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Long-term changes in an oak forest's woody understory and herb layer with repeated burning[1]

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Bowles, M. L., K. A. Jacobs (The Morton Arboretum, Lisle, IL 60532), and J. L. Mengler (U.S. Fish and Wildlife Service, Barrington, IL 60010). Long-term changes in an oak forest's woody understory and ground layer with repeated burning. J. Torrey Bot. Soc. 134: 223–237. 2007.—Although fire exclusion is thought to be linked with declining plant diversity in oak forests, few studies have examined long-term changes in their shrub and ground layers resulting from repeated burning. In this study, we compare the composition and structure of woody understory and ground layer vegetation in burned and unburned oak forest after 17 years of annual dormant season low-intensity burns. Over time, burned forest had 97% reduction of shrubs and small saplings, but only 38% loss of stems in the > 5–10 cm size class. Canopy openness was similar in burned and unburned forest plots prior to the onset of burning, but it was significantly greater in burned forest after 17 years of fire. Ground layer vegetation structure also changed significantly, with responses differing by guilds. Spring herbs were the dominant guild before burning and did not change over time. However, cover and abundance of summer herbs increased over time in burned forest, probably in response to greater light assimilation under the more open canopy. This resulted in greater overall species richness in burned plots without loss of the spring herbs. Burning eliminated most alien shrubs, although common buckthorn persisted in small numbers. The alien herb garlic mustard also persisted and had greater abundance in burned plots, apparently by re-colonizing from unburned micro-habitats and adjacent forest. These results indicate that long-term burning can eliminate shrub and small sapling canopy cover, thereby increasing canopy openness and promoting greater richness and cover of summer forbs. Fire also probably had a positive effect on seedling establishment through removal of litter. Resulting tradeoffs to this gain in diversity include loss of native vines, shrubs, understory trees and forest interior bird habitat, as well as persistence of alien plants.

Key words: alien plants, *Alliaria petiolata*, canopy openness, cover, fire effects, ground layer, guild structure, *Rhamnus cathartica*, shrub layer, species richness, spring herbs, summer herbs.

Prior to European settlement, landscape fires are thought to have maintained oak (*Quercus* spp.) dominance of midwestern forests and woodlands (Gleason 1913, Kilburn 1959, Lorimer 1987, Anderson 1991, Leitner et al. 1991, Bowles et al. 1994). Post-settlement fire suppression is often followed by replacement of oaks by shade-tolerant mesophytic tree species such as sugar maple (*Acer saccharum* L.), thereby threatening the viability of this ecosystem (McIntosh 1957, Curtis 1959, Schlesinger 1976, Miceli et al. 1977, Lorimer 1985, Pallardy et al. 1988, Abrams 1992, Roovers and Shifley 1997, Bowles et al. 2003, Abrams 2005, Bowles et al. 2005). Although ground layer vegetation has received less attention than concerns for oak regeneration, this vegetation is also thought to decline with fire protection due to loss of shade-intolerant understory plants (McIntosh 1957, Curtis 1959, Wilhelm 1991, Bowles et al. 2000). As the ground layer comprises most of the plant species in oak forests (Roberts 2004, Whigham 2004), maintaining its diversity is an important conservation need that may be facilitated by restoring fire to the system. Invasion of oak forests by alien plants, such as common buckthorn (*Rhamnus cathartica* L.) and the herb garlic mustard (*Alliaria petiolata* (M. Bieb) Cavara & Grande), also has been linked with altered fire regimes and potential for control by fire management

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(Apfelbaum and Haney 1991, Anderson et al. 1996, Schwartz and Heim 1996).

Despite a recent increase in the application of prescribed burning to restore fire processes and recover oak forest vegetation, achieving and interpreting effects may be problematic. For example, in many cases midstory tree growth appears to have exceeded a size threshold of fire sensitivity, thereby reducing effectiveness of burning (Franklin et al. 2003, Abrams 2005). Moreover, long-term fire suppression has severely reduced fire-maintained reference systems against which performance can be compared (Anderson 1991, Mendelson 1998) and may have reduced local species pools needed to facilitate recovery. Short term studies suggest that fire may increase ground layer species richness, but with individualistic species effects (Kline and McClintock 1994, Wilhelm and Masters 1994, McGee et al. 1995, Ducey et al. 1996, Schwartz and Heim 1996, Arthur et al. 1988, Luken and Shea 2000, Franklin et al. 2003). Few studies have begun to report long-term vegetation responses (e.g., Sutherland et al. 2003). Hutchinson et al. (2005) found that after five years, burning resulted in small scale increases in grasses, summer forbs and seed banking species, but argued that longer-term studies were needed to identify significant trajectories of change. In this paper we report long-term changes in the composition and structure of oak forest shrub and ground layer vegetation after 17 consecutive dormant season burns.

Resource availability is the key factor affecting abundance of ground layer vegetation and it varies across environmental gradients (Hutchinson et al. 1999, Small and McCarthy 2002, Roberts and Gilliam 2003). Light is a primary limiting resource that has selected for different phenological guilds among understory herbs (Collins et al. 1985, Gilliam and Roberts 2003, Neufeld and Young 2003, Whigam 2004). In Midwest forests, these guilds are represented primarily by shade-intolerant spring herbs that become dormant upon canopy closure, spring flowering herbs that persist with canopy closure, and more shade tolerant summer flowering herbs (Rogers 1981, 1982, 1985). These guilds should respond differently to changing canopy light levels based on their species-specific adaptations. Thus a primary process by which fire regulates ground layer composition may operate through opening of canopy cover by reduction of woody vegetation, thereby allowing the greater light assimilation required by summer flowering herbs (Sparling 1967, Bazzaz and Bliss 1971). A second important fire effect may be facilitation of herbaceous seedling establishment by removing litter (Hutchinson et al. 2005, Glasgow and Matlack 2006). Burning may increase, decrease, or have neutral effects on abundance of the alien garlic mustard *Alliaria petiolata*, a biennial with overwintering rosettes that invades after soil disturbance and fire (Anderson et al. 1996, Luken and Shea 2000).

The forest disturbance model of Roberts (2004) predicts that a reduction of woody canopy cover would be expected to increase light competition among herbs. An important question is whether an increase in summer herbs would result in competitive exclusion of spring herbs and no net gain in species richness. Rogers (1985) found no evidence of competition between spring and summer herbs under stable conditions in mesic forests, possibly due to their temporal separation. Summer flowering herbs may be more light flexible than spring herbs (Collins et al. 1985), with greater cover and flowering in light gaps (Moore and Vankat 1986, Lee et al. 1986, Dahlem and Boerner 1987, Piper 1989). However, some species decline from increased competition in larger light gaps or as gap sizes decrease (Brewer 1980, Reader and Bricker 1992, Olivero and Hix 1998). In the absence of fire, species in both guilds probably require soil disturbance patches, such as pits and mounds, for regeneration (Thompson 1980, Rogers 1985, Peterson and Campbell 1993). As a result, long-term processes may be required to cause temporal change in their abundance.

Our objectives in this study were to ascertain how repeated dormant season burning of an oak forest affected its woody understory vegetation, canopy openness, and ground layer vegetation. To do so, we compare the composition and structure of burned and unburned forest plots before and after 17 consecutive annual burns. We expected that the composition and guild structure of ground layer vegetation would change if repeated burning decreased woody canopy cover. Further, we expected effects to be neutral on spring herbs, positive on summer herbs, and negative on woody ground layer vegetation.

We also sought to determine how long-term burning affected abundance of alien shrubs, such as *Rhamnus cathartica*, and *Alliaria petiolata*, which were present in the study area at the onset of burning.

Materials and Methods. Site Description. Our research was conducted in the East Woods of The Morton Arboretum, DuPage County, Illinois, which comprises a 240 ha former prairie grove located along the East Branch of the DuPage River, 32 km west of Chicago and Lake Michigan at 41.81°N latitude and 88.05°W longitude. This area lies within the Prairie Peninsula of Eastern North America (Transeau 1935), as well as the Oak-Hickory forest region (Braun 1950). The climate is continental, with average temperatures ranging from −6.05°C in January to 22.33°C in July, and 84.9 cm annual precipitation (Mapes 1979). Unpredictable summer drought, as well as dry fall and early spring conditions, favored fire and predominance of prairie and savanna vegetation in this region (Anderson 1983, Anderson 1991). As a result, land-cover in the early 1800's was 80% prairie, with oak-dominated deciduous forest restricted to fire-protected areas of rugged topography and along watercourses (Bowles et al.1994, McBride and Bowles 2001).

The East Woods is located on the Valparaiso moraine complex and primarily on Morley silt-loam soil, a well- to moderately-well drained alfisol developed under forest conditions (Mapes 1979). This area, known historically as Kings Grove, is located within "timber" mapped by the 1840 Public Land Survey (McBride and Bowles 2001). Section line data immediately north of the study area indicate, in 1840, bur oak (*Quercus macrocarpa* Michx.) and white oak (*Q. alba* L.) dominance with hazel (*Corylus americana* Walter) undergrowth, and density < 100 trees/ha. Comparative analysis of 1925 and modern floras of the Morton Arboretum suggests a loss of summer-flowering herbs, which may have resulted from fire exclusion (Wilhelm 1981). However, it is unknown whether these species occurred within our study area. This forest currently is old second growth and typical of mature Chicago region forests, with canopy dominance by red oak (*Quercus rubra* L.), white oak (*Q. alba* L.) and bur oak (*Q. macrocarpa* Michx.) and greater sapling layer presence of *Acer saccharum*, ash (*Fraxinus* spp.) and basswood (*Tilia americana* L.) (Bowles et al. 2000, Bowles et al. 2005).

Burn Treatments. Our study area comprised adjacent east and west blocks, each about 7 ha in size and split into burned and unburned treatments by an east-west road that served as a firebreak. Seventeen dormant season burns were applied between 1986–2002. These burns usually were conducted in fall, although weather conditions caused some fires to be delayed until spring. South-west winds provided optimum burning conditions, allowing back fires set along north burn unit boundaries and head fires set along south boundaries. Ambient air temperatures during burns ranged between 5–16°C, with 30–60% relative humidity. Fuel is primarily leaf litter and persistent herbaceous vegetation. The site has very little topographic relief, and carried fires with flame lengths usually reaching 1–2 m. In different years, fuel consumption has ranged from 50–100% of the litter column, with mean surface fire temperatures ranging from about 123°C to 230°C (Jacobs et al. 2004). These qualify as light to moderate fire regimes (Franklin et al 1997), or cool fires on the scale presented by Roberts (2004). Woody stems < 1 cm diameter were often completely consumed or heavily charred by fire. Stems > 2.5 cm were less obviously damaged by burns, with mortality resulting from subsequent root disease and canker (K. Jacobs, unpublished data).

Data Collection. Pre-treatment data were collected in 1986–1988 during an inventory of Arboretum forest stands. This sampling used 0.04 ha tree plots in which were nested single 0.01 ha shrub-layer plots and multiple (8–12) 0.25 m^2 ground layer plots (Wilhelm 1991). The tree and shrub data were collected in 1986, while ground layer data were collected between 1986–1988. Our present study area includes eight of the pre-treatment tree and shrub layer plots, and 76 of the ground layer plots. Five of these tree and shrub plots and 40 of the ground layer plots occur within the burn treatment areas. Densities of sapling and shrub layer stems ≥ 1 m high were collected in three size classes measured at diameter at breast height (dbh, measured at 1.37 m above ground): < 2.5 cm, ≥ 2.5–5 cm and > 5–10cm. Ground layer vegetation was recorded by species presence and cover estimated when foliage was fully expanded, either in late spring or late summer. The amount of light penetrating the tree canopy was measured in foot-candles (fc) using a Sekonic L-398 meter with a hemispheric light receptor. Readings were taken under full sun at midday during July in the 0.04 ha plots between 1986–88, with replicates reduced to a single plot average (Wilhelm 1991).

In 2002, we expanded sample plot replicates to represent burned and unburned treatments in a balanced design. To conform data with our other Chicago region forest data sets (e.g., Bowles et al. 2000), we used nested circular 0.025 ha tree plots, 0.001 ha shrub layer plots and 1.0 m^2 ground layer plots. Three sample locations were positioned 20 m apart along each of five randomly positioned north-south transects in each burned and unburned unit in each block, for a total of 60 plot locations. Diameters of woody stems $\geq$ 2.5 cm dbh were recorded from tree plots at ten sample locations in each unit, for a total of 40 plot samples. Stem densities of woody species, primarily shrubs, $\geq$ 1 m high and $<$ 2.5 cm dbh were sampled from shrub layer plots at all 60 locations. Ground layer species, including woody plants $<$ 1 m high, were recorded by their presence and% cover at all 60 plot locations. To facilitate cover estimates, each ground layer plot was sampled with a m^2 frame divided into a 100 dm^2 grid. Some non-flowering ground layer species were treated at the genus level, including *Viola* spp., *Impatiens* spp., *Carex* spp., and *Parthenocissus* spp. *Fraxinus* spp. includes *F. americana* L. and *F. pennsylvanica* Marsh. *Ulmus americana* L. and *U. rubra* Muhl. also were combined for analysis as *Ulmus* spp. in shrub and sapling size classes. Some individuals tallied as *Quercus rubra* apparently include hybrids with other locally occurring members of *Quercus* subgenus *Erythrobalanus*, including *Q. ellipsoidalis* E. J. Hill. and *Q. velutina* Lam., and are not clearly distinguishable based on morphology (A. Hipp, pers. comm.). Nomenclature follows Swink and Wilhelm (1994).

To estimate light reaching the ground layer, the vegetation canopy above each of the ground layer plots was photographed at 1.5 m above ground level through a 180° fish-eye lens on a tripod-mounted Nikon Coolpix 800 digital camera. A level attached to the tripod camera mount was used to position the lens axis horizontally. Photos were taken during August, 2002 under overcast conditions to avoid sun flare. Each image was processed using Gap Light Analyzer (GLA) software (Frazer et al. 1999) to calculate % canopy openness.

Data Analysis. For 1986 data, woody stem densities per ha were calculated for the $<$ 2.5, $\geq$ 2.5–5 and $>$ 5–10 cm size classes in the pre-treatment burned plots. Canopy light readings from 1986–1988 were converted to% of full sun by dividing each average plot reading by the maximum value of 10,000 fc, log-transformed, and compared between burned and unburned plots in a repeated analysis of variance (ANOVA) using a general linear model (GLM). We standardized ground layer abundance data for comparison with 2002 data by calculating the relative frequencies of native vs. alien graminoid, herbaceous and woody species. These data were pooled among blocks and compared between treatments. Mean species cover and relative cover were compared between treatments for ground layer species with $>$ 1% relative cover. For the most abundant species, we used the non-parametric Mann-Whitney test to compare rank abundance between treatments. We used a split-plot nested ANOVA (GLM) to test whether ground layer guild differences occurred between the pre-treatment burned vs. unburned plots within the east and west blocks in 1988. For this test, we compared mean cover (log transformed) and mean plot species richness among spring herb, summer herb and woody plant guilds. In this analysis the spring herb group included spring ephemerals as well as spring-flowering herbs that persist with canopy closure. Graminoid vegetation was not included in this test because sample occurrences were too rare for analysis.

For the 2002 data, we calculated basal area (BA), stem densities per ha, and importance values for all trees $>$ 10 cm dbh in burned and unburned plots. For comparison with 1986 data, stem densities per ha were also calculated for the $<$ 2.5, $\geq$ 2.5–5 and $>$ 5–10 cm size classes in burned plots. Percent canopy openness was compared between treatments and blocks in a nested ANOVA with a GLM using log-transformed data. The 2002 ground layer data were analyzed similarly to pre-treatment data. This included calculating the relative frequencies of native vs. alien graminoid, herbaceous and woody vegetation in burned and unburned plots; comparing mean species cover and relative cover between treatments; and using a split-plot nested ANOVA (GLM) to compare mean plot cover and species richness among guilds by treatment and block. Linear regression was used to analyze the relationship of percent canopy openness with ground layer plot cover and plot species richness of spring and summer herb guilds. Most comparisons with pre-treatment data were by inspection because of different plot sizes, metrics or measuring devices. For the most abundant species, we used the non-parametric Mann-Whitney test to compare rank abundance over time in burned plots. For ANOVA tests, the only significant block effect was greater herb cover in the west block in 2002; but there were no significant interactions with blocks. As a result, we discuss effects on treatments.

Although other upland forest sites in the Chicago region may respond in similar ways, our use of replicate samples within a single study site limits statistical inference to that area. To infer that our results would apply to other sites with independent fire treatments would be pseudo-replication (Hulbert 1984). This necessity is often difficult to overcome in long-term studies such as ours because of lack of initial planning or availability of a fully replicated design. It is also a common situation in fire ecology studies because of the difficulty of repeatedly conducting burns in a replicated design within small areas, or due to single burn treatments (McGee et al. 1995, Luken and Shea 2000, van Mantgem et al. 2001, Taft 2003, Sutherland et al. 2003).

Results. Woody Vegetation Differences Between Burned and Unburned Treatments. In 2002, BA above 10 cm dbh was 21.7 m^2/ha in burned plots of the west block and between 28.5 and 35.4 m^2/ha elsewhere (Appendix). Basal area was 23% higher in the burned unit than in the unburned unit of the east block, but was 39% higher in the unburned unit of the west block. *Quercus alba, Q. macrocapa, Q. rubra, Fraxinus* spp. and *Tilia americana* accounted for > 70% of the BA in both burned and unburned forest. However, *Q. macrocarpa* was absent from the unburned section of the west block, where *Prunus serotina* Ehrh. and *Ostrya virginiana* (Mill.) K. Coch had 20% of the BA. Stem

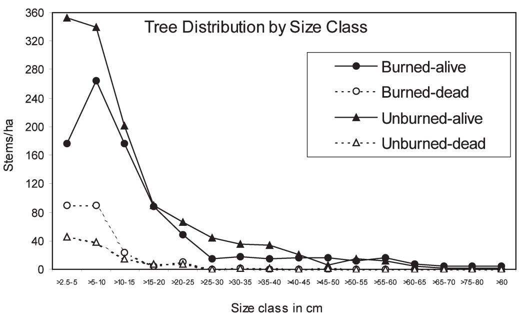

Fig. 1. Size class distribution of dead and alive trees in 2002 in burned and unburned plots in the East Woods of The Morton Arboretum.

densities exceeded 1000/ha in the unburned units of both blocks, and were 60% higher than in burned units. In burned plots, *T. americana, Ulmus americana, Fraxinus* spp. and *O. virginiana* had 65% of the stems in the east block and 47% of the stems in the west block, where *Prunus serotina* had an additional 20% of the stems. In unburned forest, *Acer saccharum, O. virginiana*, and *T. americana* accounted for 80% of the stems in the east block and 60% of the stems in the west block, where *P. serotina* accounted for an additional 10% of the stems.

Burned and unburned plots had negative exponential size-class distributions, with greater stem densities in smaller classes (Fig. 1). In the two smallest size classes, burned plots had 100% more dead stems and about 50% fewer live stems than did unburned plots. In mid size classes, unburned plots also had more live stems than burned plots, but fewer dead stems were present.

Change in Woody Understory Vegetation. In 1988, shrub and sapling densities in the pre-treatment burn plots reached almost 7000 stems/ha in the < 2.5 cm size class, 3,500 stems/ha in the ≥ 2.5–5 cm sapling size class and 460 stems/ha in the > 5–10 cm sapling size class (Table 1). Of the 24 species present, four aliens accounted for 42% of all stems in these size classes. The native shrubs *Prunus virginiana* and *Ribes missouriense* Nutt., as well as the alien *Rhamnus cathartica*, dominated the shrub layer. Four other native species and the alien shrubs *Lonicera maackii* (Rupr.) Maxim. and *Viburnum opulus* L. had intermediate stem densities. *Rhamnus cathartica* and *L. maackii* dominated the ≥ 2.5–5.0 cm size class while the native subcanopy tree *Ostrya virginiana*

Table 1. Pre-burn (1986) and post-burn (2002) woody species stem densities per ha in small size classes in annually burned plots of the East Woods of The Morton Arboretum. Stems < 2.5 cm are > 1 m high. Habit: SCT = sub-canopy tree species, CT = canopy tree species, SL = shrub layer species. Asterisks (*) indicate alien species. Ranked by overall abundance.

Habit	Species	< 2.5 cm		≥ 2.5–5 cm		> 5–10 cm	
		1986	2002	1986	2002	1986	2002
SCT*	*Rhamnus cathartica*	1200	42	1680	20	40	54
SL	*Prunus virginiana*	1400	0	0	0	0	0
CT	*Tilia americana*	500	42	260	18	120	88
SL*	*Lonicera mackii*	450	0	780	4	0	2
CT	*Ostrya virginiana*	450	0	420	20	140	52
SL	*Ribes missouriense*	900	0	0	0	0	0
SL	*Cornus racemosa*	500	0	0	0	0	0
CT	*Fraxinus* sp.	450	0	20	0	20	4
SL*	*Viburnum opulus*	400	0	0	0	0	0
CT	*Prunus serotina*	200	0	100	0	40	8
SCT	*Crataegus*	50	0	80	0	60	0
CT	*Ulmus* sp.	150	83	80	38	20	60
SL	*Viburnum dentatum*	150	0	0	0	0	0
CT	*Acer saccharum*	0	0	60	4	20	12
CT	*Carya cordiformis*	100	0	0	0	0	2
SL	*Viburnum lentago*	50	0	0	0	0	0
CT	*Carya ovata*	0	0	20	0	0	0
SL*	*Euonymus* sp.	0	0	0	0	0	2
SCT	*Carpinus carolinaina*	0	0	0	4	0	0
	Total stems	6950	167	3500	108	460	284

and the canopy tree *Tilia americana* were dominant in the > 5–10 cm size class.

By 2002, woody stem numbers in burned plots had had been reduced by 97% in the two smallest size classes, but only by 38% in the > 5–10 cm size class (Table 1). Changes in the smallest size class included loss of all native shrubs and sub-canopy trees, minor persistence of *Rhamnus cathartica* and *Tilia americana*, and a moderate decline of *Ulmus* species. In comparison, shrub layer stem density in the unburned plots was 4,400 stems/ha in 2002, including four native shrubs with *Prunus virginiana* as the most abundant species. Most of the dominant species also declined in the ≥ 2.5–5 cm size class. In the > 5–10 cm size class, dominance shifted towards *T. americana*, with secondary abundance of *Ostrya virginiana* and *Ulmus* species. *R. cathartica* continued to persist at intermediate stem numbers in both sapling size classes.

CHANGE IN GROUND LAYER STRUCTURE AND COMPOSITION. Fifty-five ground layer species had been sampled by 1988, with a 58.2% Jaccard coefficient of similarity between the pre-treatment burn and unburn plots and an equal number of species sampled in either treatment area. This vegetation was dominated by native herbs, which represented about 60% relative frequency in both burn and unburn plots (Fig. 2). Alien herbs, primarily *Alliaria petiolata*, had < 5% relative frequency in the burn plots and were less important in unburn plots. Relative frequency of woody vegetation was about 35% in both burn and unburn plots, with the alien shrubs *Rhamnus cathartica* and *Viburnum opulus* most abundant in burn plots. Relative frequency of graminoid species was < 1% in burn plots and < 3% in unburn plots. Among dominant herbs, *Circaea lutetiana* L. var. *canadensis* ($Z = -2.3425$, $P = 0.019$) and *Arisaema tryphyllum* (L.) Schott ($Z = -2.083$, $P = 0.037$), had greater cover in burn plots. The herbs *Dentaria laciniata* Willd. ($Z = 4.147$, $P < 0.001$) and *Geranium maculatum* L. ($Z = 3.149$, $P = 0.002$), had greater cover in unburn plots (Table 2).

In 2002, 77 ground layer species were sampled, with 36.4% similarity between burned and unburned plots and 10 additional species sampled in the burned plots. The burned and unburned plots differed substantially in structure in 2002. Herbs had 85% relative frequency in burned plots, but below 60% in unburned plots (Fig. 2). Relative frequency of woody vegetation dropped to < 10% in burned plots but remained at its pretreatment level in unburned plots. Graminoid vegetation remained infrequent in 2002, but shifted toward greater abundance in burned

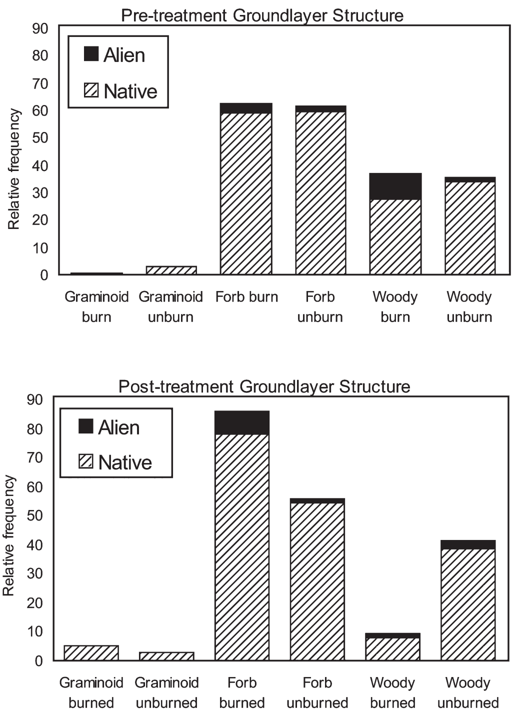

FIG. 2. Pre-treatment (upper) and post-treatment (lower) groundlayer structure of native and alien graminoid, forb, and woody vegetation in burned and unburned plots of the East Woods of The Morton Arboretum.

plots. In burned plots, significant temporal declines in rank cover occurred for *Parthenocissus* spp. ($Z = -4.015$, $P < 0.001$) and *Arisaema triphyllum* ($Z = 2.369$, $P = 0.018$). Species with increased rank cover in burned plots included *Alliaria petiolata* ($Z = 5.133$, $P < 0.001$), *Floerkia proserpinacoides* Willd. ($Z = 2.969$, $P = 0.003$), *Helianthus strumosus* L. ($Z = 2.114$, $P = 0.034$), and *Impatiens* spp. ($Z = 6.095$, $P < 0.001$). As in 1988, *Dentaria laciniata* ($Z = -3.813$, $P < 0.001$) and *Geranium maculatum* ($Z = -2.195$, $P = 0.030$), as well as *Parthenocissus* spp. ($Z = -4.066$, $P = 0.001$), had greater cover in unburned plots (Table 3).

DIFFERENCES BETWEEN GROUND LAYER VEGETATION GUILDS. Based on mean % cover, spring herbs were the dominant guild at the onset of annual burning (Fig. 3). Summer herbs and woody vegetation had less cover, with no differences between pre-treatment burn and unburn plots. In 2002, vegetation guilds differed significantly between burn and unburn treatments (Fig. 3). Burned plots had greater mean cover of summer herbs and much less woody cover. Spring herbs had similar cover in burned and unburned plots. Plot species richness was significantly correlated with plot cover in 1988 ($r = 0.557$, $P < 0.001$) and in 2002 ($r = 0.56$, $P < 0.001$), and had similar responses by guild to burn and unburn treatments (Fig. 3). Prior to burning, mean species richness was higher for spring herbs than for summer herbs in burned and unburned plots. In 2002, these guilds differed significantly between treatments, with greater mean plot richness for summer herbs in burned plots and similar richness of spring herbs in burned and unburned plots. Mean plot richness of woody species was greatest in unburned plots. In 2002, total native species richness was highest in burned plots, averaging 10.83 (± 0.59 S.E.) species/m^2.

CHANGE IN CANOPY COVER. Canopy light penetration averaged < 4% of full sun from 1986–1988, with no significant differences between pre-treatment burn vs. unburn plots over this time period (Fig. 4). In 2002, light penetration remained low in unburned stands, with about 5% canopy openness. However,% canopy openness averaged 12% in burned plots in 2002, and was significantly higher compared to unburned plots (Fig. 4).

In 2002, percent canopy openness had a significant positive linear relationship with both cover and plot species richness of summer herbs, but not with spring herb cover or richness (Fig. 5). Percent canopy cover explained about one-third of the variation in summer herb cover and richness.

Discussion. EFFECTS ON WOODY VEGETATION COMPOSITION AND CANOPY STRUCTURE. Our data indicate that long-term annual low-intensity burns substantially reduced smaller size classes of woody vegetation while increasing canopy openness by about seven%. In our study, woody ground layer vegetation also was reduced below the camera height, which would have allowed an additional unmeasured increase in available light reaching the forest floor. Similar studies of shorter duration have reported re-sprouting of most woody species top-killed by fire, leaving potential for rapid reversion to pre-burn conditions without repeated fire (Kline and McClintock 1994, Schwartz and Heim 1996, Luken and Shea 2000, Franklin et al. 2003, Chiang et al. 2005).

Table 2. Mean (± S.E.) percent cover and relative cover of dominant groundlayer plants in pre-treatment (1986–88) burn and unburn plots in the East Woods of the Morton Arboretum. Guilds: G = graminoid, SP = spring herb, SU = summer herb, W = woody. Asterisks (*) indicate alien species. Ranked by average relative cover.

		Burned			Unburned		
Guild	Species	Mean	S.E.	Rel. Cov.	Mean	S.E.	Rel. Cov.
SP	*Erythronium albidum*	23.63	4.23	28.34	16.72	3.74	20.34
SU	*Smilacina racemosa*	11.03	2.91	13.23	5.31	1.29	6.45
W	*Pathenocissus* sp.	6.55	1.58	7.86	9.44	1.54	11.49
SP	*Geranium maculatum*	0.88	0.62	1.05	6.11	1.58	7.43
SU	*Circaea lutetiana*	4.83	1.29	5.79	2.08	1.09	2.53
SP	*Allium canadense*	4.20	1.30	5.04	1.94	0.85	2.36
W	*Fraxinus* sp.	3.30	1.49	3.96	2.64	1.06	3.21
W	*Lonicera prolifera*	0.68	0.63	0.81	3.61	1.82	4.39
W*	*Rhamnus cathartica*	2.70	1.32	3.24	1.53	0.91	1.86
SP	*Dentaria laciniata*	0.13	0.13	0.15	3.78	0.96	4.59
W*	*Viburnum opulus*	3.75	1.85	4.50	0	0	0
W	*Cornus racemosa*	1.20	0.58	1.44	2.50	1.17	3.04
SU*	*Alliaria petiolata*	2.45	1.21	2.94	0.92	0.58	1.11
W	*Viburnum dentatum*	1.75	1.33	2.10	1.25	0.88	1.52
W	*Vitis riparia*	1.38	1.25	1.65	1.53	0.99	1.86
SP	*Anemonella thalictroides*	0	0	0	2.81	1.27	3.41
SP	*Arisaema tryphyllum*	2.25	0.97	2.70	0.58	0.56	0.71
SP	*Anemone quinquefolia*	0.90	0.76	1.08	1.28	0.60	1.55
SP	*Trillium recurvatum*	1.68	0.86	2.01	0.42	0.42	0.51
SP	*Floerkea proserpinacoides*	0.13	0.13	0.15	1.81	1.26	2.20
G	*Carex pennsylvanica*	0	0	0	1.89	1.01	2.30
SU	*Prenanthes alba*	0.25	0.25	0.30	1.56	0.67	1.89
W	*Rhus radicans*	0.05	0.05	0.06	1.75	0.77	2.13
W	*Prunus virginiana*	0.50	0.35	0.60	1.28	0.70	1.55
SP	*Allium tricoccum*	0.60	0.41	0.72	0.81	0.38	0.98
W*	*Lonicara maackii*	1.30	0.87	1.56	0	0	0
SP	*Caulophyllum thalictroides*	0.95	0.77	1.14	0.00	0.00	0.00
W	*Tilia americana*	0	0	0	0.83	0.83	1.01
W	*Prunus serotina*	0	0	0	0.83	0.51	1.01
W	*Ulmus americana*	0.75	0.75	0.90	0	0	0

As vines, shrubs and smaller saplings were essentially eliminated in our study, long-term burning appears effective in preventing re-sprouting as well as reducing canopy cover. However, as in short-term studies, ground layer fires were much less effective in reducing densities of stems > 5–10 cm dbh. This diameter class appears to represent a threshold beyond which greater canopy openness may be difficult to achieve without an even greater time period of burning, supplementary thinning or greater fire intensities (Franklin et al. 2003, Peterson and Reich 2001, Chiang et al. 2005, Albrecht and McCarthy 2006). Our study also indicates that alien shrubs may be reduced or eliminated by repeated burning, as they occur in smaller size classes. However, small numbers of *Rhamnus cathartica* persisted in all shrub and sapling size classes, and may constitute a source of propagules for re-invasion unless eliminated by other means.

EFFECTS ON HERBACEOUS VEGETATION. The significant shift in ground layer vegetation guild structure toward greater abundance of summer herbs without decline of spring herbs suggests that repeated burning can increase forest ground layer diversity in a predictable manner. The positive relationship of canopy light levels with summer herb cover and richness suggests an indirect fire effect on guild structure through an increase of canopy openness from about 5% to 12%. However, other factors may be important, as percent canopy cover explained only about one-third of the variation in summer herb cover and richness. Nonetheless, Lorimer et al. (1994) found that removal of understory trees in a Wisconsin forest resulted in a drop from 95% to 87% canopy cover, which enhanced oak regeneration. This effect on woody vegetation also suggests that an increase of < 10% light penetration

Table 3. Mean (+S.E.) percent cover and relative cover of dominant groundlayer plants in post-treatment (2002) burned and unburned plots in the East Woods of the Morton Arboretum. Guilds: G = graminoid, SP = spring herb, SU = summer herb, W = woody. Asterisks (*) indicate alien species. Ranked by average relative cover.

		Burn			Unburn		
Guild	Species	Mean	S.E.	Rel. Cov.	Mean	S.E.	Rel. Cov.
SP	*Erythronium albidum*	12.97	2.5	18.36	6.27	1.88	16.28
SP	*Geranium maculatum*	1.4	1.01	1.98	7.93	2.91	20.61
SU	**Alliaria petiolata*	9.5	2.65	13.45	0.1	0.07	0.26
W	*Parthenocissus quinquefolia*	0.1	0.06	0.14	4.83	2.06	12.55
SU	*Helianthus strumosus*	8.5	4.51	12.03	0	0	0
SU	*Impatiens* sp.	7.1	1.38	10.05	0.07	0.05	0.17
SP	*Floerkia prosopernoides*	6.47	3.3	9.16	0	0	0
SU	*Smilacina racemosa*	2.57	0.84	3.63	1.33	0.56	3.46
W*	*Euonymus europea*	0	0	0	2.33	2.33	6.06
SP	*Arisaema tryphyllum*	1.4	0.39	1.98	1.5	0.5	3.9
SP	*Allium canadense*	1.6	0.33	2.27	1.37	0.61	3.55
SP	*Dentaria laciniata*	0.07	0.07	0.09	1.93	0.6	5.02
W	*Prunus virginiana*	0	0	0	1.37	0.75	3.55
W	*Cornus racemosa*	0	0	0	1.33	0.71	3.46
SU	*Polygonatum canaliculatum*	1.6	1.17	2.27	0.43	0.34	1.13
G	*Carex hirtifolia*	1.6	0.81	2.27	0.33	0.33	0.87
SU	*Geum laciniatum*	1.93	0.48	2.74	0.13	0.1	0.35
SU	*Circaea lutetiana*	1.07	0.29	1.51	0.6	0.18	1.56
SU	*Tovara virginica*	1.8	0.45	2.55	0.1	0.06	0.26
W	*Fraxinus* sp.	0	0	0	1.07	0.35	2.77
SP	*Trillium recurvatum*	1.1	0.83	1.56	0.4	0.18	1.04
SP	*Anemonella thalictroides*	0.3	0.19	0.42	0.7	0.24	1.82
SU	*Hackelia virginiana*	1.17	0.83	1.65	0.1	0.06	0.26
W	*Acer saccharum*	0	0	0	0.73	0.67	1.9
W	*Crataegus* sp.	0.37	0.33	0.52	0.4	0.22	1.04
SU	*Eupatorium rugosum*	1.07	0.42	1.51	0	0	0
W	*Rubus occidentalis*	0.87	0.53	1.23	0	0	0
SP	*Podophyllum peltatum*	0	0	0	0.4	0.33	1.04
SU	*Aster shortii*	0.73	0.28	1.04	0	0	0
SP	*Claytonia virginica*	0.03	0.03	0.05	0.37	0.18	0.95

at relatively high levels of canopy cover can positively affect light-dependent understory vegetation.

An increase in cover alone might not indicate a long-lasting effect on species abundance if forest herbs are light flexible (Collins et al. 1985). However, the corresponding changes in both species richness and cover indicate that this effect represents an actual increase in species abundance in our study. In comparison, in a study that did not involve fire, Moore and Vankat (1986) linked larger gaps to greater cover of summer herbs but did not find an increase in species richness. We have no data to indicate other indirect effects. For example, removal of leaf litter by fire may have facilitated flowering, seedling establishment, and spread of summer herbs.

Our data provide partial support for processes implied in the forest disturbance model of Roberts (2004), in which low-intensity, or cool, fires decrease sub-canopy cover and shift competition from the shrub and sapling layer to the herbaceous ground layer. Elimination of the shrub and small sapling layer appears to have reduced light competition from this strata, allowing an increase in summer herbs. But, we found no strong evidence for competitive exclusion of spring herbs due to increasing abundance of summer herbs. For example, the most abundant spring herb, *Erythronium albidum* Nutt., co-occurs with *Helianthus strumosus*, which reaches > 1 m in height and had the greatest cover among summer herbs. *Erythronium albidum* is rhizomatous and clonal, and might be strongly competitive. However, its eastern congener *E. americanum* Ker Gawl., is limited by competition from other species as shown by removal experiments (Hughes 1992).

Our data support findings of others that burning does not reduce or eliminate *Alliaria petiolata* (Wilhelm and Masters 1994, Schwartz and Heim 1996, Luken and Shea

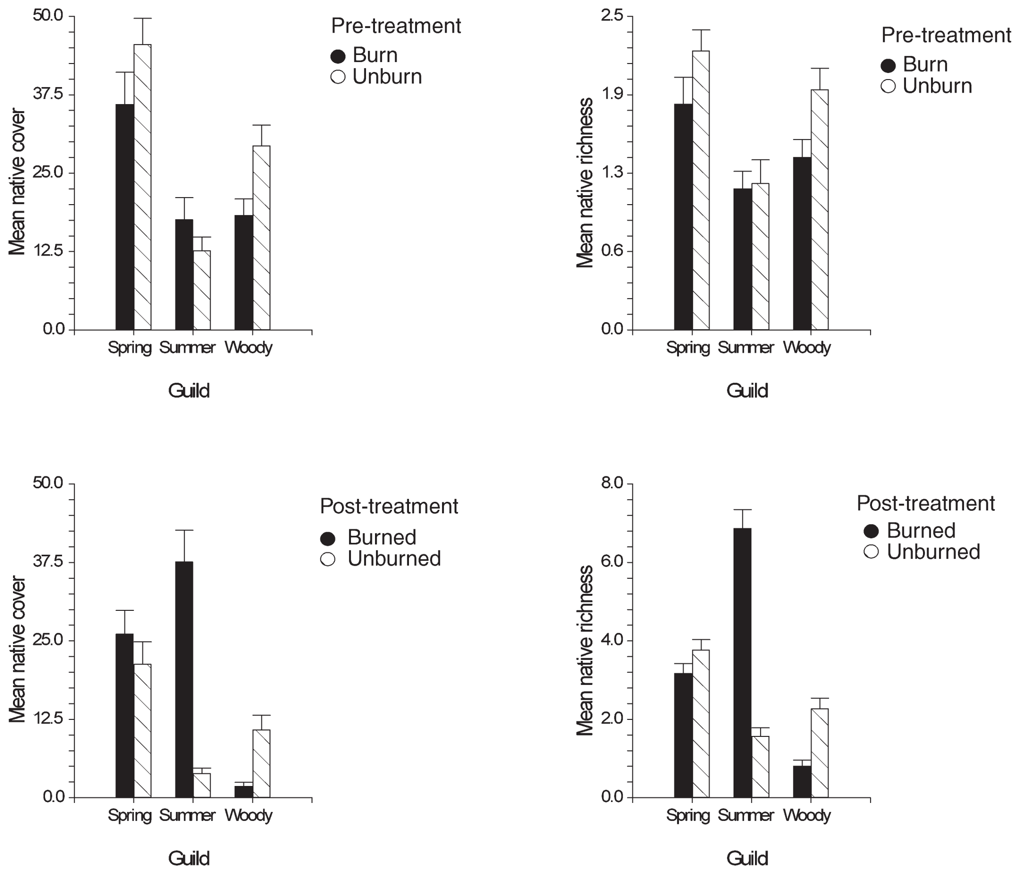

FIG. 3. Pre- and post-treatment mean% cover and plot richness of native ground layer vegetation guilds in the East Woods of the Morton Arboretum. Pre-treatment cover: guild ($F = 9.62$, $P < 0.001$), treatment ($F = 3.48$, $P = 0.064$), guild × treatment ($F = 0.98$, $P = 0.377$), block ($F = 0.39$, $P = 0.535$). Pre-treatment richness: guild ($F = 11.05$, $P < 0.001$), treatment ($F = 7.66$, $P = 0.006$), guild × treatment ($F = 0.97$, $P = 0.380$), block ($F = 0.78$, $P = 0.3785$). Post-treatment cover: guild ($F = 19.91$, $P < 0.001$), treatment ($F = 6.63$, $P = 0.011$), guild × treatment ($F = 32.69$, $P < 0.001$), block ($F = 5.94$, $P = 0.016$). Post-treatment richness: guild ($F = 45.64$, $P < 0.001$), treatment ($F = 20.74$, $P < 0.001$), guild × treatment ($F = 80.71$, $P < 0.001$), block ($F = 2.70$, $P = 0.102$). All other interactions are not significant. Bars are standard errors.

2000, Bowles et al. 2000). In our study area, garlic mustard plants survived fire in unburned microsites, and burning apparently exposed bare ground that supported seedling establishment from these refuges. The location of our study sites within a larger forested area infested with *Alliaria petiolata* also likely facilitated its re-invasion into burned plots.

PROJECTING STAND CHANGES. The impact of continued annual burning on the future woody composition and structure of these stands is somewhat uncertain. Shrub and vine species appear to be essentially eliminated. Larger saplings and midstory trees probably will continue to decrease in abundance and shift in dominance. The current dominance of *Tilia americana* may be temporary as it readily succumbs to both canker and to root disease, which appear to be increasing in larger saplings in burned plots (Jacobs et al. 2004). Although *Acer saccharum* continues to persist, its stem numbers also have declined. *Rhamnus cathartica* may persist in low numbers from root sprouts and fire-resistance of larger stems. *Ulmus americana* and *Ulmus rubra* are unlikely to enter larger classes as Dutch elm disease limits their growth. The loss of *Ostrya virginiana* regeneration and decline of larger individuals suggests that it is fire-intolerant and may eventually disappear from burned plots. We found little evidence for regeneration of *Quercus* species during this study. As a result, we cannot assess fire effects on

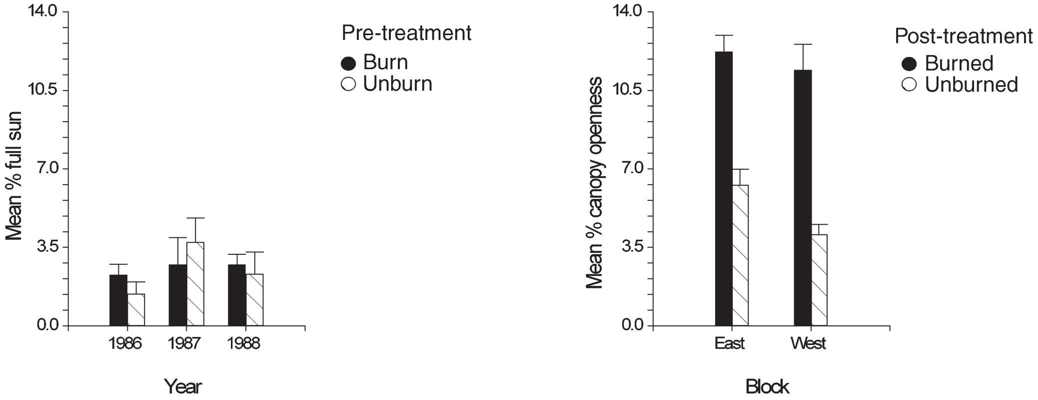

FIG. 4. Pre- and post-treatment canopy light conditions in the East Woods of the Morton Arboretum. Pretreatment: year: $F = 0.99$, $P = 0.3923$; treatment: $F = 0.05$, $P = 0.8258$; year $\times$ treatment: $F = 1.53$, $P = 0.2434$). Post-treatment: treatment ($F = 65.88$, $P < 0.0001$), block ($F = 3.41$, $P = 0.07045$), treatment $\times$ block ($F = 0.73$, $P = 0.3975$). Pre-treatment data are in% of full sun in foot-candles, post-treatment are% canopy openness. Bars are standard errors.

oaks, nor project whether they may eventually enter the canopy and help maintain oak dominance.

Further reduction of canopy cover that might facilitate additional changes in ground layer diversity may be limited by fire resistance of larger saplings and midstory trees (e.g., Franklin et al. 2003). Modeling suggests that major fire disturbance may be needed for more open canopies (Will-Wolf and Roberts 1993).

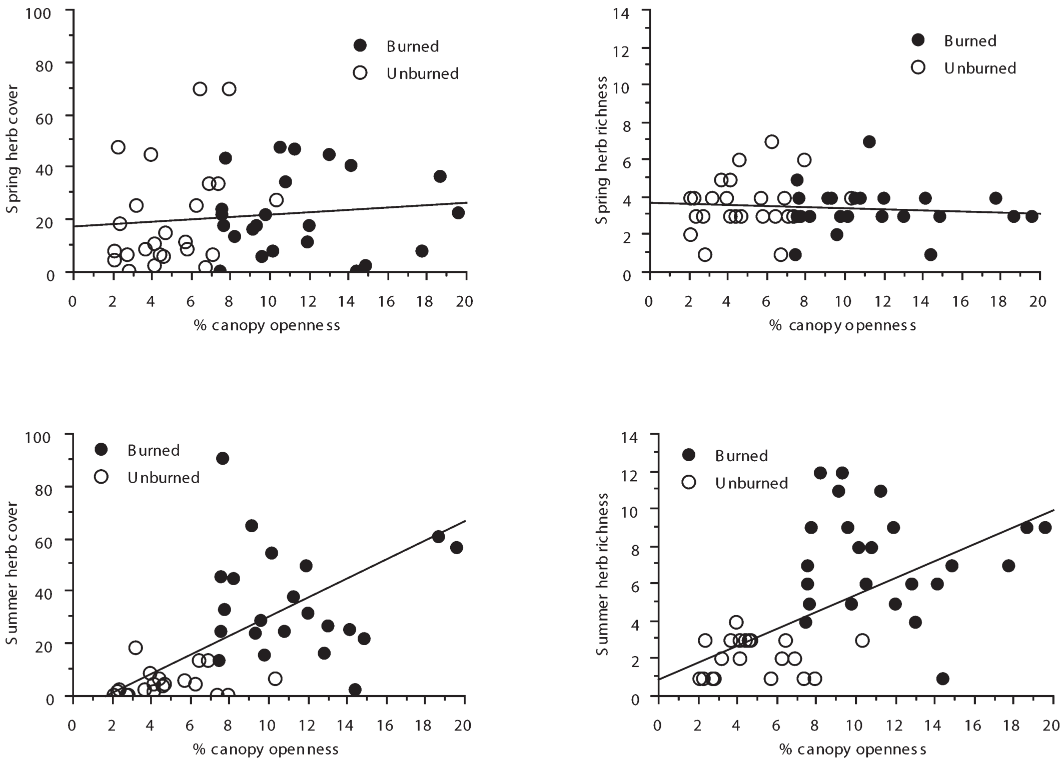

FIG. 5. Linear relationship of percent canopy openness with cover and richness of spring herb and summer herb vegetation guilds in the East Woods of The Morton Arboretum. Spring herbs: cover ($r^2 = 0.0115$, $P = 0.4672$), richness ($r^2 = 0.0102$, $P = 0.4952$). Summer herbs: cover ($r^2 = 0.3405$, $P < 0.0001$), richness ($r^2 = 0.3305$, $P < 0.0001$).

As canopy openness exceeds about 20%, species composition would be expected to shift toward woodland and savanna species, with increasing competition from grasses (Bray 1958, Bowles and McBride 1998). Although some forest herbs would persist in savanna conditions (Bray 1957, Rogers 1982), increasing plant species richness would depend upon the local species pool and dispersal abilities of potential colonizers (Franklin et al. 2003). There are severe limitations to this occurring in our area due to past elimination of most savanna and prairie vegetation. As a result, projections are difficult. However, in a Tennessee oak forest, continued burning promoted a shift toward increasing graminoid dominance and fluctuations among herbs after 27 years of repeated fire (DeSelm and Clebsch 1991). DeSelm et al. (1991) projected conversion of this site to grassland after an additional 27 annual burns.

Conclusions. Our data suggest that long-term annual burning can cause significant shifts in the guild structure and composition of oak forest ground layer vegetation through removal of shrubs and saplings that intercept canopy light. This contrasts with short-term studies, which have not detected significant ground layer changes, or permanent reduction of woody vegetation. Work is needed to understand how fire affects herbaceous plant seedling establishment in this process. Our data partially support a ground layer disturbance model that predicts a shift in competition from woody vegetation to ground layer herbaceous vegetation. Our findings do not suggest that competitive exclusion is occurring among herbaceous plants as the shifts we observed were caused by an increase in light-sensitive summer herbs not coupled with decreases in spring herbs. Thus, only an effect of decreased competition for light through shrub layer removal is implied.

Our data also indicate that repeated burning of forest ground layer vegetation can increase ground layer species richness to > 10 species/m^2, exceeding that found in Chicago region old-growth forests (Bowles et al. 2000). Further canopy cover reduction and increased ground layer diversity may be limited by larger fire resistant saplings and canopy trees, as well as by a limited local species pool of savanna and prairie species.

Despite the overall increase in ground layer species richness in our study, there are trade-offs to this gain. Old-growth Chicago region oak forests are currently multi-layered and may contain ten or more native shrubs (Bowles et al. 2000). Our data show that repeated burning essentially eliminated these species and their strata, and also reduced abundance of subcanopy trees. Loss of the forest shrub layer could have cascading effects on other organisms dependent upon this component of vegetation structure. For example, forest shrub and sapling layers, as well as leaf litter, provide nesting and migratory habitats for forest interior birds, which decline as fire removes these habitats (Artman et al. 2001, Blake 2005). Burning of forest litter also may negatively affect litter-dwelling invertebrate organisms (Brand 2002). Both *Alliaria petiolata* and *Rhamnus cathartica* may persist with repeated burning and appear to have potential to rapidly re-colonize burned habitats unless controlled by other means.

This study relied upon a single burning frequency and low fire intensity. Further work is needed to learn whether less frequent burning at higher intensities could have similar effects on ground layer vegetation while maintaining shrub-layer species. Less frequent burning also may be required to allow build-up of fuel required for more intense fires. Because we lack benchmark information on the composition and structure of former forest ecosystems and processes operating without human disturbance, replicated experimentation and feedback will be needed to maintain and maximize biodiversity in the fragmented Chicago region forest ecosystem.

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Appendix. Density/ha (D), basal area/ha in square meters (BA) and importance values (IV) in 2002 for tree species > 10 cm dbh in burned and unburned units of east and west blocks of the East Woods of the Morton Arboretum.

	Burned						Unburned					
	East Block			West Block			East Block			West Block		
Species	D	BA	IV	D	BA	IV	D	BA	IV	D	BA	IV
Quercus rubra	24	5.7	9.9	40	5.0	15.8	44	7.0	13.8	60	12.8	20.8
Quercus alba	36	11.5	18.9	28	3.2	10.4	32	3.5	7.2	36	6.8	11.2
Fraxinus sp.	64	7.2	15.6	40	2.4	10.0	28	1.3	3.4	52	5.8	10.5
Tilia americana	196	5.4	25.5	40	2.0	9.1	364	6.7	24.9	96	1.6	6.6
Ostrya virginiana	44	0.8	5.2	124	2.0	18.3	264	2.5	13.9	416	3.7	23.8
Prunus serotina	12	0.4	1.7	96	3.8	19.4	68	1.1	4.5	120	3.2	9.9
Quercus macrocarpa	20	3.2	6.1	16	2.1	6.7	16	2.0	4.2	0	0.0	0.0
Acer saccharum	24	0.4	2.8	12	0.3	2.1	484	3.6	23.7	152	0.7	7.8
Ulmus americana	88	1.7	10.5	8	0.2	1.3	16	0.3	1.1	80	0.6	4.5
Ulmus rubra	20	0.5	2.6	8	0.1	1.2	12	0.0	0.5	12	0.1	0.6
Carya cordiformis	8	0.4	1.3	4	0.0	0.5	8	0.3	0.8	0	0.0	0.0
Rhamnus cathartica	0	0.0	0.0	32	0.5	4.6	16	0.0	0.6	36	0.1	1.7
Crataegus sp.	0	0.0	0.0	0	0.0	0.0	16	0.0	0.6	40	0.1	1.9
Cercis canadensis	0	0.0	0.0	4	0.1	0.6	0	0.0	0.0	0	0.0	0.0
Populus deltoides	0	0.0	0.0	0	0.0	0.0	4	0.0	0.2	0	0.0	0.0
Carpinus caroliniana	0	0.0	0.0	0	0.0	0.0	8	0.0	0.3	8	0.0	0.4
Lonicera maackii	0	0.0	0.0	0	0.0	0.0	12	0.0	0.5	8	0.0	0.4
Total	536	37.1	100.0	452	21.7	100.0	1392	28.5	100.0	1116	35.4	100.0