Am. Midl. Nat. 157:92–105

Responses of Prairie Arthropod Communities to Fire and Fertilizer: Balancing Plant and Arthropod Conservation

MARIA K. HARTLEY, WILLIAM E. ROGERS[1] AND EVAN SIEMANN[2]
Department of Ecology and Evolutionary Biology, Rice University, Houston, Texas 77005

AND

JAMES GRACE
National Wetlands Research Center, USGS, Lafayette, Louisiana 70506

ABSTRACT.—Fire is an important tool for limiting woody plant invasions into prairies, but using fire management to maintain grassland plant communities may inadvertently reduce arthropod diversity. To test this, we established twenty-four 100 m^2 plots in a tallgrass prairie in Galveston County, Texas, in spring 2000. Plots were assigned a fire (no burn, one time burn [2000], two time burn [2000, 2001]) and fertilization treatment (none, NPK addition) in a full factorial design. Fertilization treatments allowed us to examine the effects of fire at a different level of productivity. We measured plant cover by species and sampled arthropods with sweep nets during the 2001 growing season. Path analysis indicated that fertilization reduced while annual fires increased arthropod diversity via increases and decreases in woody plant abundance, respectively. There was no direct effect of fire on arthropod diversity or abundance. Diptera and Homoptera exhibited particularly strong positive responses to fires. Lepidoptera had a negative response to nutrient enrichment. Overall, the negative effects of fire on the arthropod community were minor in contrast to the strong positive indirect effects of small-scale burning on arthropod diversity if conservation of particular taxa is not a priority. The same fire regime that minimized woody plant invasion also maximized arthropod diversity.

INTRODUCTION

Natural ecosystems are losing biodiversity at an increasing rate due to anthropogenic impacts such as habitat fragmentation or atmospheric nitrogen deposition (Wilson, 1988; Vitousek *et al.*, 1997). Such perturbations and subsequent declines in biodiversity may have effects on ecosystem functioning thus maintaining ecosystem integrity presents an important challenge for resource managers. Fire is both a natural process and common management technique that can maintain diversity in habitats where fire was historically present (Anderson, 1990). Indeed, because it is effective in limiting woody plant encroachment, fire is frequently utilized to maintain or improve grasslands (Bragg and Hulbert, 1976). Although management using fire can be beneficial for grassland vegetation (Gibson and Hulbert, 1987), it may not necessarily be an effective method for conserving arthropod diversity (Dietrich *et al.*, 1998; Panzer and Schwartz, 1998).

Because arthropods play an important role in many ecosystem processes, such as decomposition and pollination (Price, 1997; Weisser and Siemann, 2004), anthropogenic influences that substantially alter arthropod community composition or abundance could have long-term effects on ecosystem processes. In addition, arthropods are a dominant com-

---

[1] Present address: Department of Rangeland Ecology and Management, Texas A&M University, College Station, Texas 77843

[2] Corresponding author: Department of Ecology and Evolutionary Biology, Rice University, 6100 Main St., Houston, Texas 77005 USA; (713) 348-5954; FAX (713) 348-5232; e-mail: siemann@rice.edu

ponent of biodiversity on global and local scales (Wilson, 1988; Price, 1997). Although the effects of fire and nutrient enrichment upon invertebrates have been individually documented to differing extents (*e.g.*, Hansen, 1986; Strauss, 1987; Haddad *et al.*, 2000; Harper *et al.*, 2000), they have not previously been tested together.

Fire can impact arthropods directly through differential mortality and changes in phenology (Swengel, 2001; Blanche *et al.*, 2001). Arthropods have a number of adaptations that allow them to coexist with fire (Frost, 1985), for example, avoidance in space (*i.e.*, being able to flee or seek shelter) and escape in time (*i.e.*, being in the physiologically least susceptible stage at the time of burn). Despite such adaptations to fire there may be substantial short-term declines of arthropod species locally because of fire (*see* Swengel, 2001 for review) even though fire may be necessary to maintain the habitat. In that case, the short-term and long-term effects of fire on arthropod communities may differ (Siemann *et al.*, 1997). However, if fire promotes only habitat generalists then high arthropod diversity may still not achieve conservation goals.

Fire may indirectly influence arthropod communities by changing environmental conditions or altering the plant community. Arthropod communities are sensitive to changes in vegetation composition, structure and quality (Warren *et al.*, 1987; Reiske *et al.*, 2002). As a result, when fire or other factors impact the plant community by changing environmental conditions the arthropod community may also be affected. Because woody seedlings and saplings are especially vulnerable to fire, fire reduces woody plant abundance and can slow vegetative succession (Gibson and Hulbert, 1987; Anderson, 1990; Covington *et al.*, 1997). Fire also has the ability to increase net primary productivity, increase plant species richness and may alter plant tissue quality, structure and growth (Force, 1981; Collins, 2000). Changes in abiotic factors may cascade up the food chain to influence not only plants and herbivores, but higher trophic levels, such as predators and parasites, as well (Hunter and Price, 1992).

Previous studies on the effects of fire on arthropods have shown conflicting results (Frost, 1985; Blanche *et al.*, 2001; Panzer, 2002). Insect abundance and diversity have been shown to decrease (*e.g.*, Dietrich *et al.*, 1998; Anderson *et al.*, 1989), increase (*e.g.*, Force, 1981; Hanson, 1986) or show no response (*e.g.*, Hansen, 1986; Friend and Williams, 1996) to fire (also *see* Panzer, 2002 for further comparisons). Possible reasons for these variable results are differences in timing and scale of burning and the composition of local arthropod and plant communities. Recent analyses suggest that the use of fire to manage grasslands may lower arthropod species diversity and alter community structure (Reed, 1997; Dietrich *et al.*, 1998; Panzer and Schwartz, 2000), especially in smaller populations (Harper *et al.*, 2000; Panzer and Schwartz, 2000). In addition, in some cases the effects of fire on individual species may be as great a concern as the effects of fire on overall diversity (Dietrich *et al.*, 1998)

Factors other than fire, such as changes in soil nutrient availability, may indirectly affect arthropod communities through changes in the plant community and/or environmental conditions. Nitrogen deposition from sources such as high-intensity agriculture and air pollution (Galloway *et al.*, 1995; Vitousek *et al.*, 1997) can cause increases in productivity, decreases in plant species richness, changes in plant tissue quality and community composition (Faeth *et al.*, 1981; Strauss, 1987; Tilman, 1987; Haddad *et al.*, 2000). In short term studies, nitrogen addition typically increases insect species richness (Sedlacek *et al.*, 1988; Siemann, 1998) perhaps in response to transient changes of perennial vegetation but it may decrease insect species richness over longer time scales (Waring and Cobb, 1992; Haddad *et al.*, 2000). Because the effects of fire and nutrient addition on plants and arthropods may interact via mechanisms such as higher fuel loads resulting in greater fire intensity, the effect of either factor in isolation may be a poor predictor of arthropod diversity when both factors vary.

We manipulated fire and soil fertility in a tallgrass prairie to investigate their effects upon arthropod species richness and abundance directly and indirectly via changes in the plant community and to test the following predictions: (1) Plots treated with fertilizer will have increased plant productivity and increased insect diversity and (2) Fire will decrease woody plant species, and arthropod diversity will not be significantly affected in burned plots due to immigration from nearby populations.

METHODS

Study site.—The experiment was established at the University of Houston Coastal Center (hereafter ''UHCC'') located 50 km south of Houston, Texas. UHCC is a 374 ha research area managed for the restoration of native tallgrass coastal prairie in areas invaded by Chinese tallow (*Sapium sebiferum* L.) and other woody species (plant nomenclature follows Hatch *et al.*, 1990). The study site area is dominated by grasses with *Schizachyrium scoparium* (Michx.), *Spartina patens* (Ait.) and *Tripsacum dactyloides* (L.), predominating. Primary forb species are *Helianthus angustifolius* (L.), *Agalinis heterophylla* (Nutt) and *Euthamia leptocephala* (Torr. & Gray). Woody plants especially *S. sebiferum* and *Rubus riograndis* (Michx.) are also common. The topography is flat and the soils are Lake Charles clay, with a clay content of 40–60%. The average temperature is 20.9 C, with average annual rainfall (1070 mm) distributed fairly evenly throughout the year (driest average month – Mar. 56 mm; wettest average month – Sep. 150 mm). Management of the prairie to exclude further Chinese tallow invasion is accomplished through frequent mowing and more recently, controlled burning. Areas that are not mowed or burned are monospecific forests of Chinese tallow (Siemann and Rogers, 2006). Mowing was stopped in the experimental area 1 y before the experiment began.

Experimental design.—Twenty-four 100 m^2 study plots were established in UHCC prairie in Feb. 2000 and assigned two treatments in a completely randomized, full factorial design (four replications; × three fire treatments, × two fertilizer treatments). The fire treatments were: burned annually (in 2000, 2001), burned once (in 2000) or unburned. The fertilization treatments were made up of: nitrogen (8 $g/m^2/y$), phosphorus (5 $g/m^2/y$) and potassium (3 $g/m^2/y$) added or no nutrient addition. Plots were burned in late Feb. Fertilizer was added in Apr. and Jun. Fertilizer pellets were spread evenly a day before forecast rain. Maximum temperature at ground level within plots during fires was measured with two tiles that had heat sensitive stickers (Omega Engineering Inc., Stamford, CT). Alleys were mowed and maintained to a width of three meters to create areas of negligible influence between the experimental plots.

Arthropod sampling.—Arthropods were sampled four times during the 2001 growing season (Apr. 3, May. 9, Jun. 14 and Jul. 25) using a sweep net (38 cm diameter) at approximately the same time of day (mid-morning 9–11 a.m.) and similar weather conditions (sunny, warm and low wind). After 20 sweeps in a plot, the net contents were emptied into a plastic bag. The bag was subsequently frozen, and the arthropods were sorted, pinned and identified using a microscope. Specimens were identified to family, and to genus, species or morphospecies within family (arthropod nomenclature follows Arnett, 1993). Whereas sweep sampling does not sample all arthropods in a community, community measures obtained from sweep netting have been shown to be highly correlated with arthropods sampled by other methods in grasslands (Siemann, 1998; Siemann *et al.*, 1997). Sweep net sampling provides a good measure of relative abundance and relative species richness (Evans *et al.*, 1983; Evans, 1988) and has been widely used.

Vegetation measurements.—Floristic composition was determined from the relative cover of species for each whole 100 m^2 plot. This was done in mid-Sep. near the end of the growing season (2000, 2001, 2002). Percentage of woody species and effective plant species richness were calculated from the floristic cover data. Biomass (aboveground peak) was estimated from light measurements at ground level and regressions between light at ground level and above-ground biomass. The biomass model was specifically developed for the local tallgrass prairie based upon previous years of calibrating the relationship. Light penetration was determined using an Accupar Ceptometer (Decagon Devices Inc, Pullman WA, USA). Using the plant survey data, the abundances of plant functional groups were determined.

Analyses.—Four metrics were calculated for arthropods in each plot: average number of species in each sampling period (*i.e.*, average species richness); average effective species richness in each sampling period ($e^{H'}$ where H' is Shannon diversity index); total species richness over the growing season; and total abundance summed across all samples. We included all arthropod life stages (adult, nymph). Because plots may differ in species turnover, average and total species richness are different measures of diversity that give different insights into the effects of fire or fertilizer on the arthropod community.

Repeated measures analysis of variance (ANOVA) was used to include the seasonal dynamics of arthropod populations throughout the growing season. The repeated measures ANOVAs investigated whether the abundance and species richness of arthropods were responsive to fire (annual, once, unburned) or fertilization (yes, no), varied with time (April, May, June, July) or depended on interacting effects. Repeated measures ANOVAs were performed for the response variables; total arthropod species richness, total arthropod abundance, species richness and abundance at the taxonomic level of order and the 30 most common (abundant) families. Only orders with a minimum abundance of 20 individuals were examined statistically. Orders that were excluded and their relative abundance (percentage) were Dictyoptera (<1%), Odonata (<1%), Neuroptera (<1%) and unknowns (1%). In addition, ANOVA was used to determine the significance of treatments and arthropod abundance and species richness on light measurements, plant species richness, mass and plant functional groups for the 2001 data. Fishers PLSD, post hoc test were performed for all ANOVAs and repeated measures ANOVAs (StatView, Version 5. SAS Institute Inc., Cary, NC, USA.).

As we performed multiple comparisons, we applied a Bonferroni correction, which is considered conservative, and a less conservative Finner correction (reviewed in Brown and Russell, 1997). The one-step Bonferroni P-value adjustment algorithm used was: Reject H[i] if $\text{p-adjust}[j] = n*p[j] \leq \text{alpha}$ for all $j \leq i$. The step-down Finner P-value adjustment algorithm used was: Reject H[i] if $\text{p-adjust}[j] = 1 - (1 - p[j])^{(j/n)} \leq \text{alpha}$ for all $j \leq i$. Where: n = number of P-values; alpha = nominal significance level; p[i] = i^{th} smallest P-value; p-adjust[i] = adjusted value of p[i]; H[i] = hypothesis corresponding to the i^{th} P-value.

Simple regression and Spearman's Rank Correlation were used to examine correlations among plant species richness, mass, light, arthropod abundance and species richness.

Path analysis was used to examine the relative strengths of direct effects of fire vs. indirect effects of fire and fertilization mediated through changes in vegetation. Path analyses were performed for average effective arthropod species richness, average arthropod species richness, total arthropod species richness and total arthropod abundance. Each path diagram included paths for direct effects of fire on the arthropod variables, plant diversity (effective plant species richness) and plant community composition (percent cover of woody plants) together with paths for indirect effects of fire and fertilization mediated through changes in plant diversity and plant community composition (seven paths total). Additional path analyses were performed for arthropod order's species richness and abundance, using annual fire, woody plants and plant effective species richness as the predictors. Standardized multiple regression coefficients (parameter estimates divided by the ratio of the standard deviations of the response variable and predictor) were used to determine the magnitude and significance levels of each of the paths. In path diagrams, the magnitudes of direct effects are simply the coefficients for the direct paths, the magnitudes of indirect effects are the products of each direct coefficient along a path, the total magnitude of indirect effects is the sum of the magnitudes of each individual path and the sum of all possible paths between two variables is equal to their simple correlation coefficient (SAS/STAT, Version 8. SAS Institute Inc., Cary, NC, USA.).

RESULTS

Sweep net sampling caught a total of 10,348 individuals in 13 orders (Table 1). The most numerous (abundant) orders collected were Acari (30%), Homoptera (26%), Diptera (13%) and Thysanoptera (12%). The most diverse (species rich) orders were Homoptera (27%), Diptera (18%), Hymenoptera (16%) and Acari (10%). Plots averaged 46 species per sample (range 28–56) and 104 species (range 67–125) and 433 individuals (range 206–727) for the entire season. Unknown arthropods that we could not identify to order accounted for 54 individuals (1%), mainly due to bad condition or immaturity. Vegetation samples included 97 plant species with an average of 31 species per plot (range 24–42). Mean burn temperature at ground level was 280 C (SD = 48; range 110–300) for the 2000 burn and 235 C (SD = 70; range 110–300) for the 2001 burn.

Arthropod order responses.—Of the 10 orders that were analyzed by repeated measures ANOVAs, only four orders (whose abundance represented 26% of the total sample, Tables 1, 2) responded to the experimental manipulations of fire and fertilizer by changes in species richness, and only three orders (representing 42% abundance of orders sampled) by changes in abundance (Table 2). The P-value for the direct effect of fire on total arthropod species richness was $P = 0.06$ ($F_{2,18} = 3.2$) with the lowest abundances in the never burned plots. Orders that fire or fertilizer had no influence upon were Acari, Coleoptera, Hemiptera and Orthoptera.

Arthropod family responses.—Of the 30 most common families sampled, Oripodidae (Acari, mites) were the most abundant (abundance = 2036), although species richness was comparably low and dominated by morphospecies (species richness = 6) (Table 1). Other frequently sampled families were Entomybryidae (Collembola, springtails) and Chironomidae (midges), Chloropidae (frit flies) and Culicidae (mosquitoes) from the order Diptera (flies). From the Homopteran order, Aphididae (aphids), Cicadellidae (leafhoppers), Delphacidae and Psyllidae were all quite abundant and reasonably diverse. Hymenopterans from the Superfamily Chalcidoidea (Encyrtidae, Eulophidae, Eupelmidae, Eurytomidae, Mymaridae, Pteromalidae and Trichogrammatidae) were often encountered in samples, yet were never abundant. Formicidae (ants) were also regularly caught in samples, but were also never abundant. Tettigoniidae (Orthoptera, long horned grasshoppers) were more commonly encountered than Acrididae (short horned grasshoppers). Thripidae (Thysanoptera, thrips) were often found in samples and were, on occasion, very abundant.

Arthropod families had various responses to fire and fertilization. Over three-quarters of the most common families investigated (77%) showed no response to treatments (24 families species richness and 22 families abundance) (Table 3). When interactions with

TABLE 1.—Total abundance and species richness of each taxonomic order and the 30 most common families caught throughout the sampling year. Abundance was calculated as the total number of individuals within each order and family summed over all plots, over the year. Species richness for order and family is the number of different species or morpho-species encountered over the year. Trophic levels are assigned at the taxonomic level of family

Order family	Trophic level	Abundance	Species richness
Acari (mites)		**3070**	**32**
Oripodidae	Mostly detritivorous	2036	6
Coleoptera (beetles)		**236**	**69**
Chrysomelidae (leaf beetles)	Herbivore	63	21
Curculionidae (snout beetles)	Herbivore	68	12
Collembola (springtails)		**346**	**2**
Entomybryidae	Detritivore	346	2
Dictyoptera		**15**	**1**
Diptera (flies)		**1391**	**115**
Chironomidae (midges)	Fungivore	214	12
Chloropidae (frit flies)	Fungivore	679	20
Culicidae (mosquitoes)	Various	128	6
Dolichopodidae (long legged flies)	Mostly predaceous	65	12
Scatopsidae (scavenger flies)	Detritivore	43	3
Hemiptera (true bugs)		**408**	**46**
Lygaeidae (seed bugs)	Herbivore	44	7
Miridae (leaf or plant bugs)	Herbivore	43	3
Homoptera (leaf hoppers)		**2704**	**117**
Aleyrodidae (whiteflies)	Herbivore	204	4
Aphididae (aphids)	Herbivore	914	16
Cicadellidae (leaf hoppers)	Herbivore	301	20
Delphacidae	Herbivore	188	18
Membracidae (treehoppers)	Herbivore	71	4
Psyllidae	Herbivore	237	5
Hymenoptera (wasps and ants)		**702**	**190**
Encyrtidae	Parasitic	65	23
Eulophidae	Parasitic	98	22
Eupelmidae	Parasitic	33	15
Formicidae (ants)	Various	110	6
Mymaridae (fairyflies)	Parasitic	51	14
Platygasteridae	Parasitic	50	6
Pteromalidae	Parasitic	59	28
Trichogrammatidae	Parasitic	33	10
Lepidoptera (moths)		**27**	**12**
Neuroptera (lacewings)		**3**	**2**
Odonata (damselflies)		**7**	**1**
Orthoptera (grasshoppers)		**168**	**22**
Acrididae (short horned)	Herbivore	30	5
Tettigoniidae (long horned)	Herbivore	133	6
Thysanoptera (thrips)		**1217**	**19**
Aeolothripidae	Various	40	3
Phloeothripidae (tube-tailed thrips)	Various	199	3
Thripidae (common thrips)	Herbivore	834	6
Unknown		**54**	**—**
TOTAL		**10348**	**630**

TABLE 2.—Significant responses from repeated measures ANOVA showing positive (+) and negative (−) effects and interactions of treatments on order abundance and species richness. F-values in bold indicate significance ($p \leq 0.05$) after classic Bonferroni, and F-values underlined in italic indicate significance ($p \leq 0.05$) after a modified Bonferroni (Finner). *** denotes significance $p \leq 0.001$; **$p \leq 0.01$; *$p \leq 0.05$; before the Bonferroni or modified (Finner) Bonferroni correction. Degrees of freedom and residuals are as follows: fire and fire × fertilizer $F_{2,18}$; fertilizer $F_{1,18}$; time × fertilizer $F_{3,54}$; time × fire, and time × fire × fertilizer $F_{6,54}$

Order	Species richness		Abundance	
	F-value	Effect	F-value	Effect
Acari	3.334*	time × fertilizer		
Coleoptera	*3.308***	time × fire	*3.018**	time × fire
Collembola	**6.8****	fire+		
	*2.92**	time × fire	2.348*	time × fire
Diptera	**8.3****	fire+		
Homoptera			3.6*	fire+
Hymenoptera	4.4*	fire(once) × fertilizer+		
Lepidoptera	*8.9***	fertilizer−	*8.9***	fertilizer−
Thysanoptera	**5.643****	time × fertilizer	4.0*	fire− × fertilizer−
	2.616*	time × fire × fertilizer		
Total Arthropods	**78.9*****	time+	**42.0*****	time+

time were included, the species richness and abundance of 12 families and 11 families responded, respectively. After the classic Bonferroni correction, only two species richness and abundance responses retained significance ($P \leq 0.05$), and after the modified Bonferroni an additional one species richness response and three abundance responses were significant ($P \leq 0.05$).

Of the 30 most common families, treatments affected the abundance or species richness of five and seven families, respectively, at some point in the growing season (*i.e.*, significant time*treatment term, Table 3). Most of these families varied with time as well but only one family (Entomobryidae) varied with fire as a main effect (species richness and abundance) and only one family (Membracidiae) varied with fertilization as a main effect (abundance). Interestingly, a significant interaction between time and fire (nine significant results including species richness and abundance results) was more frequent than either the interaction of time and fertilizer (three significant results), or time, fire and fertilizer (three significant results).

Plant functional groups.—Of the total of 97 different plant species identified at the prairie study site, grasses (51%) dominated the total absolute cover, whereas forbs (29%) and woody vegetation (20%) were less apparent in the community. Unknown species represented less than 1% of the community (0.004%). The four most frequently encountered species (that each represent more than 10% and together equate 46%) were *Schizachyrium scoparium* (little bluestem), *Spartina patens* (salt meadow cordgrass) and *Tripsacum dactyloides* (Eastern gamma grass). The aforementioned grass species encountered are considered high quality climax species in coastal tallgrass prairie. Common forbs included *Helianthus angustifolius* (swamp or narrowleaf sunflower), *Agalinis heterophylla* (prairie false foxglove), *Solidago canadensis var. scabra* (Torr. & Gray) (tall goldenrod), and the most dominant woody species were *Rubus riograndis* (southern dewberry) and *R. louisianus* (Bergber) (sawtooth blackberry). Only two exotic species were commonly encountered: *Lonicera japonica* (Thunb.) (Japanese honeysuckle) and *Sapium sebiferum* (Chinese tallow).

TABLE 3.—Significant treatment effects from repeated measures ANOVA on the 30 most common (abundant) arthropod families total abundance and species richness within the 2001 sampling season. Families that displayed no response are not included. Significant responses indicate positive (+) or negative (−) relationship with specific treatment effects (such as fire once), and interaction effects from treatments. Degrees of freedom and residuals are as follows: fire and fire × fertilizer $F_{2,18}$; fertilizer $F_{1,18}$; time × fertilizer $F_{3,54}$; time × fire, and time × fire × fertilizer $F_{6,54}$. F-values in bold indicate significance ($p \leq 0.05$) after classic Bonferroni, and F-values underlined in italic indicate significance ($p \leq 0.05$) after a modified Bonferroni (Finner). *** denotes significance $p \leq 0.001$; $^{**}p \leq 0.01$; $^{*}p \leq 0.05$ before the Bonferroni or modified (Finner) Bonferroni correction

Order	Family	Species richness		Abundance	
		F-value	Effect	F-value	Effect
Coleoptera	Chrysomelidae	2.523*	time × fire	__3.998__**	time × fire
Collembola	Entomybryidae	__6.8__**	fire(once)	4.1*	fire(once)
		_2.92*_	time × fire	3.716*	time × fertilizer
				2.292*	time × fire × fertilizer
Diptera	Dolichopodidae	__16.0__***	fire+	__13.2__***	fire+
Homoptera	Membracidae	_8.5**_	fertilizer+	_4.8*_	fire+
				__11.4__**	fertilizer+
Homoptera	Aphididae	2.83*	time × fire		
Homoptera	Cicadellidae			2.559*	time × fire
Homoptera	Membracidae			_2.907*_	time × fire
				__6.996__***	time × fertilizer
Hymenoptera	Encyrtidae	6.3*	fertilizer−	5.0*	fertilizer−
		4.0*	fire × fertilizer	3.8*	fire × fertilizer
Hymenoptera	Eulophidae			_7.5*_	fertilizer +
Hymenoptera	Eupelmidae	4.1*	fire−		
Hymenoptera	Mymaridae	4.2*	fire × fertilizer	4.2*	fire (once)
				5.0*	fire × fertilizer
Hymenoptera	Pteromalidae			3.7*	fire × fertilizer
		_2.991*_	time × fire	_3.169**_	time × fire
Orthoptera	Tettigoniidae	2.436*	time × fire × fertilizer		
Thysanoptera	Phloeothripidae	3*	time × fertilizer		
Thysanoptera	Thripidae	__3.83__**	time × fire	_6.1**_	fire × fertilizer
		_2.908*_	time × fire × fertilizer		

In a simple regression, arthropod species richness did not depend on plant species richness ($r^2 < 0.01$; $F_{1,22} = 0.1$; $P = 0.71$). Furthermore arthropod abundance was not correlated to plant species richness ($r^2 = 0.12$; $F_{1,22} = 2.9$; $P = 0.12$). Light and biomass had no relationship to arthropod species richness or abundance.

Potential mechanisms.—Path analysis indicated that percent of woody plant cover increased with fertilization and decreased with burning (Fig. 1). All three metrics of arthropod diversity analyzed (monthly effective, monthly average and whole season) decreased with increasing woody plant cover but were independent of fire and plant diversity. Total arthropod abundance did not depend on any of the predictors (Fig. 1). Fire had a significant negative effect ($t = 2.35$, 21 df, $P = 0.03$, coefficient $= -0.43$) on the percentage of woody vegetation and fertilizer had a positive effect ($t = 1.79$, 21 df, $P = 0.09$, coefficient $= 0.33$) on woody vegetation (Fig. 1). Subsequently, the percent of woody vegetation negatively affected the monthly effective arthropod species richness ($t = 1.95$, 20 df, $P = 0.07$, coefficient $= -0.42$) and whole season arthropod species richness ($t = 1.86$, 20 df, $P = 0.07$, coefficient $= -0.40$). The percent of woody plant cover also showed a

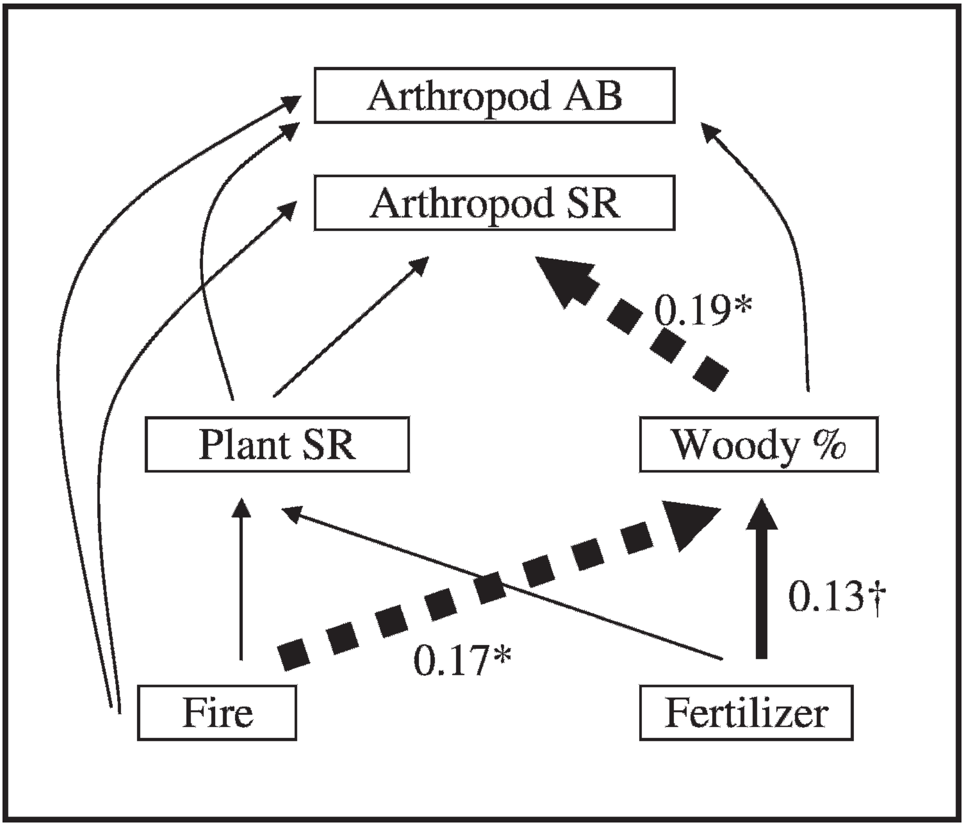

FIG. 1.—Path diagram showing the relative strengths of direct effects of fire and indirect effects of fire and fertilization treatments via changes in plant (effective) species richness and % woody cover on average monthly arthropod species richness (SR) and whole season arthropod abundance (AB). Dotted lines indicate negative relationships and solid lines denote positive relationships. Values next to the lines show the strength of effects in terms of the number of standard deviation changes in the response variable from each standard deviation change in the predictor where the thickness of the line indicates the magnitude of the path coefficient (Significance levels: *$p < 0.05$, †$p < 0.1$)

significantly negative effect ($t = 2.29$, 20 df, $P = 0.03$, coefficient = -0.47) on monthly arthropod species richness. Effective diversity and evenness (J) results did not differ from one another.

Annual fires directly increased ($P \leq 0.05$) the abundance of Coleoptera (coefficient = 0.44) and Homoptera (coefficient = 0.42) and the species richness of Acari (coefficient = -0.42). Hemiptera abundance (coefficient = -0.42) and species richness (coefficient = -0.41) decreased with plant effective species richness. Collembola and Diptera abundance (coefficient = -0.48, -0.39, respectively) and Acari and Homoptera species richness (coefficient = -0.41; $t = -3.85$, 20 df, $P = 0.001$, coefficient = -0.68 respectively) each decreased in plots with high percentages of woody species, however Hemiptera abundance (coefficient = 0.44) increased. No other paths were significant predictors of the abundance or species richness of arthropod orders. After correction for multiple comparisons, only the effect of plant diversity on Hemiptera abundance and the effect of woody plant abundance on Homoptera species richness were significant.

DISCUSSION

Fire and fertilizer influenced arthropod community structure primarily through changes in the relative abundance of woody plants (Fig. 1). Fire and fertilizer had opposing effects upon woody plant cover; fertilization increased woody plant abundance, whereas fire suppressed woody plants. The high relative allocation of woody plants to aboveground growth likely contributes to these contrasting responses. Fertilization favors plants with high aboveground allocation by increasing the importance of competition for light but fire has a strong negative effect on these same plants that lose proportionally more biomass to fires (Evans, 1984; Gibson and Hulbert, 1987; Anderson, 1990; Collins, 2000; Siemann and Rogers, 2003). Since direct effects of fire on arthropod species richness that might be caused by increases in arthropod mortality and/or increases in emigration were not evident in any analyses, changes in the abundances of plant functional groups appeared to dominate the responses of arthropods to fertilization and fire (Fig. 1).

Effects of fire on plants.—Even though fire often has been associated with higher plant diversity (Force, 1981; Fynn *et al.*, 2004), it did not affect plant diversity in this study (Fig. 1). This may be due to the short duration of the experimental treatments (two growing seasons) prior to arthropod sampling. Indeed, by the third year of this experiment (2002), fertilized plots that were not burned had lower plant diversity than those that were annually burned (50% higher when burned). However, the extreme increases in woody plant abundance in fertilized, unburned plots (mean percent woody cover = 83%) compared to unfertilized, annually burned plots (mean percent woody cover = 8%) did not allow representative arthropod community data to be collected in the third year. It does suggest, however, that the results we found for vegetation and arthropods in the second year of the experiment are conservative compared to the long-term changes in vegetation and grassland arthropods in response to fire and fertilizer treatments.

Fire effects on arthropods.—Fire had no direct negative effects on arthropod abundance or diversity at the community level (Fig. 1), possibly due to sufficient recovery time between burning (first burn was in Feb.) and first sampling (Apr.). In this southern grassland, vigorous spring growth occurs by early Mar. In addition, the small scale (100 m^2) of our fires may have contributed to the small direct negative effects of fire on arthropods we observed because arthropods escaping fires would not require long distance movement and the recolonization of plots may have been more rapid than in a large scale fire (Swengel, 2001). Compared to the scale of management fires in this area (10 to 20 ha), these plots were quite small. In cases where particular species are of conservation concern, the response of arthropod diversity or abundance may not be the appropriate metric for deciding management methods.

Arthropod diversity did depend on plant functional composition (Symstad *et al.*, 2000). Plots dominated by herbaceous vegetation had higher arthropod diversity than those heavily invaded by woody plants (Fig. 1). It has been suggested that woody plants are a poor resource base for herbivores compared to grasses and forbs due to their generally lower nitrogen content, lower moisture and higher defense chemical levels (Mattson, 1980). However, we did not find lower abundances of arthropods in plots with a greater abundance of woody plants (Fig. 1), although, the lower abundance of Homoptera in woody dominated plots does suggest that some groups of herbivores were less abundant in such plots. The independence of arthropod abundance and woody plant dominance (Fig. 1) indicates that differences in sampling efficiency among the plots due to variations in plant architecture were not the cause of differences in arthropod diversity among plots.

Although a number of studies have shown arthropod diversity is positively correlated with plant diversity (*e.g.*, Murdoch *et al.*, 1972; Kirchner, 1977; Southwood *et al.*, 1979; Siemann *et al.*, 1998), path analyses showed arthropod diversity and abundance were independent of effective plant species richness in this study. This may be the result of the short duration of the experiment that did not allow arthropod diversity to adjust to changes in plant diversity. Alternatively, the small sizes of plots may not have represented populations, but rather temporary assemblages that reflected patch choices by arthropod species (Strong *et al.*, 1984; Price, 1997). However, the positive effect of burning could be strengthened if the plots were larger and the study was longer if the positive relationship between plant diversity and arthropod diversity is important for determining arthropod diversity.

This study detected few responses of arthropods at the taxonomic level of order to fire treatments. As the individual species within orders are diverse in their life histories, behaviors, feeding and physiology, this is not unexpected given no overall responses of arthropod abundance or species richness. Repeated measures ANOVAs indicated positive effects of burning upon Collembola and Diptera species richness, and Homoptera abundance (Table 2). There was no *a priori* reason to expect this set of responses so it is difficult to generalize from these idiosyncratic results.

Fertilizer effects on plants.—Fertilizer increased woody plant cover but had no effect on effective plant species richness. Fertilizer increased woody plant species such as *Rubus, Lonicera, Baccharis halimifolia* L. and *Sapium.* The magnitude of fertilizer's effect on woody plant cover was of marginal significance ($P = 0.1$), which was not surprising, since the effects of fertilizer on plant community composition and diversity are mediated through changes in colonization and extinction rates and the dynamics may be slow (Inouye and Tilman, 1988). Supporting this, plant data recorded from the third year of this experiment showed continued increases in woody vegetation ($P < 0.05$) and a further reduction in plant species richness ($P < 0.05$) in plots that had been fertilized.

Arthropod diversity did not increase with nutrient addition although we observed two positive responses at the taxonomic level of family (Membracidae, a herbivore; and Eulophidae, a tiny parasitic wasp). At the taxonomic level of order, fertilizer addition affected only Lepidopterans that had lower numbers in unfertilized plots. Overall, the general lack of fertilizer influence on herbivores (such as Homoptera, Orthoptera, Lygaeidae and Miridae) was somewhat unexpected given that (Waring and Cobb, 1992) found almost sixty percent of reviewed fertilization studies showed a positive response by herbivores.

The diversity or abundance of some arthropod groups, such as Hymenoptera species richness and Thysanoptera abundance, only responded to the combination of fire and fertilization treatments. Interactive effects that could have influenced these orders include fertilizer increasing plant productivity which causes more intense fires, contrasting effects on plant species composition and quality or factors that cascade up the food chain. However, achieving a mechanistic understanding of the interaction of treatments upon orders is likely more complex and group specific than we can infer from this experiment.

Responses of families within orders.—Responses of families indicated there were not uniform responses within orders. Indeed, there was significant variation in the responses of individual families within orders. For example, Diptera abundance and species richness had significant fire positive responses (Table 2), yet three Diptera families showed no response to fire (Table 3). Another example is Hymenoptera in which both Encrytidae and

Mymaridae exhibited a negative relationship to fertilized plots but Eulophidae had a positive relationship to fertilized plots. With these opposing effects within order, interpretation at higher taxonomic levels should be approached cautiously.

Conclusions.—Our results showed that fire was an effective management technique for plants and arthropods in grasslands because the treatments that reduced woody encroachment also encouraged higher arthropod diversity. In the absence of concerns about particular species or information regarding the regional rarity of different taxa, preservation of high diversity *per se* may be a good strategy. The combination of altered soil nutrient levels through natural or anthropogenic sources and fire had only weak effects upon the arthropod community. Although the small scale of these experimental burns suggests caution in extrapolating these results to larger scales, the incredibly rapid rate of woody encroachment in these prairies together with such strong positive results for arthropod diversity indicate that fire is an excellent tool for managing similar grasslands.

Acknowledgments.—We thank: L. Allain, G. Aumann, A. Awantang, T. Becker, B. Butterfield, C. Donahue, J. Elias, J. Ferris, J. Hammer, S. Hsia, J. Keay, V. Keener, R. Lankau, E. Loggins, D. Mee, C. Naficy, S. Nijjer, C. Smith, L. Urban and E. Wan for assistance; J. Jackman, J. Oswald, E. Riley, J. Woolley and W. Mackay for help with identifications; Texas A&M University Entomology department for use of their collections; two anonymous reviewers for helpful comments that improved this manuscript; US EPA (EPA R82-8903), NSF (DEB-9981654) and a Wray Todd fellowship (for MKH) for support; UHCC for access.

LITERATURE CITED

ANDERSON, R. C., T. LEAHY AND S. S. DHILLION. 1989. Numbers and biomass of selected insect groups on burned and unburned sand prairie. *Am. Mid. Nat.*, **122**:151–162.

———, ——— AND ———. 1990. The historic role of fire in the North American grasslands, p. 8–18. *In*: Wallace, L. L. and Collins, S. L. (eds.). Fire in tallgrass prairie ecosystems. University of Oklahoma Press.

ARNETT, R. H. 1993. American insects. A handbook of the insects of America North of Mexico. Sandhill Cranes Press, Gainesville, Florida.

BLANCHE, K. R., A. N. ANDERSEN AND J. A. LUDWIG. 2001. Rainfall-contingent detection of fire impacts: responses of beetles to experimental fire regimes. *Ecol. Appl.*, **11**:86–96.

BRAGG, T. B. AND L. C. HULBERT. 1976. Woody plant invasion of unburned Kansas bluestem prairie. *J. Range Manage.*, **29**:19–24.

BROWN, B. W. AND K. RUSSELL. 1997. Methods correcting for multiple testing: operating characteristics. *Stat. Med.*, **16**:2511–2528.

COLLINS, S. L. 2000. Disturbance frequency and community stability in native tallgrass prairie. *Am. Nat.*, **155**:311–325.

COVINGTON, W. W., P. Z. FULÉ, M. M. MOORE, S. C. HART, T. E. KOLB, J. N. MAST, S. S. SACKETT AND M. R. WAGNER. 1997. Restoring ecosystem health in ponderosa pine forests of the Southwest. *J. For.*, **95**:23–29.

DIETRICH, C. H., M. G. HARPER, R. L. LARIMORE AND P. A. TESSENE. 1998. Insects and fire: too much of a good thing? *Ill. Nat. Hist. Surv. Rep.*, No. **349**:4.

EVANS, E. W. 1984. Fire as a natural disturbance to grasshopper assemblages of tallgrass prairie. *Oikos*, **43**:9–16.

———. 1988. Grasshopper (Insecta: Orthoptera: Acrididae) assemblages of tallgrass prairie influences of fire frequency topography and vegetation. *Can. J. Zoo.*, **66**:1495–1501.

———, R. A. ROGERS AND D. J. OPFERMANN. 1983. Sampling grasshoppers (Orthoptera: Acrididae) on burned and unburned tallgrass prairie: night trapping vs. sweeping. *Environ. Entomol.*, **12**:1449–1454.

Faeth, S. H., S. Mopper and D. Simberloff. 1981. Abundances and diversity of leaf-mining insects on three oak host species: effects of host-plant phenology and nitrogen content of leaves. *Oikos*, **37**:238–251.

Force, D. C. 1981. Postfire insect succession in southern California chaparral. *Am. Nat.*, **117**:575–582.

Friend, G. R. and M. R. Williams. 1996. Impact of fire on invertebrate communities in mallee-heath shrublands of south-western Australia. *Pacific Conserv. Biol.*, **2**:244–267.

Frost, P. G. J. 1985. The response of savanna organisms to fire, p. 232–237. *In*: J. C. Tothill and J. J. Motts (eds.). Ecology and management of the worlds savannas. Australian Academy of Science, Canberra.

Fynn, R. W. S., C. D. Morris and T. J. Edwards. 2004. Effect of burning and mowing on grass and forb diversity in a long-term grassland experiment. *Applied Vegetation Science*, **7**:1–10.

Galloway, J. N., W. H. Schlesinger, H. Levy II, A. Michaels and J. L. Schnoor. 1995. Nitrogen fixation: anthropogenic enhancement-environmental response. *Global Biogeochem. Cy.*, **9**:235–252.

Gibson, D. J. and L. C. Hulbert. 1987. Effects of fire, topography and year-to-year climatic variation on species composition in tallgrass prairie. *Vegetatio*, **72**:175–185.

Haddad, N. M., J. Haarstad and D. Tilman. 2000. The effects of long-term nutrient loading on grassland insect communities. *Oecologia*, **124**:73–84.

Hansen, J. D. 1986. Comparison of insects from burned and unburned areas after a range fire. *Great Basin Nat.*, **46**:721–727.

Harper, M. G., C. H. Dietrich, R. L. Larimore and P. A. Tessene. 2000. Effects of prescribed fire on prairie arthropods: an enclosure study. *Nat. Area J.*, **20**:325–335.

Hatch, S. L., K. N. Ghandi and L. E. Brown. 1990. A checklist of the vascular plants of Texas, MP-1655. Texas Agricultural Experiment Station, College Station, Texas.

Hunter, M. D. and P. W. Price. 1992. Playing chutes and ladders: heterogeneity and the relative roles of bottom-up and top-down forces in natural communities. *Ecology*, **73**:724–732.

Inouye, R. S. and D. Tilman. 1988. Convergence and divergence of oldfield plant communities along experimental nitrogen gradients. *Ecology*, **69**:995–1004.

Kirchner, T. B. 1977. Effects of resource enrichment on the diversity of plants and arthropods in a shortgrass prairie. *Ecology*, **58**:1334–1344.

Mattson, W. J. 1980. Herbivory in relation to plant nitrogen content. *Ann. Rev. Ecol. Syst.*, **11**:119–161.

Murdoch, W., F. Evans and C. Peterson. 1972. Diversity and pattern in plants and insects. *Ecology*, **53**:819–829.

Panzer, R. 2000. Effects of management burning on prairie insect species richness within a system of small, highly fragmented reserves. *Biol. Conserv.*, **96**:363–369.

———. 2002. Compatibility of prescribed burning with the conservation of insects in small, isolated prairie reserves. *Conserv. Biol.*, **16**:1296–1307.

——— and M. Schwartz. 1998. Effectiveness of a vegetation-based approach to insect conservation. *Conserv. Biol.*, **12**:693–702.

Price, P. W. 1997. Insect Ecology. 3rd ed. John Wiley and Sons. New York.

Reed, C. C. 1997. Responses of prairie insects and other arthropods to prescription burns. *Nat. Area J.*, **17**:380–385.

Sedlacek, J. D., G. W. Barrett and D. R. Shaw. 1988. Effects of nutrient enrichment on the Auchenorrhyncha (Homoptera) in contrasting grassland communities. *J. Appl. Ecol.*, **25**:537–550.

Siemann, E. 1998. Experimental tests of effects of plant productivity and diversity on grassland arthropod diversity. *Ecology*, **79**:2057–2070.

———, J. Haarstad and D. Tilman. 1997. Short-term and long-term effects of burning on oak savanna arthropods. *Am. Mid. Nat.*, **137**:349–361.

——— and W. E. Rogers. 2003. Changes in resources under pioneer trees may facilitate tree invasions of grasslands. *J. Ecol.*, **91**:923–931.

——— and ———. 2006. Recruitment limitation, seedling performance and persistence of exotic tree monocultures. *Biol. Inv.*, **8**:979–991.

———, D. TILMAN, J. HAARSTAD AND M. RITCHIE. 1998. Experimental tests of the dependence of arthropod diversity on plant diversity. *Am. Nat.*, **152**:738–750.

SMITH, E. F. AND V. A. YOUNG. 1959. The effect of burning on the chemical composition of little blue stem. *J. Range Manage.*, **12**:134–140.

SOUTHWOOD, T. R. E., V. K. BROWN AND P. M. READER. 1979. The relationships of plant and insect diversities in succession. *Biol. J. Linnean Soc.*, **12**:327–348.

STRAUSS, S. Y. 1987. Direct and indirect effects of host-plant fertilization on an insect community. *Ecology*, **68**:1670–1678.

STRONG, D. R., J. H. LAWTON AND T. R. E. SOUTHWOOD. 1984. Insects on Plants. Community Patterns and Mechanisms. Harvard University Press, Cambridge.

SWENGEL, A. B. 2001. A literature review of insect responses to fire, compared to other conservation managements of open habitat. *Biodivers. Conserv.*, **10**:1141–1169.

SYMSTAD, A. J., E. SIEMANN AND J. HAARSTAD. 2000. An experimental test of the effect of plant functional group diversity on arthropod diversity. *Oikos*, **89**:243–253.

TILMAN, D. 1987. Secondary succession and the pattern of plant dominance along experimental nitrogen gradients. *Ecol. Monogr.*, **57**:189–214.

VITOUSEK, P. M., J. D. ABER, R. H. HOWARTH, G. E. LIKENS, P. A. MATSON, D. W. SCHINDLER, W. H. SCHLESINGER AND D. G. TILMAN. 1997. Human alteration of the global nitrogen cycle: sources and consequences. *Ecol. App.*, **7**:737–750.

WARING, G. L. AND N. S. COBB. 1992. The impact of plant stress on herbivore population dynamics, p. 167–226. *In*: Bernays, E. A. (ed.). Plant-insect interactions, vol. 4. CRC Press, Boca Raton, Florida.

WARREN, S. D., C. J. SCIFRES AND P. D. TEEL. 1987. Response of grassland arthropods to burning: a review. *Agric. Ecosyst. Environ.*, **19**:103–130.

WEISSER, W. W. AND E. SIEMANN. 2004. Insects and ecosystem function. Springer, Heidelberg.

WILSON, E. O. 1988. Biodiversity. National Academy Press, Washington, D.C.

SUBMITTED 19 JUNE 2005 ACCEPTED 20 JUNE 2006