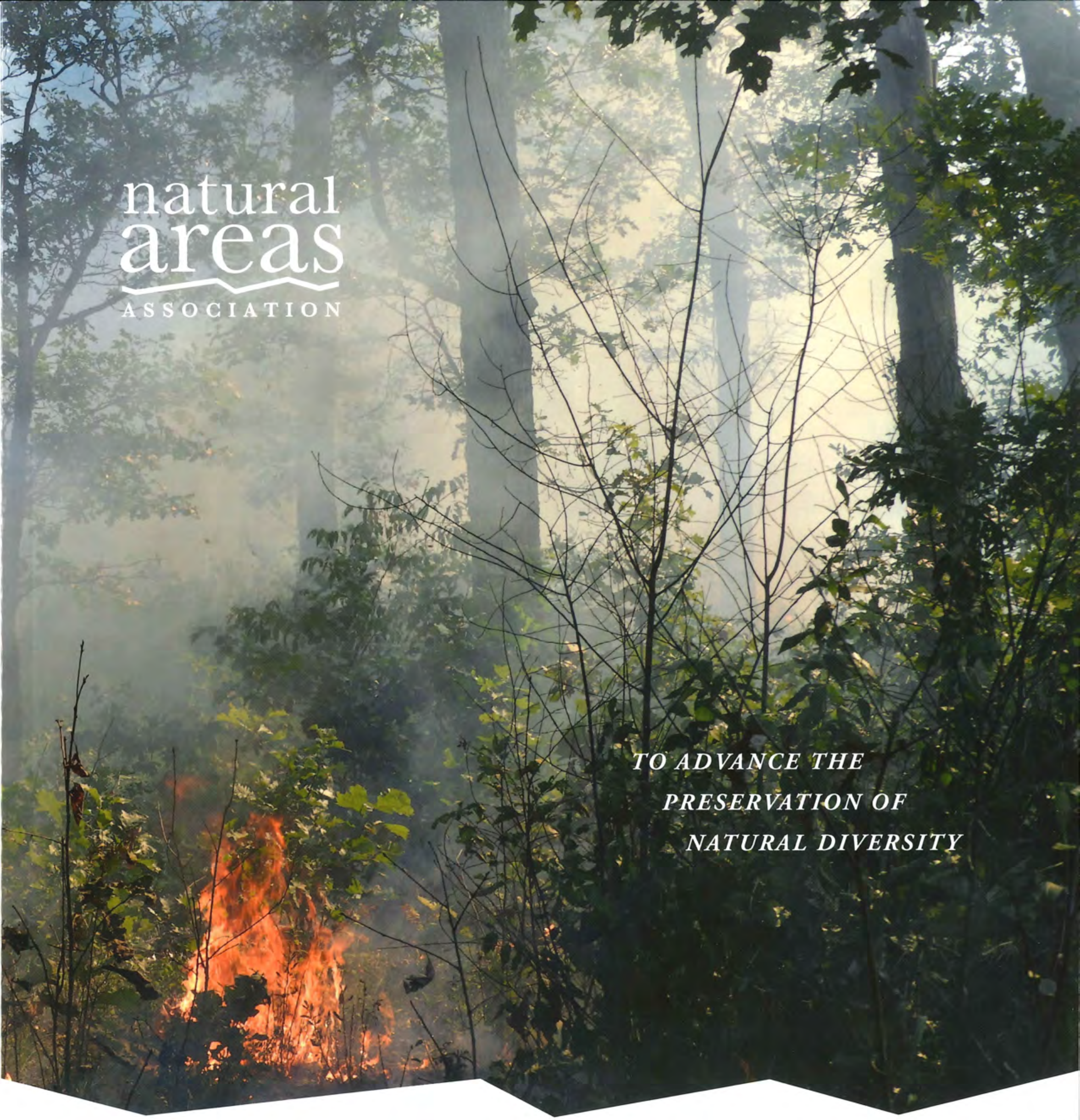

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Research Article

Changes in Groundlayer Communities with Variation in Trees, Sapling Layers, and Fires During 34 Years of Oak Savanna Restoration

Scott R. Abella,[1,2,5] LaRae A. Sprow,[3] Karen S. Menard,[3] Timothy A. Schetter,[3] and Lawrence G. Brewer[4]

[1]University of Nevada Las Vegas, School of Life Sciences, Las Vegas, NV 89154
[2]Natural Resource Conservation LLC, 1400 Colorado Street, Boulder City, NV 89005
[3]Metroparks Toledo, 5100 Central Avenue, Toledo, OH 43615
[4]Northern Kentucky University, Center for Environmental Restoration, Highland Heights, KY 41099

[5]Corresponding author: scott.abella@unlv.edu

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ABSTRACT

Like many open habitats, sustainability of oak savannas in midwestern North America depends on periodic disturbances such as fires to curtail encroachment by tall woody plants. An uncertainty in restoring and sustaining oak savannas is how frequently fires must occur to maintain the groundlayer plant diversity savannas are known for and what levels of tree canopy and sapling layer encroachment trigger shifts in groundlayers. In an oak savanna undergoing restoration in northwestern Ohio, we examined how groundlayers changed with temporal variation in tree ($\geq$10 cm in diameter) and sapling (<10 cm) layers and prescribed fires by remeasuring permanent plots up to 17 times from 1988 to 2021. Groundlayer cover was maximized when tree basal area was <13 m^2/ha (35% tree canopy cover), there were fewer than 100 trees/ha, and fire had occurred since the previous growing season. Illustrating attrition in groundlayers above these thresholds, two-thirds of savanna groundlayer cover disappeared when tree density exceeded 100/ha and over 2 y passed without fires. Through savanna species persisting at low cover, species richness endured longer between fires (4+ years), doubled during periods with at least one fire in 3 y, and increased by a third when saplings were sparse (<80 stems/ha). Savanna groundlayers during the 34 y study fluctuated with intermittent increases and decreases associated with dynamics in trees, saplings, and time since fire. Although they require a major commitment because their benefits are so transient, frequent, low-severity prescribed fires appear capable of sustaining savanna groundlayer diversity indefinitely under prevailing conditions.

Index terms: fire frequency; overstory–understory relationships; shrubby layer; species richness; woody plant encroachment

INTRODUCTION

The vascular plant community of midwestern oak savannas is viewed as containing three dynamic and interacting layers: a tree canopy layer of large oaks, a sapling layer of varying height in the understory including young stems of tree species of seedling or sprout origin, and a groundlayer of herbaceous and woody plants (Leach and Givnish 1999; Peterson and Reich 2001; Taft 2009). By producing sunny and shady microsites, the overstory layer can interact with the groundlayer by creating a gradient of light availability (Pavlovic et al. 2006). Indeed, the high plant diversities of oak savannas arise in part from coexistence of species varying in light requirements (Noble and Bauer 2022). The overstory layer before Euro-American settlement is thought to have varied in tree density in space and time, perhaps fluctuating between open savanna and denser woodland with factors such as weather events (e.g., droughts, wind storms) and variable fire frequency and severity (Haney et al. 2008). On likely all but the driest sites, the sapling layer, much as it does contemporarily, is thought to have increased during fire-free periods (Bowles et al. 2011). During fire-free periods as the sapling layer matures, groundlayers are hypothesized to undergo a community disassembly process whereby increasing numbers of light-demanding species disappear (Taft and Kron 2014).

Fire can affect the savanna groundlayer directly and indirectly by influencing tree and sapling layers and soils (Peterson et al. 2007; Plenzler and Michaels 2015). Direct fire effects include processes such as consuming biomass and seeds but stimulating resprouting, flowering, or seed germination (Pavlovic et al. 2011). The low-severity, prescribed fires commonly used in contemporary savanna restoration and management do not necessarily have much influence on large, thick-bark, fire-resistant oaks (Cole et al. 1992). However, low-severity fires can affect the sapling layer, especially by top-killing less fire-resistant species encroaching into savannas (e.g., red maple [*Acer rubrum* L.]) and small oaks not yet fire resistant (Abella et al. 2021). Fire can influence soils through processes such as incinerating seeds and reducing thickness of surficial organic layers (O horizons), which can filter groundlayer species composition (Plenzler and Michaels 2015). Variation in fire frequency, described using measures such as length of a fire-free period (time since fire) and number of fires within a certain period, can be a major regulator of savanna sapling and groundlayers (Taft 2009).

After covering at least 11 million hectares historically in the Midwest, oak savanna is nearly absent on the modern midwestern landscape primarily from land use change (e.g., conversion to agriculture and urban lands) and transition to forest without fires, which were historically ignited predominantly by Native Americans (Nuzzo 1986). The high biodiversity, unique habitat values, and precipitous decline of oak savannas have stimulated interest in restoring them (e.g., Packard 1988; Bowles et al. 2011; Bassett et al. 2020). One of the major uncertainties in restoring and sustaining midwestern savanna groundlayers is whether thresholds exist along gradients of tree canopies, sapling layers, and fire frequencies that trigger shifts in groundlayers through time. For example, knowledge of how long savanna groundlayer plants can persist between fires and how much woody plant encroachment savanna plants can tolerate could aid planning multi-decade savanna restoration and management projects.

Here, we present a case study of temporal change in groundlayers, tree canopy and sapling layers, and fire frequency during 34 y of oak savanna restoration. Our study objectives included (1) determining how temporal change in groundlayer cover, species richness, and constituent species were related to change in canopy tree and sapling layers and prescribed fires; and (2) identifying thresholds of tree and sapling layer abundance and fire intervals at which major shifts in groundlayer cover, species richness, and composition occur.

METHODS

Study Area

Our study area was within the 45,000 ha Oak Openings region in northwestern Ohio, USA. Climate is temperate, including daily average low/high temperatures of −9/0°C in January and 16/29°C in July and 85 cm/y of precipitation (34 cm in summer from May through August; 1955–2021 records, Toledo Airport weather station, Midwestern Regional Climate Center, Champaign, Illinois). Analysis of public land survey records revealed that, in the early 1800s before Euro-American settlement, this sandy region contained a mixture of oak savanna (4–43 trees/ha and averaging 14 trees/ha for trees larger than approximately 10 cm in diameter at 1.4 m) and woodland (>43 trees/ha and averaging 90 trees/ha; Brewer and Vankat 2004). Both habitats were dominated by white oak (*Quercus alba*) and black oak (*Quercus velutina*). Similar to much of the broader midwestern oak savanna region, these open habitats are thought to have been historically maintained largely by frequent, Native American–ignited fires (Wolf 2004). Within decades without fires or disturbances that hinder forest development, the open habitats convert to forest (Schetter and Root 2011).

We performed the study in the 1737 ha Oak Openings Preserve, managed by Metroparks Toledo. By the 1980s with no known fires since perhaps the 1800s, oak savanna was essentially absent from the preserve, having converted to closed-canopy oak forest with dense tree sapling layers of non-oak species on all but the driest sites (Abella et al. 2020c). These non-oak species were predominantly red maple, black cherry (*Prunus serotina*), and sassafras (*Sassafras albidum*), which were present, but not dominant, in pre-settlement savannas (Brewer and Vankat 2004). Our study site was the 40 ha Mary's Savanna (41°32′15″N, 83°51′00″W), on sandy soil classified as Udipsamments of the Ottokee and Oakville series (Stone et al. 1980). The site was mapped as oak savanna in the early 1800s public land survey (Brewer and Vankat 2004). When our study began in 1988, the site contained a forest with predominantly black oak overstory trees (with the oldest typically age 70–100 y at that time) averaging 21 m^2/ha oak basal area (for trees ≥10 cm in diameter at 1.4 m) and a tree sapling layer (stems ≥ 1 < 10 cm in diameter) of 800 stems/ha of red maple-sassafras-black cherry and 300 stems/ha of black oak-white oak. Groundlayers in 1988 were dominated by mostly shade-tolerant species or those that can inhabit forests such as brackenfern (*Pteridium aquilinum*), Pennsylvania sedge (*Carex pensylvanica*), and ericaceous shrubs (e.g., black huckleberry [*Gaylussacia baccata*] and Blue Ridge blueberry [*Vaccinium pallidum*]).

Prescribed Fires and Ecological Events

Beginning in autumn 1988 and continuing through 2021, prescribed fires were implemented at the site in spring (March–April) or autumn (October–November) on a variable schedule based on availability of personnel, weather, and seeking to burn often but intermittently (Table 1). Typical conditions during the dormant-season fires included relative humidity of 30–70%, wind <16 km/hr, and surface fire behavior with flames <2 m high from backing or head fires. One prescribed fire also occurred during the growing season, in August 2020, under light winds (<12 km/hour). As none of the fires readily killed larger (≥10 cm in diameter) oak trees, overstory oak tree density and basal area remained relatively constant until 2010, when high winds from an EF1 tornado damaged the overstory and halved density and basal area of large oaks (Figure 1).

Data Collection

In summer 1988 before the first prescribed fire, five permanent plots (each 20 m × 25 m, 0.05 ha) were systematically established approximately 50 m from each other. A sixth plot was added in 1998. Beginning with pre-treatment sampling in 1988 and the first post-fire sampling in 1989, plots were sampled irregularly but frequently based on availability of personnel over 34 y through 2021. As fires burned different parts of the study site depending in part on ignition locations and variable fire behavior across the site, individual plots had unique fire histories. Plots were burned 4–16 times and sampled up to 17 times during the study, providing data on plant community condition at different intervals since fires and dynamic tree and sapling structures (Table 1, Figure 1).

In each plot each sample year, we visually categorized aerial cover by species for 42 vascular, savanna groundlayer plant species from among the site's flora. For plants rooted in plots, we categorized cover as 0.1%, 0.25%, 0.5%, and 1%; 1% intervals to 10% cover, and 5% intervals to 100% cover. Cover could exceed 100% in total for all savanna species on a plot if foliage of multiple species overlapped. We chose the 42 savanna

Table 1.—Summary of sampling schedule, prescribed fires and disturbance, and precipitation during a 34 y study of changes in oak savanna plant abundance, northwestern Ohio.

			Precipitation (%)[b]	
Year[a]	Sampled[a]	Events (on number of plots of 5 or 6)	May–Jun	Jul–Aug
1988	×	Autumn fire (3/5)	24	135
1989		Spring fire (3/5)	167	151
1990		Spring fire (3/5)	112	80
1991	×		91	38
1993	×	Autumn fire (3/5)	83	42
1994		Autumn fire (3/5)	68	79
1997	×	Spring fire (3/5)	151	102
1998	×	Autumn fire (3/6)	55	124
1999	×		98	65
2000	×		178	98
2001		Autumn fire (3/6)	114	66
2002	×		77	48
2004	×	Autumn fire (3/6)	123	102
2006	×		152	190
2007	×		75	178
2008		Spring fire (3/6)	116	99
2010		Winds reduce tree density (6/6)	142	114
2012	×	Spring fire (3/6); autumn fire (3/6)	64	128
2013		Spring fire (3/6)	129	91
2015	×	Spring fire (3/6); autumn fire (3/6)	165	141
2016		Autumn fire (3/6)	44	121
2018	×		136	90
2019	×	Spring fire (3/6); autumn fire (3/6)	126	178
2020	×	Summer fire (1/6)	96	86
2021	×	Spring fire (3/6)	128	105

[a] Only years that were sampled (×) or experienced a fire or disturbance event are listed.

[b] Percent of the long-term (1955 through 2021) average.

species (29 forbs, 9 graminoids, and 4 shrubs) based on the following criteria: being part of the local flora of the study site; were native species with a coefficient of conservatism of at least 4 (out of 10) in Ohio signifying fidelity to high-quality natural habitats (Andreas et al. 2004); and were species identified as inhabiting pre-settlement or high-quality contemporary remnant savannas based on published literature from the broader midwestern oak savanna region (e.g., Bray 1958; Pruka 1995; Leach and Givnish 1999; Bader 2001; Meisel et al. 2002; Pavlovic et al. 2011) and locally from the Oak Openings region (Moseley 1928; Brewer and Vankat 2004, 2006; Supplemental Table S1). Sampling typically occurred in July–August, near the

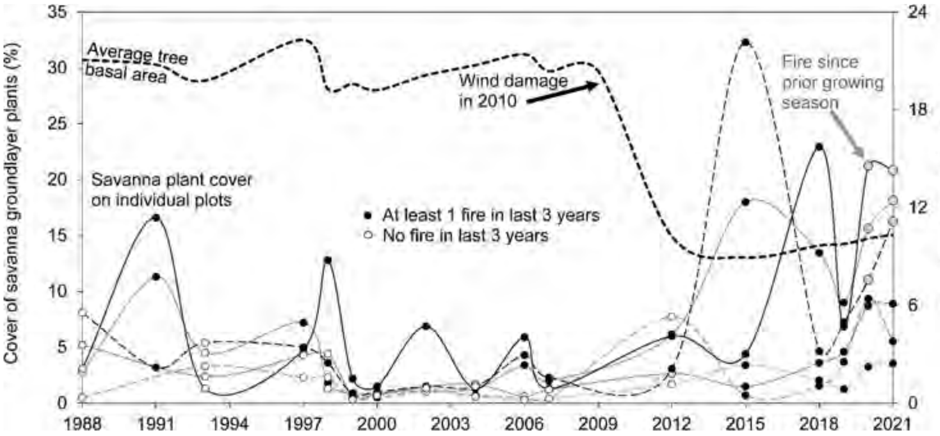

Figure 1.—Summary of prescribed fire history, change in basal area of trees (≥10 cm in diameter), and cover of savanna groundlayer plants during 34 y of oak savanna restoration, northwestern Ohio. Data are from six plots, five sampled beginning in 1988 and the sixth beginning in 1998 (circles represent sample years). Only three plots were able to be sampled in 1991. Tree basal area is averaged across plots. Total cover of savanna plants is shown for each individual plot through time. For the last 2 y of the study in 2020–2021, fire history is further subdivided into whether a plot received prescribed fire since the prior growing season (gray circle = yes; black circle = no but still burned at least once in the last 3 y).

period of peak cover and flowering of savanna plants. Also in each plot, we measured the stem diameter at a height of 1.4 m for each stem ≥1 cm in diameter of tree species. Nomenclature and classification of species by growth form follow Natural Resources Conservation Service (2022).

Data Analysis

We prepared a dataset containing the response variables cover (%) and species richness (0.05 ha) of the 42 savanna groundlayer species and the estimators density and basal area of overstory trees (≥10 cm in diameter) and saplings (≥ 1 < 10 cm), time since fire (years), number of fires in the 3 y prior to the vegetation sampling year, and whether a fire occurred since the growing season prior to sampling (categorical as yes, no). We used tree density and basal area to represent tree layers because we collected these data all years. As tree canopy cover is also often used to characterize midwestern oak savannas, we developed regression equations with tree canopy cover data we collected some years to estimate canopy cover from tree density and basal area to enable converting among these measures (Supplemental Appendix S1). We selected <10 cm as a cutoff for saplings because these smaller stems are more readily top killed (although root systems can survive) by typical low-severity fires (Abella et al. 2021) and to represent the dense sapling layer below overstory trees that can form on savanna sites during fire-free periods (Taft 2009; Figure 2). We based the number of fires in the last 3 y on calendar years preceding a sampling year, but excluding any fires in autumn the calendar year of sampling as autumn fires would be after summer sampling that calendar year. Whether a fire occurred since the prior growing season was based on whether fire occurred in the autumn or spring preceding a summer sampling. The dataset contained 96 observations for each variable, representing 17 sampling years for five plots (excluding two plots not measured in 1991 due to time constraints) and 13 sampling years for the sixth plot (Figure 1, Table 1).

We conducted several preliminary data analyses to evaluate suitability of candidate statistical approaches. For example, we screened for temporal autocorrelation (which was minimal to absent among plots) in groundlayer measures, tested for departure from randomness in prescribed fire seasonality through time (no significant departure occurred), and tested for relationships between climate and fire events (no significant relationships were detected). We report these analyses in Supplemental Appendix S2, and based on the findings, we treated each observation for plots independently and did not include fire seasonality in statistical analyses.

To model variation in savanna groundlayer cover and species richness through time as a function of tree, sapling, and fire estimators, we used regression trees (Breiman et al. 1984). We chose these nonparametric analyses because they accommodate mixtures of continuous and categorical estimators and hierarchically partition data into increasingly homogeneous subsets, useful for our goals of identifying shifts in savanna plant abundance at potential thresholds of tree abundance and fire prevalence. We implemented the regression trees in WEKA 3.8

Figure 2.—Repeat photos of recent change on an example plot during a 34 y study of change in oak savanna plant abundance, northwestern Ohio. This plot received 15 burns between 1988 and 2021. Most recently, the plot burned in autumn 2016 (3 y preceding the 2019 photo), autumn 2019 preceding the 2020 photo, and in spring 2021 preceding the 2021 photo. A savanna forb, *Baptisia tinctoria*, is circled in gray in the bottom left of each photo for reference. Photos by S.R. Abella in July–August each year.

Table 2.—Single-estimator regression trees estimating cover and species richness of savanna groundlayer plants for partitions of tree (≥10 cm in diameter), sapling (≥ 1 < 10 cm in diameter), and prescribed fire estimators during a 34 y period, northwestern Ohio. Estimated groundlayer cover and species richness values are mean ± standard error of mean.

	Modeling savanna plant cover			Modeling savanna species richness		
Predictors	Partition	Cover (%)	*r*	Partition	Species/0.05 ha	*r*
Tree density	≥100/ha[a]	3 ± 1	0.63	≥200/ha	7 ± 1	0.47
	<100/ha	13 ± 2		<200/ha	11 ± 1	
Tree basal area	≥13 m^2/ha	3 ± 1	0.34	≥10 m^2/ha	9 ± 1	0.23
	<13 m^2/ha	9 ± 1		<10 m^2/ha	13 ± 1	
Sapling density	≥2000/ha	9 ± 2	0.16	≥40/ha	9 ± 1	0.24
	<2000/ha	5 ± 1		<40/ha	12 ± 1	
Time since fire	≥2 years	3 ± 1	0.44	≥4 years	6 ± 1	0.69
	<2 years	8 ± 1		<4 years	11 ± 1	
No. fires last three years	≥1	7 ± 1	0.26	≥1	11 ± 1	0.68
	<1	2 ± 1		<1	6 ± 1	
Fire since prior growing season	Yes	10 ± 2	0.40	Yes	12 ± 1	0.38
	No	4 ± 1		No	9 ± 1	

[a] Tree canopy covers corresponding with partition values for tree density and basal area, based on regressions in Supplemental Appendix S1, are as follows: 100 trees/ha: 29% tree canopy cover, 200 trees/ha: 45%, 10 m^2/ha basal area: 28%, and 13 m^2/ha: 35%.

using the RandomTree algorithm, a minimum of five observations at terminal nodes, and Pearson *r* computed via five-fold cross-validation (Bouckaert et al. 2017). We calculated regression trees for each estimator individually and for all estimators to model savanna plant cover and richness. To assess associations of cover of the 42 savanna species individually with tree and fire estimators, we used indicator species analysis (Dufrêne and Legendre 1997). This analysis used 9999 permutations for significance and was computed in PAST 4.09 (Hammer 2022). Indicator values integrate frequency (fidelity of a species to a particular group) and abundance (cover in our case) into an indicator value ranging from 0 (no association of a species with a group) to 100 (maximum association).

RESULTS

In single-estimator models, savanna groundlayer plant cover and species richness were maximized when tree basal area and density were low, time since fire was short, there was at least one fire within the last 3 y, and fire had occurred in autumn or spring preceding a current growing season (Table 2). For example, savanna plant cover quadrupled when there were fewer than 100 trees/ha (29% tree canopy cover). It approximately tripled when fire had occurred since the prior growing season, time since fire did not exceed 2 y, or at least one fire had occurred within the last 3 y. Savanna plant cover declined by two-thirds after 2 y without fire. The main differences between responses of cover and species richness were that cover increased, but species richness decreased, when sapling density was high and that elevated richness persisted at higher density of trees and longer time since fire. Under cross-validation, single-estimator models portrayed 3–40% of variance in cover and 5–48% in richness.

In multi-estimator models (those containing only trees and trees combined with sapling and fire estimators), a hierarchical pattern emerged whereby overstory trees formed a primary partition followed by partitions using saplings or fire estimators (Table 3). For example, when tree basal area was <13 m^2/ha (35% tree canopy cover), savanna groundlayer plant cover was high and increased further if fire had occurred since the prior growing season. The combined tree and fire model for savanna species richness illustrated that at least one fire occurring within a 3 y period could also promote richness, even when tree density exceeded 200/ha (45% tree canopy cover), although not to the maximum levels of richness occurring when fire coincided with low tree density. In models using only tree and sapling layers, both savanna plant cover and richness were maximized under a combination of low density of both trees and saplings. In models using only fire estimators, groundlayer cover was lower if a fire had not occurred since the prior growing season but increased if a fire had at least occurred within the last 3 y. For species richness modeled using only fire estimators, richness increased if at least one fire had occurred within 3 y and was further boosted by 10% if fire had occurred since the prior growing season. The multi-estimator models portrayed 11–46% of variance in cover and richness under cross-validation.

Of 42 savanna species in the study, 11 (26%) were significantly associated (indicator values ≥50, $P < 0.05$) with one or more partitions of tree or fire estimators (Table 4). All significant indicator values were in the direction of increasing savanna species cover with lower amounts of trees and more frequent fire. No species was ever significantly associated with partitions toward more trees or infrequent fire. These patterns occurred across savanna species in different growth forms of forbs, grasses, and shrubs.

DISCUSSION

Groundlayer Cover and Species Richness Patterns and Sapling Density

The data were consistent with an idea that after 2 y without fires during which time the sapling layer rapidly redeveloped,

Table 3.—Regression trees estimating cover and species richness of savanna groundlayer plants for multi-estimator partitions of tree ($\geq$10 cm in diameter), sapling ($\geq 1 < 10$ cm in diameter), and prescribed fire estimators during a 34 y period, northwestern Ohio.

Savanna plant cover	Savanna species richness
Trees and saplings only	
Trees $\geq$ 100/ha 3 ± 1%[a,b]	Tree basal area $\geq$ 10 m^2/ha
Trees < 100/ha	Saplings $\geq$ 40/ha 9 ± 1 species
Saplings $\geq$ 2500/ha 8 ± 1%	Saplings < 40/ha 11 ± 1 species
Saplings < 2500/ha 15 ± 2%	Tree basal area < 10 m^2/ha
	Saplings $\geq$ 80/ha 11 ± 1 species
	Saplings < 80/ha 16 ± 2 species
Fire history only	
Fire since prior growing season = yes 10 ± 2%	No. fires last three years $\geq$ 1
Fire since prior growing season = no	Fire since prior growing season = yes 12 ± 1 species
No. fires last three years $\geq$ 1 5 ± 1%	Fire since prior growing season = no 11 ± 1 species
No. fires last three years < 1 2 ± 1%	No. fires last three years < 1 6 ± 1 species
All estimators	
Tree basal area $\geq$ 13 m^2/ha	Trees $\geq$ 200/ha
Time since fire $\geq$ 10 years 1 ± 1%	No. fires last three years $\geq$ 1 11 ± 1 species
Time since fire < 10 years 4 ± 1%	No. fires last three years < 1 6 ± 1 species
Tree basal area < 13 m^2/ha	Trees < 200/ha
Fire since prior growing season = yes 14 ± 2%	Fire since prior growing season = yes 13 ± 1 species
Fire since prior growing season = no 6 ± 1%	Fire since prior growing season = no 11 ± 1 species

[a] Estimated cover and species richness values, shown at terminal nodes of regression trees, are mean ± standard error of mean.

[b] For each set of models, cross-validated *r* values listed for plant cover then species richness are: trees and saplings only: 0.57, 0.33; fire history only: 0.34, 0.61, and all estimators: 0.51, 0.68.

cover of savanna groundlayer plants declined first followed by species richness. The delayed decline in species richness appeared from savanna species able to persist at low, declining cover before many species disappeared altogether as time since fire increased, until the next fire. This sequence is akin to a pulse ecosystem fluctuating through time, whereby an ecological event (fire in this case) triggers a pulse of biological activity (Taft 2003). As the fire-free period subsequently lengthens, community disassembly, through species attrition (Taft and Kron 2014), reverses the increase, producing a temporally fluctuating series of transient increases and decreases in savanna plants contingent on time since fire (Abella et al. 2020c). This pattern played out across multiple decades in our study and could apparently continue indefinitely given frequent fires, absent some type of disruption to the pattern.

This fluctuating pattern also could account for the seemingly paradoxical positive association of sapling density with savanna plant cover (specifically in the single-estimator model) but the negative association between saplings and species richness. Particularly after wind damage to the overstory in 2010 increased light, vigorous post-fire resprouting produced a dense sapling layer of tree species within 1–2 growing seasons after fire. This is precisely when savanna groundlayer plants were simultaneously increasing the most in cover, producing a positive association. On the other hand, species richness of savanna plants had a negative association with even relatively low density of saplings. The delayed decline in species richness as time since fire increased and the negative association of richness with sapling density may have reflected saplings growing larger, thereby having a greater negative influence per sapling on savanna plants (Wilcox et al. 2005). This therefore could have heightened sensitivity of richness to even low density of saplings. Negative influences of saplings on savanna plants as the sapling layer developed could include greater shading and competition for soil resources, coupled with accumulation of litter that can hinder fitness of savanna plants (Pavlovic and Grundel 2009). It is also noteworthy that while savanna plant cover was high when sapling density was high in the first few post-fire years, the sapling layer may have actually been negatively affecting savanna plant cover, just not to the extent of fully suppressing a positive response by savanna plants to fire. Further resolving these possibilities likely requires experimental approaches disentangling direct effects from fire and the sapling layer on savanna plants, such as applying fire coupled with removing resprouting trees.

Tree Layer

A threshold for maximal savanna groundlayer plant cover and species richness was below 10–13 m^2/ha basal area of trees ($\geq$10 cm in diameter), or a third the amount typically in closed-canopy oak forests around the study area (Abella et al. 2020b). The threshold for tree density was below 100–200 trees/ha. Trees generally remained above these thresholds for the first 23 y of the study, as prescribed fires had minimal influence on survival of large oaks, consistent with their resistance to low-severity fires (Abella et al. 2021). It was after 2010, after wind damage halved overstory tree basal area and density, when some of the highest savanna plant cover and richness values appeared. In fact, 9 of the 10 highest savanna plant cover values (ranging from 13% to 32%) on plots during the study occurred in 2015 or later. These observations suggest that unplanned, natural disturbances in some cases can act synergistically with planned restoration treatments to achieve restoration goals, in our case increasing savanna plants. Maximum abundance of savanna plants occurred when tree abundance was low, partly a function of the wind disturbance, and planned restoration burns were frequent. Had the wind disturbance not occurred, mechanical cutting or other treatments to reduce tree density would apparently have been required to increase savanna plant abundance beyond what fire alone could accomplish (Bassett et al. 2020).

Prescribed Fire Frequency

Our study was not designed to compare specific burn frequencies (e.g., annual cf. decadal burns) replicated in time, but within our study context of irregular burn occurrences through time, we found that the most frequent burning was consistently associated with elevated savanna plant cover and

Table 4.—Indicator species analysis across tree and prescribed fire estimators of plant species occurrence and cover during a 34 y study of changes in groundlayer communities of oak savannas, northwestern Ohio. Indicator values shown are for cutoff values (e.g., <13 m^2/ha for tree basal area) of estimators corresponding with Table 2 at which total savanna plant cover was maximized (no species had significant indicator values for the higher levels of trees or less frequent fire).

	Tree basal area	Tree density	Time since fire	No. fires last 3 years	Fire since prior season
	<13 m^2/ha	<100/ha	≤2 years	3 fires	Yes
Forbs					
Baptisia tinctoria	**63 (<0.001)**[a]	**88 (<0.001)**	**51 (0.008)**	27 (0.199)	**68 (<0.001)**
Comandra umbellata	48 (0.053)	**57 (0.021)**	46 (0.034)	11 (0.442)	**51 (0.048)**
Euphorbia corollata	46 (0.170)	38 (0.480)	35 (0.707)	**51 (0.036)**	46 (0.209)
Helianthemum canadense	**49 (<0.001)**	**58 (<0.001)**	47 (<0.001)	2 (0.663)	32 (0.082)
Lespedeza capitata	**55 (<0.001)**	**53 (<0.001)**	**53 (<0.001)**	4 (0.719)	47 (<0.001)
Lupinus perennis	31 (0.248)	**82 (<0.001)**	**70 (<0.001)**	30 (0.136)	**88 (<0.001)**
Grasses					
Andropogon gerardii	47 (0.026)	**87 (<0.001)**	**75 (<0.001)**	**68 (0.002)**	**75 (<0.001)**
Dichanthelium sabulorum	**52 (0.001)**	**50 (0.008)**	36 (0.038)	3 (0.613)	29 (0.195)
Shrubs					
Rhus copallinum	**62 (<0.001)**	**63 (<0.001)**	**54 (<0.001)**	7 (0.392)	47 (0.004)
Rosa carolina	**68 (0.001)**	**67 (0.006)**	**62 (0.026)**	40 (0.072)	58 (0.137)
Tephrosia virginiana	57 (0.119)	**75 (0.001)**	56 (0.154)	45 (0.083)	**66 (0.021)**

[a] Values are indicator value (P value). Indicator values ≥50 with $P < 0.05$ are in bold. Among 42 species analyzed (Supplemental Table S1), only species that had at least one instance of a significant indicator value (≥50 out of a maximum 100 possible and with $P < 0.05$) are shown in the table.

species richness. This raises a question of whether annual burning may be most beneficial for oak savanna restoration. However, previous research suggests some negative trade-offs of long-term annual burning. In our study area, for example, Grigore and Tramer (1996) found that fitness of wild lupine (*Lupinus perennis*), a savanna perennial forb, improved under biennial compared with annual burning. This related to factors such as fire-free periods enabling seeds to escape fire and seedlings to become established (Grigore and Tramer 1996). Oaks can fail to regenerate under annual burning, as multi-year, fire-free regeneration windows may be unavailable in space (e.g., overlapping fires burning any unburned patches skipped by earlier fires) or time (Peterson and Reich 2001). Although a maturing oak sapling layer can hinder persistence of savanna groundlayer plants and open savanna structure, it can also supply individuals transitioning to the overstory occasionally needed to maintain oak savannas (Brudvig and Asbjornsen 2008). How practitioners can best vary fire frequency, severity, or spatial patterns (e.g., unburned refugia for oak sapling-to-overstory transition) to balance groundlayer diversity, sapling layers, and sustainability of overstory structure could benefit from refinement in further research.

Individual Groundlayer Species

Without exception, all significant indicator species responded in the positive direction to lower amounts of trees and more frequent fire. This raises questions regarding traits of species that facilitated such positive responses across all savanna plant growth forms (Taft 2003). Some indicator species in our study, such as wild lupine and the shrub winged sumac (*Rhus copallinum*), have seeds triggered to germinate by heat (Bolin 2009). C_4 grasses, such as big bluestem (*Andropogon gerardii*), are often restricted to the sunniest microsites within savannas (Pavlovic et al. 2006; Noble and Bauer 2022). Our results supported these observations, as the grasses were associated with the most open plots through time. Big bluestem may have further benefited from fires through processes such as litter reduction and warmer soil temperature during the growing season (Hulbert 1988). In a previous study by Niering and Dreyer (1989) in a Connecticut grassland, wild indigo (*Baptisia tinctoria*) doubled in cover under annual burning and quadrupled under biennial burning. In our study in which wild indigo also increased after fires, most burns on plots were not consecutive, so the frequent, but often not successive, fires may have been optimal for this species (Figure 2). Soil seed bank longevity is unknown for most oak savanna species, a notable knowledge gap as this information could be useful for identifying how long propagules of savanna species could persist on-site during fire-free or tree encroachment periods. A prior seed bank inventory we conducted in the study area established that several species in the present study (e.g., winged sumac, wild indigo, and Canada frostweed [*Helianthemum canadense*]) at least form seed banks living more than a year (Abella et al. 2020a). A seed burial experiment in Georgia revealed that two species present in our study, hairy bush clover (*Lespedeza hirta*) and goat's-rue (*Tephrosia virginiana*), lived at least 8 y in seed banks (Kaeser and Kirkman 2012).

Other increasing species in our study were parasitic plants, including the annual forb fernleaf false foxglove (*Aureolaria pedicularia*) and the perennial forb toadflax (*Comandra umbellata*). Although fernleaf false foxglove was not a significant indicator species, likely because it was absent or had no more than 0.1% cover until 2018, it surged to 20% cover on one plot and inhabited at least half of plots in 2020–2021. As an annual, fernleaf false foxglove must be capable of forming soil seed banks but was not detected in the seed bank inventory of the study area (Abella et al. 2020a). Toadflax never achieved cover as high as fernleaf false foxglove, instead being present throughout much of the study at low cover (typically 0.1%) that increased when there were fewer than 100 trees/ha and a fire had occurred since the prior growing season. Whether increases in these root parasites after fires and when tree density was low contributed to increasing savanna plant richness remains unclear. Parasitic plants in general often increase community diversity, perhaps by weakening otherwise dominant species to limit competitive exclusion of other species or via other ecological interactions (DiGiovanni et al. 2017). In an Illinois prairie, toadflax did not reduce one of its dominant hosts, big bluestem, but was nevertheless associated with increased floristic quality (DiGiovanni et al. 2017). Whether increasing parasitic plants is another process whereby fires increase species richness warrants further investigation.

Multiple Limiting Factors, Shade Tolerance, and Groundlayer Community Disassembly

Further work that mechanistically examines potential limiting factors to savanna plant persistence—including combinations of light availability, competition with woody plants, and lack of fire—could help identify processes by which savanna plants begin disappearing as tall woody plants encroach as time since fire increases. The idea that groundlayer community disassembly processes commence as shade increases while woody encroachment proceeds concurs with studies of savanna species along light gradients (e.g., Leach and Givnish 1999; Pavlovic and Grundel 2009; Michaels et al. 2019) and limited ecophysiological data for some species (e.g., Knapp and Gilliam 1985). The finding in our study that savanna groundlayer plants sharply increased after 2010 wind damage halved overstory canopy cover is consistent with the idea that overstory trees, perhaps by providing too much shade, had limited savanna groundlayer plants. Before 2010, overstory density resembled that normally found in the region's pre-Euro-American settlement woodlands and forests, rather than savannas (Brewer and Vankat 2004). However, the increases in savanna groundlayer plants that had occurred post-fire before 2010 even under dense overstories and that subsequently occurred after 2010 under relatively constantly open overstories suggest that factors other than overstory light gradients could be secondary factors (under dense overstories) or primary factors (in a context of open overstories) regulating savanna groundlayers. Beyond overstory shade limitation, some of these limiting factors, as time since fire increases, could include shading and belowground competition from the sapling layer, litter accumulation, lack of fire-related germination cues, and pollinator limitation in woody-encroached conditions (Lettow et al. 2018). Additionally, as it redeveloped after fires to a high density, the sapling layer could have competed with groundlayer plants for growing space (*sensu* Figure 2). The maximum density of saplings ($\geq 1 < 10$ cm in diameter) we recorded was an exceptionally high 12,540 stems/ha. There were also 18 instances during our study of saplings exceeding 1000 stems/ha, and all six plots contained a density exceeding 1000 saplings/ha at least once.

Specifically in the single-estimator model using only saplings, the seemingly paradoxical positive relationship we observed between sapling density and savanna plant cover is potentially explained by both being initially stimulated by fire under open overstory conditions, then the relationship becomes asymmetrically negative as the dense sapling layer outcompetes groundlayer plants. From this perspective, if competition is deterministically asymmetrically negative for groundlayer plants (irrespective of species or their traits) as a group with sapling layers, then persistence of groundlayer plants at low cover as time since fire increases could be primarily related to microsite effects. Groundlayer plants, irrespective of species, could persist in the few microsites that, by chance or by some environmental constraint, have not filled with tree saplings.

Shade tolerances of the groundlayer species in our study further suggest potential that factors in addition to light could be influencing savanna plant persistence (or lack thereof) as time since fire increased. We compiled shade tolerance ratings from Bader (2001), who categorized species as mainly inhabiting areas of shade, partial sun, or full sun in southern Wisconsin oak savannas. Ratings were available for 29 (69%) of the 42 species in our study. Of the 29 species, 1 (3%) was categorized as occurring across the complete shade–full sun gradient (flowering spurge [*Euphorbia corollata*]), 2 (7%) were shade–partial sun (winged sumac and woodland sunflower [*Helianthus divaricatus*]), 2 (7%) partial sun (fernleaf false foxglove and two-flower dwarf dandelion [*Krigia biflora*]), 21 (73%) partial–full sun, and 3 (10%) were full sun (dwarf dandelion [*Krigia virginica*], little bluestem [*Schizachyrium scoparium*] and big bluestem; Supplemental Table S1). Thus, nearly all (90%) of the 29 species were rated as tolerating partial shade, yet these species as a group fluctuated widely through time in our study during extended periods of nearly constant overstory canopy cover (Figure 1). Moreover, in indicator species analysis in our study across tree and fire variables, the species rated by Bader (2001) as most sensitive to shade were not the most strongly related to tree basal area and density. Of our 11 significant indicator species, 8 were included in Bader et al. (2001). Only one of those (big bluestem) was a full-sun species; the rest were all partial–full sun or even rated as tolerant of shade. For example, winged sumac, although rated as tolerant of shade–partial sun, was among the most susceptible to decline as trees and time since fire increased among all 42 species in our study.

Management Implications

Prescribed fires stimulated rapid but transient pulses in savanna groundlayer plant cover and species richness. Groundlayer condition was therefore contingent on when the most recent fire had occurred, and high levels of savanna plant cover depended on both open overstories and fires occurring every 2–3 y. Even multiple decades into savanna restoration after 10+ fires, gains in savanna plant cover could be lost after just 3 y without fire. An encouraging result for savanna plant persistence was that species richness of savanna plants showed some ability to endure for 4+ years between fires via species persisting at low cover. Nevertheless, as the sapling layer matured during longer fire-free periods and became negatively associated with savanna plant richness, most of the savanna species appeared unlikely to extensively persist much longer than 4 y between fires, at least as aboveground plants.

Results suggested that sustained management resources for frequent fire (or potentially alternative treatments to limit tree sapling encroachment) would continue to be required to maintain restoration gains, even after 34 y into restoration management. Although our study site has been prioritized to receive management resources, this frequency of prescribed fires may not always be feasible in the future at this site or at other sites. We agree with recommendations from other authors to explore complementary treatments for curtailing woody plant encroachment, such as potential for fewer but more severe fires to have longer-lasting effects (Haney et al. 2008), mastication or other cutting treatments useful in years with weather unfavorable for burning or if burn personnel are unavailable (Bassett et al. 2020), managed herbivory or trampling (Harrington and Kathol 2009), or other alternatives in combination (Reinhardt et al. 2017). These could at least provide other options to complement use of low-severity fires. Although frequent prescribed fires do represent a long-term commitment, an encouraging result suggested by our 34 y study is that frequent fires at least every 2–4 y appear capable of stimulating a series of intermittent increases to sustain savanna groundlayer plants indefinitely under prevailing conditions.

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Scott Abella is Associate Professor in the School of Life Sciences at the University of Nevada Las Vegas and founder of Natural Resource Conservation LLC. His research focuses on restoration, conservation, and fire ecology and ecological research supporting those fields.

LaRae Sprow is Natural Resources Supervisor with Metroparks Toledo. She manages the park district's natural resource conservation and fire program in the Oak Openings region.

Karen Menard is Research and Monitoring Supervisor with Metroparks Toledo. She conducts and oversees botany and wildlife research programs across the park district.

Timothy Schetter is Chief Natural Resources Officer with Metroparks Toledo. He directs district-wide natural resource and land acquisition operations.

Lawrence Brewer is Botanist with the Center for Environmental Restoration at Northern Kentucky University. He is conducting plant community, rare plant, and bird surveys.

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Table S1. List of 42 savanna groundlayer species and their coefficient of conservatism (C of C), shade tolerance, and frequency (%, out of 5 plots from 1988-1997 and 6 plots from 1998-2021) across 17 sample years during 34 years of oak savanna restoration in northwestern Ohio.

	C of C	1988	1991	1993	1997	1998	1999	2000	2002	2004	2006	2007	2012	2015	2018	2019	2020	2021	Shade[b]
Forbs		Frequency (%)																	
Asclepias amplexicaulis	7	20	–[a]	20	20	–	–	17	17	–	–	–	17	17	–	–	–	–	PS-SU
Asclepias tuberosa	4	20	40	20	40	–	17	17	17	17	–	33	33	17	–	33	33	33	PS-SU
Aureolaria pedicularia	9	–	20	40	–	33	33	–	–	33	–	33	–	17	33	17	50	50	PS
Baptisia tinctoria	6	60	20	60	60	50	67	50	50	67	50	33	83	83	67	67	83	83	
Comandra umbellata	5	40	40	40	60	83	50	50	17	83	67	50	33	33	67	83	67	67	PS-SU
Desmodium sessilifolium	8	–	–	–	–	–	–	–	–	–	–	–	–	–	33	–	–	–	
Euphorbia corollata	4	80	60	100	100	50	83	100	100	33	33	17	83	100	83	83	100	100	SH-SU
Helianthemum bicknellii	9	20	60	20	–	–	17	83	67	–	–	–	–	100	83	17	17	17	PS-SU
Helianthemum canadense	9	–	–	–	–	–	17	–	–	67	67	50	67	17	33	100	100	100	PS-SU
Helianthus divaricatus	4	60	40	20	20	50	17	17	–	33	17	33	33	33	–	33	17	33	SH-PS
Helianthus occidentalis	7	–	–	20	–	–	–	–	–	–	–	–	–	17	–	–	–	–	PS-SU
Krigia biflora	5	–	–	–	–	–	17	–	–	17	17	–	–	–	–	–	–	–	PS
Krigia virginica	8	–	–	–	–	–	–	–	–	17	–	–	–	–	–	–	–	–	SU
Lechea mucronata	7	–	–	–	20	17	–	–	–	33	–	–	–	–	–	–	–	33	
Lespedeza capitata	5	20	–	–	20	17	17	17	17	17	–	33	50	83	33	83	67	100	PS-SU
Lespedeza procumbens	5	–	–	–	–	–	–	–	–	17	–	–	–	–	–	–	–	–	
Liatris aspera	6	20	20	–	20	–	–	50	–	33	33	–	33	17	–	17	17	17	PS-SU
Liatris spicata	7	–	–	–	20	–	–	–	–	–	17	–	–	–	–	–	–	–	
Liatris squarrosa	8	–	–	–	–	–	17	–	–	–	–	–	–	–	–	–	–	–	
Lithospermum caroliniense	9	60	40	60	20	17	33	33	33	33	33	17	33	–	–	–	17	–	PS-SU
Lupinus perennis	7	40	40	80	60	50	50	50	50	50	50	50	50	50	33	50	50	50	PS-SU
Monarda punctata	7	–	–	–	–	–	–	–	–	–	–	–	–	17	17	–	–	–	PS-SU
Polygala polygama	10	20	60	20	–	67	17	33	–	33	50	33	17	17	–	17	50	17	PS-SU
Pycnanthemum verticillatum	5	–	–	–	–	–	–	–	–	–	–	–	17	–	–	–	–	–	
Sisyrinchium albidum	6	–	–	–	–	–	–	–	17	–	17	–	–	–	–	–	–	–	
Symphyotrichum laeve	6	–	–	–	–	–	–	–	–	–	–	–	33	–	–	–	–	–	PS-SU

Tephrosia virginiana	6	100	60	100	80	100	100	100	100	100	33	100	100	100	83	100	100	100	PS-SU
Verbena hastata	4	–	–	–	–	–	–	–	–	–	–	–	17	17	–	–	–	–	PS-SU
Viola pedata	8	–	20	40	40	17	33	67	17	83	67	33	33	33	17	67	–	17	PS-SU
Graminoids																			
Andropogon gerardii	5	40	60	60	60	67	50	67	50	50	33	50	67	50	50	67	67	67	SU
Danthonia spicata	4	–	–	–	–	–	–	–	–	–	–	–	50	17	17	17	17	33	PS-SU
Dichanthelium dichotomum	4	–	–	–	–	–	–	–	–	–	–	–	–	–	–	17	17	33	
Dichanthelium meridionale	9	–	–	–	–	–	–	–	–	–	17	–	–	–	–	–	–	–	
Dichanthelium oligosanthes	6	–	–	–	–	–	–	–	–	–	–	–	–	–	17	–	–	33	PS-SU
Dichanthelium sabulorum	6	–	–	–	–	–	–	–	33	100	17	100	100	33	33	83	83	83	
Dichanthelium spretum	9	–	–	–	–	–	–	–	–	–	–	–	–	–	–	17	17	17	
Koeleria macrantha	10	–	–	–	–	–	–	–	17	17	–	17	33	–	17	33	33	17	PS-SU
Schizachyrium scoparium	5	–	20	–	–	–	–	33	–	–	17	–	17	17	17	17	17	17	SU
Shrubs																			
Hypericum kalmianum	8	–	–	–	–	–	–	–	–	–	–	–	–	–	17	–	–	–	
Rhus copallinum	4	20	20	20	20	17	–	17	17	–	–	17	17	83	67	83	100	100	SH-PS
Rosa carolina	4	100	60	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	PS-SU
Salix humilis	4	40	20	–	–	–	–	–	–	–	–	–	–	–	–	17	33	17	PS-SU

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[a] Not present.

[b] Shade tolerance ratings (SH, tolerant of shade; PS, partial sun; and SU, full sun) for species available in Bader (2001; Bader, B.J. Developing a species list for oak savanna/oak woodland restoration at the University of Wisconsin-Madison arboretum. Ecological Restoration 19:242–250.)

Appendix S1. Development of regression equations to relate tree density and basal area with tree canopy cover.

Studies in Midwestern savannas have commonly used density, basal area, and tree canopy cover to characterize overstories and relate these measures to groundlayers. In addition to measuring tree density and basal area, in 1998-2000, 2002, and 2020-2021, we measured aerial canopy cover of trees above a height of 3 m using a densitometer. We averaged eight measurements, spaced every 5 m along the diagonal within each plot, to estimate tree canopy cover per plot. To convert between tree density (≥ 10 cm in diameter) and basal area and canopy cover, we developed linear regressions. The regression equations were as follows: tree canopy cover (%) = 2.284(tree basal area in m^2/ha) + 5.56 ($r^2 = 0.49$); and tree canopy cover (%) = 0.158(tree density in trees/ha) + 13.14 ($r^2 = 0.57$).

Appendix S2. Preliminary screening of the dataset to identify suitable statistical approaches.

To evaluate suitability of candidate statistical approaches, we screened for temporal autocorrelation and covariance of response and estimator variables with climate in PAST 4.09 (Hammer, Ø. 2022. PAST 4.09, paleontological statistics reference manual. University of Oslo, Norway). We tested if the savanna plant cover and species richness response variables were temporally autocorrelated for each plot by calculating correlations and 95% confidence intervals for up to seven lags. Temporal autocorrelation was absent to minimal, with no significant ($P < 0.05$) autocorrelation for any lag for four of six plots for both groundlayer cover and richness and autocorrelation only for lags 1 or 2 for two plots for cover or richness. Next, we evaluated if early (May + June) or late (July + August) summer precipitation (measured at the Toledo Airport, 7 km northeast of the study site) correlated with savanna plant cover or richness. Precipitation was uncorrelated (Pearson $r < |0.20|$, $P > 0.05$) with cover and richness. Minimal temporal autocorrelation in response variables and lack of relationships with precipitation within the dataset are consistent with the idea that savanna plants fluctuated with tree characteristics or recent fire history, with high variability from one year to the next limiting autocorrelation. As a result, we treated each observation independently in statistical analyses.

Next, to evaluate if prescribed fire years were patterned according to early or late summer precipitation, we compared mean precipitation in fire and non-fire years using *t* tests. Neither early ($t_{23} = 0.85$, $P = 0.407$) nor late-summer precipitation ($t_{23} = 0.28$, $P = 0.782$) differed between fire and non-fire years. Finally, we tested for a non-random pattern in fire seasonality through time (including years with either only spring or autumn fires which were most years) using a runs test. Fire seasonality did not differ from random through time ($Z = 0.31$, Monte Carlo $P = 0.771$). The study was not designed to assess fire seasonality because it could be confounded with other factors during the 34-year period (e.g., an autumn fire could be followed by a spring fire prior to the next sampling, precluding distinguishing effects of one or the other). While we therefore did not include fire seasonality in the statistical analysis, lack of association of fire years with precipitation generally and the random pattern of fire seasons through time supported using presence or absence of any type of fire as an independent estimator.