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Short-term and Long-term Effects of Burning on Oak Savanna Arthropods

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ABSTRACT.—We investigated the effects of prescribed burning on the composition, abundance, species richness and diversity of oak savanna arthropod communities in a replicated, large-scale, 30-y experiment. We employed four sampling methods over 3 y and caught 11,215 arthropods of 551 species. Species had varied and often negatively correlated short vs. long-term responses to burning. In the years savannas were burned, species richness and abundance of arthropods, especially Homoptera and Lepidoptera, were reduced and species compositions were sometimes more similar. However, despite its major effect on vegetation, frequency of burning did not affect arthropod abundance and species richness, but sometimes caused savannas to be similar in species or taxonomic order composition. The Shannon diversity index was unaffected by burning. On the whole, prescribed burns necessary to maintain grasslands and savannas do not appear to be harmful to, or to greatly impact, the arthropod fauna.

INTRODUCTION

Prescribed burning is an essential tool for preserving many plant communities, such as grasslands and savannas (Daubenmire, 1968; Hurlbert, 1969; Tester, 1989), but it has been hypothesized to modify, and perhaps harm, their arthropod communities. Fire can be a source of arthropod mortality (Gillon, 1971; Fay and Samenus, 1993) and is used to control agricultural and silvicultural pests (Bolton and Peck, 1946; Komarek, 1970; Miller, 1978). Arthropod species differ in their life histories and may be in different life stages (*i.e.*, egg, larva or nymph, adult) when a fire occurs. They also differ in their location relative to the heat of a fire and in their escape abilities and therefore their susceptibility (Gillon, 1971; Gillon, 1971a; Evans, 1984). Fire also has indirect effects on the arthropod community through changes in plant community species composition (Tester and Marshall, 1961; Lawton, 1983; Evans, 1984), reduced litter, modified soil moisture and temperature (Tester and Marshall, 1961; Bulan and Barrett, 1971; Lussenhop, 1976; Van Amburg *et al.*, 1981; Seastedt, 1984), changes in cover which alter predator hunting efficiency (Andow, 1991) and changes in food quality from altered plant growth patterns (Evans, 1971; Stein *et al.*, 1992). Arthropods vary in trophic roles (*i.e.*, detritivore, herbivore, predator or parasite) and may change roles during development from egg to adult (Borror *et al.*, 1989). For all these reasons, species responses to fire are likely to vary.

Studies of individual arthropod species have shown that some are more abundant in burned areas and others less abundant (*e.g.*, Rickard, 1970; Harris and Whitcomb, 1971; Harris and Whitcomb, 1974; Evans, 1984; Gardner and Usher, 1989; Bock and Bock, 1991). Numerous studies have shown some groups of arthropods, typically single orders, are more (*e.g.*, Tester and Marshall, 1961; Cancelado and Yonke, 1970; Hurst, 1970; Nagel, 1973; Force, 1981; Holliday, 1984; Warren *et al.*, 1987) or less abundant in burned areas (*e.g.*, Buffington, 1967; Bulan and Barrett, 1971; Seastedt, 1984; Warren *et al.*, 1987) or unaffected by fire (*e.g.*, Rice, 1932; Warren *et al.*, 1987; Anderson *et al.*, 1989; Bock and Bock, 1991). However, few studies have looked at the long-term effects of burning, employed multiple sampling methods, or measured abundance and diversity in multiple taxonomic orders.

To determine the effects of burning on arthropod community composition, diversity and abundance, we sampled arthropods using four sampling methods over 3 yr in a large replicated burning experiment begun in 1964 (Irving, 1970). We sought to answer five questions: (1) How do individual species respond to frequency of burning and to burning in the sampling year? (2) Are savannas with similar burn histories more similar to each other in their arthropod species compositions than to savannas with different burn histories? (3) Does burning in the sampling year affect arthropod abundance, species richness and diversity (H′) in that year? (4) Has the frequency of burning over approximately 30 yr caused changes in the abundance, species richness and diversity (H′) of oak savanna arthropod communities? (5) Which taxonomic orders are especially sensitive to short and long-term effects of burning?

METHODS

Sampling.—Cedar Creek Natural History Area is located 50 km N of Minneapolis, Minnesota, on the Anoka sandplain, and was probably originally a mosaic of prairie, oak savanna (*Quercus macrocarpa, Q. ellipsoidalis*) and oak woodland maintained by periodic wildfires of human or lightning origin (Tilman, 1987; Tester, 1989). Fire suppression and cultivation converted most of the oak savanna into deciduous forest and croplands. In 1964, an experiment was begun to investigate restoration of oak savanna from oak forest by prescribed burning (Irving, 1970). Plots ranging from 2.6–27.5 ha have been subjected to moderate-intensity, spring, head-fires at different frequencies, ranging from never burned to burned 9 out of 10 yr, at a time of year fires likely occurred historically (Hurlbert, 1973), late April to early May (for details on burning procedure *see* Irving, 1970; White, 1983). Sampling of arthropods was done in permanent vegetation sampling areas within the savannas which were used by Tester (1989) and Faber-Langendoen and Tester (1993).

In 1992 and 1993, we sampled 10 savannas with sweep nets (Table 1). In 1992, they were sampled semimonthly from the beginning of June to the end of August (five samples for each savanna). In 1993, they were sampled semimonthly from late May to late June (three samples for each savanna). Sampling was done during midday when the vegetation was dry. Each sample consisted of all the arthropods caught in 100 standard swings of a 38-cm diam muslin net swung with each step while walking. The same person (JH) collected all the samples which should increase comparability between samples. Sweep net sampling is a good measure of relative abundance and relative species richness for all but the smallest vegetation-dwelling arthropods for areas with similar vegetation structure (Turnbull and Nicholls, 1966; Evans *et al.*, 1983). Our study areas were all sparsely vegetated, with at most 66% vegetation cover, and had statistically indistinguishable amounts of shrub and tree cover (Tester, 1989; D. Peterson, pers comm.) and sampling efficiencies should have been similar.

In 1992, four of the 10 sweep-sampled savannas were also sampled with pitfall traps (Table 1). Pitfall traps were 950-cc plastic containers with drainage pin holes in the bottom and lids with 2.5-cm holes. In late May, each savanna had four traps buried with their rims flush with the ground and lid holes covered. They were open from 10 July until 10 October and all dead and living arthropods were removed every 10 days. Pitfall traps sample only motile ground-dwelling arthropods (Southwood, 1978) but are a good companion method to sweep net sampling since they intensively sample a different part of the arthropod community.

We sampled 11 savannas using visual surveys on 3 August 1994 to estimate Lepidoptera

TABLE 1.—Total abundance and species richness for each savanna and sampling method

Savanna	Burn freq	Sweep 1992		Sweep 1993		Pitfall trap		Light trap		Visual
		AB	SR	AB	SR	AB	SR	AB	SR	LEP
109[a]	0	—	—	—	—	—	—	37	23	76
209[a]	0	—	—	—	—	—	—	12	8	23
14	0	1099	138	224	53	—	—	—	—	—
13[b]	0.03	731	126	125	42	—	—	—	—	—
115	0.1	548	105	206	43	—	—	—	—	—
113[a]	0.1	—	—	—	—	—	—	415	35	12
111[a]	0.1	—	—	—	—	—	—	24	14	30
107[a]	0.33	—	—	—	—	—	—	62	18	121
108[a]	0.33	693	115	97	32	—	—	89	31	20
116	0.4	656	93	120	33	—	—	—	—	—
101[a]	0.5	1107	42	116	22	55	5	33	15	47
105[a]	0.5	1070	114	161	34	228	14	63	24	8
106[a]	0.67	1050	166	130	38	—	—	37	19	9
103[a]	0.9	771	94	113	34	77	9	40	14	14
104[a]	0.9	840	117	87	31	70	6	29	10	10

Savanna number: [a] part of the burn experiment described in the text which was begun in 1964; [b] burned once by a wildfire in 1988. Burn freq is the frequency of burning, AB and SR are total arthropod abundance and species richness; LEP is the total number of Lepidoptera. Negative signs mean that the savanna was not sampled by the method

abundances but not individual species abundances (Table 1). Three observers slowly and simultaneously walked parallel 50-m transects, 5 m apart and counted each lepidopteran seen. A lepidopteran was counted as only one observation even if it could be seen by more than one observer. Lepidoptera are thought to be especially sensitive to burning if fires occur when they are present as eggs, larvae or pupae (Warren *et al.*, 1987). Furthermore, the majority of Minnesota and federally protected arthropod species are Lepidoptera (USFWS, 1980; Coffin and Pfannmuller, 1988) and this sampling method enhanced our ability to detect effects of burning on this important group.

The 11 visually surveyed savannas were light-trapped on the night of 3 August 1994 at sometime between 1 h after sundown and 1 h before sunrise. To control for effects of time of night of sampling, the savannas were assigned to replicate blocks and sampled in random order within blocks with one randomly chosen block sampled in the first half of the night and the other block sampled in the second half of the night. A single 10-watt UV-light trap (Bioquip model 2851A, 2851U) was taken to a previously selected location within each savanna with no nearby visual obstructions, hung 2 m off the ground and turned on for 20 min. All arthropods in the trap were collected. This method enhanced our ability to detect changes in Lepidoptera, as well as giving information about species that could have been missed by sweep net sampling or pitfall trapping.

For all sampling methods except visual surveys, specimens were manually sorted and identified to species or morphospecies within known genera or families. Coleoptera, Hemiptera, Homoptera and Orthoptera were particularly well-identified. When possible, we had appropriate outside experts re-examine questionable specimens.

Analyses.—We measured the response of each species' abundance summed over the sampling season to burning using Generalized Linear Models (GLM) regression with frequency of burning as a continuous variable and burned or not burned in the sampling year as a categorical variable. We report Bonferroni-corrected significance levels, to control for multiple comparisons. The uncorrected significance levels necessary for significant responses were 0.0001, 0.0004, 0.003 and 0.0005 for 1992 sweep samples, 1993 sweep samples, pitfall samples and light trap samples, respectively. To test whether long- and short-term responses of species to burning were independent, each species was classified into one of four possible categories based on whether the coefficient for effect of burning frequency on its abundance was positive or negative and whether it was more or less abundant in savannas burned in the sampling year, whether or not the effects were significant. Species caught by more than one sampling method or in more than 1 yr were counted as multiple observations and species which had zero response to one or both variables were excluded. A chi-square test of independence was applied to this 2 by 2 contingency table to determine if species' short- and long-term responses to burning were correlated.

In order to test for similarities of arthropod community species composition, two measures of faunal similarity were used. The Jaccard index (JI) is the proportion of the combined set of species present in either of two savannas that are present in both savannas (Southwood, 1978). It ranges from 0 to 1, with 0 meaning no species occur (*i.e.,* are present) in both savannas, and 1 meaning all species are present in both. Proportional similarity (PS) is a measure of how similar the compositions of two communities are in terms of proportional abundances of individual species and it is roughly equivalent to the proportion of the individuals of two savannas that are of shared species (Evans, 1984). It ranges from 0 to 1, with 0 meaning no individuals of the same species occur in both savannas and 1 meaning the same species make up the same proportions of the arthropod communities of both savannas. These two measures of similarity emphasize differences in rare species versus common species, respectively. Using regression, we tested whether the similarity of the arthropod species composition of pairs of savannas (JI or PS) depended on the difference in their burning frequencies (Delta-BF). Using AOV, we tested whether savannas in the same category for burned or not burned in the sampling year were more similar to each other in their arthropod species composition than to savannas in the other category. We repeated these analyses to test whether the proportional similarity of taxonomic order composition of savannas depended on the difference in their burning frequencies or whether or not they were burned in the sampling year. Using data from Tester (1989), we tested whether the similarity of plant species composition of pairs of savannas depended on the difference in their burning frequencies.

For each sampling method and year, we tested for response of total arthropod abundance, summed over the sampling season, to burning using GLM regression with frequency of burning as a continuous variable and burned or not burned in the sampling year as a categorical variable. For all but the visual survey data, we also tested for effects on overall summed species richness and Shannon's diversity index. In order to test how taxonomic orders responded to burning, we used GLM regressions to test for effects of burning frequency and of burning in the sampling year on summed abundance, species richness and diversity of the most abundant taxonomic orders and to report Bonferroni-corrected significance levels.

RESULTS

Sweep net, pitfall and light trap sampling combined caught 11,215 individuals of 534 insect species and 17 noninsect arthropod species (Table 1). The abundances of 141 families of 14 orders that represented more than 2% of the samples for any sampling method are given in Table 2. The abundances of the five most abundant species are given in Table 3. An additional 370 lepidopterans were counted in visual surveys.

TABLE 2.—Abundances of families representing more than 2% of the specimens for any sampling method. Abundance is total number of individuals of all species in the family (or families for the miscellaneous category) summed over all savannas and the sampling year

Order	Family	'92 Sweep	'93 Sweep	Pitfall	Light trap
Araneida	Araneidae	114	33	0	6
	Misc (5 families)	66	0	2	0
Coleoptera	Carabidae	0	1	17	36
	Chrysomelidae	128	58	0	0
	Helodidae	164	5	0	47
	Scarabaeidae	1	2	134	0
	Staphylinidae	5	2	0	81
	Misc (23 families)	477	56	4	30
Diptera	Anthomyiidae	262	172	0	6
	Chamaemyidae	27	29	0	0
	Chironomidae	0	0	0	43
	Chloropidae	87	1	0	83
	Culicidae	0	6	0	114
	Dolichopodidae	315	117	0	0
	Platystomatidae	345	137	0	0
	Syrphidae	100	29	0	0
	Tephritidae	191	3	0	0
	Misc (26 families)	438	111	0	27
Hemiptera	Miridae	2177	55	0	8
	Misc (10 families)	150	29	0	4
Homoptera	Aphididae	0	0	0	28
	Cicadellidae	1465	86	0	10
	Delphacidae	272	21	0	7
	Membracidae	265	23	0	0
	Misc (6 families)	132	4	0	15
Hymenoptera	Formicidae	0	0	200	3
	Misc (28 families)	316	24	0	6
Lepidoptera	Noctuidae	72	5	0	62
	Pyralidae	13	20	0	85
	Tortricidae	8	0	0	19
	Misc (4 families)	73	0	0	10
Odonata	Coenagrionidae	0	202	0	0
	Misc (2 families)	0	2	0	6
Orthoptera	Acrididae	564	138	6	2
	Gryllidae	4	0	65	0
	Tettigoniidae	264	0	0	0
	Misc (3 families)	3	0	2	0
Trichoptera	Leptoceridae	0	0	0	45
	Phryganeidae	0	0	0	146
Miscellaneous	(3 orders, 4 families)	63	8	0	5

No individual species showed significant responses of its abundance, after Bonferroni correction, to either burning frequency or burning in the sampling year. Some species were more abundant in the year of a fire such as a *Sepsis* morphospecies (Diptera: Sepsidae, mean = 2.4, P = 0.05 for 1993 sweep samples before Bonferroni correction) and others were less abundant, such as a *Herculia* morphospecies (Lepidoptera: Pyralidae, mean = 0.2,

TABLE 3.—The five most abundant species caught by each sampling method summed across savannas and sampling year. Abundance is the number of individuals caught and % is the percentage of the total sample of this species

Species	Family	Order	Abundance	%
1992 Sweep				
Lygus lineolaris	Miridae	Hemiptera	1125	13.1
Labops hirtus	Miridae	Hemiptera	709	8.3
Macrosteles fascifrons	Ciccadellidae	Homoptera	459	5.4
Rivellia morphospecies	Platystomatidae	Diptera	345	4.0
Doratura stylata	Ciccadellidae	Homoptera	196	2.3
1993 Sweep				
Nehalennia irene	Coenagrionidae	Odonata	185	13.4
Rivellia morphospecies	Platystomatidae	Diptera	137	9.9
Hylemya morphospecies	Anthomyiidae	Diptera	129	9.4
Dolichopus morphospecies	Dolichopodidae	Diptera	105	7.6
Melanoplus dawsoni	Acrididae	Orthoptera	45	3.3
Pitfall traps				
Formica obscuripes	Formicidae	Hymenoptera	200	44.4
Canthon nigrocornis	Scarabaeidae	Coleoptera	132	29.3
Gryllus pennsylvanicus	Gryllidae	Orthoptera	63	14.0
Carabus serratus	Carabidae	Coleoptera	7	1.6
Percosia obesa	Carabidae	Coleoptera	7	1.6
Light traps				
Aedes morphospecies	Culicidae	Diptera	114	13.6
Triaenodes morphospecies	Leptoceridae	Trichoptera	93	11.1
Oscinella morphospecies	Chloropidae	Diptera	83	9.9
Oecetis morphospecies	Leptoceridae	Trichoptera	68	8.1
Aleocharinae morphospecies	Staphylinidae	Coleoptera	56	6.7

$P = 0.02$ for light trap samples before Bonferroni correction) and a *Neoscona* morphospecies (Araneae: Araneidae, mean = 2.8, $P = 0.02$ for 1992 sweep samples before Bonferroni correction). Some species increased in response to burning frequency such as *Melanoplus dawsoni* (Orthoptera: Acrididae, mean = 17.5, $P = 0.05$ and mean = 4.5, $P = 0.01$ for 1992 and 1993 sweep samples, respectively, before Bonferroni correction) and *Pachyschelus laevigatus* (Coleoptera: Buprestidae, mean = 8.3, $P = 0.05$ for 1992 sweep samples before Bonferroni correction) and others decreased, such as *Doratura stylata* (Homoptera: Ciccadelidae, mean = 19.6, $P = 0.01$ for 1992 sweep samples before Bonferroni correction). Within some orders such as Hemiptera and Hymenoptera not even the most abundant species (*Lygus linolaris*, Hemiptera: Miridae, mean = 112.5 and *Dialictus pillosus*, Hymenoptera: Colletidae, mean = 4.1) showed responses as strong as $P = 0.05$ before Bonferroni correction.

The number of species responding negatively to increased burning frequency, 341, was significantly greater ($\chi^2 = 6.94$, 1 d.f., $P < 0.01$) than the number responding positively, 277, and the number of species responding negatively to burning in the sampling year, 344, was significantly greater ($\chi^2 = 15.86$, 1 d.f., $P < 0.001$) than the number of species responding positively, 274 (Table 4). Responses to the two variables were not independent ($\chi^2 =$

TABLE 4.—Numbers of species responding positively and negatively to burning frequency and burning in the sampling year

		Response to burning in sampling year		
		Positive	Negative	Totals
Response to 30 year frequency of burning				
Positive	Observed	62	215	277
	Expected	123	154	
Negative	Observed	212	129	
	Expected	151	190	341
Totals		274	344	618

Species responses to burning, as measured by GLM regression, were cross-classified depending on whether they were more or less abundant in more frequently burned savannas and whether they were more or less abundant in savannas burned in the year of sampling, regardless of significance level

98.04, 1 d.f., $P < 0.001$), but rather species responding positively to frequency of burning were more likely to respond negatively to burning in the sampling year and vice versa.

For 1992 sweep samples, savannas with more similar burning frequencies were more similar in their species composition as measured by proportional similarity (PS = 0.468 − 0.118 × Delta-BF, N = 45, $P < 0.05$), but in all other analyses they were not. Pairs of savannas in the same category for burned or not burned in the sampling year were significantly more similar to each other than to savannas in other burning categories as measured by proportional similarity for 1993 sweep samples (Same Category PS = 0.434, Different Category PS = 0.397, N = 45, $P < 0.05$) and by the Jaccard index for light trap samples (Same Category JI = 0.176, Different Category JI = 0.141, N = 55, $P < 0.05$). Savannas within the same light trap time of night sampling block were not more similar to each other than to those sampled in the other block. For 1992 sweep samples, savannas with more similar burning frequencies were significantly more similar to each other in ordinal composition (PS = 0.826 − 0.233 × Delta-BF, N = 45, $P < 0.001$) but other samples were not.

Based on data from Tester (1989), savannas with more similar burning frequencies were more similar in their plant species composition as measured by the Jaccard Index (JI = 0.418 − 0.123 × Delta-BF, N = 66, $P < 0.05$) and proportional similarity (PS = 0.698 − 0.133 × Delta-BF, N = 66, $P < 0.01$).

Savannas burned in 1992 had significantly lower total arthropod abundances (GLM t = 3.49, 7 d.f., $P < 0.05$) and species richness (GLM t = 2.83, 7 d.f., $P < 0.05$) in 1992 sweep samples than savannas not burned in 1992 (Fig. 1a, b). The six most abundant taxonomic orders (those with > 10 species: Coleoptera, Diptera, Hemiptera, Homoptera, Hymenoptera and Orthoptera) also declined in abundance and species richness with burning in 1992, although only the decline of Homoptera abundance (Fig. 1c) was significant (GLM t = 4.03, 7 d.f., $P < 0.05$). The responses of diversity (H′) of the entire arthropod community and of every abundant taxonomic order were not significant.

Abundance, species richness (Fig. 1a, b) and diversity (H′) of 1992 sweep samples did not respond significantly to burning frequency (GLM t = 0.80, 7 d.f., P = 0.45; GLM t = 0.31, 7 d.f., P = 0.77; GLM t = 1.97, 7 d.f., P = 0.09). The responses of abundance and diversity of the six most abundant taxonomic orders were not significant and only species richness of Homoptera (Fig. 1d) responded significantly (GLM t = 4.09, 7 d.f., $P < 0.05$).

Abundance, species richness and diversity (H′) of 1993 sweep samples did not respond significantly to burning frequency (GLM t = 1.29, 7 d.f., P = 0.24; GLM t = 1.15, 7 d.f., P

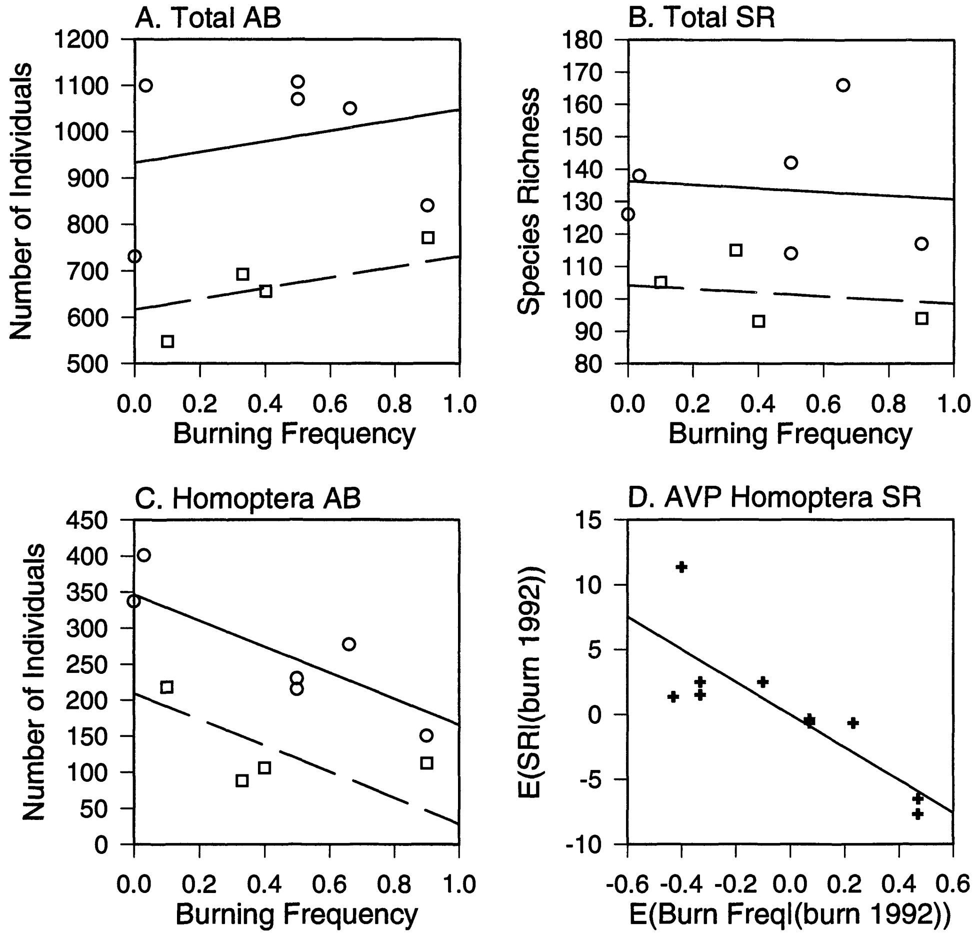

FIG. 1.—Relationships between burning history and arthropod abundance and species richness in 1992 sweep samples. A–C. Squares are savannas burned in the sampling year, circles are those which were not. Solid lines are the regression for burning frequency within savannas not burned in 1992; dashed lines are the regression for buring frequency within savannas burned in 1992. D. Added Variable Plot to show the dependence of Homoptera species richness on burning frequency, while controlling for the effect of buring in 1992

= 0.29; GLM t = 0.28, 7 d.f., P = 0.79) or burning in 1993 (GLM t = 0.04, 7 d.f., P = 0.97; GLM t = 0.08, 7 d.f., P = 0.94; GLM t = 0.59, 7 d.f., P = 0.57). There was a nonsignificant trend for higher burning frequency to reduce abundance and species richness. Of the six most abundant taxonomic orders, none responded significantly to burning frequency.

Abundance, species richness and diversity (H′) of 1992 pitfall samples did not respond significantly to burning frequency (GLM t = 0.47, 1 d.f., P = 0.72; GLM t = 0.45, 1 d.f., P = 0.73; GLM t = 0.10, 1 d.f., P = 0.94) or burning in 1992 (GLM t = 0.04, 1 d.f., P = 0.97; GLM t = 0.33, 1 d.f., P = 0.80; GLM t = 0.22, 1 d.f., P = 0.86).

Abundance, species richness (Fig. 2a, b) and diversity (H′) of 1994 light trap samples did not respond significantly to time of sampling, burning frequency (GLM t = 1.46, 8 d.f., P

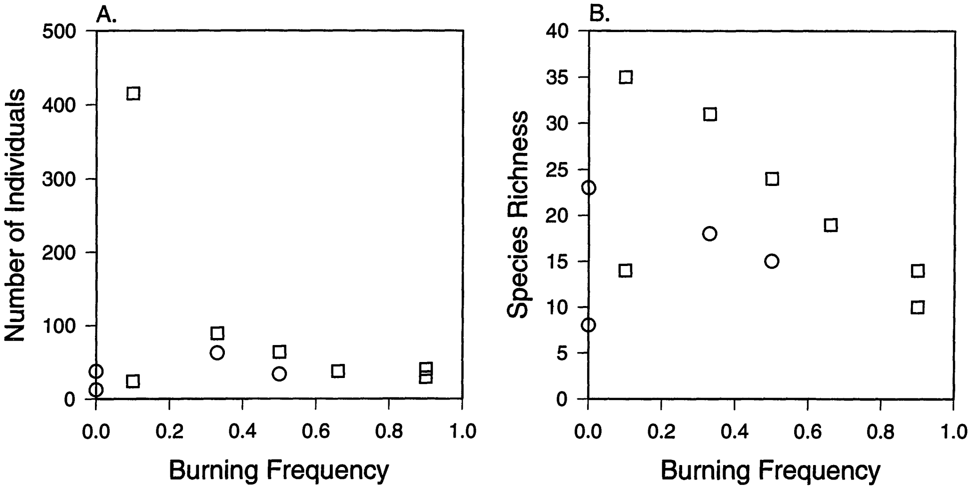

FIG. 2.—Relationships between burning history A, total arthropod abundance and B species richness in light trap samples. Squares are savannas burned in the sampling year, circles are those which were not

= 0.38; GLM t = 1.62, 8 d.f., P = 0.35; GLM t = 1.84, 8 d.f., P = 0.32) or burning in 1994 (GLM t = 1.48, 8 d.f., P = 0.18; GLM t = 1.64, 8 d.f., P = 0.14; GLM t = 1.49, 8 d.f., P = 0.17). However, total abundance, species richness and diversity, as well as abundance, species richness and diversity within the three most abundant taxonomic orders (Coleoptera, Diptera and Lepidoptera) decreased with increased burning frequency and increased with burning in 1994, though not significantly.

The number of Lepidoptera counted in visual transects in 1994 declined significantly with burning in 1994 (GLM t = 2.77, 8 d.f., $P < 0.05$) and declined nonsignificantly with burning frequency (Fig. 3).

DISCUSSION

Burning of oak savanna at Cedar Creek caused significant changes such as increased soil pH, decreased soil organic matter, increased bare mineral soil, decreased litter, increased plant species richness and increased cover of native plants (White, 1983; Tester, 1989). These changes are similar to those brought about by burning of grasslands and savannas in many areas of the world (Daubenmire, 1968). Oak savanna arthropods could respond to fire either directly or indirectly in response to changes in the environment, such as increased plant diversity and enhanced food quality.

Studies of the abundances of individual arthropod species have shown that they may vary in response to fire (Warren *et al.*, 1987). In our samples, species abundance showed a range of responses, though none was significant (Table 4). Interestingly, species' short and long-term responses to fire were negatively correlated so species that were less abundant in the growing season following a spring burn were more likely to be more abundant in savannas burned frequently during the last 30 yr, and vice versa. One possible reason may be that even though fire increases mortality, it also maintains necessary host plants or environmental conditions. The weakness of our species responses to fire agrees with a study of grassland arthropod families (Van Amburg *et al.*, 1981) and suggests most grassland and savanna arthropod species are adapted to fire (Evans, 1984; Anderson *et al.*, 1989).

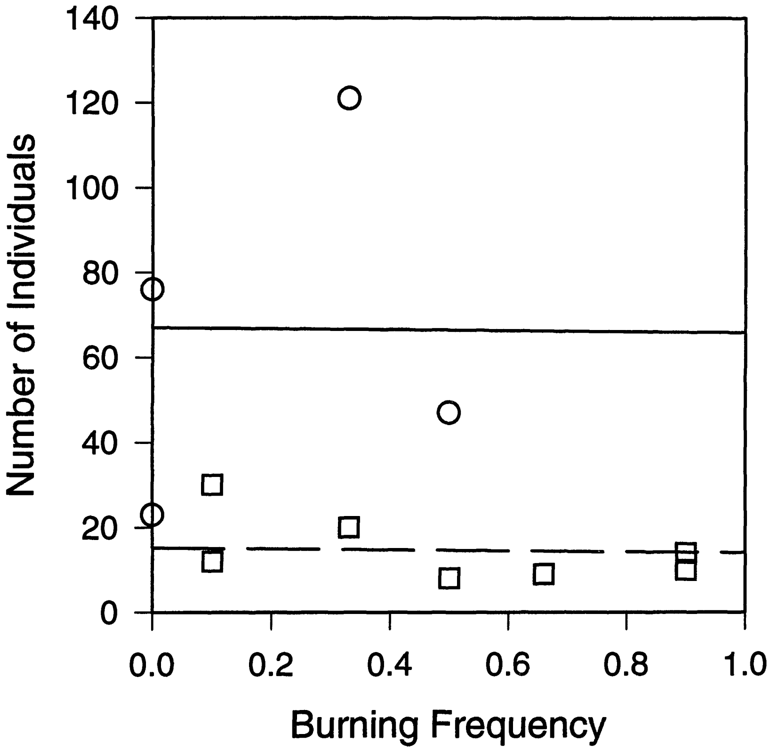

FIG. 3.—Relationships between burning history and total Lepidoptera abundance in visual surveys. Squares are savannas burned in the sampling year, circles are those which were not

It has been suggested that areas with similar burning histories may have similar arthropod species compositions (Evans, 1984), but our results do not clearly support or reject this conjecture. On the whole, savannas with similar burning histories had similar plant communities and physical environments (White, 1983; Tester, 1989; D. Peterson, pers. comm.), yet were not more likely to have similar arthropod species composition since most of our tests show no significant similarity. Jaccard indices of light trap samples and proportional similarities of 1993 sweep samples were greater for savannas within the same category for burned or not burned in the sampling year but the magnitude of the response was small (<5% difference). Proportional similarity was significantly greater for savannas with similar burning frequencies as measured by 1992 sweep samples, but the magnitude of the response was also small (an 11% difference between burning frequencies of 0 and 0.9). Evans (1984) found that grasshopper communities were more similar in grasslands burned at similar frequencies but he asserted that the effect was due to years since last burning. The high variance of abundance and species richness in infrequently burned savannahs, as measured by light traps and visual surveys (Figs. 2, 3) suggests the number of years since the last fire may also be important at Cedar Creek. Even though burning influences grasshopper species composition, Evans (1988), in a separate study, showed that frequency of burning had no effect on grasshopper species richness or abundance.

In our data, frequency of burning over the past 30 yrs has not caused any significant changes in overall arthropod abundance, species richness or diversity despite decreased abundance and species richness in the year of a fire as shown by significant decreases in species richness (1992 sweeps) and abundance (1992 sweeps and visual surveys). However, the dominant taxonomic orders changed with burning frequency as measured by proportional similarity for 1992 sweep samples. The proportions of Diptera and Homoptera declined with increased burning frequency and the proportion of Hemiptera increased. These results suggest that regional factors, such as climate, soil types, productivity and available pool of arthropod species, may determine the abundance and species richness of oak savanna arthropod communities, but that fire is important in determining the dominant groups in a local community.

Our different sampling methods show different results, perhaps because, in part, they intensively sample different parts of the arthropod community and in part because they differ in the intensity of sampling effort. However, our sampling methods never gave conflicting significant results. The time of sampling relative to the time of fires would increase the likelihood of finding effect for 1993 sweep net and pitfall samples compared to 1992 sweep net, light trap and visual survey samples.

The sizes of our burns were smaller than presettlement fires (Hurlbert, 1973) and may allow faster recolonization than occurred in the past. However, they may be a relevant size for two reasons. First, for some species recolonization is from unburned patches within burned areas (Hughes, 1943) or else occurs yearly from across the continent (Setiawan, 1986). Secondly, regardless of the historical size of fires, remnant savannas are presently much smaller.

Natural resource managers are unlikely to change the diversity of the entire arthropod community by burning but could jeopardize or favor populations of some arthropods, such as locally or globally endangered species which are typically Lepidoptera (USFWS, 1980; Coffin and Pfannmuller, 1988). Even though species responses to fire are generally weak, perturbations of rare species may result in their extinction (Pimm *et al.*, 1988; Lande, 1993). At this point, the most reliable way to predict the effect of different burning regimes on particular species seems to be to examine them on a case by case basis, though Homoptera and Lepidoptera seem to be more vulnerable. In general, species that are benefitted in the short term are harmed in the long term and vice versa. In fact, many arthropods have host plants which need fire to persist and burning may be necessary for the survival of these arthropod species even if they are highly susceptible to fire in some life stages. The frequency, method and time of year of burning could be chosen to minimize impact on certain species or maximize benefits to them, while still maintaining grassland or savanna plants. On the whole, using fire to preserve plant communities need not require the sacrifice of arthropod communities.

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