RESEARCH ARTICLE

Effects of Prescribed Fire on Prairie Arthropods: An Enclosure Study

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ABSTRACT: We assessed the relative contributions of in situ survival and recolonization to overall recovery of arthropod populations following prescribed fire by monitoring arthropod morphospecies richness and abundance in enclosed and open plots in adjacent burned and unburned units within two remnant Illinois prairies. Vacuum sampling of arthropods at semimonthly intervals following spring burns at each site indicated that fire strongly depressed arthropod abundance initially, but that abundance and species richness tended to recover toward the end of the summer, mostly due to recolonization from adjacent unburned refuges. Nevertheless, arthropod groups (taxa or guilds) were affected differently by fire, and differences in arthropod species composition among burned and unburned plots persisted. Sampled arthropod groups significantly reduced by fire at one or both study sites included springtails (Collembola), deltocephaline leafhoppers (Homoptera: Cicadellidae: Deltocephalinae), aphids (Homoptera: Aphididae), delphacid planthoppers (Homoptera: Delphacidae), parasitoid wasps (Hymenoptera), and spiders (Araneae). Only one group, typhlocybine leafhoppers (Homoptera: Cicadellidae: Typhlocybinae), exhibited a significant positive response to fire. These results indicate that in situ populations of many arthropod species are substantially reduced by prescribed fire. Thus, to preserve native arthropod faunas, land managers should ensure that unburned refuges are maintained and that the intervals between burns are sufficient to allow recolonization of burned areas to occur.

Index terms: arthropods, insects, management effects, prescribed burning, recolonization

INTRODUCTION

Prairies throughout the midwestern United States are being managed with pre-scribed fire (Collins and Wallace 1990). Prescribed fire releases nutrients into the soil, discourages growth of some woody and invasive species, and encourages production and flowering of some native grass-es and forbs. The assumption that fire benefits native animal species by restoring their habitat has been questioned by some entomologists (reviewed by Warren et al. 1987, Panzer 1988, Swengel 1996, Reed 1997), who have noted marked declines in insect abundance in recently burned areas and expressed concern over possible long-term, detrimental effects on populations of insects restricted to prairie habitats. De-tailed study of the effects of fire on native arthropods is needed because many prairies today persist as small remnants that represent habitat islands upon which many arthropod species depend for their survival (Panzer et al. 1995).

Management practices that maintain a di-verse arthropod community are important not only because arthropods represent the dominant component of terrestrial biodiversity, but also because of the crucial roles played by insects and other arthropods in ecosystem function (e.g., pollination and nutrient cycling). Unfortunately, responses to management remain largely unknown for most arthropod communities. Because many native arthropod species are apparently restricted to isolated patches of relatively high-quality habitat (Panzer et al. 1995), survival of these species may hinge on the development of management strategies that not only maintain native vegetation, but also avoid harming resident arthropod populations.

Previous studies (reviewed by Warren et al. 1987, Panzer 1988, Reed 1997) indicate that short-term responses to fire vary among arthropod taxa. The reasons for such variation in fire sensitivity are not well understood, partly because it is not known whether most prairie arthropod species can survive fire in situ (in soil or plant tissue, for example) or whether they must recolonize from unburned refuges. Direct evidence of high levels of insect mortality due to fire (e.g., Miller 1979) as well as information on insect life histories suggest that few arthropods other than those inhabiting the soil survive prescribed fire in situ. This has led to the recommendation that sites supporting remnant-dependent arthropod populations (i.e., those having an obligatory association with remnants of fragmented ecosystems; Panzer et al. 1995) should be burned infrequently, and that sites managed with fire should be divided so that only a portion is burned in any given year (Panzer 1988, Moffat and McPhillips 1993). Recent experimental evidence (Panzer 1988, Dana 1991, Swengel 1996) suggests that some remnant-dependent prairie arthropods either survive fire in situ or easily overcome barriers to recolonization (habitat gaps, etc.). Nevertheless, the debate over how fire affects arthropod communities will likely continue until the mechanisms of postburn population response and the long-term effects of bum management on the community are better understood. Knowledge of whether, and under what conditions, arthropods can survive prescribed bums in situ would improve our ability to design management strategies that enhance over-all ecosystem structure and function in native prairie remnants.

Although several studies have examined the effects of fire on insect communities in prairies (Rice 1932, Cancelado and Yonke 1970, Nagel 1973, Anderson et al. 1989) and other ecosystems thought to be fire-dependent (Delettre 1994, Collett and Neumann 1995, Moya-Raygoza 1995, Siemann et al. 1997), specific information on the relative importance of in situ survival and recolonization for maintaining insect populations in fire-managed prairies is available for only a few species (Borth and Barina 1991, Dana 1991, Fay and Samenus 1993, Swengel 1995). If in situ survival of fire by prairie arthropods is rare, and near-by refuges are not available to serve as sources for recolonization, then frequent burning of such isolated preserves risks reducing the viability of, or even extirpating, some arthropod populations.

We compared in situ arthropod survival with general arthropod survival (recolonization plus in situ) after a prescribed fire. Arthropod abundance and diversity were measured in burned and unburned sites, and in both enclosed and open plots. We assumed that arthropods found within the enclosures survived in situ, whereas those in open sites represented in situ survival, recolonization, or both. We predicted that arthropods occurring within the soil during spring and fall (e.g., eggs or immatures of many Araneae, Coleoptera, Diptera, and Orthoptera) would be insulated from the hot temperatures of fires and would consequently show greater in situ survival than other arthropods. We predicted that arthropods occurring in lit-ter or aboveground vegetative tissues (e.g., leafhoppers [Homoptera], which overwinter as eggs in plant tissue or as adults in litter; various bees and wasps [Hymenoptera], which overwinter in plant stems) would be more vulnerable to fire, and therefore would suffer higher levels of mortality than would other arthropods.

METHODS

Study sites

Native prairie remnants at Richardson Wildlife Foundation (RWF), Lee County, Illinois, and Windfall Prairie Nature Pre-serve (Windfall) in Vermilion County, Illinois, were chosen for study (Figure 1). Based on sampling in 1996 (C.H. Dietrich, unpubl. data), the arthropod fauna of RWF was known to include numerous remnant-dependent leafhopper species (e.g., *Dorydiella kansana* Beamer, *Graminella* spp., *Laevicephalus unicoloratus* [Gillette and Baker], *Limotettix truncatus* Sleesman). Windfall Prairie was also expected to sup-port a variety of native, remnant-dependent arthropod species, based on its location and vegetation. Two adjacent areas of approximately equal size, designated as "unburned" and "burned," were selected for study in each prairie in the autumn of 1996. The burned areas were subjected to prescribed fire the following spring, where-as the adjacent areas remained unburned.

The RWF prairie consists of dry-mesic, and mesic to wet-mesic sand prairie. Grass-es such as Indian grass *(Sorghastrum nu-tans [L.]* Nash), big bluestem *(Andropogon Berardi* Vitman), bluejoint grass *(Calamagrostis canadensis* [Michx.] P. Beauv.), and prairie cord-grass *(Spartina pectinata* Link) characterize the prairie (nomenclature follows Mohlenbrock 1986). Patches of blackberry *(Rubus* spp.) and other woody shrubs occur throughout the prairie (maximum height ca. 1.5 m), but these patches were avoided for the purpose of insect sampling (i.e., no plot was located within 1 m of a shrub patch).

Figure 1. Map of Illinois showing the locations of the two sample sites: Richardson Wildlife Foundation, Lee County (square) and Windfall Prairie, Vermilion County (circle).

The study areas at RWF consisted of north and south management units, approximately 6 m apart, separated from each other by a shallow ditch. Each unit is approximately 1 ha in size, but both occur within a native prairie that is approximately 9 ha in size. The eastern boundaries of both units grade into a pond. Both had been managed by prescribed burning for several years prior to the present study; the south unit (burned treatment) had been burned annually in the spring between 1989 and 1996, and the north unit had been burned between 1989 and 1995. Qualitative sampling during the 1996 growing season (C.H. Dietrich, unpubl. data) indicated the presence in these areas of a variety of insect species typical of native wet-mesic prairie habitats. This suggested that populations of these species either survived in situ or recolonized quickly from the surrounding unburned habitat. Nevertheless, because we lacked data on the arthropod fauna of these areas prior to the onset of burn management, we were unable to address the question of whether certain species were extirpated by fire at RWF prior to our study. Because intensive previous fire management at this site presumably favored fire-tolerant species and may have extirpated the most fire-sensitive species, our experiments conducted at RWF represent a relatively conservative test of the effects of prescribed fire on arthropods.

Windfall Prairie is a glacial drift hill prairie occurring on a high, southwest-facing bluff overlooking the Middle Fork of the Vermilion River, Vermilion County, Illinois. Grasses such as little bluestem *(Schizachyrium scoparium* [Michx.] Nash), Indian grass, and side-oats grama *(Bouteloua curtipendula* [Michx.] Ton.) characterize the prairie. Red-cedar *(Juniperus virginiana* L.) currently forms patches that dominate 30—40% of the prairie, but these areas were excluded from the study plots. The prairie is surrounded by calcareous seeps occurring on the lower slopes of the bluff, upland forests dominated by oak *(Quercus* spp.) and hickory *(Carya spp.),* and forests dominated by sugar maple *(Ater saccharum* Marshall) and basswood *(Tilia americana* L.) on slopes and ravines. Because of its small size (ca. 12 ha) the entire prairie was used for the study, so all sample plots were relatively close to forest and were shaded at various times during the day.

The prairie consists of a south and a north unit, which are approximately 30 m apart and separated from each other by a wooded ravine. The south unit was last burned in late March 1996. Prior to this, there is no written record of burn management at the site, but it was probably burned some-time between 1990 and 1992. Prior to those dates, the areas were burned sporadically if at all (M.K. Solecki, Illinois Nature Pre-serves Commission, pers. corm). For our study the north unit was burned and the south unit was left unburned in spring 1997.

Sampling Methods

Prior to the burn at each study site, locations for placement of enclosed and open circular sample plots, each 1 m in diameter, were chosen at random and marked with metal tags. We rejected plots if they did not meet all of the following criteria: (1) vegetation cover > 50% dominant prairie grasses; (2) total cover of vegetation > 75%; (3) relatively level, so enclosures could be set up properly; and (4) no large trees or shrubs (such sites could not be enclosed easily). These criteria were selected in order to minimize variation in vegetation among sites and to maximize the likelihood of capturing prairie arthropods. Fourteen (Windfall) or 16 (RWF) plots were selected for arthropod sampling in each treatment at the two study areas. The minimum distance between plots was 1 m, but most plots were several meters from their nearest neighbors.

Litter (dead plant tissue produced in previous growing seasons) might affect arthropod diversity or abundance at sites, as well as modify the burn. Thus, we measured litter depth at each plot location prior to the burn by estimating the height of the litter above the mineral soil at the center point of each plot. Standing dead material (i.e., dead tissue produced during the cur-rent growing season) was not included in this estimate.

To provide a rough characterization of conditions prior to each prescribed burn, we took several additional measurements immediately before burning began. We measured water content of vegetation by collecting all standing and dead vegetation (litter and stalks) from two 30-cm x 30-cm areas selected at random at each site. These samples were weighed, dried in an oven at 130° C for approximately 3 days, and reweighed to determine percent dry mass. Wind direction, speed, temperature, and humidity were monitored prior to and after each burn using a portable weather kit. Flame length was estimated visually during the burn. Immediately after the fire, we visually estimated percent area burned in each plot. Plots that remained unburned were excluded from the analysis.

To estimate burn temperature and intensity within each sample plot, we painted aluminum tags (2.5 cm x 8.9 cm x 0.02 cm) with Tempilac (Air Liquide America Corp., Plainfield, N.J.) fire-sensitive paints, designed to melt at different temperatures, and placed these in plots prior to the burn (see Cole et al. 1992). Thirteen different paints that melted at the following temperatures (°C) were painted in this order on each tag: 39, 59, 79, 101, 121, 139, 198, 260, 316, 371, 427, 500, 566. We also used the melting point of aluminum (660° C) (Cole et al. 1992) as an additional temperature measurement. At opposite edges of each plot, we placed a tag under the duff at the mineral soil surface, and placed another tag on top of the duff layer; an attached wire was driven into the soil to hold the tag in place. Following the burn, the temperature noted for each tag was that of the paint that melted at the highest temperature, or if part of the tag was melted, the temperature noted was 660°. Burns were conducted at around noon on 27 March 1997 at RWF and on 11 March 1997 at Windfall.

In each study site half of the plots, selected at random, were enclosed immediately after the burn and half remained open. Each enclosure was a cylinder (1.2 m high and 1 m in diameter) made of rectangular mesh wire fence (5.1-cm x 10.2-cm mesh) covered with white nylon no-see-em netting. Microclimatic alteration due to these enclosures appeared to be negligible; we noted no consistent differences in plant growth or arthropod mortality between enclosed and open plots. To reduce the possibility of contamination of the enclosed plots by outside arthropods, we placed enclosures at Windfall on a foam gasket (4 cm high x 4.5 cm wide). At RWF the bottom of each enclosure was buried to a depth of approximately 10 cm. Each en-closure was secured in place with four tent stakes. Care was taken to minimize disturbance to the prairie.

Arthropods were sampled in plots at both study sites at semimonthly intervals between 24 May and 1 August 1997. Sampling occurred between 0011 and 0014 hours on each sample date. Arthropods were captured by vacuuming the vegetationllitter at a height of approximately 10 cm above the ground in each plot for 10 seconds using a gasoline powered lawn vacuum (Model BG 75, Stihl Inc., Virginia Beach, Va.) with a fine-mesh insect net bag duct-taped to the end of the intake nozzle. This method efficiently captures nearly all arthropods present within a few centimeters of the intake nozzle, causes only minor disturbance to the vegetation, and appears to result in negligible mortality among the arthropods sampled (Mac-Leod et al. 1994). To minimize the chances of arthropods entering or leaving enclosures during sampling, the enclosure was left in place with the vacuum collector inserted through an opening in the roof. Sampling of open plots was accomplished by vacuuming within a plastic ring of diameter equal to that of the enclosed plots. Each sample was placed in a clear plastic bag and visually inspected to determine how many of each morphospecies were present. Arthropods were then released alive back into the plot from which they were sampled (usually within 5 minutes).

Leafhoppers and planthoppers (auchenorrhynchous Homoptera), the group for which one of us (C.H.D.) has the most taxonomic expertise, were identified to genus or species. This group includes numerous species thought to be remnant-dependent and indicative of high-quality prairie habitats (Panzer et al. 1995; Hamilton 1995, 1999). Members of other arthropod groups were identified to family and morphospecies. The number of individuals of each arthropod species or morphospecies was recorded for each sample. Shannon-Weaver diversity (Poole 1974) and species richness (Southwood 1978) were estimated for each sampling date, based on numbers of individuals of each morphospecies. Species in many arthropod taxa (e.g., braconid and chalcidoid wasps, acalypterate muscoid flies) cannot be reliably distinguished in the field. Thus, each morphospecies in these groups probably represented more than one true species, resulting in an underestimate of species richness and diversity. Additional samples from areas adjacent to the study sites were taken to obtain voucher specimens for the sampled morphospecies. These vouchers were deposited in the Illinois Natural History Survey Insect Collection, Champaign, Illinois.

Plant species composition and percent cover were also recorded for each plot at the end of the sampling season, since these could affect arthropod diversity and abundance. Areal coverage was determined for each plant species by estimating the pro-portion of the plot covered by plant foliage for all plants rooted within the plot. Data are reported as mean ± 1 SE.

Statistical Analyses

Statistical analyses were conducted using commercial software (SYSTAT 5.2.1, SPSS Inc., and JMP 3.1, SAS Institute). For univariate analyses, the assumptions of parametric analysis were tested by evaluating the normality of the sample distributions using the Shapiro-Wilk test, and homogeneity of variances was evaluated using Levene's test (SAS Institute 1996). Results of statistical tests were considered significant at $p < 0.10$.

Kruskal-Wallis rank-sum tests were used to determine whether litter depth differed significantly between burned and unburned treatments prior to the burn. Nonparametric tests were used because assumptions of parametric tests were not met.

Plant species cover data were averaged across plots to determine percent cover for the burned/unburned treatments. This in-formation was used to determine qualitatively whether burn and control treatments were similar in vegetative cover at the end of the growing season, since this could affect arthropod diversity and abundance.

Tests for treatment effects (burning and enclosures) on arthropod diversity (Shannon-Weaver diversity index, H') were per-formed using repeated measures multivariate analysis of variance (RMANOVA).

Because the small population sizes of most arthropod species sampled presented difficulties for the statistical analyses, we grouped arthropods into higher taxa or guilds (see Table 2), comprising species thought to have similar behaviors and life histories. Data on these groups were used to test for treatment effects on overall arthropod abundances and the taxonomic composition of the arthropod fauna. Estimated abundances from the five sampling dates were averaged to produce one value per plot for each arthropod group. Thus, whether or not abundance of each arthropod group varied over time was not analysed.

Two-way nonparametric analysis of variance (ANOVA) tests were performed on ranked data for each of the 10 most abundant arthropod groups to determine which groups were affected by the burn and en-closure treatments. The two-way ANOVA design for ranked data is the Scheirer-Ray-Hare extension of the Kruskal-Wallis test (Sokal and Rohlf 1981). P-values were corrected for the number of tests performed ($n=10$) using the Bonferonni method. Nonparametric tests were used because many groups did not meet the assumptions of parametric ANOVA. Ranked data produced results similar to unranked data.

Nonparametric Spearman tests were used to assess the relationship of (a) Shannon-Weaver diversity and (b) abundance of each of the 10 most abundant arthropod groups to burn temperature at soil and duff levels. The P-value was adjusted for the number of tests performed ($n=2$) using the Bonferonni method. Nonparametric tests were used because assumptions of parametric tests were not met.

RESULTS

Weather conditions at the time of burning at RWF were: air temperature = 26°C, relative humidity = 25.5%, windspeeds = 10–16 km per hour, winds south/southwest. Average fuel moisture at RWF was 4.6 ± 0.6% ($n=2$). Backfire flame lengths varied from 1.5 to 6.1 m, and headfires were approximately 9.1–12.2 m high. However, the majority of the plots were burned with the backfire.

Weather conditions at the time of burning at Windfall Prairie were: air temperature = 12°C, relative humidity = 69%, windspeeds = 5–10 km per hour, winds north/northeast. Average fuel moisture at Windfall was 13.5 ± 4.5% ($n = 2$). Backfire flames

Table 1. Percent areal cover for the dominant plant species on burned and unburned prairies approximately 4 months after burning at Richardson Wildlife Foundation (RWF) and 5.5 months after burning at Windfall Prairie (only plants that made up at least 10% cover in either the burned or the unburned study site were included). Plant nomenclature follows Mohlenbrock (1986).

	RWF		Windfall	
Species	Burned	Unburned	Burned	Unburned
Andropogon gerardi	21.7	32.7	22.3	12.9
Bouteloua curtipendula			30.9	56.8
Calamagrostis canadensis	36.6	13.8	—	—
Carex sp.	16.6	11.6		
Coreopsis triptera	—	—	12.3	5.4
Euthamia graminifolia	14.8	11.4		
Helianthus grosseseratus	15.1	4.2	—	—
Parthenium integrifolium	0	16.6		
Sorghastrum nutans			14.6	23.4
Silphium terebinthinaceum	—	—	9.2	12.6

were less than 0.6 m high, and headfire flames were less than 1.8 m high.

Burn temperatures varied substantially between and within sites. At RWF the burn was hot (mean soil temperature 118.5° ± 11.0°C, n=16; mean duff temperature 392.9°C ± 48.2°C, n=16) with nearly all (93.8% ± 3.4%, n=16) aboveground vegetation in burned plots reduced to mineral ash. At Windfall, the burn was relatively cool (mean soil temperature 30.8° ± 12.7°C, n = 13; mean duff temperature 122.6° ± 16.3°C, n=13) and patchy (92.3% ± 3.8%, n = 13, burned within plots, excluding one plot that did not burn at all).

At both RWF and Windfall, mean litter depth (cm) prior to the burn was significantly greater in the burned treatment (RWF: 8.8 ± 0.9, n=16; Windfall: 3.3 ± 0.5, n=13) than the control treatment (RWF: 6.4 ± 0.8, n=16; Windfall: 0.7 ± 0.2, n=14) (RWF: s = 212.0, z = -1.98, p = 0.048; Windfall: s = 263.5, z = 3.98, p = 0.0001).

At the end of the sample season, dominant plant species appeared similar between burned and control treatments at RWF and Windfall (Table 1), with one exception. At RWF *Parthenium integrifolium* L. (wild quinine) was dominant in the control area plots, but did not occur in the burned area plots.

Sample plots at RWF yielded a total of 79 arthropod morphospecies, whereas those at Windfall yielded 62 morphospecies. The data on sample abundances of individual morphospecies were used to calculate species richness and Shannon-Weaver diversity. However, because many of these morphospecies were represented by very few individuals, we consolidated the morphospecies data into groups (higher taxa or guilds) prior to testing for treatment effects. Morphospecies at RWF represented 28 such groups and there were 21 groups present at Windfall. The taxonomic compositions of these groups are shown in Table 2. Despite the fact that we pooled data for several arthropod morphospecies into a single group, too few individuals were sampled to facilitate statistical tests for treatment effects on several such groups; therefore, we used only the 10 most abundant groups for our statistical comparisons.

Arthropod diversity and richness were similar at RWF and Windfall (Figures 2 and 3). Repeated measures MANOVA indicated significant burn and enclosure effects on species diversity (RWF: burn $^{F}128$ = 40.23, p<0.001, enclose $F_{1\ 28}$=9.54, p = 0.005; Windfall: burn $F_{1,22}$ = 50.51, p < 0.001, enclose F1 22 = 33.12, p < 0.001). Average diversity was greater in unburned than in burned treatments. However, there was a significant burn-by-enclosure interaction at Windfall (F122=20.22, p<0.001) and a marginally nonsignificant one at RWF (F_{128}=2.88, p=0.101), suggesting that the diversity response to enclosures varied depending on whether the treatment was burned or unburned. Therefore, we ran ANOVAs separately for the burned and unburned treatments. At RWF and Windfall, enclosures affected diversity in the burned treatments (RWF: F1 $_{14=11.23,}$ p=0.005; Windfall: $F_{1\ 11}$=41.57, p < 0.001) but not in the unburned treatments (RWF: $F_{1\ 14}$= 0.99, p = 0.337; Windfall: F1 11=1.08,p = 0.32). In the burned treatments, diversity was lower in the enclosed sites (RWF: 1.18 ± 0.10; Windfall: 1.11 ± 0.08) than in the open sites (RWF: 1.58 ± 0.06; Windfall: 1.70 ± 0.05). There was significant variation in diversity over time at RWF $^{(F}$41112 = 8.90, p < 0.001) and Windfall $^{(F}$4 88 = 2.80, p = 0.03), but the data did not exhibit any clear directional trends (Figure 2).

Results of two-way nonparametric ANOVA on each of the top 10 arthropod groups showed that at RWF, the burned treatment had significantly fewer Collembola (F128=41.077, adjustedp <0.01), Cicadellid 4 $_{(F128=53.508,}$ adjusted p < 0.01), and Hymenoptera 2 (F_{128}=9.348, adjusted p = 0.05; Figure 4A). The burned treatment at RWF had significantly more Cicadellid 1 ($F_{1,28}$=10.229, adjusted p = 0.03; Figure 4A). At Windfall the burned treatment had significantly fewer Collembola ($F_{1,23}$=65.816, adjusted p < 0.01), Cicadellid 4 (F1 $_{23=7.966,}$ adjusted p=0.10), Sternorrhyncha ($F_{1\ 23}$=54.882, adjusted p < 0.01), and Delphacid (F_{123}=40.320, adjusted p<0.01; Figure 4B). At RWF enclosures significantly reduced Coleoptera numbers ($F_{1\ 28}$=8.467, adjusted p=0.07; Figure 4A). At Windfall enclosures reduced Diptera 1 (F_{123}=18.083, adjustedp < 0.01) and Diptera 2 numbers ($F_{1\ 23}$=8.238, adjusted p=0.09; Figure 4B). At RWF a significant burn-by-enclosure interaction for the Araneae ($F_{1\ 28}$=15.492, adjusted p < 0.01) indicated that spiders were affected

Table 2. Taxonomic composition of arthropod groups at Richardson Wildlife Foundation and Windfall Prairie, Illinois, ranked in order of average abundance within each site. Species were grouped by taxonomic affiliation and, within taxa, by life history characteristics. Groups thought to be remnant-dependent are marked with an asterisk (*).

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Delphacidae	Delphacinae (delphacid planthoppers)
Cicadellidae 1	*Forcipata loca* (DeLong and Caldwell), *Empoasca fabae* (Harris), *Dikraneura angustata* Ball and DeLong, *Erythroneura* spp. (typhlocybine leafhoppers)
Cicadellid 4	*Athysanus argentarius* Metcalf, *Cicadula melanogaster* (Provancher)*, *Laevicephalus unicoloratus* (Gillette and Baker)*, *Limotettix cuneatus* (Sanders and DeLong)*, *L. elegans* Hamilton*, *Polyamia caperata* (Ball)*, *Scaphytopius acutus* (Say), *Endria inimica* (Say), *Cosmotettix delector* (Sanders and DeLong)*, *Chlorotettix* sp.* (deltocephaline leafhoppers)
Sternorrhyncha	*Izyphia flabella* (Sanborn), *Subsaltusaphis wanica* (Hottis and Frison), Aphidae spp., Psyllidae sp. (aphids and psyllids)
Hymenoptera 2	Chalcidoidea, Braconidae (parasitoid wasps).
Araneae	spiders
Collembola	Entomobryidae, Sminthuridae (springtails)
Diptera 1	Cecidomiidae, Chironomidae, Sciaridae, Tipulidae (nematocerous flies)
Diptera 2	Chloropidae, Drosophilidae, Muscidae (brachycerous flies)
Coleoptera	Cantharidae, Curculionidae, Chrysomelidae, Lathridiidae, Nitidulidae, Staphylinidae (beetles)
Hymenoptera 1	Formicidae (ants)
Opiliones	harvestmen
Cicadellidae 3	*Agallia* spp., *Agalliopsis novella* (Say) (agalliine leafhoppers)
Lepidoptera	undetermined larvae, Pyralidae (moths)
Fulgoroidea 1	*Scolops* sp.*, *Acanalonia* spp., *Ormenoides venusta* (Melichar) (planthoppers)
Heteroptera 2	Pentatomidae, Miridae, Lygaeidae (phytophagous bugs)
Fulgoroidea 3	*Bruchomorpha* spp.* (planthoppers)
Heteroptera 1	Nabidae (predaceous bugs)
Orthoptera 1	Tettigoniidae, Gryllidae (katydids and crickets)
Fugoroidea 2	*Cedusa* spp., *Otiocerus* spp. (derbid planthoppers)
Orthoptera 2	Acrididae (grasshoppers)
Thysanoptera	thrips
Cicadellidae 2	*Balclutha neglecta* (DeLong and Davidson), *Macrosteles variata* (Fallen), *M. quadrilineata* (Forbes) (macrosteline leafhoppers)
Psocoptera	bark lice
Phasmatidae	walking sticks
Hymenoptera 4	Tenthredinidae (sawfly larvae)
Hymenoptera 3	Andrenidae (bees)
Other	various small insect orders

WINDFALL PRAIRIE

Collembola	Entomobryidae, Sminthuridae (springtails)
Cicadellidae 4	*Dorydiella kansana* Beamer*, *Flexamia clayi* Young and Beirne*, *Polyamia caperata*, Laevicephalus minimus* (Osborn and Ball)*, *Scaphytopius acutus, Chlorotettix* sp.*, *Texananus* sp.*, *Xestocephalus desertorum* (Berg) (leafhoppers)
Hymenoptera 1	*Formica* spp. (ants)
Araneae	spiders
Stemorrhyncha	*Izyphia flabella,* Aphidae spp. (aphids)
Diptera 1	Cecidomyiidae, Chironomidae, Tipulidae (nematocerous flies)
Delphacidae	*Delphacinae* (delphacid planthoppers)*
Diptera 2	Chloropidae, Drosophilidae, Muscidae (brachycerous flies)
Hymenoptera 2	Chalcidoidea, Braconidae (parasitoid wasps)
Coleoptera	Buprestidae, Chrysomelidae, Ciidae, Curculionidae, Mordellidae, Melyridae, Phalacridae, Nitidulidae, Lathridiidae, Scarabaeidae (beetles)
Cicadellidae 1	*Forcipata loca, Empoasca fabae, Dikraneura angustata* (typhlocybine leafhoppers)
Lepidoptera	undetermined larvae, Pyralidae (moths)
Opiliones	harvestmen
Orthoptera 2	Tettigoniidae, Gryllidae (katydids and crickets)
Fulgoroidea	*Bruchomorpha* spp.*, *Nersia* sp., *Ormenoides venusta, Acanalonia* spp., *Cixius* sp. (planthoppers)
Hymenoptera 3	Apidae, Vespidae, Pompilidae (bees and predaceous wasps)
Heteroptera	Miridae, Pentatomidae (true bugs)
Cicadellidae 3	*Agallia constricta* (Say) (agalliine leafhopper)
Orthoptera 1	Acrididae (grasshoppers)
Membracidae	*Campylenchia latipes* (Say) (treehopper)
Other	Thysanoptera (thrips), Ephemerida (mayflies), Psocoptera (bark lice), Diplopoda (millipeds)

by enclosures differently, depending on whether they were in the burned or unburned treatment. Therefore, we ran non-parametric ANOVAs separately for burned and unburned treatments. In the burned area only, average numbers of Araneae were lower in the enclosed sites (1.00 ± 0.17) than in the open sites (1.93 ± 0.27; F1114=7.861, p= 0.014).

At RWF, in the burned/open treatment, there was a significant, negative correlation between average duff temperature and diversity (Spearman Rho = -0.7711, $p < 0.10$). No significant correlations between burn temperature and diversity were found at Windfall.

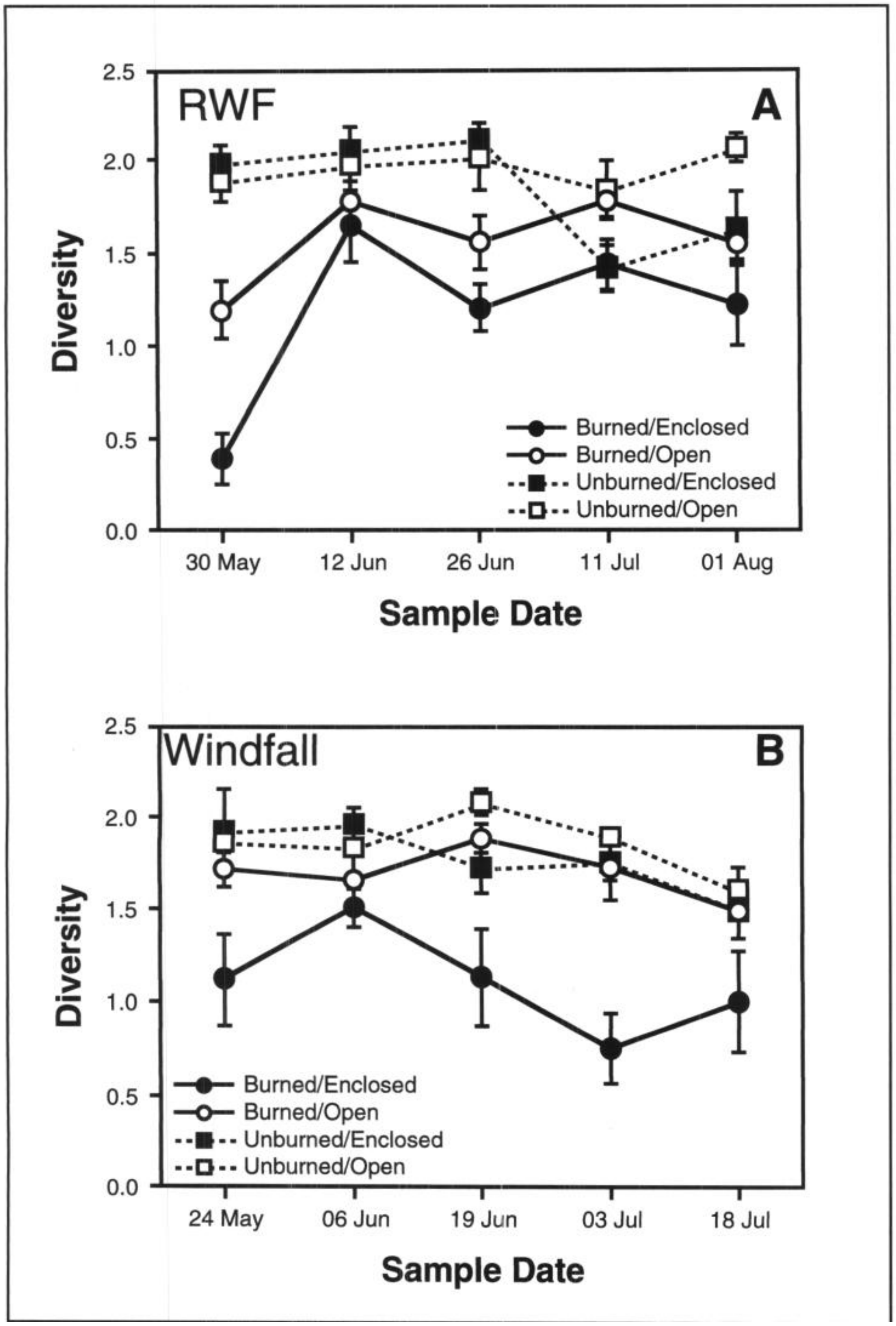

Figure 2. Effects of experimental treatments on Shannon-Weaver index of diversity of arthropods, as estimated over five sampling dates in 1997. (A) Richardson Wildlife Foundation (n=8 for each treatment); (B) Windfall Prairie ($n_{\text{burned-enclosed}} = 6$, $n_{\text{unburned-enclosed}} = 7$; $n_{\text{burned-open}} = 7$, $n_{\text{unburned-open}} = 7^*$; except data for an unburned, open plot were missing for 18 July). Symbols represent mean diversity (± 1 SE) for each treatment on each sampling date.

DISCUSSION

Our data from two Illinois remnant tallgrass prairies suggest that prescribed burning has profound effects on prairie arthropod communities. Overall, species richness and diversity were substantially reduced by burning (Figure 2 and 3), and these negative burn effects were due to the failure of many arthropods to survive the fires in situ. At both study sites, arthropod diversity was significantly lower in enclosed plots than in open plots, but only in the burned treatments (Figure 2). This result demonstrates that many arthropods failed to survive the fires in situ and that the higher diversity in open plots was due to recolonization.

Because of the small number of plots included in the study and small arthropod sample sizes, we were unable to test for the effects of burn temperature on individual arthropod taxa. However, not surprisingly, plots at RWF in which the duff temperature of the fire was hotter tended to have lower arthropod diversity. A similar correlation between fire temperature and arthropod diversity was not found among plots at Windfall. Overall, however, the cool, patchy fire at this site seemed to have as profound an effect on the arthropod community as did the nearly uniform, hot fire at RWF (Figure 2-4).

Not surprisingly, given the diversity of life history strategies found among arthropods, different groups of arthropods responded differently to fire. At RWF (Figure 4A), burning significantly reduced abundance of springtails (Collembola), deltocephaline leafhoppers (Cicadellid 4), and parasitoid wasps (Hymenoptera 2) in both en-closed and open plots. Abundance of spiders was also reduced, but in enclosed plots only, suggesting that spiders failed to survive in situ but readily recolonized the burned area. The only arthropod group that responded positively to fire, typhlocybine leafhoppers (Cicadellid 1), comprises highly vagile, host- and habitat-generalist species such as the potato leafhopper (*Empoasca fabae* [Harris]) that may have been attracted by the relatively lush green vegetation of the burned treatment. In contrast, the deltocephaline leafhoppers, many of which are capable of only limited flight and specialize on prairie grasses and sedges, were scarce in the burned treatment.

At Windfall (Figure 4B), the four groups significantly reduced by fire were springtails, deltocephaline leafhoppers, aphids (Sternorrhyncha), and delphacid plant-hoppers (Delphacidae); none of the 10 most abundant arthropod groups at Windfall exhibited a positive burn response. These results are also not surprising in light of the life histories of these insect groups. Springtails inhabit leaf litter, which is substantially reduced by burning. Deltocephaline leafhoppers, aphids, and planthoppers typically overwinter as eggs inserted into the aboveground tissues of their herbaceous host plants, which are also usually destroyed by fire. Many parasitoid wasps overwinter as larvae or pupae in dead plant stems.

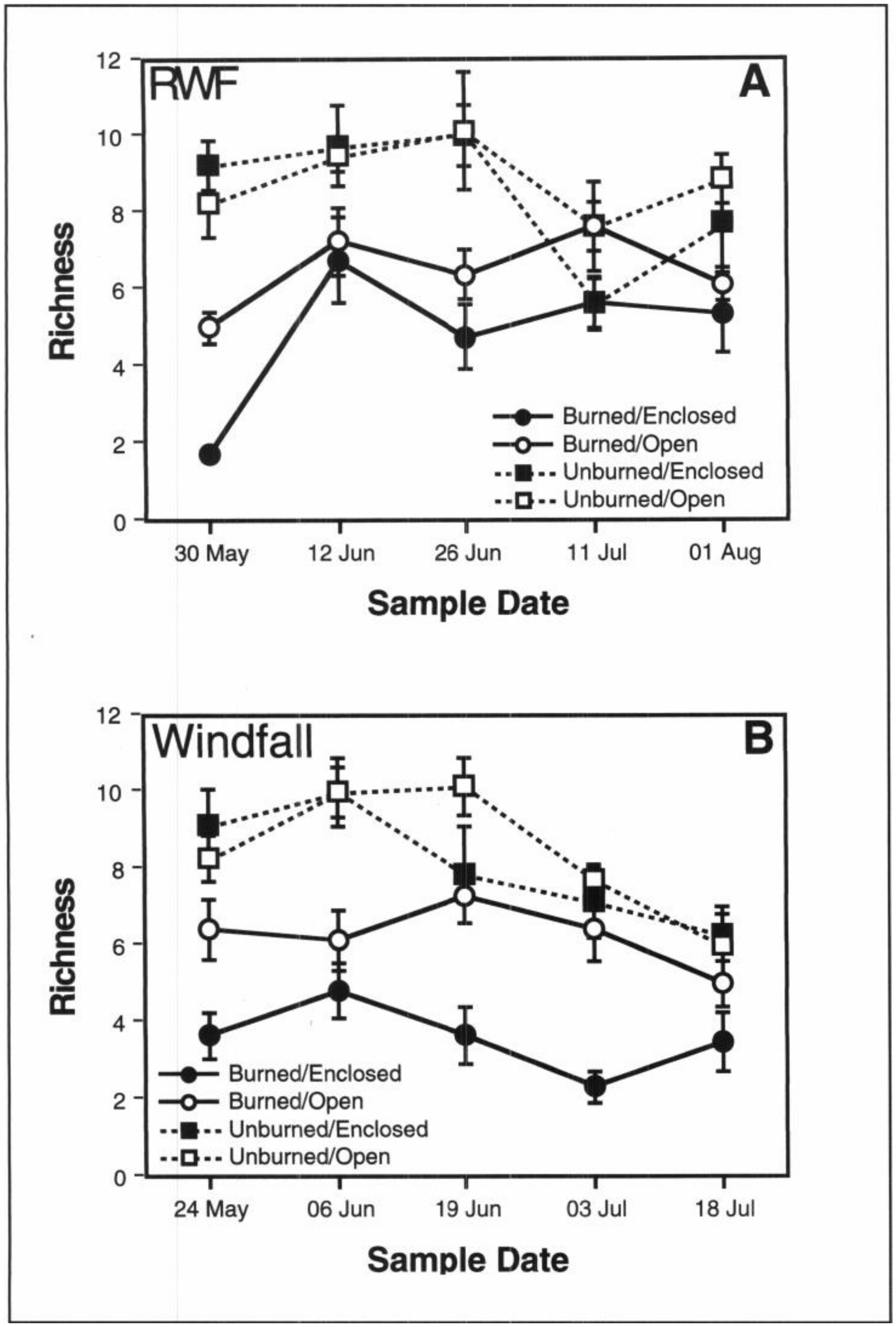

Figure 3. Effects of experimental treatments on morphospecies richness of arthropods, as estimated over five sampling dates in 1997. (A) Richardson Wildlife Foundation; (B) Windfall Prairie. Symbols represent mean richness (±1 SE) for each treatment on each sampling date (sample sizes as in Figure 2).

Somewhat surprisingly, despite the highly significant reduction in overall arthropod diversity due to enclosure effects, abundance of only 2 of the top 10 arthropod groups at either site was significantly affected by enclosures. At RWF there were significantly fewer beetles (Coleoptera) in the enclosed plots in both burned and unburned treatments; at Windfall, there were significantly fewer flies (Diptera 1 and 2) in enclosed plots. These results suggest that many of the flies and beetles present in both burned and unburned parts of the prairie during the growing season over-wintered in other habitats. For several other arthropod groups, although average abundances tended to be higher in open plots (Figure 4), high levels of variation among plots rendered these differences nonsignificant.

Despite observed reductions in arthropod diversity and abundance at both RWF and Windfall, apparently in response to pre-scribed fire, the arthropod faunas of open plots showed marked recovery by the end of the sampling period in 1997. This is not surprising, because not only were the burned treatments closely adjacent to the unburned treatments, but both study sites were surrounded by extensive areas of unburned native vegetation, which presumably provided ample sources of new arthropod colonists. These study sites are, therefore, somewhat atypical of tallgrass prairie remnants, many of which are small habitat islands surrounded by agroecosystems or other anthropogenic habitats. Given that much of the postburn recovery of prairie arthropod populations is due to re-colonization, burning an isolated preserve in its entirety may risk extirpating some arthropod populations.

Failure of certain species to survive fire in situ is probably the most important cause of short-term alterations in the arthropod species composition of burned prairies. The extent to which such differences in species composition persist may be influenced by numerous factors including vegetation, burn characteristics, distance to refuges, prevailing wind direction, and the relative mobilities and fecundities of the species involved. In our study, some species quickly colonized the burned areas but others failed to appear, despite an abundance of suitable host plants. For example at Windfall, *Laevicephalus minimus (Os*-born and Ball), a leafhopper that specializes on side-oats grama, was initially absent from the burned area, but adult individuals began appearing in the open plots by mid-June. In contrast, *Izyphia flabella* (Sanborn), a grass-feeding aphid, was abundant in the unburned plots but remained absent in the burned area at the end of the sampling period. Apparently, *I. flabella is* less mobile and may require more time to recolonize the burned area.

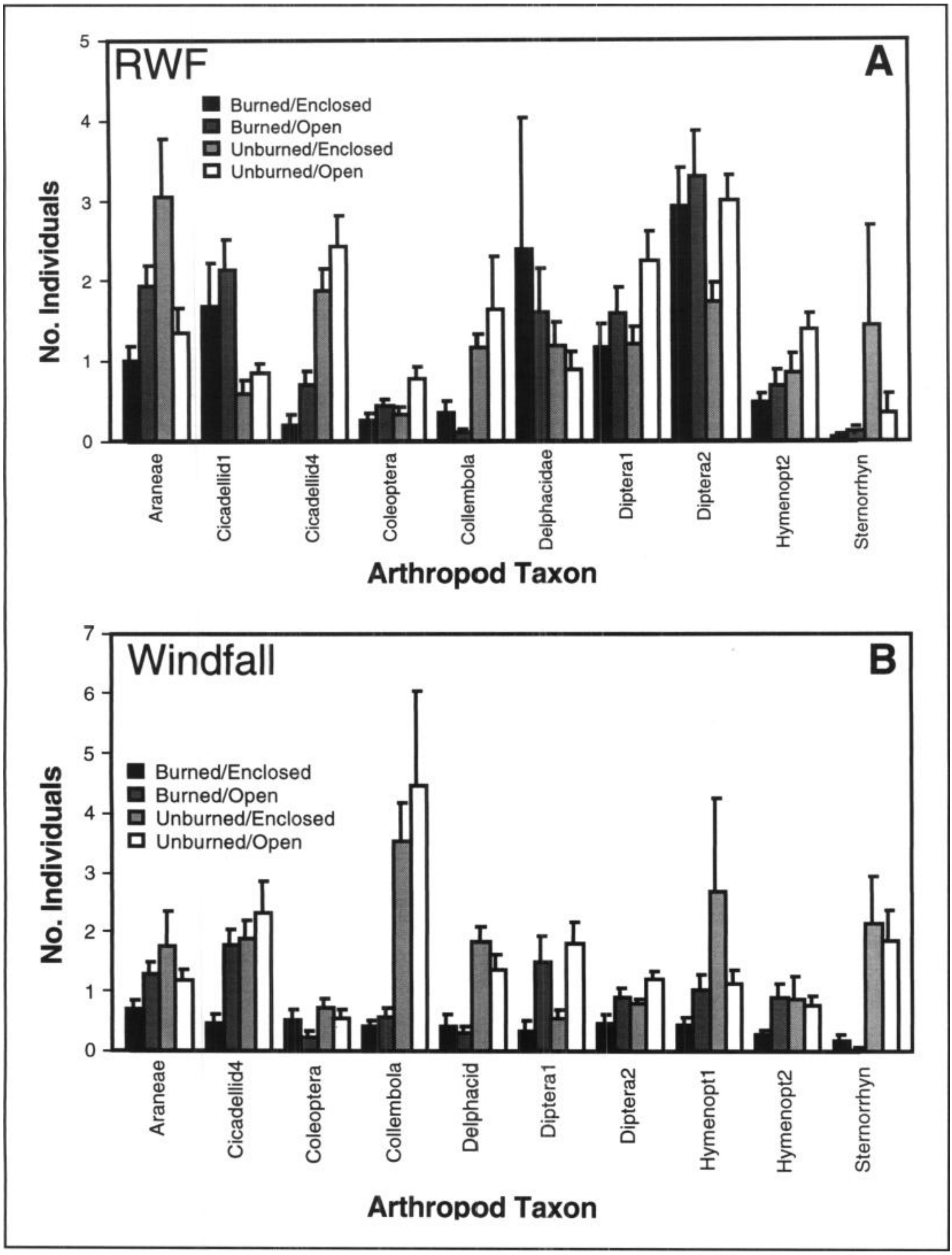

Figure 4. Effects of experimental treatments on the 10 most abundant arthropod groups at Richardson Wildlife Foundation and Windfall Prairie (see Table 2 for composition of groups). Each bar represents the mean number of individuals (±-1 SE) sampled per group, for each treatment averaged over five collection dates in 1997 (sample sizes as in Figure 2).

Despite our overall finding that prescribed fire can significantly alter the prairie arthropod communities, the results presented here should be interpreted with caution. By attempting to address management effects on an entire community rather than individual species or populations we undoubtedly failed to detect finer-scale patterns of response to our experimental treatments. For example, our failure to detect significant treatment effects in many of the groups of arthropods en-countered in our samples may indicate that these groups were unaffected by burning. How-ever, this failure could also have resulted from different species within some groups responding to the treatments in different ways. Because the two most abundant groups of leafhoppers in our samples exhibited the opposite responses to burning (typhlocybines responded positively; deltocephalines responded negatively), if we had pooled data for these two groups, our results may have indicated that the overall response of leafhoppers to fire was neutral. Similarly, in other arthropod groups, although we pooled data for species thought to have similar life history patterns, by doing so we may have obfuscated significant but contradictory patterns of response among individual species.

Another reason for interpreting our results with caution is the lack of quantitative data on the preburn arthropod faunas of the study sites. Because the burn units at both study sites differed somewhat in their burn histories, we cannot be certain that the burned and unburned treatments were comparable prior to our study. The burned treatment at RWF had been burned the previous year (1996), while the unburned treatment had remained so since 1995. Thus observed reductions in arthropod diversity in the burned treatment at RWF may have resulted partly from the previous year's burn. In contrast, at Windfall, there was no record of the burned treatment having been burned in recent years, while the unburned treatment had been burned in 1996. Thus, the lower diversity found in the burned treatment (burned 1997) at this site is of greater significance. Also, although the vegetation appeared similar in burned and unburned treatments at both sites, preburn litter depth in the unburned treatment at both sites was significantly less than in the burned treatment. Because many arthropods inhabit litter during the winter, the burned treatment may have had a greater proportion of litter-dwelling arthropods prior to our study.

More work is needed to further elucidate the effects of prescribed burning on arthropods. Information on arthropod ecology and life history, lacking for many species, may allow one to predict their responses to fire. In our study, the responses of various arthropod groups to fire tended to fit such life history predictions, al-though small sample sizes and high levels of variability for individual arthropod species (as well as most of the composite groups we recognized) prevented us from examining these responses in detail. More-over, the myriad sources of variability in arthropod populations might be expected to confound attempts to make such predictions. For example, the response of a particular plant-feeding insect species to fire may depend as much on the effects of the fire on its predators, pathogens, parasitoids, and host plants as it does on the direct mortality effects of the burn on its own population. Arthropod populations often undergo significant natural fluctuations from year to year, and significant changes in arthropod species composition due to management effects may not be-come apparent for many years following the onset of a particular management pro-gram. Thus, long-term monitoring is needed to more accurately assess the effects of management on the entire arthropod community. Perhaps most urgently, monitoring of arthropod faunas should begin prior to the onset of management. Because many remnant prairies are currently being man-aged by fire, it is already difficult to find suitable study sites that have not been burned recently. For many of these sites no information is available on the composition of the arthropod fauna prior to the onset of management.

Although there is growing awareness among preserve managers that arthropod communities need to be considered during the design of effective disturbance-based management strategies, fundamental knowledge of the effects of management on arthropod populations and communities lags far behind that available for other groups of organisms. Most previous studies of the responses of arthropods to fire have indicated that arthropod populations reduced by fire eventually recover, al-though recovery times vary. Generally, it is assumed that postburn recovery is due to recolonization of the burned area. Our results, which indicate that few prairie arthropods survive fire in situ, corroborate this general pattern. Therefore, under most circumstances, burn management of prairies should probably be kept to the mini-mum required to maintain native vegetation, and unburned refuges sufficiently representative of the prairie as a whole should always be maintained to facilitate recolonization of burned areas by fire-sensitive arthropod species. Clearly, more than a single year is required for some prairie arthropod populations to recover from fire, even under a best-case scenario (as in our study sites) in which unburned refuges exist immediately adjacent to the burned area. Thus, managers may be wise to use burn rotations of two or more years and to consider alternatives to prescribed burning, such as mowing and grazing.

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