning with burning, relative to burning alone. We suggest that these differing intensities of oak savanna restoration may be appropriate under different temporal, financial, and ecological scenarios. Our work highlights the potential for restoration of understory forb communities by low or high intensity approaches, where relict populations and/or viable seedbanks exist.

1. Introduction

Temperate savanna ecosystems are among the rarest and least-protected biomes on Earth today (Hoekstra et al., 2005). Oak savannas were once widespread in the Midwestern United States, but have all but disappeared (Nuzzo, 1986). Most of these lands have been directly converted for agricultural or residential purposes, making rehabilitation difficult and unlikely. Most remaining savannas exist as remnants in altered ecological states due to disruption of their historical disturbance regimes (Nuzzo, 1986; O'Connor, 2006; Nowacki and Abrams, 2008). Thus, restoration efforts on remnants are key to the persistence of savannas in the Midwestern landscape.

Midwestern oak savannas were formerly abundant and share structural and vegetative characteristics with both tallgrass prairie and eastern deciduous forest biomes, including well-developed herbaceous understories and scattered overstory oak trees. Spanning the ecotone between prairie and Eastern deciduous forest, oak savannas display wide variation in plant species composition, soil type, disturbance regime, and structure. A defining feature is

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the co-dominance of the overstory and understory plant community (Curtis, 1959; Packard and Mutel, 2005; Chapman and Brewer, 2008), with tree canopy cover typically ranging from 10–60% (Curtis 1959, Kost et al., 2007). Importantly, oak savanna understories are also noted for their high proportion of forbs relative to graminoids, opposite that of grassland understories (Pruka, 1994; Leach and Givnish, 1999).

The structure and biological communities of Midwestern oak savannas are maintained through disturbance, particularly frequent low-intensity surface fires that were historically largely ignited by humans (Heikens and Robertson, 1994; Wolf, 2004; O'Connor, 2006; Nowacki and Abrams, 2008). Fires act to suppress encroachment of woody vegetation, promoting a scattered canopy and the higher light levels necessary to maintain a dense herbaceous understory (Bowles and McBride, 1998; Leach and Givnish, 1999; Reich et al., 2001; Pavlovic et al., 2006). Records of regional historical fire return intervals in oak savannas are uncommon and, where available, appear highly dependent on local conditions (e.g. annual precipitation, human activity). Fire return intervals maintained by Native Americans are thought to range from one to ten years (Abrams, 1996), with documented pre-European settlement mean intervals of 2.8 (Cutter and Guyette) and 3.7 years (Dey et al., 2004; Wolf, 2004). In these studies, the majority of burns occurred during the dormant or late growing season, with occasional early season burns. European settlement and subsequent cessation of historical fire regimes resulted in a number of key changes in abiotic conditions and biological communities. Fast-growing mesophytic tree species, once marginalized by frequent fire, rapidly colonized savannas in the absence of fire. This "mesophication" process increases occurrence of mesophytic tree species, woody plant density and soil moisture, decreased light availability, and produces a shift to less-flammable litter (Nowacki and Abrams, 2008). Thus, many oak savanna remnants today exist in a fire-suppressed state with a closed canopy, dominance by mesophytic tree species, declining prevalence of oaks, a relatively thick, moisture-retaining litter layer, and reduced density and diversity of the understory plant community (Nowacki and Abrams, 2008).

The decline of oak savanna understory communities is well documented. Research from Wisconsin (Cottam, 1949), Illinois (Bowles and McBride, 1998), Iowa (Brudvig and Mabry, 2008), and the larger Eastern United States (Nowacki and Abrams, 2008) all note reductions in remnant oak savanna understory plant diversity and/or cover following fire suppression. Increased canopy cover and shifts in tree species composition following fire suppression are two of the presumed mechanisms causing this understory decline (Nowacki and Abrams, 2008). Moreover, the understory plant communities in fire-suppressed savanna remnants support more shade-tolerant species characteristic of woodland or forest, with light-loving plant species historically prevalent in savannas confined to edges, canopy openings, the seed bank, or absent altogether (Bowles and McBride, 1998; Brudvig and Mabry, 2008).

Biodiversity in oak savanna communities in the Midwest can be restored by reversing the effects of mesophication in fire-suppressed remnants (Leach and Givnish, 1999; Davis et al., 2000). An overarching goal of these efforts is to return historical savanna structure and biological diversity by decreasing canopy cover and increasing herbaceous understory plant communities (Asbjornsen et al., 2005). Prescribed fire during oak ecosystem restoration can reduce canopy and overall woody cover (Faberlangendoen and Davis, 1995, Haney et al. 2008), increase understory light availability (Kay et al., 2007), promote a dense herbaceous understory plant community (Nuzzo et al., 1996; Leach and Givnish, 1999), and facilitate recruitment of understory plant species through stimulation of the seed bank (Glasgow and Matlack, 2007). However, burning alone may not achieve some restoration objectives, such as canopy cover reduction, particularly at fire-suppressed sites where encroaching mesophytic tree species have achieved high densities and large diameters (White, 1983; Abella et al., 2004). Therefore, some managers advocate direct removal of mesophytic trees and shrubs through mechanical harvest and subsequent herbicide treatment (Nielsen et al., 2003; Brudvig and Asbjornsen, 2007; Abella, 2010). This practice can accelerate savanna restoration by more rapidly increasing understory light availability, shifting woody species composition and abundance, and facilitating the development of the understory plant community (Brudvig and Asbjornsen, 2009). However, woody vegetation removal is costly relative to prescribed fire and, if carried out too quickly, could result in stress or mortality of remaining overstory oak trees, or invasion by exotic or aggressive native understory plant species. Either of these unintended impacts could compromise the core goals of promoting characteristic savanna overstory structure and understory plant communities during restoration.

The objectives of this study were to measure the effects of two oak savanna restoration strategies on (1) structural metrics of vegetation which define savannas (i.e. 10–60% canopy cover, low shrub cover, high understory cover), (2) understory light availability, and (3) flowering response of understory forb species. This study examines the first two-years of a 10-year effort to examine the long-term ecological effects of utilizing burn only and thinning and burning management approaches to oak savanna restoration. Specifically, we monitored the effects of prescribed burning-alone, as well as tree thinning coupled with prescribed fire on understory and canopy cover, shrub layer cover, light availability, and abundance and richness of understory forb species in flower. We did not include a "thin only" treatment as previous research has demonstrated that thinning by itself may yield short-term benefits but ultimately prescribed burning is necessary for these benefits to persist (Brudvig and Asbjornsen, 2007). Forb species are important to pollinators and comprise a large percentage of the ground layer in oak savannas – both in terms of richness and abundance, yet effects of savanna management on flowering forbs is lacking (Leach and Givnish, 1999; Huffman and Werner, 2000; Pavlovic et al., 2011). We focused on forbs in bloom because flowering is necessary for sexual reproduction of forbs, flowering rates are likely to influence the recovery of relict forb populations, and because of our broader interest in the role of pollinators in ecological restoration. We hypothesized that many heliophytic (light-loving) savanna forb species are suppressed due to decades of mesophication and resultant shading, but that these effects may be ameliorated through restoration. Specifically, we predicted that with increasing management intensity, light availability, floral abundance, and richness of forbs in flower would increase, while shrub and canopy cover would decrease.

2. Material and methods

2.1. Study site

The study site was located on the ∼165 ha Michigan State University MacCready Reserve in Jackson County, MI (42°07′36″ N, 84°23′38″). The reserve lies in the Jackson Interlobate Region, an area formed at the intersection of three separate glacial lobes (13–16,000 years ago). Glacial landscape features such as outwash plains and moraines, as well as ice-contact topography such as eskers, kettles, and kames characterize the region (Albert, 1995). This diversity of landscape features in the region has led to a diversity of natural communities, which are well represented at the study site. These include oak opening savannas, hillside prairies, prairie fen wetlands, and southern wet meadows (Michigan Natural Features Inventory, www.mnfi.anr.msu.edu/communities).

These communities span a range of human-induced disturbances including historical tilling, historical grazing, hydrological impediments, fire suppression, and encroachment from invasive plant species.

An esker ridge within MacCready Reserve that supports remnant fire-suppressed oak savanna communities was the focus of this study. The esker is dominated by soils in the Boyer-Leoni complex (alfisols), characterized by sandy loams and gravelly loams in the upper portion of the soil profile with 18 to 40 percent slopes (USDA NRCS Web Soil Survey). Despite the ample precipitation ($\sim$79 cm/year), the coarse textured soils promote effective drainage, and is thought to have resulted in relatively low productivity of overstory trees compared to surrounding areas (O'Connor, 2006). In aerial photos from 1938 (Fig. 1), an open canopy structure of scattered mature trees is evident and large oak trees with open-grown (laterally spreading limbs) architecture remain to the present day.

In the years since 1938, mesophication (Nowacki and Abrams, 2008) resulting from cessation of the historical burning and grazing disturbance regime has altered the canopy composition and increased the density of woody plants in remnant savanna patches (Fig. 1). Overstory trees common on site prior to the initiation of restoration included white oak (*Quercus alba* L.), black oak (*Quercus velutina* Lam.), northern red oak (*Quercus rubra* L.), pignut hickory (*Carya glabra* (Mill.) Sweet), red maple (*Acer rubrum* L.), and black cherry (*Prunus serotina* Ehrh.).

Common understory plants in the pre-management stage included Pennsylvania sedge (*Carex pensylvanica* Lam.), licorice bedstraw (*Galium circaezans* Michx.), northern dewberry (*Rubus flagellaris* Willd.), Virginia creeper (*Parthenocissus quinquefolia* (L.) Planch.), enchanter's nightshade (*Circaea canadensis* (L.) Hill), black cherry (*P. serotina* Ehrh.), red maple (*A. rubrum* L.), summer grape (*Vitis aestivalis* Michx.), pointed leaf ticktrefoil (*Hylodesmum glutinosum* (Willd.) H. Ohashi and R. R. Mill), sassafrass (*Sassafrass albidum* (Nutt.) Nees), ash (*Fraxinus* sp.), American hogpeanut (*Amphicarpaea bracteata* (L.) Fernald), and roundlobe hepatica (*Hepatica americana* (DC.) Ker Gawl).

2.2. Experimental design

In fall of 2010 through spring of 2011, we identified 15 comparable fire-suppressed patches of remnant oak savanna. Criteria for selection of patches included the presence of open grown oaks, and logistical feasibility of restoration (minimal density of planted pines, minimal presence of exotic understory species). We randomly assigned half of the ten fall-selected remnant patches to each of "burn only" or "thin and burn" management treatments (hereafter referred to as "BO" and "TB" respectively). The BO treatment received a controlled burn in alternate springs, while the TB treatment received controlled burns in alternative springs and three additional stages of woody plant removal. These were compared to five spring-selected reference areas that received no management (hereafter referred to as "UN"). Thus, there were 15 experimental units with five replicates of each treatment (UN, BO, and TB), which span a gradient of management intensity. Experimental unit size ranged from 0.2 to 1.2 ha, with size determined by the distribution of savanna remnants, locations of fire breaks (e.g., two track roads), and property boundaries (Fig. 1).

During woody plant removal stage one (fall 2010), we cut non-oak woody plant species with diameter-at-breast-height (1.3 m; DBH) $\leqslant$ 10.2 cm at ground level with chainsaws. A glyphosate-based herbicide (Cornerstone Plus) was mixed according to manufacturer's instructions and applied to cut stumps to prevent re-sprouting. During stage two (fall 2011), we cut and applied

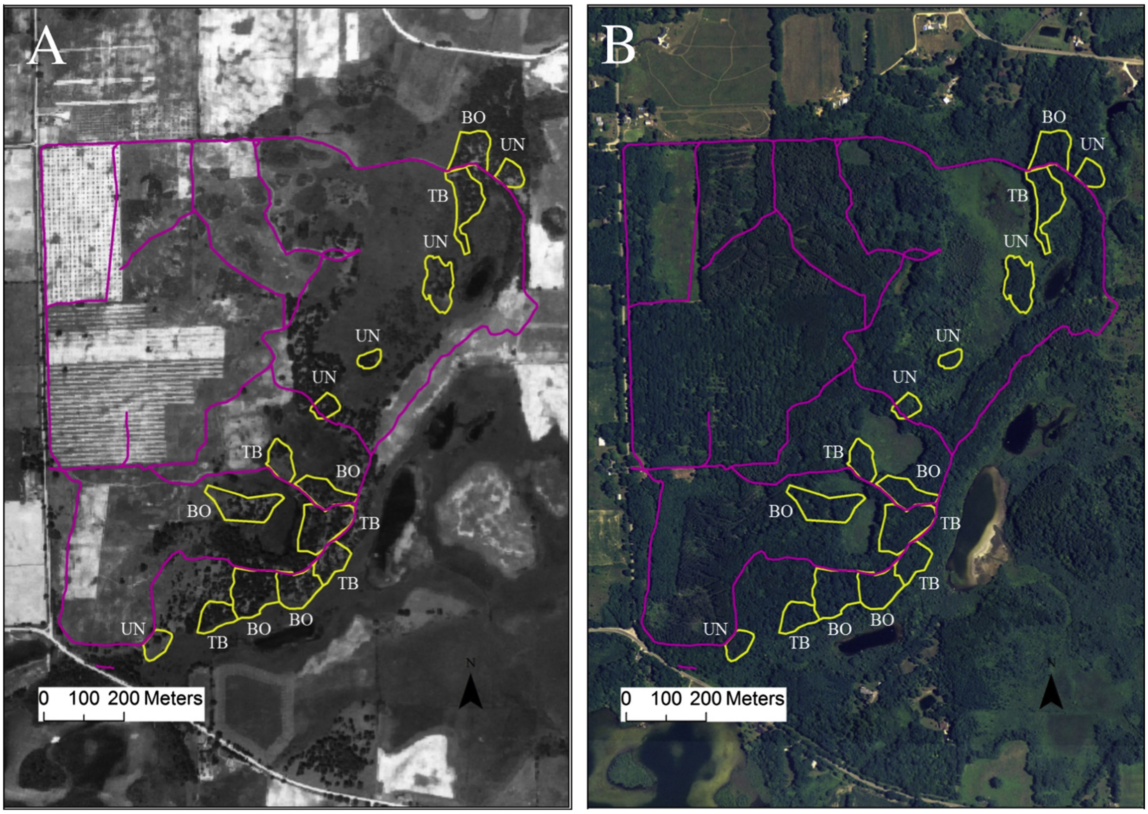

Fig. 1. 1938 (A) and 2005 (B) aerial photos of MacCready Reserve. Experimental plots outlined in yellow and labeled with treatment type UN (unmanaged), BO (burn only), or TB (thin and burn) (pink lines show public trail system). Compare the relatively scattered canopy of 1938 to the closed canopy in 2005.

herbicide to stumps of woody plants of the aforementioned characteristics up to DBH ⩽ 17.8 cm. Downed woody material was removed near the perimeters of the experimental units in order to reduce fuel for appropriate prescribed fire control and safety. In addition, a portion of the downed woody material was removed in selected TB units where it was found in great excess after cutting, resulting in all units containing similar amounts of woody litter. In spring 2011, prescribed burns were conducted at all 10 BO and TB experimental units. Burns occurred largely with backing fires during two days (5/4/11, 5/11/11). The mean relative humidity, mean temperature, and mean wind direction and speed on 5/4/11 were 59%, 10 °C, and NNW at 6 km/h respectively, and 57%, 19 °C, and ESE 14 km/h respectively on 5/11/11 (www.wunderground.com – Jackson, MI). Both burns produced similar effects on vegetation and litter. Mean fire temperature was 379.6 °C ± 15.5 (SEM) for the 66/81 pyrometers (temperature sensitive paints applied to copper tags, deployed at ground level; Wally et al., 2006) that registered during burns. A future stage three will involve cutting and treatment of larger non-oak stems once the herbaceous ground layer develops to the point that litter inputs from these trees are no longer necessary as fuel for prescribed fires. Woody vegetation thinning was conducted in a gradual manner to avoid encouraging invasive plant species, as our management activities have the potential to stimulate both desirable native plants as well as aggressive species. We also wanted to allow initial burns to reduce fuel loads before further thinning. We consider our ecological restoration endeavors to be a multi-step long-term process, and we wished to capture the results of initial stages before the woody thinning process was finished.

2.3. Vegetative structure

We assessed tree canopy cover in experimental plots using a spherical densiometer. We conducted densiometer measurements every 10 m along transects running from the base to the top of the esker ridge at each experimental unit ($n = 6–11$ points/unit). Most units contained a single transect; however, we established two transects in smaller units to permit sufficient sampling points. Individual transect lengths therefore varied from 20 to 100 m. We took four densiometer measurements during August 2012 at 1.5 m above each point, at 90° intervals relative to the sampling transect, and averaged values across all measurements and sampling points to derive one canopy cover value for each unit, for analyses. The sampling point at the esker base was located at the edge between oak savanna and fen wetland and, while excluding this point had no effect on our qualitative conclusions and little quantitative impact on our results, we decided to exclude this point so that all canopy cover measurements were representative of oak savanna alone.

We assessed understory and shrub cover with a vertical "cover board" (Nudds, 1977). The cover board was 3.48 cm wide, 2.5 m high, with five alternating painted black and white 0.5 m bands on the vertical axis. We used the eight sampling points created by the two 5 × 5 m sampling grids in each plot (Fig. 2). After selecting one random sampling point in one grid, a consistent observer (M.L.) would walk 15 m away from the point in a random compass direction. Facing the cover board, cover was visually assessed by estimating the percentage of each of the five alternating bands obscured by vegetation. This was repeated for another random compass direction for the same sampling point, and then repeated for the second 5 × 5 grid. Two measurements per sampling point and two sampling points per experimental unit were used, resulting in a total of 20 individual measurements per unit (four points × five height bands). If tree trunks completely obscured three or more bands of the cover board, we shifted 15° counter clockwise before estimating cover in order to prevent inflating estimates of under and mid-story cover by mature trees. Here, we designate understory cover as vegetation obscuring the 0.5 m band (first from ground), and shrub cover as vegetation obscuring bands from 1.0–2.5 m (four bands). Herbaceous and woody vegetation were not separated when taking understory and shrub cover measurements.

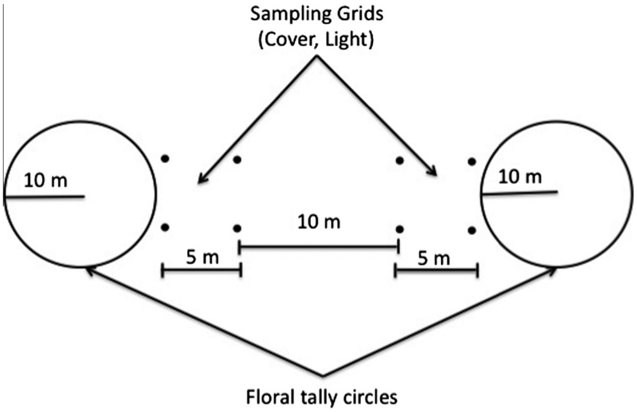

Fig. 2. Schematic of sampling design in research plot. Sampling points were randomly chosen from the two 5 m × 5 m grids for light and cover measurements. Circular floral tally plots were repeatedly measured (5–6 times) over the season.

2.4. Light availability

We assessed light availability among treatments using a 1 m long ceptometer (Sunfleck, Decagon Devices Inc., Pullman, WA). Photosynthetically active radiation (PAR) was measured on clear sunny days at three random sampling points per unit (Fig. 2) at 1 m height, consistently pointing north, between 10 a.m. and 2 p.m. on July 13th and August 15th in 2011, and August 6th and 7th in 2012.

2.5. Floral response

We made visual assessments of the flowering forb communities among treatments. Two species of woody angiosperms (i.e. *Ceanothus americanus* L. and *Elaeagnus umbellata* Thunb.) were also documented flowering in the understory of our plots, and are hereafter included in our forb category. In each experimental unit, two "tally circles" with 10 m radii (area: 314 m^2) were established adjacent to sampling grids (Fig. 2) where once every two weeks (six dates/season) a consistent observer (M.L.) would walk the perimeter of the circle and identify each forb species actively flowering within the circle, and tally the number of floral units for each flowering plant. A floral unit was defined as a discrete inflorescence separated in space from an adjacent inflorescence such that a medium-sized bee (e.g. honeybee) could not walk from one to another (Dicks et al., 2002). Species richness is defined here as the number of actively flowering forb species in each tally circle. The first date of floral sampling was standardized with base 10 °C degree-day model (Baskerville and Emin, 1969) using temperatures from a weather station ~40 km away (42°47′14″ N, 84°45′75″ W). Floral metrics are reported in this paper per 314 m^2 (the area of our circular subsample units).

2.6. Data analysis

We performed two-way (on height and treatment) repeated measures ANOVA procedures on percent cover across all three treatments (i.e. UN, BO, & TB). For these analyses we utilized arcsin square root transformations as suggested for proportional data (Crawley, 2013) to rectify non-normal error distributions and heterogeneous variances (PROC MIXED; SAS 9.3). Plot was treated as a random variable in ANOVA models to account for covariance in subsamples within plots. We analyzed light availability and floral abundance data using generalized linear mixed models that utilized Poisson distributions to reflect the non-normal error distribution of our data. We then applied a repeated measures ANOVA to analyze light availability and floral abundance data (PROC GLIMMIX; SAS 9.3). We compared canopy cover among all treatments using one-way ANOVA (PROC MIXED; SAS 9.2), on arcsin square root transformed canopy cover values.

Due to the difficulty in meeting assumptions of the error distribution in floral richness data, a non-parametric test was used to compare floral richness between all treatments and both years. The average number of species of forbs in flower for each treatment across each season was ranked (PROC RANK; SAS 9.3), giving the plot with the highest average species richness the highest rank, and so forth. A one-way ANOVA was then applied to ranked data using a general linear mixed model (PROC GLIMMIX; SAS 9.3). Model comparisons determined which random factors would be retained in all mixed models using Akaike's Information Criterion.

We also examined frequency occurrences of individual forb species within each treatment and across all treatments. This was based on the percentage of plots occupied within each treatment ($n = 10$) and across all treatments ($n = 30$), given that each treatment had five replications and each plot had two floral tally circles. Occupation was defined as presence of a forb in bloom in one tally circle in either year. In all analyses, pairwise differences among treatments were analyzed using Tukey's HSD.

3. Results

Restoration treatments consistently displayed stepwise increases as management intensity increased (i.e. UN < BO < TB) in mean light availability, floral abundance and richness, while showing stepwise decreases in mean values for vegetative cover and canopy cover. In general, treatment differences were more pronounced in 2012 than 2011.

3.1. Vegetative structure

Canopy cover in 2012 differed among experimental treatments ($F_{2,12} = 16.54$, $p = 0.0004$), with values ranging from 79.1% ± 2.2 (SEM) in the TB treatment to 91.7% ± 2.2 and 93.4% ± 2.2 in the BO and UN treatments, respectively. This resulted in less canopy cover in the TB than BO ($t_{12} = 4.43$, $p = 0.0007$) or UN treatments ($t_{12} = 5.43$, $p = 0.0002$), whereas there was no difference between the BO and UN treatments $t_{12} = 0.81$, $p = 0.43$).

Understory cover (0.5 m) was never different among treatments in either year, whereas treatment effects were often apparent in the shrub (1.0–2.5 m) cover (Figs. 3 and 4). In 2011, there was no difference in shrub cover from between UN and BO treatments, while TB always had less shrub cover than the other two treatments at these heights (Fig. 3). In 2012 shrub cover from 1.0 to 2.5 m declined with increasing management intensity (Fig. 4). However, the only significant treatment differences in shrub cover were between TB and UN from 1.5 to 2.5 m above ground in 2012 (1.5 m: $t_{572} = -3.77$, $p = 0.015$, 2.0 m: $t_{572} = -5.34$, $p = < 0.001$, 2.5 m: $t_{572} = -5.48$, $p = < 0.001$).

3.2. Light availability

Light availability differed among treatments in 2012 ($F_{2,27} = 9.56$, $p = 0.001$), but not 2011 ($F_{2,27} = 1.54$, $p = 0.233$) (Fig. 5). In 2012, light availability was greater in TB than BO or UN ($t_{27} = -3.14$, $p = 0.011$ and $t_{27} = 4.20$, $p = 0.001$), while BO and UN treatments were not different ($t_{27} = 0.30$, $p = 0.549$). Overall, mean light availability was lowest in UN (63.3 μmol/m^2), moderate in BO (100.1 μmol/m^2), and highest in TB (210.3 μmol/m^2).

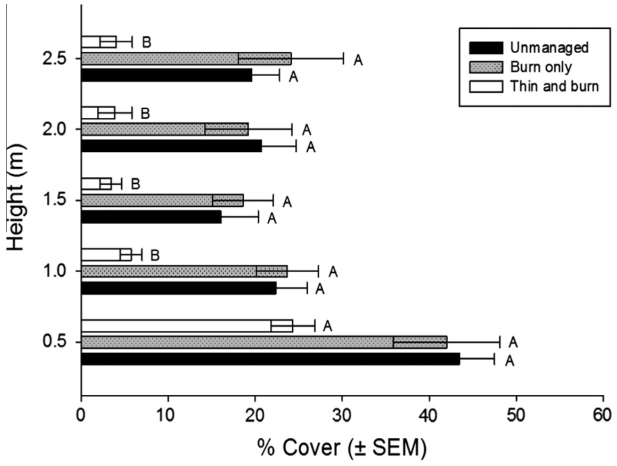

Fig. 3. Means ± SEM for 2011 under and mid-story cover among the three management treatments. A two-way ANOVA was performed using Tukey's HSD for treatment comparisons within height level. Different letters indicate statistically significant differences α = 0.05.

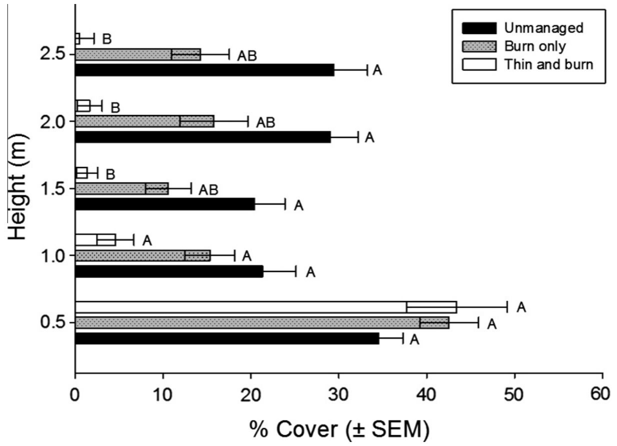

Fig. 4. Means ± SEM for 2012 under and mid-story cover among the three management treatments. A two-way ANOVA was performed using Tukey's HSD for treatment comparisons within height level. Different letters indicate statistically significant differences α = 0.05.

3.3. Floral response

In 2011 floral abundance was not affected by treatment ($F_{2,60} = 2.15$, $p = 0.126$), despite a greater mean number of floral units in TB than either BO or UN (Fig. 6). In 2012, however, floral abundance varied significantly by treatment ($F_{2,72} = 12.16$, $p = <0.001$), with an increase in mean floral abundance from UN to BO to TB (Fig. 7). While the mean floral abundance was comparable in the UN treatment between years (2.26–2.76 mean floral units/314 m^2), mean floral abundance increased from 2011 to 2012 by more than five times in BO (mean 8.3–44.3 mean floral units/314 m^2), and increased by more than seven times in TB (mean of 16.4–115.9 mean floral units/314 m^2). Changes in floral abundance from 2011 to 2012 trended toward significance for the BO and TB treatments, and both BO and TB supported greater floral abundance than UN in 2012 ($t_{72} = 3.55$, $p = 0.002$ and $t_{72} = 4.78$, $p = <0.001$ respectively).

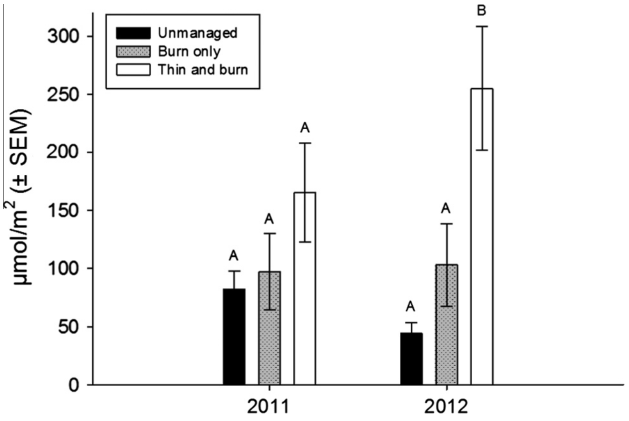

Fig. 5. Means ± SEM for light availability at 1 m among the three management treatments. A one-way ANOVA was performed using Tukey's HSD for treatment comparisons within year. Different letters indicate statistically significant differences within years $\alpha = 0.05$.

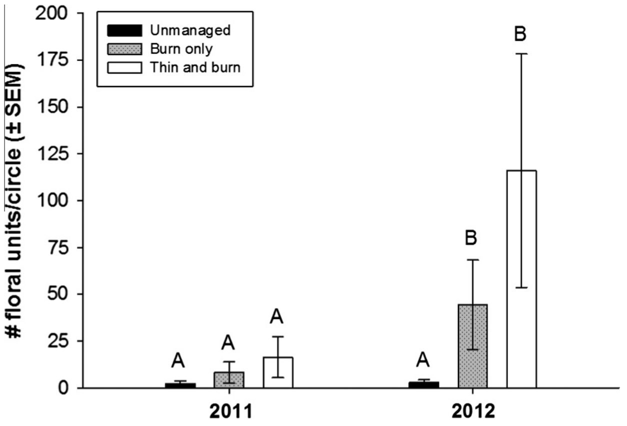

Fig. 6. Mean floral abundance ± SEM per 314 m^2 sampling circle among the three management treatments between years. A one-way ANOVA was performed using Tukey's HSD for treatment comparisons within year. Different letters indicate statistically significant differences $\alpha = 0.05$.

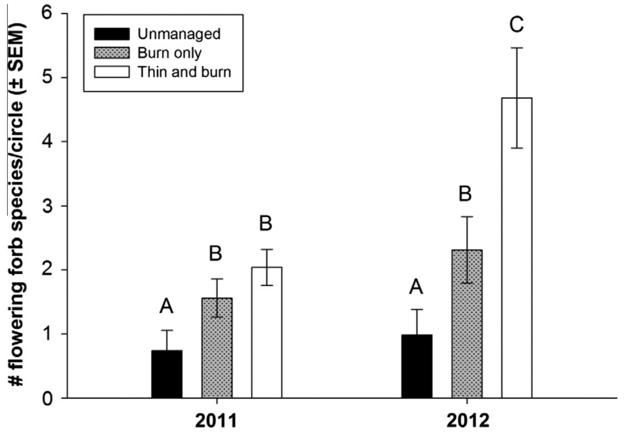

Fig. 7. Mean number of species ± SEM for floral richness per 314 m^2 sampling circle among the three management treatments between years. A one-way ANOVA was performed using ranked plot means. Tukey's Honestly Significant Difference for treatment comparisons within year. Different letters indicate statistically significant differences $\alpha = 0.05$.

In 2011 and 2012 floral richness was affected by treatment ($F_{2,48} = 3.88$, $p = 0.027$, $F_{2,60} = 9.90$, $p = <0.001$ respectively) (Fig. 7). Due to increases in the mean richness of BO and TB treatments in 2012, floral richness was affected by year ($F_{1,159} = 31.07$, $p = <0.001$), with an interaction between treatment and year ($F_{2,159} = 4.99$, $p = 0.008$). In 2011, floral richness did not differ between the BO treatment and either the UN or TB treatments ($t_{48} = 1.85$, $p = 0.164$, $t_{48} = -0.88$, $p = 0.658$), while the TB treatment supported greater floral richness than the UN treatment ($t_{48} = 2.73$, $p = 0.024$). In 2012 all treatments differed, with an increase in mean richness from UN to BO to TB.

We documented a total of 60 species of forbs in flower representing 27 taxonomic families (Table 1), including 49 forb species native to Michigan, and 11 exotic species. Species' frequency of occurrence among all floral plots (i.e., across treatments) ranged from 3% to 97% and from 0% to 100% within individual treatments. The ten forb species with the highest frequency of occurrence were: *G. circaezans* (97%), *Hylodesmum nudiflorum*, *Potentilla simplex*, *Rubus sp.* (70%), *C. canadensis*, *H. glutinosum* (67%), *Geum canadense*, *Hackelia virginiana* (60%), *Phryma leptostachya* (50%), and *Galium aparine* (43%).

4. Discussion

Our objectives were to assess how oak savanna restoration methods impact (1) structural metrics of vegetation which define savannas, (2) understory light availability, and (3) the abundance and diversity of flowering forb species. We found that defining structural metrics were mixed in their responses to high (thinning and burning) vs. low-intensity restoration (burning alone), relative to unrestored savannas. Canopy cover was reduced by thinning and burning, but not burning alone, understory cover (0.5 m) did not differ among treatments, and shrub cover reductions were variable depending on height above ground and treatment. Light availability increased in the second sampling season in the highest intensity restoration, reflecting managed reductions to shrub, mid, and overstory woody vegetation. Both management methods resulted in a greater abundance and richness of flowering forbs. Many of these effects of management were only realized in the second year of the study, and highlight the effects of multi-staged restoration practices, lagged responses of plant communities to these efforts, and the importance of multi-year studies for documenting these impacts. It should also be reiterated that these represent the results from the first two years of a planned 10-year study, and they should be interpreted as an initial response to ecological restoration on a previously unmanaged system.

4.1. Vegetative structure

Restoration by thinning and burning reduced canopy cover by 14%, relative to unrestored sites, but fell short of our long-term target canopy cover of 10–60% indicative of intact savannas (Curtis, 1959; Kost et al., 2007). Restoration by prescribed burning alone had little impact on canopy cover. This pattern mirrored the lack of strong effects of burning-alone on shrub cover and understory light levels (see below) and, together, suggest minimal short-term impact of the single prescribed fire on woody vegetation structure at our sites. Similar trends have been observed elsewhere in Minnesota and Ohio oak savannas/forests (Peterson and Reich, 2001; Hutchinson et al., 2005) where in each case, there was little effect of a single prescribed fire, yet multiple fires reduced overstory tree density, and effects were most pronounced for fire-sensitive species (Peterson and Reich, 2001; Hutchinson et al., 2005). We recognize that a higher intensity prescribed burn could have resulted in different fire effects in our study, such as lower canopy cover and basal area (Haney et al., 2008). In the Michigan oak savanna system, we anticipate a reduction in fire-sensitive species such as red maple (*Acer rubra*) and black cherry (*P. serotina*) with repeated

Table 1
Flowering forb species and % occupation of 314 m^2 circular sampling units at MacCready Reserve, 62 total, * = exotic species. *Rubus sp.* refers to both *R. flagellaris* Willd. and *R. pubescens* Raf. which were not separated in the field and were combined in analysis.

Family	Genus species	Common name	% Occupation			
			Total	UN	B	TB
Rosaceae	*Agrimonia gryposepala* Wallr.	Tall agrimony	0.23	0.00	0.30	0.40
Brassicaceae	*Alliaria petiolata* (M. Bieb.) Cavara & Grande*	Garlic mustard	0.10	0.10	0.00	0.20
Apocynaceae	*Apocynum androsaemifolium* L.	Spreading dogbane	0.03	0.00	0.00	0.10
Apocynaceae	*Apocynum cannabinum* L.	Indian-hemp	0.03	0.00	0.00	0.10
Apocynaceae	*Asclepias exaltata* L.	Poke milkweed	0.03	0.00	0.10	0.00
Brassicaceae	*Berteroa incana (L.) DC.**	Hoary alyssum	0.03	0.00	0.00	0.10
Brassicaceae	*Boechera canadensis* (L.) Al-Shehbaz	Sickle-pod	0.23	0.10	0.20	0.40
Urticaceae	*Boehmeria cylindrica* (L.) Sw.	False nettle	0.03	0.00	0.10	0.00
Rhamnaceae	*Ceanothus americanus* L.	New Jersey tea	0.03	0.00	0.10	0.00
Amaranthaceae	*Chenopodium simplex* Raf.	Maple-leaved goosefoot	0.03	0.00	0.00	0.10
Onagraceae	*Circaea canadensis* (L.) Hill	Enchanter's-nightshade	0.67	0.40	0.70	0.80
Asteraceae	*Cirsium vulgare* (Savi) Ten.*	Bull thistle	0.03	0.00	0.00	0.10
Lamiaceae	*Collinsonia canadensis* L.	Stoneroot	0.07	0.00	0.20	0.00
Asteraceae	*Conyza canadensis* (L.) Cronq.	Horseweed	0.23	0.00	0.10	0.60
Elaeagnaceae	*Elaeagnus umbellata* Thunb.*	Autumn-olive	0.03	0.10	0.00	0.00
Asteraceae	*Erechtites hieraciifolius* (L.) Raf.	Fireweed	0.10	0.00	0.10	0.20
Asteraceae	*Erigeron philadelphicus* L.	Common fleabane	0.20	0.00	0.10	0.50
Asteraceae	*Eurybia macrophylla* (L.) Cass.	Large-leaved aster	0.17	0.00	0.20	0.30
Asteraceae	*Eupatorium perfoliatum* L.	Boneset	0.03	0.00	0.00	0.10
Rubiaceae	*Galium aparine* L.	Cleavers	0.43	0.10	0.50	0.70
Rubiaceae	*Galium boreale* L.	Northern bedstraw	0.10	0.00	0.10	0.20
Rubiaceae	*Galium circaezans* Michx.	White wild licorice	0.97	0.90	1.00	1.00
Rubiaceae	*Galium concinnum* Torr. & A. Gray	Shining bedstraw	0.03	0.10	0.00	0.00
Geraniaceae	*Geranium maculatum* L.	Wild geranium	0.20	0.10	0.10	0.40
Rosaceae	*Geum canadense* Jacq.	White avens	0.60	0.30	0.70	0.80
Boraginaceae	*Hackelia virginiana* (L.) I. M. Johnst.	Beggar's lice	0.60	0.10	0.80	0.90
Asteraceae	*Hieracium caespitosum* Dumort.*	King devil	0.03	0.00	0.10	0.00
Fabaceae	*Hylodesmum glutinosum* (Willd.) H. Ohashi & R. R. Mill	Clustered-leaved tick-trefoil	0.67	0.40	0.80	0.80
Fabaceae	*Hylodesmum nudiflorum* (L.) H. Ohashi & R. R. Mill	Naked tick-trefoil	0.70	0.20	0.90	1.00
Asteraceae	*Krigia biflora* (Walter) S. F. Blake	False dandelion	0.30	0.10	0.00	0.20
Asteraceae	*Lactuca canadensis* L.	Wild lettuce	0.03	0.00	0.10	0.00
Lamiaceae	*Leonurus cardiaca* L.*	Motherwort	0.20	0.10	0.20	0.30
Campanulaceae	*Lobelia inflata* L.	Indian tobacco	0.07	0.00	0.00	0.20
Campanulaceae	*Lobelia spicata Lam.*	Pale spiked lobelia	0.03	0.00	0.00	0.10
Myrsinaceae	*Lysimachia quadrifolia* L.	Whorled loosestrife	0.07	0.00	0.10	0.10
Convallariaceae	*Maianthemum racemosum* (L.) Link	False spikenard	0.03	0.00	0.00	0.10
Fabaceae	*Melilotus albus* Medik.*	White sweet-clover	0.03	0.00	0.00	0.10
Fabaceae	*Monarda fistulosa* L.	Wild-bergamot	0.03	0.00	0.00	0.10
Apiaceae	*Osmorhiza claytonii* (Michx.) C. B. Clarke	Hairy sweet-cicely	0.03	0.10	0.00	0.00
Oxalidaceae	*Oxalis stricta* L.	Yellow wood-sorrel	0.10	0.00	0.00	0.30
Asteraceae	*Packera aurea* (L.) À. Löve & D. Löve	Golden ragwort	0.03	0.00	0.00	0.10
Caryophyllaceae	*Paronychia canadensis* (L.) Alph. Wood	Tall forked chickweed	0.10	0.00	0.10	0.20
Polygonaceae	*Persicaria virginiana* (L.) Gaertn.	Jumpseed	0.37	0.40	0.30	0.40
Phrymaceae	*Phryma leptostachya* L.	Lopseed	0.50	0.10	0.90	0.50
Phytolaccaceae	*Phytolacca americana* L.	Pokeweed	0.30	0.20	0.30	0.40
Berberidaceae	*Podophyllum peltatum* L.	May-apple	0.03	0.00	0.00	0.10
Rosaceae	*Potentilla norvegica* L.	Rough cinquefoil	0.03	0.00	0.00	0.10
Rosaceae	*Potentilla simplex* Michx.	Common cinquefoil	0.70	0.50	0.90	0.70
Lamiaceae	*Prunella vulgaris* L.	Self-heal	0.10	0.10	0.10	0.10
Rosaceae	*Rubus allegheniensis* Porter	Common Blackberry	0.10	0.10	0.00	0.20
Rosaceae	*Rubus sp.*	Raspberry	0.70	0.30	1.00	0.80
Asteraceae	*Rudbeckia hirta* L.	Black-eyed Susan	0.03	0.10	0.00	0.00
Caryophyllaceae	*Silene latifolia* Poir.*	White campion	0.03	0.00	0.00	0.10
Solanaceae	*Solanum ptychanthum* Dunal	Black nightshade	0.20	0.00	0.20	0.40
Apiaceae	*Taenidia integerrima* (L.) Drude	Yellow-pimpernel	0.03	0.10	0.00	0.00
Apiaceae	*Torilis japonica* (Houtt.) DC.*	Japanese hedge-parsley	0.23	0.20	0.00	0.50
Commelinaceae	*Tradescantia ohiensis* Raf.	Ohio spiderwort	0.17	0.00	0.10	0.40
Campanulaceae	*Triodanis perfoliata* (L.) Nieuwl.	Venus's looking-glass	0.07	0.00	0.00	0.20
Scrophulariaceae	*Verbascum thapsus* L.*	Common mullein	0.10	0.00	0.00	0.30
Verbenaceae	*Verbena urticifolia* L.	White vervain	0.20	0.00	0.20	0.40

burns. Even repeated burns are likely limited in their capacity to reduce larger size classes of trees; however, and mechanical treatments may be ultimately necessary to achieve our target canopy cover of 60%. Even long-term burn studies where as many as 13 fires have been conducted annually, have demonstrated that tree mortality of stems >25 cm is rare (White, 1983). In our study system, although thinning and burning reduced canopy cover in the short-term, canopy cover was not reduced below 60%. In this sense, our planned reductions in canopy cover through future clearing of larger size class trees will be important for successfully restoring canopy cover to levels that typify oak savannas (Curtis, 1959; Kost et al., 2007).

The development of a native, dense, and herbaceous understory is a goal of our oak savanna management (Asbjornsen et al., 2005), and if this goal is being met, it should be reflected in treatment differences of cover from 0 to 1 m. However, all treatments were comparable in mean vegetative cover at 0.5 m in 2011, and 0.5 and 1.0 m in 2012 (Figs. 3 and 4). From this, it could be concluded that management did not affect understory development, yet this is not reflective of our floral data or our general observations. A more likely explanation is the fact that our assessment of vegetative cover did not separate woody cover from herbaceous cover, and of particular importance may be the post-fire re-sprouting shoots of small top-killed trees and shrubs present in BO treatments.

The initial reduction in shrub cover (1–2.5 m) in the TB, relative to BO treatment, that we observed in 2011 did not persist to 2012 (Figs. 3 and 4). An additional level of thinning took place in TB treatments in the fall of 2011. We expected this to lower mean shrub cover in TB, and further separate its mean from the BO treatments, yet the two treatments were more similar in 2012. The reductions in mean shrub cover in 2012 from both TB and BO treatments related to this change are visually evident (Fig. 4). An increase in standard error of the mean of the shrub cover for one or both the TB and BO treatments would reflect an increase in variability and could cause this change in the statistical relationship from 2011 to 2012. However, we did not observe an increase in error (Figs. 3 and 4). As such, we suspect that this observation results from an authentic biological process. One hypothesis is that there is a delayed pattern of mortality or reduced vigor in fire-sensitive woody species that contributes to a lower mean cover in 2012 but not 2011 in BO treatments. In 2011 we observed substantial woody vegetative cover in BO treatments resulting from resprouting of fire-intolerant woody species (e.g. *P. serotina*), presumably as a physiological stress response to the spring burn (M.L. personal observation). A study of the effects of fire in an oak forest in Kentucky, USA, found a similar response with a rapid flush of stump sprouts that was responsible for a short-term decline in understory openness or "gap fraction" (Chiang et al., 2005) following initial prescribed burns. In some cases, a reduction in the canopy and/or shrub layer may not occur with repeated burnings if the recovery of woody species outpaces the setbacks induced by fire (Alexander et al., 2008; Haney et al., 2008). This same vigorous regrowth at MacCready Reserve could have maintained adequate vegetative cover in 2011 to create similar mean vegetative cover between unmanaged and burn only treatments.

In 2012 the MacCready Reserve region received approximately half its normal accumulation of rainfall from January 1st to August 30th (41.86 cm), compared with the same period in 2011 (75.41 cm) (www.enviroweather.msu.edu, Leslie, Michigan station). This atypical reduction in precipitation combined with a decrease of the moisture retaining capacity of the litter layer (burned off the spring prior) could have created droughty soil conditions and exerted additional stress on mesic-adapted woody species already stressed from burning. The overall effect could be a delayed reduction in cover of fire-sensitive mesic forest species resulting from direct (e.g. heat damage) and indirect (e.g. reduction of moisture retaining capacity of the soil) physiological stresses from our prescribed burn and low precipitation, although we do not have data to directly test this hypothesis. The conceptual intent of the restoration methods presented here are to reverse the degradative effects rendered by the successional process of mesophication. Our hypothesis of this reduction in fire-sensitive woody plants through the effects from fire on litter, soil moisture, and direct stress supports this concept, and these species-specific mortality effects are documented in similar studies (Peterson and Reich, 2001; Alexander et al., 2008).

4.2. Light availability

Light availability was only effectively increased within the two year study period by the TB treatment, while the BO treatment failed compared to the UN treatment. When light availability was measured during 2011, both BO and TB plots had received one burn the spring prior, and additionally, TB plots had their non-oak woody shrub layer ($\leqslant$10.2 cm DBH) removed. Although the mean light availability was numerically greater in TB in 2011, the treatments were not statistically different (Fig. 5). This suggests that simply burning once, or burning and conducting thinning of the shrub layer may not be sufficient to increase light availability to the understory. In 2012, when the second stage of thinning had occurred, light availability increased in the TB treatment, suggests that thinning larger trees (10.2–$\leqslant$17.8 cm DBH) was necessary to increase light availability. In contrast, BO treatments did not have greater light availability than unmanaged treatments in 2012. Given the significantly greater richness of flowering forbs, and greater mean floral abundance of TB as compared to BO (Figs. 6 and 7, and Table 1), increased light availability in TB may be a driver of increased floral diversity. Leach and Givnish (1999) presented light availability as one of two principal ecological gradients affecting plant community composition in a comprehensive study of oak savanna groundlayers in Wisconsin (the other being soil texture). Light was also found to be the strongest predictor of understory vegetation growth in a study of variable sizes of canopy gaps in longleaf pine savannas (McGuire et al., 2001), and declines in canopy cover from management were associated with 100% increases in understory species richness of research plots in a remnant Eastern sand savanna (Bowles et al., 2011). Although we saw no significant increase in light availability in the ground layer of our BO treatment, this does not necessarily mean that using a burn only management method is ineffective at achieving increased light availability, as more than one burn may be necessary to achieve significantly increased light penetration. This observation underscores the importance of sustained management (e.g. a long-term burning regime) once restoration of a remnant community is initiated.

4.3. Floral response

Flowering forb communities (abundance and richness) responded positively to increasing management intensity (Figs. 6 and 7). These patterns developed over time and were mixed in significance in 2011 but consistent in 2012. Mean abundance of floral units in TB treatments was greater than both UN, and BO treatments in 2011, yet there were no statistically significant treatment differences until 2012 (Fig. 6). Similarly, modest treatment differences in floral richness in 2011 became more pronounced in 2012 (Fig. 7). In a similar system, Thomas et al. (1999) found that silvicultural thinning increased richness of understory plants, as well as understory vegetative cover relative to non-manipulated forest stands. It appears that a more intense management method (i.e. TB) in our study similarly leads to greater mean floral abundance than a less intense (i.e. BO) approach, although this trend was not statistically significant.

In managed treatments, we observed a delayed flowering response for many species following prescribed burning as management progresses and/or more time is allowed for physiological recovery of the understory vegetation. This delayed flowering response could be explained by several mechanisms. Dormant seed could be stimulated into germination with removal of leaf litter, scarification, and/or smoke (Keeley and Fotheringham, 1998; Glasgow and Matlack, 2007) associated with burning, and simply require two seasons (biennial flowering species or perennial) to build up the energy required to flower. Additionally, flowering individuals may simply produce more flowering units during the second season than the first, potentially set back by the harmful short-term effects of fire in the first year. *H. virginiana*, a biennial native forb species, was not observed blooming at the study site until 2012, in spite of its high abundance (occupying 60% of total floral tally plots, though 10% of UN plots; Table 1)). *Verbascum thapsus*, an exotic biennial forb, also followed a similar trend. It occupied only 10% of total plots, all of which were TB plots, but also was only observed in 2012. It is reasonable to suggest that these species were stimulated by the disturbance of our restoration activities and subsequently bloomed in their second year of growth. Alternatively, the combined long-term effects of fire suppression and short-term effects of disturbance by fire (as associated damage to plants), could require multiple years of recovery before flowering occurs. There are inherent short-term impacts that using prescribed fire as a management tool can have on desirable flora. Yet burning will be required in long-term oak savanna management to stimulate understory growth through maintenance of high light levels, litter removal, and reduce competition from fast growing fire-sensitive woody species.

The flowering forb species we observed in treatment floral tally plots spanned a range of habitat associations and abundances. The combination of understory species adapted to forest, savanna, and prairie-like conditions documented in our study support the concept that oak savannas retain their high diversity through niche heterogeneity across physical gradients (e.g. light). Forest-adapted species such as *Podophyllum peltatum*, *Persicaria virginiana*, and *Boehmeria cylindrica* might decrease in frequency over time due to increased fire mortality, light intensity, competition, and a reduction of forest-microsites as restoration progresses. Conversely, species associated with prairies and open areas like *Monarda fistulosa* and *Triodanis perfoliata* might increase in abundance as restoration produces prairie-like microsites. Each of these open-site adapted species was only present in one tally plot (Table 1), a likely reflection of the smaller number of prairie-like microsites at this early stage of restoration. Putative oak savanna specialist species such as *Apocynum androsaemifolium*, *Asclepias exaltata*, *C. americanus*, *Krigia biflora*, *Lysimachia quadrifolia*, and *Taenidia integerrima* that have been discussed in recent oak savanna restoration works (e.g. Bader, 2001) and classic savanna studies (Curtis, 1959) were observed in floral plots of our study in low abundances (Table 1). We anticipate increases of abundance over time of these savanna species, as well as those indicative of prairie. Sources of oak savanna specialists and open-adapted species could come from continued seed bank emergence, increased vigor in light-suppressed vegetative forms, and migration from light gaps, trailsides, and forest edges where light levels may retain historical intensity. Several understory species documented in our study (e.g. *Boechera canadensis*, *Erigeron philadelphicus*, *G. aparine*) displayed a gradual increase in their presence in floral tally plots along a gradient of management intensity. This trend may reflect a direct response of understory plant vigor (i.e. flowering) to the gradual increase in mean light availability across our restoration treatments.

In addition to plant species typical of savannas, prairies, and forests, we documented a number of ruderal species that had increased abundance or exclusive presence in TB treatments as compared to BO and UN (Table 1). This suggests that high light levels and/or physical disturbance associated with mechanical removal of woody vegetation favored these weedy species. The ruderal native species include *Chenopodium simplex*, *Conyza canadensis*, *E. philadelphicus*, *Lobelia inflata*, *Oxalis stricta*, *Potentilla norvegica*, while exotics include; *Cirsium vulgare*, *Leonurus cardiaca*, *Melilotus albus*, *Silene latifolia*, *Torilis japonica*, and *V. thapsus*. We do not consider the aforementioned weedy natives to be a management concern. In fact, these annual disturbance-adapted species may play an important role of early colonization of exposed soil following a disturbance. Given the mixed response of the understory in this study, these weedy natives may help compete for resources with exotics, and will likely decrease in abundance in time as more conservative, perennial species increasingly dominate at the site. Hutchinson et al. (2005) for example, found that *Erechtites hieraciifolius* (fireweed), a seedbanking annual species also documented in our study, increased sharply during the season immediately following a spring fire, but returned to pre-burn levels during years when fire was absent. Although the exotic species we documented were not widespread in our floral tally plots (Table 1), their early detection at the site is important and points out key considerations regarding savanna restoration. There is a grazing history at MacCready Reserve, as is common with many oak savanna remnants (Curtis, 1959; Considine et al., 2013). The presence of grazing by livestock might have maintained structural openness after regular burning ceased and potentially delayed the effects of mesophication, and has even been investigated as an oak savanna restoration tool (Harrington and Kathol, 2009). However, this land use may have introduced and maintained many of the exotic species found in this study into the understory plant community.

Kudo et al. (2008) suggested that flowering and fruit set of early summer flowering species (the period when most of our sampling took place) in a deciduous forest understory was most limited by light. The critical role of light availability in driving dynamics of oak savanna understory communities demonstrated in other research (Leach and Givnish, 1999) in combination with our results (Figs. 5–7, Table 1), suggests that even modest increases in light availability could produce dramatic effects on flowering of forb species in the understory of oak savannas.

This study demonstrates that in the short-term (e.g. two to three years, and the length of many grant supported restoration efforts), a more intensive restoration method could achieve a higher degree of success of restoration objectives related to increases in light availability, reduction of canopy and shrub cover, and rehabilitation of the flowering of the understory plant community. However, we observed delayed effects from burn only restoration in mean shrub cover reduction, increases in light availability, and floral diversity. This suggests that burn only treatments may be on a trajectory to approach the degree of success that thin and burn treatments have attained, but require longer term monitoring to detect. In contrast, many researchers have pointed out that due to the great periods of fire suppression of many oak savanna remnants, large increases in girth of fire-sensitive trees are realized and increase fire resistance in all overstory trees. Therefore, in some cases burning alone may not be sufficient to reduce canopy cover to presettlement levels; meeting such restoration objectives could therefore require a more intensive method, such as mechanical thinning (White, 1983; Abella et al., 2004; Wolf, 2004; Karnitz and Asbjornsen, 2006; Considine et al., 2013).

5. Conclusions

Restoration methods of varying intensity may be pursued under different temporal, financial, and ecological scenarios. Intensive management by thinning and burning may be necessary to rapidly meet goals if financial support is limited. Conversely, if funds for initial restoration are limited, but the time frame to achieve restoration objectives is long, a lower intensity burn only method may be sufficient and we demonstrate many positive management outcomes of this approach even over the short-term. Maintaining high biodiversity in oak savanna restorations may require a range of disturbance regimes and, by extension, multiple restoration methods (Leach and Givnish, 1999). Given the differential yet generally positive results on abiotic conditions and floral diversity from the two restoration methods presented here, both could be utilized at the same site to create greater within-site heterogeneity. This utilization of multiple restoration methods and their resultant heterogeneity could serve to further promote the notably high biodiversity of oak savanna ecosystems.

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