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Vegetation and Avian Response to Oak Savanna Restoration in the Mid-South USA

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ABSTRACT.—Oak (*Quercus* spp.) savannas are among the most imperiled ecosystems in the United States. Consequently, associated vegetation and avian communities are also in decline. Furthermore, restoration of savanna communities may be an important strategy for conserving avian species that require early successional habitat, a type underrepresented on regional landscapes. Therefore, we evaluated savanna restoration on twelve sites in the Mid-South USA. Specifically, we examined grass, forb, legume, and woody understory cover, regeneration and sapling density, and breeding bird use of the sites following mechanical overstory thinning and dormant-season fire using a hierarchical linear model. Total grass cover was negatively related to canopy cover ($P < 0.01$) and total forb cover was negatively related to total basal area ($P = 0.04$). Oak regeneration density was positively related to canopy cover ($P < 0.01$), while oak competitor regeneration density was positively related to percent slope ($P = 0.01$) and sapling density ($P = 0.01$). Shrub/scrub birds were common within sites undergoing restoration. Only three obligate grassland bird species, eastern kingbird (*Tyrannus tyrannus*), Bachman's sparrow (*Aimophila aestivalis*) and dickcissel (*Spiza americana*), were detected on one site. Presence of indigo buntings (*Passerina cyanea*) was positively related to groundlayer development. Canopy reduction and burns outside the dormant season may both be critical to restoration of savannas and associated avifauna in the region.

INTRODUCTION

Oak (*Quercus* spp.) savannas once encompassed >11 million ha in the Midwest USA including Minnesota, Iowa, Missouri, Illinois, Wisconsin, Michigan, Indiana, and Ohio but have been reduced to less than 1% of their original extent (Nuzzo, 1986). Savannas stretched into the southern Appalachians (Van Lear and Waldrop, 1989) and the Piedmont where historic documents describe a ''grande savanne'' that exists now only in isolated remnants (Davis *et al.*, 2002). Most savannas were cleared for cropland, converted to pasture or succeeded into closed-canopy forests as a result of fire exclusion (Curtis, 1959; Noss and Peters, 1995; Anderson, 1998; Bowles and McBride, 1998). Noss and Peters (1995) also concluded savannas are one of the most imperiled ecosystems in the United States, further highlighting the need for restoration.

In the Mid-South (defined here as the oak-dominated region that lies south of glacial influence and north of the Gulf Coastal Plain typified by Tennessee and Kentucky), where early successional forest landscapes are under-represented, only approximately 3% of the land is non-forested (Forest Inventory and Analysis, 2011). The loss of savannas has contributed to the decline of many grassland avian species (Askins, 1993; North American Bird Conservation Initiative, 2009). Two species described as savanna obligates, Bachman's sparrow (*Aimophila aestivalis*) and red-headed woodpecker (*Melanerpes erythrocephalus*), have declined annually between 1966–2007 by −0.67% and −1.53%, respectively, throughout the Central Hardwoods Bird Conservation Region (Sauer *et al.*, 2008). Grassland species such as Henslow's sparrow (*Ammodramus henslowii*) have also experienced population declines due

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to loss of suitable habitat (Galligan *et al.*, 2006). Brawn *et al.* (2001) concluded that 40% of disturbance-dependent species associated with grassland, shrub-scrub, and open woodlands declined between 1966 and 1998, whereas restoration of oak savannas may help reverse such trends by providing high quality habitat (Askins, 1993; Packard, 1993).

Despite the need to restore these habitats (Leach and Ross, 1995), research evaluating the effects of mechanical thinning (*i.e.*, selective removal of overstory trees through commercial logging) and prescribed fire for oak savanna restoration is limited. Although there has been some research conducted on the western periphery of the range of oak savannas including Illinois, Indiana, Iowa, Minnesota, and Wisconsin (Apfelbaum and Haney, 1990; Rebertus and Burns, 1997; Davis *et al.*, 2000; Peterson and Reich, 2001; Brudvig and Asbjornsen, 2009), studies in the Mid-South are entirely lacking. Several investigators have concluded that fire alone may not be sufficient to restore oak savanna ecosystems and that mechanical thinning may reduce the time required for restoration to years, rather than the decades, when using burning alone (Abella *et al.*, 2001; Peterson and Reich, 2001; Nielson *et al.*, 2003).

Research incorporating both mechanical thinning and prescribed fire has been typically conducted in partially degraded savannas that have not reached closed-canopy stature (Apfelbaum and Haney, 1987; Nielson *et al.*, 2003; Au *et al.*, 2008). Research addressing or quantifying oak savanna restoration starting from closed-canopy conditions have not been conducted regionally. Furthermore, research focused on savanna restoration has not addressed changes to avian communities when fire and mechanical overstory thinning are used together. Only one study addresses avian response to overstory thinning and prescribed fire within oak-dominated forests in the southeastern USA (Lanham *et al.*, 2002). They determined that both overstory thinning and prescribed fire could be a viable option given that various avian species would fill the habitat niches provided by the edge, some overstory retention, and open understories.

We collected data from 12 active savanna restoration projects in the Mid-South in various stages of development to improve our understanding of vegetation and avifaunal responses to restoration. Specific objectives were to (1) document changes in herbaceous vegetation, woody vegetation, and avifauna within mature, oak-dominated forests in the Mid-South in response to disturbances imposed for the purpose of savanna restoration, (2) evaluate the influence of topographic variables on vegetation during the restoration process, and (3) evaluate the relationship between breeding bird observations and vegetation during the restoration process.

STUDY AREAS

We chose twelve sites from five properties in Kentucky and Tennessee based on current savanna restoration activities. The first property was the 32,374 ha Catoosa Wildlife Management Area (CWMA) located in Cumberland County, Tennessee. The second property, Land Between the Lakes National Recreation Area (LBL), located in Stewart County, Tennessee, encompassed approximately 69,201 ha. The third and fourth properties were the Sterns (STERNS) and Cumberland (CUMB) Ranger Districts, respectively, of the 286,113 ha Daniel Boone National Forest in eastern Kentucky. The fifth property was Fort Campbell Military Base (FCMB), a 43,180 ha tract located in Stewart and Montgomery Counties, Tennessee and Trigg and Christian Counties, Kentucky, and included an established oak savanna. Within these five properties, we selected 12 sites (Table 1) representing a continuum of overstory structure and disturbance history. One site also was treated with drum-chopping, which entailed pulling a large drum (1.5 m diameter by 4 m

TABLE 1.—Descriptions of twelve oak savanna restoration sites in Tennessee and Kentucky sampled during 2008 and 2009

Site	Management history	Disturbance acronym	Basal area (m^2 ha^{-1})	Soil description	Latitude/Longitude
CWMA[1]	unburned unthinned	C-cont	22.4	Mesic Typic Hapludults, Mesic Typic Dystrudepts	84°84′59.10″ 36°07′81.70″
CWMA[1]	Thin only	C-cut	14.4	Mesic Typic Hapludults	84°87′06.72″ 36°06′76.95″
CWMA[1]	thin and burned 3×*	C-cut/burn3	10.6	Mesic Typic Hapludults	84°86′61.66″ 36°06′13.12″
CWMA[1]	thin and burned 5×*	C-cut/burn5	11.7	Mesic Typic Hapludults, Mesic Typic Dystrudepts	84°87′86.54″ 36°05′63.85″
CWMA[1]	thinned and burned 5×* and drum chopped	C-cut/burn5 and chop	9.0	Mesic Lithic Dystrudepts, Mesic Typic Hapludults	84°87′89.08″ 36°05′97.16″
STERNS[2]	unburned unthinned	S-cont	25.8	Mesic Typic Hapludults	84°45′03.59″ 36°86′55.45″
STERNS[2]	burned 5×*	S-burn5	11.5	Mesic Typic Hapludults, Mesic Typic Dystrudepts	84°23′01.18″ 36°95′84.65″
LBL[3]	unburned unthinned	L-cont	19.9	Thermic Typic Hapludults, Thermic Typic Paleudults	87°92′80.47″ 36°64′23.22″
LBL[3]	burned 1×*	L-burn1	20.3	Thermic Typic Paleudults, Thermic Typic Hapludults	87°95′69.72″ 36°64′05.32″
CUMB[4]	unburned unthinned	CU-cont	26.3	Mesic Typic Hapludalfs, Mesic Typic Dystrudepts	83°56′68.33″ 38°04′83.14″
CUMB[4]	burned 4×*	CU-burn4	21.9	Mesic Typic Hapludalfs, Mesic Typic Dystrudepts	83°55′82.85″ 8°05′92.19″
FCMB[5]	current savanna	FC-savanna	1.8	Mesic Typic Paleudults, Thermic Glossic Fragiudults	87°64′82.53″ 36°63′35.96″

[1] Catoosa Wildlife Management Area

[2] Sterns District of the Daniel Boone National Forest

[3] Land Between the Lakes National Recreation Area

[4] Cumberland District of the Daniel Boone National Forest

[5] Fort Campbell Military Base

* All burns completed two growing seasons prior to sampling were dormant season burns

wide) behind a bulldozer as a means of toppling and then crushing midstory hardwood stems.

These areas were characterized by topography that ranged from moderately rolling hills and broad drainages to those with narrow ridges dissected by steep ravines. Elevations ranged from 150–549 m above sea level and slopes between 6 and 80%. Between 1971–2000, average annual temperatures ranged from 11.7–14.4 C and average annual rainfall was 117–152 cm (NOAA, 2009). Soils were mesic Hapladults or typic Hapladults over weathered sandstone and weathered cherty limestone parent materials (NRCS websoil survey, 2009). Forest in these areas were dominated by white (*Quercus alba*), black (*Q. veluntina*), scarlet (*Q. coccinea*), and southern red oaks (*Q. falcata*), and shortleaf pine (*Pinus echinata*). Shortleaf pine and Virginia pine (*Pinus virginiana*) became a minimal component of the stands as a result of pine mortality from a southern pine bark beetle (Dendroctonus frontalis) outbreak in 1999–2000 and as a result of this pine mortality and ensuing management involving prescribed fire and mechanical thinning, the ground layer developed a rich flora of native grasses and forbs common to prairie and savanna ecosystems and not associated with forest conditions. Because of this vegetative response, we considered these areas to be former oak savannas or woodlands. Furthermore, local residents have described free-range grazing of open woodlands with bluestem-dominated understories in the vicinity of these study sites as recently as the 1930s. They also described burning these woodlands each spring to encourage the growth of the grasses.

Within these study areas, we selected four undisturbed (*i.e.*, unlogged and unburned) sites (C-cont, L-cont, S-cont, and CU-cont), characterized by mature closed-canopy hardwood forests with some pine, to provide reference forest sites (Table 1). These four sites typified conditions in the disturbed sites prior to implementation of savanna restoration activities. Three burn-only sites (L-burn1, CU-burn4, S-burn5) were located in closed-canopy forest and had been subjected since 2002 to one, four, and five prescribed fires, respectively. All prescribed fires were conducted during the dormant season (Feb.–Apr.) at least two growing seasons prior to sampling. Ring or head firing techniques were used in each prescribed fire, but no fire behavior data were available for any burn. An eighth site (C-cut) was subjected in 2005 to mechanical thinning only with no prescribed fire. The mechanical thinning for all harvested sites used in our project was a salvage harvest targeted at removing dead pines and leaving a partial canopy comprised primarily of oak species with diameters of residual stems ranging from 25–50 cm DBH. Some oaks were removed during these harvests in order to leave a more open canopy. The ninth (C-cut/burn3) and tenth sites (C-cut/burn5) were harvested as described previously and treated with three and five prescribed fires, respectively, since 2004. The eleventh site had a timber harvest; five prescribed fires and was drum-chopped (C-cut/burn5 and chop). Drum-chopping was conducted during Jan. of 2008. The twelfth site (FC-savanna) was included because it was representative of an established oak savanna (strong herbaceous understory with widely spaced overstory trees) as a result of 60+ y of annual and biennial burning associated with military training. None of the 12 sites had been exposed to appreciable disturbances beyond those described here during the years leading up to and including the study. Collectively, these sites represented the broadest gradient in disturbance histories available and the most advanced stages of oak savanna restoration we were aware of in the region.

METHODS

Within each site, we systematically selected a 40-ha unit, the largest area common to all 12 sites available, for sampling. If the size of any restoration site exceeded 40 ha, we limited

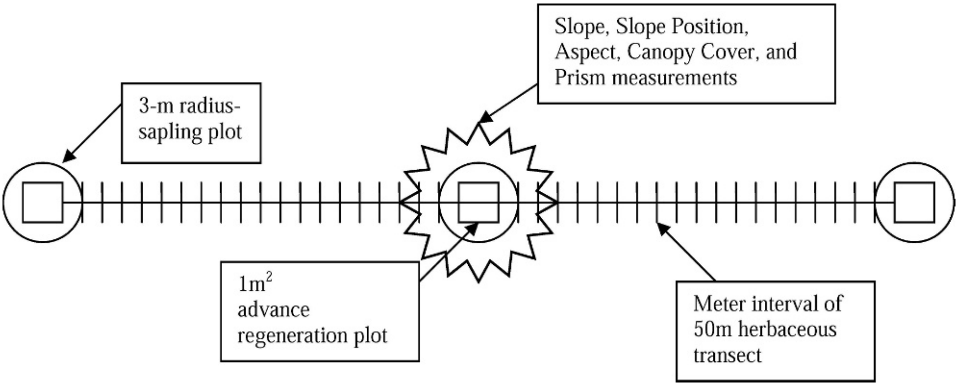

FIG. 1.—Plot layout of both herbaceous transects and woody vegetation plots (1 m^2 and 3-m radius). Herbaceous transect is 50 m in length with woody vegetation plots nested at the 0, 25, and 50 m intervals along the herbaceous transect

sampling to a 40-ha area representative of the treated area and configured to maximize core (*i.e.*, interior) area. To reduce bias associated with edge effects, we limited sampling to the inner 20 ha of each area. Data were conducted during 2008 for eight sites and 2009 for four sites.

To sample vegetation, we established plots beginning at a randomly located point within each 20-ha core area (Fig. 1). From that random starting point, subsequent plots were placed on a 70 × 70 m grid, allowing for a total of 30 plots per 20 ha core area within each study site (Avery and Burkhart, 2002). At each plot, we centered a 50-m transect perpendicular to the slope and identified plants to species that were intercepted at 1-m intervals (*i.e.*, point) along its length and recorded them as grass, forb, legume, or woody plant to characterize understory cover (Owensby, 1973). We also sampled vegetation in 1-m^2 and 3-m radius sub-plots (28 m^2) placed at plot center and both ends of the transect (0, 25, 50-m marks). On the three 1-m^2 sub-plots, we counted tree regeneration and vines and shrubs 30.5 cm–1.37 m tall. On the three 3-m radius sub-plots, we counted woody sapling stems 2.54–12.7 cm DBH. We sampled the overstory using an 11.3-m radius sub-plot placed at plot center. A 2.5× metric prism was used to measure basal area (m^2 ha^{-1}) of live and dead trees from plot center (25-m mark). We also recorded percent slope, azimuth, and slope position (ridge, shoulder, mid-slope, toe-slope, cove, or alluvial) for each plot at plot center. A spherical densitometer measurement was taken at plot center in each cardinal direction to estimate canopy cover.

We sampled the avian community using standard point count protocol (Ralph *et al.*, 1993). Eight 50-m fixed-radius points, separated by >200 m, were systematically located within the 20-ha core area of each sampling unit (Ralph *et al.*, 1993). This was the maximum number of points that could be placed in each area without overlapping fixed radius survey plots. At each point an observer proficient in identifying birds by both sight and sound recorded all species seen or heard during a 10-min period. Each point was sampled between 10 May and 15 Jun., in 2008 or 2009 depending on the site. Points were sampled only once. While using multiple point counts for a given location can be desirable where density estimates, detection probabilities, or occupancy models are to be developed, our objective was to characterize bird species composition and proportional (relative) abundances as a function of the ''effect'' (*e.g.*, disturbance level). Therefore, we relied on single surveys per location and study site. Single point count visits have been considered appropriate to develop indices of impact relative to ''treatment'' level or other gradient (*see* Bryce *et al.*, 2002; Bryce, 2006; Larsen *et al.*, 2010). No sampling was conducted during rain or when wind was inhibiting avian detection (Ralph *et al.*, 1993).

ANALYSIS

We analyzed our vegetation data using hierarchical linear modeling (HLM) in SAS 9.1 using PROC MIXED (SAS Ins., Cary, N.C, USA). Hierarchical linear modeling is a statistical approach that fits a regression model to cross-level data (Wech and Heck, 2004), in this case fitting regression equations for related variables across all plots ($n = 360$ for vegetation, $n = 96$ for avian). Use of HLM allowed us to test our dependent variables collected at individual plots ($n = 360$) across all 12 sites while accounting for variability within and between levels and has been used previously in oak savanna research (Peterson *et al.*, 2007). Separate models were developed for groundcover, midstory, and avian measures. Interclass correlation (ICC) was calculated in PROC MIXED to determine the amount of variation in the dependent variables explained in the sites (Wech and Heck, 2004).

Dependent variables were tested for normality using a Wilks' test ($W > 0.90$) using PROC Univariate and transformed, if necessary, using square root, log, or natural log transformation. We tested each of the dependent variables against our independent variables to determine if they could be modeled as random slopes in the final model by entering the independent variable in the random statement in our model. If the relationship was not random, independent variables were removed and not modeled. We then performed backwards selection regression using all independent variables, where variable inclusion criteria was maintained at alpha = 0.05.

Dependent variables included mean percent grass, forb, and legume cover, herbaceous species richness (groundcover model), vine and shrub density, oak regeneration, competitor regeneration density, oak sapling, and competitor sapling density (midstory model). We calculated percent cover of the dependent variables by dividing the intercepts for a given cover class by 50 (total number of potential intercepts). Means stem densities from the three 1-m^2 and 3-m radius sub-plots were calculated on a per plot basis ($n = 3$). All oaks were pooled in the regeneration and sapling size classes as a result of low sample sizes for individual species. Also, maples (*Acer* spp.), tulip poplar (*Liriodendron tulipifera*), and sweetgum (*Liquidambar styraciflua*) were classed together as oak competitors.

Our independent variables for both models were percent slope, slope-position, aspect, percent canopy cover, sapling density (except in midstory model), canopy cover, and total basal area (m^2 ha^{-1}), and were selected a priori, based on their expected influence on the vegetation. In both models, aspect was transformed following Beers *et al.* (1966), where a value of 0.00 represents a southwest aspect and a value of 2.00 represents a northeast aspect. We used this transformation to account for site productivity based on aspect. We assigned the slope positions as numerical categorical variables such that alluvial, cove, toe-slope, mid-slope, shoulder, and ridge were classified 1–6, respectively.

Seven avian species documented during surveys were used in regression analyses following the same HLM approach as described above. Bird species included in our analysis were selected based on their presence on at least half of the sites ($n = 6$) and >46 observations. The next most frequently encountered species, eastern towhee (*Pipilo erythrophthalmus*), was only observed 22 times across six sites; thus towhee's and less frequently observed species were not included in the model. The seven species were ovenbird (*Seiurus aurocapillus*; OVEN), red-eyed vireo (*Vireo olivaceus*; REVI), hooded warbler (*Wilsonia citrina*; HOWA), blue-gray gnatcatcher (*Polioptila caerulea*; BGGN), tufted titmouse (*Baeolophus bicolor*; TUTI),

TABLE 2.—Mean (SE) percent understory vegetation cover on twelve oak savanna restoration sites located in Tennessee and Kentucky and sampled during the summers of 2008 and 2009

Disturbance treatment	Grass cover %	Forb cover %	Legume cover %	Understory woody cover %	Herbaceous species richness
STERNS S-cont	0.7 (0.3)	0.9 (0.3)	3.2 (0.8)	28.8 (2.0)	1.3 (0.3)
CWMA C-cont	1.6 (0.5)	1.1 (1.1)	0.0 (0.0)	22.3 (2.4)	0.8 (0.2)
LBL L-cont	5.3 (2.1)	0.6 (0.2)	0.0 (0.0)	15.1 (2.2)	0.9 (0.2)
CUMB CU-cont	2.0 (0.5)	2.5 (0.6)	1.0 (0.5)	31.1 (3.3)	2.0 (0.0)
CWMA C-cut	10.9 (1.8)	1.2 (0.4)	0.1 (0.1)	31.1 (2.6)	2.9 (0.3)
LBL L-burn1	7.1 (0.9)	2.1 (0.6)	1.0 (0.3)	25.3 (3.0)	3.1 (0.4)
CUMB CU-burn4	9.0 (1.4)	14.1 (1.9)	2.3 (0.6)	42.5 (3.3)	6.1 (0.0)
STERNS S-burn5	14.3 (1.7)	7.3 (1.3)	1.1 (0.3)	68.6 (3.8)	6.3 (0.6)
CWMA C-cut/burn3	17.8 (2.3)	1.6 (0.6)	0.1 (0.1)	39.4 (2.7)	3.8 (0.3)
CWMA C-cut/burn5	41.2 (2.9)	6.3 (0.9)	1.5 (0.4)	44.3 (2.8)	5.9 (0.4)
CWMA C-cut/burn5 and Chop	24.9 (2.6)	2.8 (0.5)	0.3 (0.2)	42.9 (3.6)	4.2 (0.4)
FCMB FC-savanna	38.3 (2.3)	20.3 (2.1)	2.6 (0.6)	10.7 (1.2)	9.2 (0.0)

indigo bunting (*Passerina cyanea*; INBU), and prairie warbler (*Dendroica discolor*; PRAW), and represented a continuum from mature forest species to early successional species. Detections at each point (n = 96) for each of these species was used as our dependent variable in the HLM. Independent variables were percent grass, forb, and woody understory cover, vine and shrub density, seedling density, sapling density, total basal area, and the basal area of dead trees. These variables were chosen because of their contribution to savanna structure and their influence on avian site selection along a gradient from forest to savanna (Dickson *et al.*, 1995; Davis *et al.*, 2000; Grundel and Pavlovic, 2007a).

For all three final models (groundcover, midstory, avian), we tested for normality of the residuals using Wilke's test ($W > 0.90$) in PROC Univariate. Intercepts were compared among sites with a chi-square test. We determined avian species richness and diversity at the site level (8 point counts per site) using Shannon-Wiener's Diversity Index (Magurran, 1988). Avian species were also separated into three guilds (grassland, shrub/scrub, and forest) based on breeding habitat groups as defined by the Breeding Bird Survey (Sauer *et al.*, 2008). We assigned species not belonging to any of these groups, such as chipping sparrow (*Spizella passerina*), to an ''other'' guild.

RESULTS

Herbaceous species richness ranged from 0.83 under closed-canopy forest to 9.2 in FC-savanna (Table 2). Grass cover ranged from 0.7% under closed-canopy forest to 38.3% in FC-savanna (Table 2). Needlegrass (*Piptochaetium avenaceum*) was the most abundant species and accounted for 29% of the grass cover in C-burn5 (Table 3). Deertongue (*Dicanthelium* spp.) and sedge (*Carex* spp.) were both common and found in all sites with cover ranging from 0.1–9.2% and 0.3–3.3%, respectively. Two common grasses in savannas, big bluestem (*Andropogon gerardii*) and indiangrass (*Sorghastrum nutans*), were absent in most of the sites but were present in sites that were subject to overstory thinning and multiple prescribed fires though their percent cover remained minimal. Three non-native grass species were encountered [johnsongrass (*Sorghum halepense*), tall fescue (*Lolium arundinaceum*), and cheat (*Bromus tectorum*)], however, these species had low percent cover (<0.5%) in the five sites where present. These non-native species tended to be found around the periphery of the site that encroached from roadways.

Forb cover ranged from 0.6% under closed-canopy forest to 20.3% in FC-savanna, the highest forb cover of any site (Table 2). Goldenrod (*Solidago* spp.) was the most abundant forb among the sites. Two non-native forb species were identified, ox-eyed daisy (*Leucanthemum vulgare*), only found in C-cut/burn5 and Chop, and red sorrel (*Rumex acetosella*), only found in C-cut/burn3. These two species only made up 0.1% cover in their respective stands.

Native legume cover was minimal, with cover ~3% in FC-savanna and S-cont (Table 2). Beggarlice (*Desmodium* spp.) and lespedeza (*Lespedeza* spp.) were the most frequent legumes detected among the sites. Three non-native legumes were identified. Crown vetch (*Securigera varia*) was identified only at CU-burn4 and made up 0.9% cover. Serecia lespedeza (*Lespedeza cuneata*) and sweet clover (*Melilotus* spp.) were both identified in the FC-savanna and made up 4.3% and 0.1% cover, respectively. Fern cover was minimal in all sites and moss cover almost non-existent. Understory woody vegetation cover ranged from 15% under closed canopy to 69% in the S-burn5 but was only 10.7% in the FC-savanna site (Table 2).

Vines and shrubs, oak regeneration, competition regeneration, and oak sapling densities did not show trends with increased disturbances, but oak competitor sapling densities appeared to decrease as disturbance increased (Table 4). Blackberry (*Rubus* spp.) and greenbrier (*Smilax* spp.) were most common among all sites, ranging from 0–67% and 0–36%, respectively. Multiflora rose (*Rosa multiflora*), the only exotic shrub identified, was only found in the S-burn5 and comprised <2% of the total shrub stems. Red maple was the most common regeneration species, where stem densities ranged from 0–70% among sites. Black oak and white oak were the dominant regenerating oaks, but each comprised a small ~20% portion of the regeneration on any site. Red maple, black gum, and sourwood were the most common sapling species among the 12 sites, with red maple making up the greatest proportion of saplings at each site. Black oak and white oak made up the largest proportion of oak saplings within each of the sites. However, oak sapling proportion remained low among all sites <12%.

Prairie warblers and indigo buntings were detected more often as disturbance increased (Table 5). Prairie warblers were absent on three of the four controls as well as FC-savanna (Table 5). Fewer ovenbirds and hooded warblers were detected on sites with increased disturbance, while tufted titmice and blue-gray gnatcatchers did not appear to be affected relative to disturbance. Avian species diversity ranged from 2.5–3.2 (Table 6). The number of forest guild species ranged from 15–18 in the controls to seven in FC-savanna. Only one shrub/scrub species was encountered in the controls and 11 in FC-savanna. We encountered grassland-obligate species at only two sites (Table 6): four eastern kingbirds (*Tyrannus tyrannus*) at C-cut/burn5 and Chop and one Bachman's sparrow (*Aimophila aestivalis*) and two dickcissel's (*Spiza americana*) at FC-savanna.

Based on the HLM for groundcover variables, herbaceous species richness was negatively related to sapling density only ($P = 0.03$), while grass cover was negatively related to percent canopy cover ($P < 0.01$), and forb cover was negatively related to total basal area ($P = 0.04$) (Table 7; Fig. 2). Species richness and grass and forb cover all tended to increase with increasing disturbance (Fig. 2), while legume cover was positively related to slope ($P = 0.03$). Woody understory plant cover was negatively related to both percent canopy cover ($P = 0.02$) and sapling density ($P < 0.01$). Vine and shrub density was positively related to sapling density ($P = 0.04$) (Table 8). Oak regeneration was positively related to canopy cover ($P < 0.01$) (Fig. 2). Competition regeneration was positively related to percent slope ($P = 0.01$) and sapling density ($P = 0.01$). Oak sapling density was not significantly related to any of the variables tested, while oak competition sapling density was positively related to

TABLE 3.—Percent cover (standard errors) for most common herbaceous species among any of the twelve oak restoration sites located in Tennessee and Kentucky, 2008–2009

	STERNS S-cont	CWMA C-cont	LBL L-cont	CWMA CU-cont	CWMA C-cut
Grass					
broomsedge (*Andropogon virginicus*)	–	–	–	–	0.7 (0.7)
deertounge (*Dicanthelium spp.*)	0.1 (0.1)	0.6 (0.3)	3.7 (2.1)	1.3 (0.4)	2.4 (0.7)
little bluestem (*Schizachyrium scoparium*)	–	–	–	–	0.2 (0.1)
needlegrass (*Piptochaetium avenaceum*)	0.1 (0.1)	0.7 (0.3)	–	–	2.3 (0.8)
povertygrass (*Danthonia spp.*)	–	–	0.1 (0.1)	0.1 (0.1)	2.3 (0.7)
sedge (*Carex spp.*)	0.3 (0.1)	0.3 (0.2)	1.5 (0.4)	0.5 (0.2)	0.3 (0.2)
slender woodoats (*Chasmanthium laxum*)	–	–	–	–	1.7 (0.7)
Forb					
common ragweed (*Ambrosia artemisifolia*)	–	–	–	–	–
goldenrod (*Solidago spp.*)	–	–	–	–	–
sunflower (*Helianthus spp.*)	–	–	–	0.1 (0.1)	0.1 (0.1)
Legume					
desmodium (*Desmodium spp.*)	–	–	–	0.7 (0.5)	–
lespedeza (*Lespedeza spp.*)	–	–	–	–	–
nakedleaf trefoil (*Desmodium nudiflorum*)	2.7 (0.7)	1.1 (1.1)	–	0.3 (0.1)	–
serecia lespedeza (*Lespedeza cuneata*)	–	–	–	–	–

total basal area (P = 0.02). With the exception of legume cover, site factors such as aspect, slope and slope position were not related to any groundcover category and were not significant in any models. Approximately half of the variation among sites was explained by the dependent variables as indicated by our ICC values, with the exception of legume cover (Table 7) and oak regeneration and competitor saplings (Table 8). Slope intercept estimates also differed among the study sites for each dependent variable (Tables 7 and 8).

Based on the HLM for avian species presence ovenbird detections were positively related to total basal area (P = 0.01) and negatively to basal area of dead trees (P = 0.02), red-eyed vireo detections were negatively related to grass cover (P = 0.07), forb cover (P = 0.04), and woody understory cover (P = 0.03) (Table 9). Detections for hooded warblers were only related to grass cover ($P < 0.01$), indigo bunting detections were related to grass ($P < 0.01$),

TABLE 3.—Extended

LBL L-burn1	CWMA CU-burn4	STERNS S-burn5	CWMA C-cut/burn3	CWMA C-cut/burn5	CWMA C-cut/ burn5 and chop	FCMB FC-savanna
–	0.1 (0.1)	–	0.2 (0.2)	–	0.1 (0.1)	1.9 (0.5)
3.4 (0.6)	6.0 (1.1)	7.3 (1.1)	4.5 (0.9)	9.2 (1.2)	2.9 (0.6)	0.7 (0.3)
–	–	0.3 (0.2)	0.1 (0.1)	0.6 (0.4)	0.5 (0.2)	31.4 (2.6)
–	–	4.6 (0.9)	5.9 (1.4)	29.7 (3.2)	17.5 (2.4)	–
0.1 (0.1)	0.3 (0.2)	0.7 (0.3)	4.0 (1.2)	0.4 (0.2)	0.9 (0.3)	–
3.3 (0.6)	1.7 (0.4)	0.7 (0.3)	0.7 (0.3)	1.7 (0.4)	0.7 (0.7)	1.8 (0.4)
–	–	0.1 (0.1)	2.5 (1.0)	1.1 (0.3)	0.7 (0.7)	–
–	–	–	–	–	–	1.2 (0.6)
0.1 (0.1)	0.4 (0.2)	2.0 (0.5)	0.3 (0.3)	2.1 (0.4)	1.0 (0.3)	1.7 (0.4)
–	3.0 (0.8)	0.3 (0.2)	0.1 (0.1)	–	–	–
0.8 (0.3)	0.4 (0.2)	0.2 (0.1)	–	0.3 (0.1)	0.1 (0.1)	1.3 (0.7)
0.2 (0.1)	0.1 (0.1)	1.1 (0.3)	–	0.7 (0.2)	–	2.4 (0.4)
–	0.9 (0.3)	0.5 (0.2)	–	0.1 (0.1)	–	–
–	–	–	–	–	–	4.3 (1.2)

forb ($P = 0.06$), and woody plant cover ($P = 0.12$). Blue-gray gnatcatcher, tufted titmouse, and prairie warbler detections were not related to any of the variables tested.

DISCUSSION

Despite increased interest in restoration of oak savannas, our understanding of how this process is best accomplished and how such ecosystems function remains limited (Leach and Ross, 1995). In particular, few investigators have addressed oak savanna restoration beginning from a mature close-canopied forest, or the use of mechanical overstory thinning and prescribed fire in combination, especially in the Mid-South.

Based on our results and the work of others (Scholes and Archer, 1997; Leach and Givnish, 1999; Peterson *et al.*, 2007), it appears that overstory reduction is important to the

TABLE 4.—Mean (SE) woody vegetation density (stems/ha) for twelve oak savanna restoration sites located in Tennessee and Kentucky and sampled during the summers of 2008 and 2009

Disturbance treatment	Vines and shrubs[1]	Oak regeneration[2]	Competitor regeneration[2]	Oak saplings[3]	Competitor saplings[3]
STERNS S-cont	14,333 (2656)	4667 (1496)	4333 (1774)	83 (33)	354 (74)
CWMA C-cont	12,000 (4584)	1333 (1043)	6333 (2170)	47 (37)	177 (63)
LBL L-cont	667 (463)	667 (463)	333 (333)	71 (49)	142 (55)
CUMB CU-cont	10,222 (2114)	1778 (654)	1556 (472)	55 (17)	373 (131)
CWMA C-cut	19,000 (4633)	2000 (1006)	2667 (1263)	165 (84)	71 (31)
LBL L-burn1	3667 (1312)	2000 (1006)	0 (0)	212 (67)	24 (16)
CUMB CU-burn4	11,889 (2100)	1889 (591)	778 (381)	16 (7)	4 (4)
STERNS S-burn5	31,111 (3575)	4778 (1092)	9778 (1836)	346 (62)	563 (94)
CWMA C-cut/burn3	13,667 (3698)	4000 (1702)	7000 (2498)	24 (16)	59 (48)
CWMA C-cut/burn5	10,000 (2626)	6667 (2316)	8333 (2449)	47 (28)	0 (0)
CWMA C-cut/burn5 and Chop	20,000 (5274)	4000 (1633)	6000 (2068)	47 (22)	0 (0)
FCMB FC-savanna	5889 (1285)	0 (0)	0 (0)	0 (0)	0 (0)

[1] Vines and shrubs 30.5 cm–1.37 m tall

[2] Regeneration 30.5 cm–1.37 m tall

[3] Sapling stems 2.54–12.7 cm DBH

development of the herbaceous layer and, therefore, should be viewed as a critical step in restoring oak savannas. Scholes and Archer (1997) discuss in depth the role of overstory trees on grasses and cite many factors that influence the presence of grass, including competition for resources with overstory trees and the shading effect caused by overstory canopies. Similarly, Peterson *et al.* (2007) found forb cover was negatively related to tree canopy cover. We often found native warm-season grasses [big bluestem, little bluestem (*Schizachyrium scoparium*), and indiangrass] growing in canopy gaps within mature hardwood stands where these species did not otherwise occur. We also found some locally extirpated species, including rattlesnake master (*Eryngium yuccifolium*), yellow indigo (*Baptisia tinctoria*), blazing star (*Liatris* spp.), and five species of bluestem (*Andropogon* spp.), growing in the more open areas in our study. All of the native herbaceous species counted across the

TABLE 5.—Mean (SE) species detections per point count (n = 8) on twelve oak savanna restoration sites located in Tennessee and Kentucky between 15 May–15 Jun. 2008 and 2009

Disturbance treatment	PRAW	TUTI	RHWO	INBU	OVEN	BGGN	HOWA	REVI
STERNS S-cont	0.0 (0.0)	0.4 (0.3)	0.0 (0.0)	0.0 (0.0)	1.5 (0.3)	0.3 (0.2)	1.4 (0.3)	1.3 (0.3)
CWMA C-cont	1.3 (1.1)	0.3 (0.2)	0.0 (0.0)	0.0 (0.0)	1.6 (0.2)	0.0 (0.0)	1.0 (0.3)	2.0 (0.4)
LBL L-cont	0.0 (0.0)	1.3 (0.3)	0.0 (0.0)	0.0 (0.0)	0.9 (0.3)	1.1 (0.4)	0.4 (0.2)	1.0 (0.3)
CUMB CU-cont	0.0 (0.0)	1.1 (0.4)	0.0 (0.0)	0.1 (0.1)	0.9 (0.2)	1.6 (0.3)	0.8 (0.2)	0.6 (0.3)
CWMA C-cut	1.0 (0.3)	0.5 (0.2)	0.1 (0.1)	0.8 (0.2)	0.8 (0.3)	0.4 (0.2)	0.6 (0.2)	0.9 (0.2)
LBL L-burn1	0.1 (0.1)	0.6 (0.3)	0.0 (0.0)	0.1 (0.1)	0.0 (0.0)	1.4 (0.3)	0.4 (0.3)	0.8 (0.3)
CUMB CU-burn4	0.1 (0.1)	0.5 (0.5)	0.0 (0.0)	1.8 (0.4)	0.4 (0.3)	0.4 (0.3)	0.3 (0.2)	0.4 (0.3)
STERNS S-burn5	0.4 (0.3)	0.9 (0.6)	0.3 (0.3)	1.3 (0.5)	0.0 (0.0)	1.3 (0.5)	0.5 (0.3)	0.0 (0.0)
CWMA C-cut/burn3	0.9 (0.2)	0.3 (0.2)	0.8 (0.3)	0.9 (0.4)	0.0 (0.0)	0.4 (0.2)	0.5 (0.3)	0.8 (0.3)
CWMA C-cut/burn5	1.1 (0.2)	0.0 (0.0)	0.4 (0.2)	0.8 (0.3)	0.3 (0.2)	0.4 (0.2)	0.1 (0.1)	0.5 (0.2)
CWMA C-cut/burn5 and Chop	1.1 (0.1)	0.1 (0.1)	0.1 (0.1)	1.5 (0.3)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	1.3 (0.4)
FCMB FC-savanna	0.0 (0.0)	0.3 (0.2)	0.0 (0.0)	1.3 (0.3)	0.0 (0.0)	0.4 (0.2)	0.0 (0.0)	0.0 (0.0)

TABLE 6.—Avian species diversity and richness on twelve oak restoration sites located in Tennessee and Kentucky between 15 May and 15 Jun. 2008 and 2009

	STERNS S-cont	CWMA C-cont	LBL L-cont	CUMB CU-cont	CWMA C-cut	LBL L-burn1	CUMB CU-burn4	STERNS S-burn5	CWMA C-cut/burn3	CWMA C-cut/burn5	CWMA C-cut/burn5 and chop	FCMB FC-savanna
Species diversity	2.63	2.54	2.6	2.63	2.88	2.65	2.95	3.19	2.99	2.99	2.83	2.81
Species richness												
All guilds	20	21	18	21	24	20	26	33	24	26	25	23
Forest guild	18	15	15	18	14	14	15	14	11	10	9	7
Shrub/scrub guild	1	2	1	2	7	3	6	10	8	10	7	11
Grassland guild	–	–	–	–	–	–	–	–	–	–	1	2
Other guild	1	4	2	1	3	3	5	9	5	6	8	3

TABLE 7.—Hierarchical linear model results for groundcover variables on twelve oak savanna restoration sites located in Tennessee and Kentucky and sampled during 2008 and 2009

Dependent variables	Independent variables	ICC	df	F	P	Estimate (SE)
Herbaceous Species Richness	Sapling/ha	60.32%	1, 347	4.62	0.03	−0.060 (0.030)
Grass Cover	Canopy Cover (%)	65.50%	1, 347	18.28	<0.01	−0.001 (0.000)
sqrt(Forb Cover)	Total Basal Area (m^2 ha^{-1})	53.69%	1, 347	4.46	0.04	−0.002 (0.001)
sqrt(Legume Cover)	Slope (%)	17.47%	1, 347	5.07	0.03	−0.040 (0.010)
Woody Understory Cover	Canopy Cover (%)	49.39%	1, 346	5.94	0.02	−0.001 (0.000)
	Sapling/ha		1, 346	19.14	<0.01	−0.009 (0.002)

various sites are known to occur in prairie and savanna communities. Without historic data, it is difficult to determine the original species composition and relative cover of each plant. However, these grasses and forbs are likely an indication of pre-European understory composition in disturbed oak or oak-grass communities of this region. In our study, sapling density also negatively influenced herbaceous species richness. This could have important consequences for savanna restoration by limiting species richness and, potentially, occurrence of rare species. Overstory thinning could potentially accomplish two goals quickly: provide revenue from harvested timber and reduce canopies to acceptable levels. During overstory reduction, species common to savannas should be left, shifting the overstory composition towards conditions similar to those reported in historic accounts (Peterson and Reich, 2001).

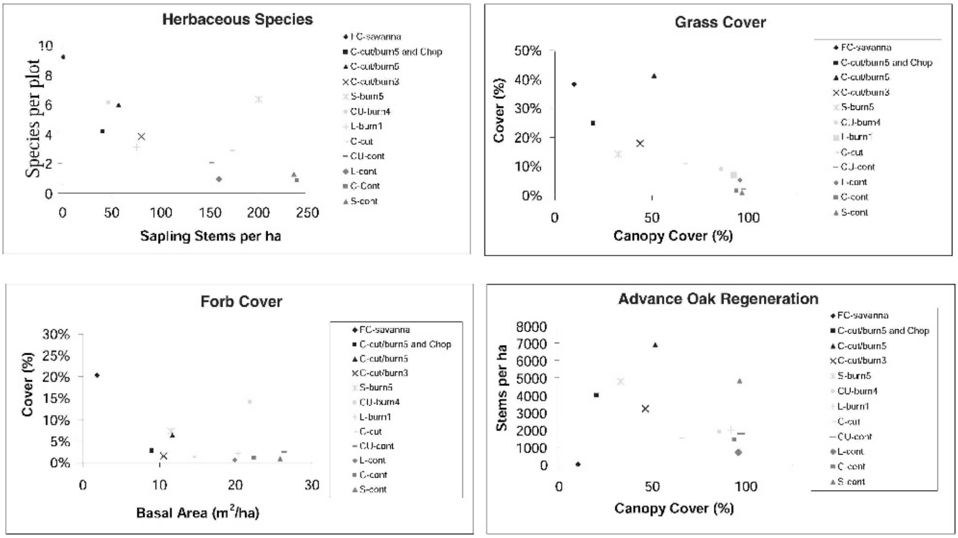

FIG. 2.—Restoration site means (n = 12) of variables with significant ($P < 0.05$) models developed under hierarchical linear model for twelve oak savanna sites in Tennessee and Kentucky during the summers of 2008 and 2009. Restoration sites with red symbols are undisturbed sites, those with green are either burned or cut only, and those with blue are burned and cut

TABLE 8.—Hierarchical linear model results for midstory variables on twelve oak savanna restoration sites located in Tennessee and Kentucky and sampled during in 2008 and 2009

Dependent variable	Independent variable	ICC	df	F	P	Estimate (SE)
sqrt (Vines and Shrubs)	Sapling/ha	40.53%	1, 347	4.33	0.04	0.12 (0.06)
ln(Oak Regeneration)	Canopy Cover (%)	18.79%	1, 337	0.17	<0.01	0.03 (0.01)
ln(Competitor Regeneration)	Slope (%)	41.29%	1, 336	6.91	0.01	0.06 (0.02)
	Sapling/ha		1, 336	7.53	0.01	0.14 (0.05)
ln(Oak Saplings)	No Predictors	44.89%				
ln(Competitor Saplings)	Total Basal Area (m^2 ha^{-1})	26.98%	1, 337	5.65	0.02	0.03 (0.01)

Although savannas are rich in forb diversity (Bray, 1960) and may even be forb- rather than grass-dominated (Leach and Givnish, 1999), we did not see forb cover >20.3%. This might be a reflection of the current stage of development of the sites in our study and indicate the slow response of fire-adapted forbs to reintroduced fire. Other studies have also found forbs respond positively to fire but with only small increases in cover after multiple fires (Hartman and Heumann, 2003; Hutchinson *et al.*, 2005). We also found legumes to be a minor component of the herbaceous layer, even in stands that had been cut and received multiple burns. Nielson *et al.* (2003) also noted legumes failed to respond positively, or were absent, after overstory thinning and prescribed fire and suggested that the seedbank may have been depleted after canopy closure. This could explain the minimal cover of legumes in our study given that the age of timber on our sites exceeded 60 y. Understory woody plant cover was negatively related to canopy cover and sapling density. This relationship has also been shown in Iowa, where the distance between trees within the savanna was directly correlated with increasing woody plant cover (Brudvig and Asbjornsen, 2009). The understory woody plant cover in our study was dominated by *Vaccinium* spp. and hardwood stems, most arising from the sprouting of stumps and extant root systems. In early stages of savanna restoration, the presence of woody sprouts arising from cut stumps is common (McCarty, 2002) and is likely caused by the increase in nitrogen availability following overstory thinning (Reich *et al.*, 2001) and increase in light reaching the ground (Larson and Johnson, 1998).

TABLE 9.—Hierarchical linear model results relating avian species detections to habitat metrics on twelve oak savanna restoration sites sampled in Tennessee and Kentucky during 2008 and 2009

Species	Independent variables	ICC	df	F	P	Estimate (SE)
log(ovenbird)	Total Basal Area	52.39%	1, 82	7.92	0.01	−0.02 (0.01)
	Basal Area of Dead Trees		1, 82	5.92	0.02	−0.03 (0.01)
log(red-eyed vireo)	Grass Cover	29.59%	1, 81	3.31	0.07	−0.86 (0.47)
	Forb Cover		1, 81	4.42	0.04	−1.69 (0.80)
	Woody Understory Cover		1, 81	5.16	0.03	−0.77 (0.34)
log(hooded warbler)	Grass Cover	25.93%	1, 83	11.15	<0.01	−1.35 (0.40)
log(blue-gray gnatcatcher)	No Predictors	30.25%				
sqrt(tufted titmouse)	No Predictors	7.69%				
sqrt(indigo bunting)	Woody Understory Cover	37.16%	1, 81	2.46	0.12	0.52 (0.33)
	Forb Cover		1, 81	3.38	0.06	1.43 (0.78)
	Grass Cover		1, 81	8.43	<.01	1.34 (0.46)
log(prairie warbler)	No Predictors	46.66%				

We identified nine non-native species in the grass, forb, legume, and vine and shrub categories, eight of which never exceeded 0.9%, and the ninth, serecia lespedeza at FC-savanna, made up only 4.3% of the groundcover. Other research has noted the invasion of European buckthorn (*Rhamnus cathartica*) (Apfelbaum and Haney, 1990) and serecia lespedeza into established savannas (Eddy and Moore, 1998). Grace *et al.* (2001) observed the response of various invasive plants to prescribed fire and concluded that the different species respond differently to fire, requiring other management strategies to achieve control. The invasive species were found near the peripheries of the sampling area and encroached from nearby roads indicating that the roads, rather than the restoration process itself, were the source for these plants. This pattern also suggests that before any restoration activities begin, the control of invasive plants near the periphery of the project area should be addressed. Though continued monitoring is needed on these sites, the limited abundance of non-native species, despite substantial disturbances associated with mechanical overstory thinning and prescribed fire, suggests that protection of the integrity of this ecosystem during restoration is possible.

Site factors such as aspect, slope, and slope position did not influence groundcover in our study. Because these factors do not appear to be influencing herbaceous groundcover development, managers may be able to restore savannas on large scales and not be constrained by topographic limitations. Elliot *et al.* (1999) observed similar results in the mountains of North Carolina, reporting that though there were some community differences related to topography [*e.g.,* dry mixed-oak vs. mesic hemlock-poplar (*Tsuga-Populus*) or cove hardwoods], individual species were found over a wide range of topographic positions. In another North Carolina study, Clinton *et al.* (1994) found that seedling density did not differ between ridges, mid-slope, or toe-slopes. However, some studies have concluded there were topographic effects on individual herbaceous species and the diversity of herbaceous species (Anderson and Anderson, 1975; Abrams and Hulbert, 1987; Nielson and Haney, 1998).

Although we were unable to isolate site and fire effects under our approach, the substantial site-level effects demonstrated by the ICC values, differing model intercepts, and consistent patterns in the 12 study site means all suggest that this disturbance was a valuable component of restoration with important effects on herbaceous vegetation (Fig. 2). A replicated experiment with differing fire and canopy treatments would be required to clarify fire effects; however, we did not have access to such an opportunity in our study. Indeed, such research is lacking in savanna restoration literature.

Season of fire is important in managing understory woody vegetation during restoration. There is historical evidence that fires typically occurred during the growing season in both oak-pine forest (Barden and Woods, 1973) and pine savanna ecosystems (Huffman, 2006). In our study, understory woody vegetation was not adequately reduced with dormant-season (*i.e.,* late Feb. through Mar. and prior to bud-break) fires. Other workers have concluded that dormant-season fires are not effective at reducing hardwood stems because of prolific resprouting (Thor and Nichols, 1973; Blewett, 1976; Waldrop *et al.*, 1987). Conversely, growing-season fires may reduce woody stem densities, including oak, albeit to a lesser extent (Waldrop *et al.*, 1987; Keyser *et al.*, 1996; Brose and Van Lear, 1998). A change to growing-season fire is likely needed to restore savannas more quickly by reducing density of resprouting woody stems.

We found that regeneration and sapling strata were influenced by sapling density and by overstory metrics, respectively. Hutchinson and Sutherland (2000) concluded some species with greater sprouting abilities (*e.g.,* oaks) would persist longer with repeated fires. We did not detect consistent trends for oak or oak competitor regeneration or oak sapling density with increasing disturbance. The low proportion of oak regeneration may have been a result of herbaceous vegetation competing for limited resources (Scholes and Archer, 1997; Davis *et al.*, 1999). The black and white oaks that remained dominant within the regeneration and sapling pool could reflect the adaptation of these species to fire. As was the case with the oaks, we did not observe any trends associated with competitor regeneration, a finding that could have been a result of the competitors' (*e.g.*, red maple), ability to continue resprouting prolifically, even after multiple fires (Arthur *et al.*, 1998; Blankenship and Arthur, 2006). However, we did find, in agreement with others, that competitor saplings decreased in density with the increase in disturbances such as fire (Wendel and Smith, 1986; Elliot *et al.*, 1999; Blankenship and Arthur, 2006), likely as a result of these species being less fire tolerant and, therefore, being top killed. Such stems may have sprouted back but would have been accounted for within a smaller vegetation size class.

For several of the avian species, we were able to document relationships between detections and vegetative characteristics. The lack of such relationships for blue-gray gnatcatchers and tufted titmice is likely a result of their presence across a wide gradient of site conditions ranging from mature forest to open savanna. Other workers have shown titmice and blue-gray gnatcatchers persist under a wide range of deciduous overstory and shrub conditions (Ellison, 1992; Grubb and Pravasudov, 1994). Indeed, Grundel and Pavlovic (2007a) concluded the variation in multiple vegetation strata from the ground to the canopy was not useful in predicting density for 33% of the avian species they tested.

That ovenbirds were positively related to basal area is predictable given they require mature forest stands (Annand and Thompson, 1997), whereas past research has demonstrated ovenbird densities are related to basal area (Van Horn and Donovan, 1994). Red-eyed vireo and hooded warbler presence was related to groundcover metrics may be an artifact of overstory condition, likely because the structural requirements these species require are more complex than could be discussed in this study. Understory development may actually be a better index of the complex and somewhat open canopy architecture important to these species (Ogden and Stutchbury, 1994; Cimprich *et al.*, 2000) than any direct measures we had available. In any case, that these relationships were documented across 12 sites representing a wide geographic area with a broad gradient of disturbance suggests that the results are important.

Grundel and Pavlovic (2007b) and Au *et al.* (2008) both concluded savannas were an ecotone, harboring both prairie and forest species. This contention is supported by our observation that forest species persisted in the more disturbed sites in our study. However, conditions at the time of our study were more like woodlands than savannas. Thus, because savannas provide some benefit to forest species while fostering habitat useful to early successional species, savanna restoration may represent an optimal approach for the conservation of scrub/shrub or grassland species, and in any case, can enhance avian species diversity (Lanham *et al.*, 2002). Prairie warblers were counted numerous times, though not related to any independent variables tested. This may be a result of species selecting other aspects of vegetation structure that we did not measure, such as lateral branching or specific trees, such as elm (*Ulmus* spp.) (Nolan *et al.*, 1999). The absence of prairie warblers from FC-savanna, a site where they otherwise commonly occur, may have been a result of a recent fire that reduced shrub density within our sampling area.

In our study, the lack of grassland obligate species is likely a result of continued presence of a woody rather than grass-dominated understory. The presence of grassland and shrub/scrub species at FC-savanna is likely a result of a strong herbaceous layer and the presence of a shrub component and a likely reason that we documented a bachman's sparrow at the site. At FCMB, we observed similar shrub/scrub species to those on the other disturbed sites. However, the presence of grassland species at FCMB is likely influenced by the presence of large open tracts of grasslands, which provide a more favorable landscape context for grassland species such as Henslow's sparrow (Herkert *et al.*, 2002) and grasshopper sparrows (*Ammodramus savannarum*) (Vickery, 1996). With the continued use of prescribed fire and the reduced frequency of woody stems, there will likely be a greater presence of grassland species at our other sites as grass-dominated understories develop.

Our study provides insight into important factors affecting oak savanna restoration and provides additional insight into the combined use of fire and canopy reduction. It also provides information that is lacking in the literature involving oak savanna restoration from mature hardwood forest and extends our understanding of these processes into the Mid-South region. Further, research that is continuing on these sites is likely to help us gain a better understanding of the responses of herbaceous vegetation and woody stems to overstory thinning and prescribed fire.

LITERATURE CITED

ABELLA, S. R., J. F. JAEGER, D. H. GEHRING, R. G. JACKSY, K. S. MENARD, AND K. A. HIGH. 2001. Restoring historic plant communities in the oak openings region of Northwest Ohio. *Ecol. Restor.*, **19**:155–160.

ABRAMS, M. D. AND L. C. HULBERT. 1987. Effect of topographic position and fire on species composition in tallgrass prairie in Northeast Kansas. *Am. Midl. Nat.*, **117**:442–445.

ANNAND, E. M. AND F. R. THOMPSON, III. 1997. Forest bird response to regeneration practices in central hardwood forests. *J. Wildl. Manage.*, **61**:159–171.

ANDERSON, R. C. 1998. Overview of Midwestern oak savanna. *Trans. Wisconsin Acad. Sci., Arts, and Lett.*, **86**:1–18.

——— AND M. R. ANDERSON. 1975. The presettlement vegetation of Williamson County, Illinois. *Castanea*, **40**:345–363.

APFELBAUM, S. AND A. HANEY. 1987. Management of degraded oak savanna remnants in the upper Midwest: preliminary results from three years of study. *In:* G. V. Burger, J. E. Ebinger, and G. S. Wilhelm (eds.). Proceedings of the Oak Woods Management Symposium. Eastern Illinois University, Charleston, Illinois.

——— AND ———. 1990. Structure and dynamics of Midwest oak savannas, p. 19–30. *In:* J. M. Sweeney (ed.). Management of dynamic ecosystems. North Central Section, The Wildlife Society, West Lafayette, Indiana.

ARTHUR, M. A., R. D. PARATLEY, AND B. A. BLANKENSHIP. 1998. Single and repeated fires affect survival and regeneration of woody and herbaceous species in and oak-pine forest. *J. Tor. Bot. Soc.*, **125**:225–236.

ASKINS, R. A. 1993. Population trends in grassland, shrubland, and forest birds in eastern North America, p. 1–34. *In:* D. M. Power (ed.). Current Ornithology. Vol. 11. Plenum Press, New York, New York.

AU, L., D. E. ANDERSEN, AND M. DAVIS. 2008. Patterns in bird community structure related to restoration of Minnesota dry oak savannas and across a prairie to oak woodland ecological gradient. *Nat. Areas J.*, **28**:330–341.

AVERY, T. E. AND H. E. BURKHART. 2002. Forest measurements, 5th ed. McGraw-Hill, New York, New York. 456 p.

BARDEN, L. S. AND F. W. WOODS. 1973. Characteristics of lightning fires in southern Appalachian forest. *Tall Timbers Fire Ecol. Conf. Proc.*, **13**:345–361.

BEERS, T. W., P. E. DRESS, AND L. C. WENSEL. 1966. Aspect transformation in site productivity research. *J. For.*, **64**:691–692.

BLANKENSHIP, B. A. AND M. A. ARTHUR. 2006. Stand structure over 9 years in burned and fire-excluded oak stands on the Cumberland Plateau, Kentucky. *For. Ecol. Manage.*, **225**:134–145.

BLEWETT, T. 1976. Prairie and savanna restoration in the Necedah National Wildlife Refuge. D.C., p. 154–157. *In:* Glenn-Lewin and R. Q. Landers, Jr. (eds.). Fifth Midwest Prairie Conference Proceedings. Iowa State University, Ames, Iowa.

BOWLES, M. L. AND J. L. MCBRIDE. 1998. Vegetation composition, structure, and chronological change in a decadent Midwestern North American savanna remnant. *Nat. Areas J.*, **18**:14–27.

BRAWN, J. D., S. K. ROBINSON, AND F. R. THOMPSON. 2001. The role of disturbance in the ecology and conservation of birds. *Ann. Rev. Ecol. System.*, **32**:251–276.

BRAY, J. R. 1960. The composition of savanna vegetation in Wisconsin. *Ecology*, **41**:721–732.

BROSE, P. H. AND D. H. VAN LEAR. 1998. Responses of hardwood advance regeneration to seasonal prescribed fire in oak-dominated shelterwood stands. *Can. J. For. Res.*, **28**:331–339.

BRUDVIG, L. A. AND H. ASBJORNSEN. 2009. The removal of woody encroachment restores biophysical gradients in Midwestern oak savannas. *J. Appl. For.*, **46**:231–240.

BRYCE, S. A. 2006. Development of a Bird Integrity Index: measuring avian response to disturbance in the Blue Mountains of Oregon, USA. *Environ. Manage.*, **38**:470–486.

———, R. M. HUGHES, AND P. R. KAUFMANN. 2002. Development of a bird integrity index: using bird assemblages as indicators of riparian condition. *Environ. Manage.*, **30**:294–310.

CIMPRICH, D. A., F. R. MOORE, AND M. P. GUILFOYLE. 2000. Red-eyed Vireo (*Vireo olivaceus*), The Birds of North America Online, A. Poole (ed.). Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America Online: http://bna.birds.cornell.edu/bna/species/527doi:10.2173/bna.527

CLINTON, B. D., L. R. BORING, AND W. T. SWANK. 1994. Regeneration patterns in canopy gaps of mixed-oak forests of the Southern Appalachians: influences of topographic position and evergreen understory. *Am. Midl. Nat.*, **132**:308–319.

CURTIS, J. T. 1959. The vegetation of Wisconsin. University of Wisconsin Press, Madison. 657 p.

DAVIS, J. E., JR., C. MCRAE, B. L. ESTEP, L. S. BARDEN, AND J. F. MATTHEWS. 2002. Vascular flora of Piedmont prairies: evidence from several prairie remnants. *Castanea*, **67**:1–12.

DAVIS, M. A., D. W. PETERSON, P. B. REICH, M. CROZIER, T. QUERY, E. MITCHELL, J. HUNTINGTON, AND P. BAZAKAS. 2000. Restoring Savanna using Fire: Impact on the Breeding Bird Community. *Restor. Ecol.*, **8**:30–40.

———, K. J. WRAGE, P. B. REICH, M. G. TJOELKER, T. SCHAEFFER, AND C. MUERMANN. 1999. Survival, growth, and photosynthesis of tree seedlings competing with herbaceous vegetation along a water-light-nitrogen gradient. *Plant Ecol.*, **145**:341–350.

DICKSON, J. G., F. R. THOMPSON, III, R. N. CONNER, AND K. E. FRANZREB. 1995. Silviculture in Central and Southeastern Oak-Pine Forest, p. 245–265. *In:* T. E. Martin and D. M. Finch (eds.). Ecology and management of neotropical migratory birds: A synthesis and review of critical issues. Oxford University Press, New York, New York.

EDDY, T. AND C. MOORE. 1998. Effects of sericea lespedeza on oak-savannas in Kansas. *Trans. Wisconsin Acad. Sci., Arts and Lett.*, **86**:57–62.

ELLIOT, K. J., R. L. HENDRICK, A. E. MAJOR, J. M. VOSE, AND W. T. SWANK. 1999. Vegetation dynamics after a prescribed fire in the southern Appalachians. *For. Ecol. Manage.*, **114**:199–213.

ELLISON, W. G. 1992. Blue-gray Gnatcatcher (*Polioptila caerulea*), The Birds of North America Online, A. Poole (ed.). Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America Online: http://bna.birds.cornell.edu/bna/species/023doi:10.2173/bna.23

GALLIGAN, E. W., T. L. DEVAULT, AND S. L. LIMA. 2006. Nesting success of grassland and savanna birds on reclaimed surface coal mines of the midwestern United States. *Wil. J. Ornith.*, **118**:537–546.

GRACE, J. B., M. SMITH, S. L. GRACE, S. COLLINS, AND T. J. STOHLGREN. 2001. Interactions between fire and invasive plants in temperate grasslands in North America, p. 40–65. *In:* K. Galley and T. Wilson (eds.). Fire Conference 2000: the first national congress on fire, ecology, prevention and management. Invasive species workshop: the role of fire in the control and spread of invasive species. Tall Timbers Research Station, Tallahassee, Florida.

GRUBB, T. C., JR. AND V. V. PRAVASUDOV. 1994. Tufted Titmouse (*Baeolophus bicolor*), The Birds of North America Online, A. Poole (ed.). Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America Online: http://bna.birds.cornell.edu/bna/species/086doi:10.2173/bna.86

GRUNDEL, R. AND N. B. PAVLOVIC. 2007a. Response of bird species densities to habitat structure and fire history along a Midwestern open-forest gradient. *Condor*, **109**:734–749.

——— AND ———. 2007b. Distinctiveness, use, and value of Midwestern oak savannas and woodlands as avian habitats. *Auk*, **124**:969–985.

HARTMAN, G. W. AND B. HEUMANN. 2003. Prescribed fire effects in the Ozarks of Missouri: the Chilton creek project 1996–2001. Proceedings of the Second International Wildland Fire Ecology and Fire Management Congress.

HUFFMAN, J. 2006. Historical fire regimes in southeastern pine savannas. Ph.D. Dissertation. Louisiana State University, Baton Rouge, Louisiana.

HUTCHINSON, T. F. AND S. SUTHERLAND. 2000. Fire and understory vegetation: a large-scale study in Ohio and a search for general response patterns in central hardwood forest. General Technical Report. NE-274. US. Department of Agriculture, Forest Service, Northeastern Research Station. 13 p.

———, E. K. SUTHERLAND, AND D. A. YAUSSY. 2005. Effects of repeated prescribed fires on the structure, composition and regeneration of mixed-oak forests in Ohio. *For. Ecol. Manage.*, **218**:210–228.

KEYSER, P. D., P. H. BROSE, D. H. VAN LEAR, AND K. M. BURTNER. 1996. Enhancing oak regeneration with fire in shelterwood stands: preliminary trials. *N. Am. Wildl. Nat. Res. Conf.*, **61**:215–219.

LANHAM, J. D., P. D. KEYSER, P. H. BROSE, AND D. H. VAN LEAR. 2002. Oak regeneration using the shelterwood-burn technique: management options and implications for songbird conservation in the southeastern United States. *For. Ecol. Manage.*, **155**:143–152.

LARSEN, S., A. SORACE, AND L. MANCINI. 2010. Riparian bird communities as indicators of human impacts along Mediterranean streams. *Environ. Manage.*, **45**:261–273.

LARSON, D. R. AND P. S. JOHNSON. 1998. Linking the ecology of natural oak regeneration to silviculture. *For. Ecol. Manage.*, **106**:1–7.

LEACH, M. K. AND T. J. GIVNISH. 1999. Gradients in the composition, structure, and diversity of remnant oak savannas in Southern Wisconsin. *Ecol. Monog.*, **69**:353–374.

——— AND L. ROSS (eds.). 1995. Midwest oak ecosystem recovery plan. Midwest Oak Savanna and Woodland Conference, Springfield, Missouri, USA.

MAGURRAN, A. E. 1988. Ecological diversity and its measurement. Princeton University Press, Princeton, New Jersey. 179 p.

MCCARTY, K. 2002. Fire management for Missouri savannas and woodlands, p. 40–57. *In:* G. Hartman, S. Holst and B. Palmer (eds.). Proceedings of SRM 2002. Savanna/Woodland Symposium, Kansas City, Missouri.

NIELSEN, S. N., C. KIRSCHBAUM, AND A. HANEY. 2003. Restoration of Midwest oak barrens: structural manipulation or process-only? *Conserv. Ecol.*, **7**:10.

NOAA. 2009. Comparative Climate Data. National Oceanic and Atmospheric Administration. URL: www.noaa.gov

NOLAN, V., JR., E. D. KETTERSON, AND C. A. BUERKLE. 1999. Prairie Warbler (*Dendroica discolor*), The Birds of North America Online, A. Poole (ed.). Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America Online: http://bna.birds.cornell.edu/bna/species/455

NORTH AMERICAN BIRD CONSERVATION INITIATIVE, U.S. COMMITTEE. 2009. The State of the Birds, United States of America, 2009. U.S. Department of Interior, Washington, DC. 36 p.

NOSS, R. F. AND R. L. PETERS. 1995. Endangered ecosystems in the United States. A status report on America's vanishing habitat and wildlife. Defenders of Wildlife, Washington, DC.

NUZZO, V. 1986. Extent and status of Midwest oak savanna: presettlement and 1985. *Nat. Areas J.*, **6**:6–36.

OGDEN, L. J. AND B. J. STUTCHBURY. 1994. Hooded Warbler (*Wilsonia citrina*), The Birds of North America Online, A. Poole (ed.). Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America Online: http://bna.birds.cornell.edu/bna/species/110doi:10.2173/bna.110

OWENSBY, C. E. 1973. Modified step-point system for botanical composition and basal cover estimates. *J. Ran. Manage.*, **26**:302–303.

PACKARD, S. 1993. Restoring oak ecosystems. *Restor. Manage. Notes*, **11**:5–16.

PETERSON, D. W. AND P. B. REICH. 2001. Prescribed fire in oak savanna: fire frequency effects on stand structure and dynamics. *Ecol. Appl.*, **11**:914–927.

———, ———, AND K. J. WRAGE. 2007. Plant functional group responses to fire frequency and tree canopy cover gradients in oak savannas and woodlands. *J. Veg. Sci.*, **18**:3–12.

RALPH, C. J., G. R. GEUPEL, P. PYLE, T. E. MARTIN, AND D. F. DESANTE. 1993. Handbook of field methods for monitoring landbirds. General Technical Report. PSW-144. U.S. Department of Agriculture. Forest Service. Pacific Southwest Research Station, 41 p.

REBERTUS, A. J. AND B. R. BURNS. 1997. The importance of gap processes in the development and maintenance of oak savannas and dry forests. *J. Ecol.*, **85**:635–645.

REICH, P. B., D. W. PETERSON, D. A. WEDIN, AND K. WRAGE. 2001. Fire and vegetation effects on productivity and nitrogen cycling across a forest-grassland continuum. *Ecology*, **82**:1703–1719.

SAUER, J. R., J. E. HINES, AND J. FALLON. 2008. The North American Breeding Bird Survey, Results and Analysis 1966–2007. Version 5.15. USGS Patuxent Wildlife Research Center, Laurel, Maryland.

SAS INSTITUTE INC. 2004. SAS OnlineDoc® 9.1.3. SAS Institute Inc, Cary, North Carolina.

SCHOLES, R. J. AND S. R. ARCHER. 1997. Tree-grass interactions in savannas. *Ann. Rev. Ecol. Syst.*, **28**:517–544.

THOR, E. AND G. NICHOLS. 1973. Some effects of fires on litter, soil, and hardwood regeneration. *Tall Timbers Fire Ecol. Conf. Proc.*, **13**:317–329.

VAN HORN, M. A. AND T. M. DONOVAN. 1994. Ovenbird (*Seiurus aurocapilla*), The Birds of North America Online, A. Poole (ed.). Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America Online: http://bna.birds.cornell.edu/bna/species/088doi:10.2173/bna.88

VAN LEAR, D. H. AND T. A. WALDROP. 1989. History, uses, and effects of fire in the Appalachians. General Technical Report. SE-54. U.S. Department of Agriculture, Forest Service, Southeastern Forest Experiment Station. 20 p.

VICKERY, P. D. 1996. Grasshopper Sparrow (*Ammodramus savannarum*), The Birds of North America Online, A. Poole (ed.). Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America Online: http://bna.birds.cornell.edu/bna/species/239doi:10.2173/bna.239

WALDROP, T. A., D. H. VAN LEAR, F. T. LLOYD, AND W. R. HARMS. 1987. Long-term studies of prescribed burning in loblolly pine forests of the Southeastern Coastal Plain. General Technical Report. SE-45. U.S. Department of Agriculture, Forest Service, Southeastern Forest Experiment Station. 23 p.

WEBSOIL SURVEY. 2009. NRCS websoil survey, URL: www.websoilsurvey.nrcs.usda.gov

WECH, B. A. AND A. L. HECK. 2004. An introduction to hierarchical linear modeling for marketing researchers. *Market. Bull.*, **15**:1–8.

WENDEL, G. W. AND H. C. SMITH. 1986. Effects of prescribed fire in a central Appalachian oak-hickory stand. General Technical Report. NE-594. U.S. Department of Agriculture, Forest Service, Northeastern Forest Experiment Station. 8 p.

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