TIMING OF PRESCRIBED BURNS AFFECTS ABUNDANCE AND COMPOSITION OF ARTHROPODS IN THE TEXAS HILL COUNTRY

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ABSTRACT—Prior research has demonstrated that fire can be an important structuring force for plant communities in prairies and grasslands. However, investigations of land-management techniques, such as prescribed fire, often overlook responses of local fauna, particularly the arthropods. In this study, we examined a previously unappreciated, although potentially important, component of fire ecology by asking, does the timing of prescribed burns alter community structure of arthropods? At a site in the Texas Hill Country, we used sweep-net sampling to collected arthropods from experimental plots that had been treated with a summer-burn or winter-burn regime. Summer-burn plots supported >170% more individual arthropods than winter burns. Although overall diversity of arthropods did not significantly differ between treatments, there were significantly more carnivorous arthropods and marginally more herbivorous arthropods after fire in summer relative to fire in winter. Effects of timing were particularly strong for Cicadellidae (leaf hoppers) and Tetragnathidae (long-jawed spiders). Our results demonstrate that timing of prescribed fire can substantially alter composition of resident communities of arthropods. Furthermore, these data highlight the importance of examining composition of the community, in addition to diversity indices, when assessing response of arthropods to land-management techniques.

RESUMEN—Investigaciones previas han mostrado que el fuego puede ser una fuerza importante en la estructuración de comunidades vegetales en praderas y pastizales. Sin embargo, las investigaciones acerca de las técnicas de manejo del terreno, tales como quemas prescritas, pasan por alto la respuesta de la fauna local, particularmente la de los artrópodos. En este trabajo, examinamos un previamente poco apreciado, aunque potencialmente importante, componente de la ecología del fuego, preguntando si la temporada de quemas prescritas altera la estructura de la comunidad de los artrópodos. En un sitio en Texas Hill Country, usamos redes de golpeo para colectar los artrópodos de las parcelas experimentales previamente tratadas con quemas invernales y quemas veraniegas. Las parcelas con quemas veraniegas mantuvieron >170% más individuos que las parcelas de quemas invernales. Aunque la diversidad total de artrópodos no difirió significativamente entre tratamientos, hubo significativamente más artrópodos carnívoros y, marginalmente, más artrópodos herbívoros en el tratamiento de quemas veraniegas relativas a las invernales. El efecto de la temporada de quema fue particularmente marcado para los Cicadélidos (chicharritas) y Tetragnátidos (arañas obitelas de grandes quelíceros). Nuestros resultados muestran que la temporada de las quemas prescritas puede alterar substancialmente la composición de las comunidades residentes de artrópodos. Así mismo, estos resultados destacan la importancia de examinar la composición de la comunidad, y no sólo los índices de diversidad, al evaluar la respuesta de los artrópodos a las técnicas de manejo del terreno.

Historically, fire, grazing by American bison (*Bison bison*), and seasonal extremes in temperature and precipitation regulated vegetation dynamics in North American prairies and grasslands (Parton and Risser, 1980; Risser and Parton, 1982; Diamond and Smeins, 1985; Gibson and Hulbert, 1987; Leach and Givnish, 1996; Collins et al., 1998; Knapp et al., 1999; Radeloff et al., 2000; Steinauer and Collins, 2001; Collins and Smith, 2006). Due to suppression of fire by humans, fire has been all but eliminated from most systems, and the brief but intense grazing by American bison has been replaced primarily by year-round grazing by domestic cattle. Studies have shown that elimination of periodic fires can lead to an annual loss of 0.45–1.03% of the original species of plants (Leach and Givnish, 1996). Alteration of historical disturbance factors has reduced ecological integrity of prairie ecosystems, with loss of herbaceous species and a general encroachment of woody species of plants. In attempts to reverse these changes, disturbance by fire frequently is re-introduced to sites under highly prescribed conditions.

Prescribed fire has long been used as a tool for the management and restoration of grasslands and savannas; enhancing production of grass, controlling growth and spread of woody species, and modifying composition of herbaceous species (Collins, 1992; Collins and Smith, 2006; see Collins and Wallace, 1990, for a review]. Although responses by plants to fire may depend on the season in which the burns occur (Towne and Owensby, 1984; Glenn-Lewin et al., 1990; Howe, 1994*a*, 1994*b*, 1995; Engle and Bidwell, 2001), prescribed fires generally increase biodiversity of plants (Copeland et al., 2002), limit the spread of some invasive plants (Emery and Gross, 2005), reduce encroachment by woody plants (Pendergrass et al., 1998), and increase reproductive fitness of some fire-adapted, native species of plants (Brewer, 2006).

In prairie and grassland systems, arthropods not only function as important pollinators and decomposers, but also dominate many communities in both biodiversity and abundance (Triplehorn and Johnson, 2005; Losey and Vaughan, 2006; Marshall, 2006). However, quantitative responses of arthropods to fire have received far less attention than responses of plants (Seastedt, 1984; Panzer, 1988; Schwartz, 1994; Swengel, 2001; Hartley et al., 2007). Occurrence of fire can affect arthropods directly through mortality (Swengel, 2001), or indirectly by inducing changes in composition or cover of plants. For example, if fire increases diversity of plants, the diversity of arthropods may increase in response to these indirect changes in the plant community, as has been shown in studies that directly manipulated diversity or species richness of plants (e.g., Siemann et al., 1998; Symstad et al., 2000). In addition, fires, particularly patchy ones, create a variety of habitats and refugia for fire-intolerant species of arthropods, and refugia can be critically important to survival, particularly for insects with limited dispersal ability (Panzer, 2003; Knight and Holt, 2005). With the exception of highly mobile arthropods, most population densities of arthropods decline on sites burned during the dormant-season (winter) the first year following a burn (Swengel, 2001). However, these insects often rebound to pre-burn or greater levels by the second year provided there are individuals that can re-colonize from unburned sites (Cancelado and Yonke, 1970; Evans, 1984; Anderson et al., 1989; but see Swengel, 1996, who found adverse effects from dormant season fires on prairie specialist butterflies lasting 3–5 years). In addition to fire, timing of burns may also influence arthropod communities, just as timing can be important in structuring the composition of vegetation.

In the Texas Hill Country, historical wildfires were likely most common during the growing season, when frequencies of cloud-to-ground lightning strikes are at their highest (Smeins, 1982; Higgins, 1984). In addition to natural fires, historic burning by Native Americans would have increased frequency of fires, as well as introduced fire to new locations (Smeins, 1997). Current management techniques primarily use dormant-season (winter) fire to encourage productivity of warm-season (C_4) grasses, and for convenience and perceived safety (Copeland et al., 2002).

In ecosystems of the Texas Hill Country, appropriately timed burns may help control invasions by plants. For example, King Ranch bluestem (*Bothriochloa ischaemum*) is an invasive grass from Central Europe and Asia that can constitute 60–80% of the canopy cover when untreated. This invader was significantly reduced by summer (growing-season) fire (Simmons et al., 2007). In an ongoing study (M. T. Simmons and S. Windhager, unpublished data) that examines how timing of prescribed fire affects herbaceous species of plants, preliminary data indicate that annual productivity of plants is higher, and diversity of plants is lower on winter burns compared to summer burns. Furthermore, responses by plants appear to be species specific. For example, native firewheel (*Gaillardia pulchella*) is the dominant spring forb on winter burns and untreated prairie, whereas native black-eyed Susan (*Rudbeckia hirta*) dominates summer burns (M. T. Simmons and S. Windhager, unpublished data).

Although some studies have compared richness, abundance, and diversity of arthropods

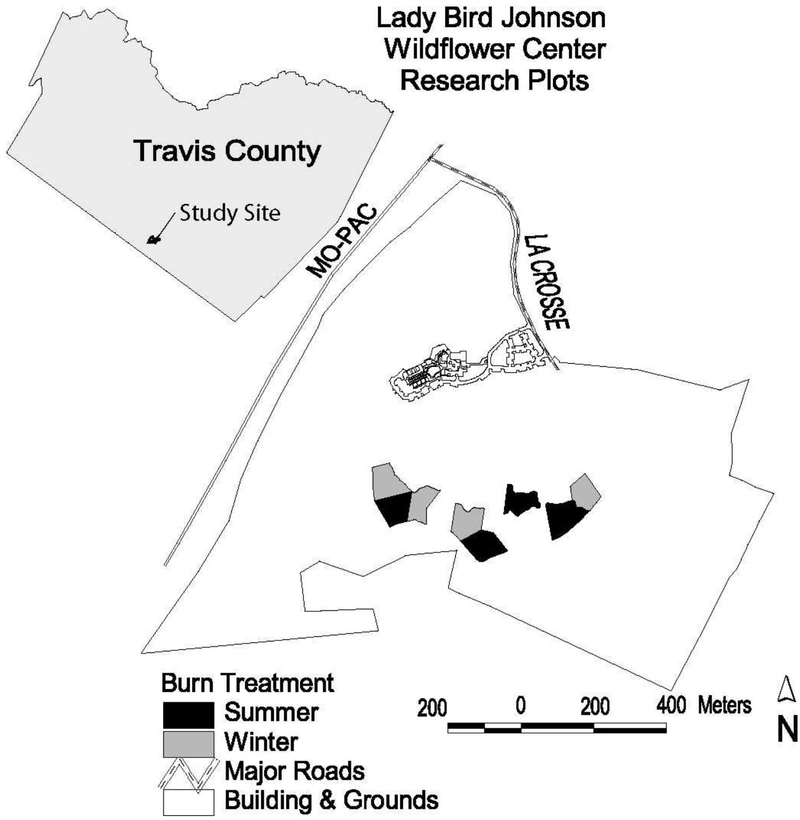

FIG. 1—Locations of summer-burn and winter-burn plots sampled in grasslands of the Texas Hill Country at Lady Bird Johnson Wildflower Center, near Austin, Travis Co., Texas.

between burned and untreated areas (Siemann et al., 1997; Harper et al., 2000; Panzer, 2002; Hartley et al., 2007), to our knowledge, no study has explored whether timing of fire affects arthropods. Because timing can significantly affect composition of plants in the Texas Hill Country, timing may indirectly influence communities of arthropods, as arthropods often track changes in composition, structure, and quality of plants (e.g., Siemann et al., 1998; Symstad et al., 2000). Here, we asked the question, does the timing of prescribed burns (winter or summer) affect abundance, richness, evenness, or diversity of arthropods? Because summer burns significantly reduce canopy cover of the invasive warm-season grass *B. ischaemum* and potentially promote diversity of native plants, we expected that abundance, diversity, and richness of arthropods would be greater in summer burns relative to winter burns.

MATERIALS AND METHODS—We conducted this study at the Lady Bird Johnson Wildflower Center, an organized research unit within the University of Texas at Austin, located southwest of Austin, Travis Co., Texas (30°11′7.35″N, 97°52′27.73″W). We collected arthropods on 17 February 2007, a sunny, windy day with a mean temperature of ca. 18°C at time of collection. The Lady Bird Johnson Wildflower Center has maintained 64.7 ha of experimental burn, mow, and control plots for the past 6 years. There are six plots each of winter, summer, and autumn burns. Each plot is 0.6 ha in size and treatments were assigned at random. For each plot, burns have been performed 3 times during the past 6 years (2001, 2002, and 2004).

We compared four summer-burn and four winter-burn plots (Fig. 1). Insects were collected using canvas sweep nets (diameter = 30 cm). Sweep-netting samples only a subset of arthropods in a community, but this method of collection correlates with community measures obtained from other methods for sampling arthropods and has been used widely (Siemann et al., 1997). In each plot, a single collector used two linear transects of 30 net-strokes each. Transects began ≥1.5 m from the edge of the plot. Contents of the sweep net were emptied into a plastic bag after each transect. We collected a total of 16 bags, 8 from summer-burn plots and 8 from winter-burn plots. All samples were collected 1100–1430 h. After collection, bags were frozen. All arthropods >2 mm in length (including wings) were thawed, sorted to morphospecies, and counted.

All morphospecies were keyed to order and family using Marshall (2006) and Triplehorn and Johnson (2005). We classified damaged specimens that could not be identified as unidentifiable, assigned them to order when possible, and included them in calculations of abundance, richness, evenness, and diversity. These included ca. 2% of individuals collected. When possible, insects were classified as carnivores (predators and parasites) or herbivores according to feeding habits of their family as described by Triplehorn and Johnson (2005). We calculated diversity of morphospecies using Hurlbert's PIE (Hurlbert, 1971), and evenness of morphospecies using the Shannon evenness index (Begon et al., 1996). Additionally, we examined abundance of individuals for each of the three most commonly collected families of arthropods (Cicadellidae, Tetragnathidae, and Oxyopidae).

We analyzed effects of timing of burn using mixed-model ANOVA, with plot (nested within burn treatment) as a random effect and timing of burn (winter or summer) as a fixed effect (SAS Institute, Inc., version 9.1, Cary, North Carolina, 2004). Richness, total abundance, and abundance of herbivores were log transformed to meet assumptions of normality of residuals and homogeneity of variances. Normality of residuals could not be achieved by transformations of abundance of Cicadellidae or Hurlbert's PIE; these responses were rank transformed to apply non-parametric analyses following Conover and Iman (1981). Analyses of all other response variables satisfied assumptions of normality and homogeneity without transformation.

Results—Sweep-net sampling yielded 245 individuals, representing 7 orders, 26 families, and 46 morphospecies. There were five individuals in unknown families, three of which were also of unidentifiable orders, due to damage caused by sweep-net sampling (Table 1).

Timing of burns had strong effects on abundance and composition of arthropods. There were >170% more total individuals in summer-burn than winter-burn plots (Fig. 2A, Table 2, $P = 0.014$). The statistical model (including treatment and plot) explained substantial variation in total abundance ($r^2 = 0.84$). In addition, summer burns significantly increased abundance of carnivores by 120% (Fig. 2B, Table 2, $P = 0.023$) and marginally increased abundance of herbivores (Fig. 2C, Table 2, $P = 0.083$). Neither the Shannon diversity index, Hurlburt's PIE, nor the Shannon evenness index significantly differed between treatments (Table 2). However, there was a marginally significant difference in richness of morphospecies, with 60% more species in the summer burn (mean = 8.4 morphospecies ± 1.4 *SE*) than winter burn (mean = 5.4 morphospecies ± 0.2 *SE*; Table 2, $P = 0.080$).

When data were decomposed by family, summer-burn plots had significantly more long-jawed spiders (Tetragnathidae) and leaf hoppers (Cicadellidae), the two most abundant families collected (Fig. 3A–B; Table 2; $P = 0.014$ and $P = 0.007$, respectively). Timing of burns had no significant effect on the third most abundant family, Oxyopidae (lynx spiders; Fig. 3C, Table 2, $P = 0.914$).

Discussion—We expected to find different communities of arthropods inhabiting summer

Table 1—Abundance and morphospecies richness of arthropod families (organized by order) from sweep-net samples at Ladybird Johnson Wildflower Center, near Austin, Travis Co., Texas.

Order	Family	Richness	Abundance
Araneae	Araneidae	3	8
	Linyphidae	1	1
	Lycosidae	1	1
	Oxyopidae	1	38
	Salticidae	1	1
	Tetragnathidae	3	70
	Therididae	1	1
	Thomisidae	1	2
	Unknown	1	1
Coleoptera	Chrysomelidae	1	1
	Cleridae	1	3
	Curculionidae	1	1
Diptera	Agromyzidae	2	2
	Ceratopogonidae	1	1
	Chironomidae	1	1
	Chloropidae	1	1
	Muscidae	2	4
	Rhagionidae	1	1
	Tephritidae	2	5
	Tipulidae	1	1
Hemiptera	Unknown	1	1
	Alydidae	1	2
	Cicadellidae	7	82
	Delphacidae	2	4
Hymenoptera	Braconidae	3	3
	Eulophidae	1	1
	Torymidae	1	1
	Unknown	1	1
Lepidoptera	Unknown	1	1
Orthoptera	Acrididae	1	1
Unknown			3

versus winter burns, given the reported changes in composition of plants between treatments, particularly the decline in invasive *B. ischaemum* in summer-burn plots (Simmons et al., 2007). Here, timing of burns significantly affected both abundance and composition of arthropods in grasslands of the Texas Hill Country, with greater total abundance, as well as more carnivores, tetragnathids, and cicadellids in the summer-burn treatment. Summer burns also had marginally more total herbivores and morphospecies than winter burns. However, species evenness and diversity indices did not significantly differ between summer and winter burns.

Winter burns traditionally have been the preferred treatment for prairie ecosystems, but reliance on this season for prescribed fire is increasingly being called into question when floral composition or historic restoration is the goal (Howe, 1994*b*, 1995). If plant richness or diversity is the only metric evaluated, important effects of timing of burns on vegetational composition may be overlooked. Research on the plant component of the system (M. T. Simmons and S. Windhager, unpublished data) revealed that, overall, most species of plants in this study reacted weakly to fire, but exhibited strong yearly variation, possibly due to climatic factors. However, several dominant species of grass showed strong treatment responses. For example, winter fire appears to have increased cover of both *B. ischaemum* and *Bothriochloa laguroides*. Conversely, these two species were dramatically reduced under summer fire and effectively replaced by *Eragrostis intermedia* and *Panicum halei* (both of which are warm-season C_4 grasses) and by *Nassella leucotricha*, a cool-season C_3 grass. Although dominant grasses did respond to the fire season, the general result was that most annual and perennial forbs seem well adapted to fire throughout the year. Most (75 of 92) species of plants analyzed (of which most were forbs) showed no difference in response to fire treatments. Consequently, summer and autumn fires are dominated by a suite of mid-grasses and short C_3 and C_4 grasses, whereas winter fires have higher biomass but are dominated by taller warm-season grasses (M. T. Simmons and S. Windhager unpublished data).

Similar to these results for plants, using diversity of arthropods as the only indicator to guide management decisions also is not always the best choice. Here we report that significant effects of timing of burns occurred only for some taxonomic groups; effects that would be missed if we had only examined standard diversity indices.

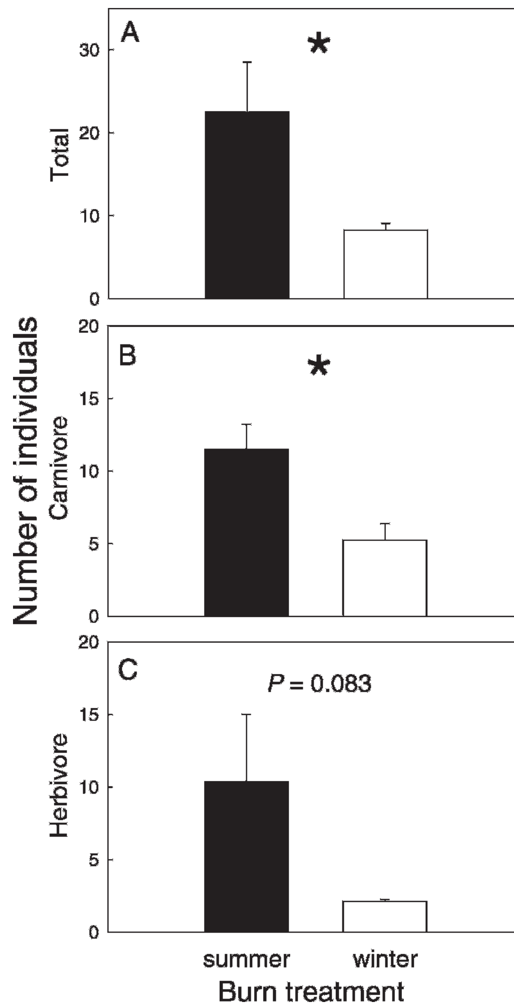

Fig. 2—Responses of arthropods to summer-burn and winter-burn treatments in grasslands of the Texas Hill Country at Lady Bird Johnson Wildflower Center, near Austin, Travis Co., Texas: A) total abundance (number of individuals/sweep-net transect) of arthropods; B) abundance of arthropods classified as carnivores, based on feeding habits of each family of arthropod; and C) abundance of arthropods classified as herbivores, based on feeding habits of each family of arthropod. Bars give means ± *SE*, which were calculated from means/plot (i.e., $n = 4$ plots/treatment). Asterisks indicate statistical significance ($P < 0.05$) according to mixed-model ANOVA (see Table 2).

TABLE 2—Results obtained from using mixed-model-ANOVA to test the effect of summer-burn and winter-burn treatments on several response variables for arthropods at Ladybird Johnson Wildflower Center, near Austin, Travis Co., Texas. Results for the random effect of plot (nested within-burn treatment) are not presented here; the plot effect was statistically significant only for abundance of carnivores ($P = 0.006$). Means are per sweep-net transect and standard errors were calculated from mean/plot (i.e., $n = 4$ plots/treatment).

	Summer		Winter				
Indices	Mean	*SE*	Mean	*SE*	*df*	*F*	*P*
Total abundance	22.50	6.02	8.25	0.78	1	11.6	0.014
Morphospecies richness	8.38	1.40	5.38	0.24	1	4.4	0.080
Hurlbert's PIE	0.83	0.01	0.81	0.07	1	0.4	0.562
Shannon diversity index	1.77	0.11	1.48	0.12	1	3.4	0.117
Shannon evenness index	0.61	0.02	0.71	0.09	1	1.5	0.271
Abundance of carnivores	11.50	1.72	5.25	1.13	1	9.2	0.023
Abundance of herbivores	10.38	4.65	2.13	0.13	1	4.3	0.083
Abundance of Cicadellidae	9.25	4.29	0.75	0.32	1	16.3	0.007
Abundance of Tetragnathidae	6.75	1.16	2.00	0.74	1	11.9	0.014
Abundance of Oxyopidae	2.38	0.83	2.50	0.74	1	<0.1	0.914

Our results suggest that timing of burns is important for managing small, native prairies and grasslands for the conservation of arthropods. Arthropods play important roles in ecosystems, as pollinators, decomposers, predators of pests, and food for larger animals (Losey and Vaughan, 2006), and are important to consider in conservation management (Panzer, 1988; Schwartz, 1994). Previous work has revealed that populations of arthropods can recover following burns (Siemann et al., 1997; Harper et al., 2000), and burns have remained a preferred management technique. For example, Panzer (2002) concluded that burning should be used to manage small prairies, so long as they are cool-weather burns and occur on a rotational basis. While our study did not examine frequency of burns, our results conflict with the recommendation that burns should occur in winter (dormant-season), because abundance and richness of arthropods were, in fact, much greater under a summer-burn regime. We found that summer fire allowed populations of arthropods to reach higher numbers (>170% more total individuals) than winter fire, perhaps due to timing of life-cycles relative to the burn. For example, many arthropods reach adulthood in early summer, and the mobile adult stage may escape fire more easily than immatures, allowing populations to rebound more rapidly after a burn. In addition, carnivores were significantly more abundant in summer burns (with only marginally more herbivores), suggesting changes in structure of the food web. Increase in carnivores was driven, in part, by the greater number of tetragnathid spiders in summer burns. Spiders often are responsive to changes in habitat (e.g., web-building sites), and perhaps are responding to changes in vegetation structure, composition, or both in summer burns (Robinson, 1981; Gunnarsson, 1990; Halaj et al., 2000; Denno et al., 2002; Buddle and Rypstra, 2003). Differences between treatments may also be explained by responses of arthropods to changes in composition of plants (e.g., Siemann et al., 1998; Symstad et al., 2000), and future work will aim to disentangle the direct versus indirect effects of burning on arthropods in this system. Additionally, the effect of autumn and spring burns on both plant and arthropod communities should be examined, as there is little information available on how these non-traditional timings of burns would influence community structure.

Our results are consistent with other studies suggesting that fire-management plans should consider timing of treatment. Prior studies have revealed that changing timing of prescribed burns can significantly alter composition of plants (Howe, 1994*a*, 1994*b*, 1995; Copeland et al., 2002; Simmons et al., 2007). In addition, some effects of season that burns occurred have been reported for invertebrates in other ecosystems. In a Californian forest system, there were no large effects of timing of burns on composition of arthropods on the forest floor, with the exception that species richness was lower in early season relative to late-season burns (Ferrenberg et al., 2006). Similarly, in

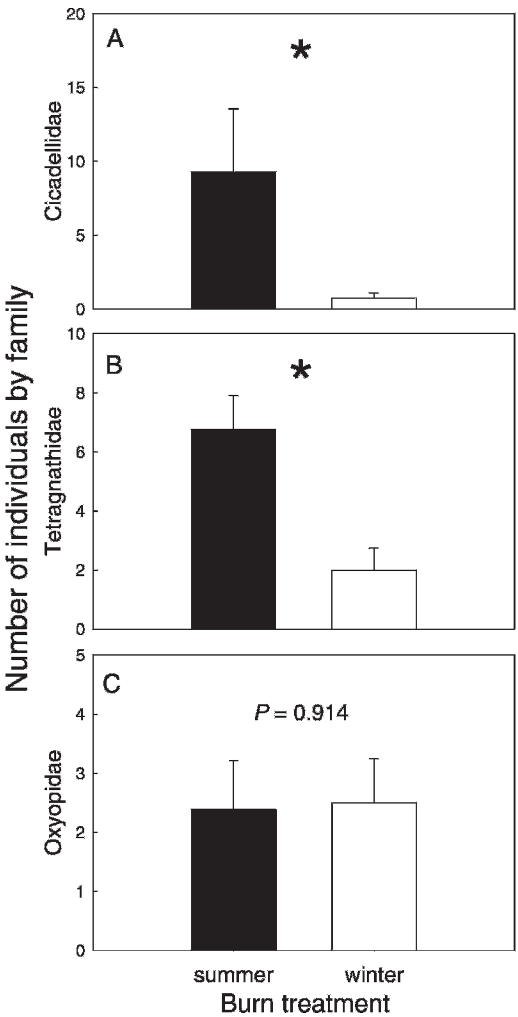

Fig. 3—Responses of the three most abundant families of arthropods to summer-burn and winter-burn treatments in grasslands of the Texas Hill Country at Lady Bird Johnson Wildflower Center, near Austin, Travis Co., Texas: A) abundance (number of individuals/sweep-net transect) of Cicadellidae; B) Tetragnathidae; and C) Oxyopidae. Bars give means ± *SE*, which were calculated from means/plot (i.e., n = 4 plots/treatment). Asterisks indicate statistical significance ($P < 0.05$) according to mixed-model ANOVA (see Table 2).

an Iowa prairie system, arthropods in soil also were unaffected by timing of burn, with the exception of flies (Diptera), which were more abundant after summer than after spring burns (Kirkwood et al., 2000). In the present study, we found that altering the timing of fire had strong effects on abundance and composition of arthropods. These effects may cascade to other species in the ecosystem, particularly through changes in arthropods that function as biocontrol agents of herbivores, such as the observed increase in abundance of carnivores in summer burns. Treatment technique has long been considered in management of plants, and it is time to look beyond plants and include their most ecologically important associates, the arthropods. Results presented here are among the first to show that timing of prescribed burns can affect abundance and composition of the arthropod community.

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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. American Midland Naturalist 122:151–162.

Begon, M., J. L. Harper, and C. R. Townsend. 1996. Ecology: individuals, populations and communities. Blackwell Science Ltd., Oxford, United Kingdom.

Brewer, J. S. 2006. Long-term population changes of a fire-adapted plant subjected to different fire seasons. Natural Areas Journal 26:267–273.

Cancelado, R., and T. R. Yonke. 1970. Effect of prairie burning on insect populations. Journal of the Kansas Entomological Society 43:274–281.

Collins, S. L. 1992. Fire frequency and community heterogeneity in tallgrass prairie vegetation. Ecology 73:2001–2006.

Collins, S. L., and M. D. Smith. 2006. Scale-dependent interaction of fire and grazing on community heterogeneity in tallgrass prairie. Ecology 87: 2058–2067.

Collins, S. L., and L. L. Wallace. 1990. Fire in North American tallgrass prairie. University of Oklahoma Press, Norman.

Collins, S. L., A. K. Knapp, J. M. Briggs, J. M. Blair, and E. M. Steinauer. 1998. Modulation of diversity by grazing and mowing in native tallgrass prairie. Science 280:745–747.

Conover, W. J., and R. L. Iman. 1981. Rank transformations as a bridge between parametric and nonparametric statistics. American Statistician 35:124–133.

Copeland, T. E., W. Sluis, and H. F. Howe. 2002. Fire season and dominance in an Illinois tallgrass prairie restoration. Restoration Ecology 10:315–323.

DENNO, R. F., C. GRATTON, M. A. PETERSON, G. A. LANGELLOTTO, D. L. FINKE, AND A. F. HUBERTY. 2002. Bottom-up forces mediate natural-enemy impact in a phytophagous insect community. Ecology 83: 1443–1458.

DIAMOND, D. D., AND F. E. SMEINS. 1985. Composition, classification and species response patterns of remnant tallgrass prairies in Texas. American Midland Naturalist 113:294–308.

EMERY, S. M., AND K. L. GROSS. 2005. Effects of timing of prescribed fire on the demography of an invasive plant, spotted knapweed *Centaurea maculosa*. Journal of Applied Ecology 42:60–69.

ENGLE, D. M., AND T. BIDWELL. 2001. The response of central North American prairies to seasonal fire. Journal of Range Management 54:2–10.

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

FERRENBERG, S. M., D. W. SCHWILK, E. E. KNAPP, E. GROTH, AND J. E. KEELEY. 2006. Fire decreases arthropod abundance but increases diversity: early and late season prescribed fire effects in a Sierra Nevada mixed-conifer forest. Fire Ecology 2:79–102.

GIBSON, D. J., AND L. C. HULBERT. 1987. Effect of fire, topography and year-to-year climactic variation on species composition in tallgrass prairie. Vegetatio 72:175–185.

GLENN-LEWIN, D. C., L. A. JOHNSON, T. W. JURIK, A. KOSEK, M. LEOSCHEKE, AND T. ROSBURG. 1990. Fire in central North American grasslands: vegetative reproduction, seed germination, and seedling establishment. Pages 28–45 in Fire in North American tallgrass prairie (S. L. Collins and L. L. Wallace, editors). University of Oklahoma Press, Norman.

GUNNARSSON, B. 1990. Vegetation structure and the abundance and size distribution of spruce-living spiders. Journal of Animal Ecology 59:743–752.

HADDAD, N. M., J. HAARSTAD, AND D. TILMAN. 2000. The effects of long-term nitrogen loading on grassland insect communities. Oecologia (Berlin) 124:73–84.

HALAJ, J., A. CADY, AND G. W. UETZ. 2000. Modular habitat refugia enhance generalist predators and lower plant damage in soybeans. Environmental Entomology 29:383–393.

HARPER, M. G., C. H. DIETRICH, R. L. LARIMORE, AND P. A. TESSENE. 2000. Effects of prescribed fire on prairie arthropods: an enclosure study. Natural Areas Journal 20:325–335.

HARTLEY, M. K., W. E. ROGERS, E. SIEMANN, AND J. GRACE. 2007. Responses of prairie arthropod communities to fire and fertilizer: balancing plant and arthropod conservation. American Midland Naturalist 157: 92–105.

HIGGINS, K. F. 1984. Lightning fires in North Dakota grasslands and in pine-savanna lands of South Dakota and Montana. Journal of Range Management 37:100–103.

HOWE, H. F. 1994*a*. Managing species diversity in tallgrass prairie: assumptions and implications. Conservation Biology 8:691–704.

HOWE, H. F. 1994*b*. Response of early- and late-flowering plants to fire season in experimental prairies. Ecological Applications 4:121–133.

HOWE, H. F. 1995. Succession and fire season in experimental prairie plantings. Ecology 76:1917–1925.

HURLBERT, S. H. 1971. The nonconcept of species diversity: a critique and alternative parameters. Ecology 52:577–586.

KIRKWOOD, M., L. SHAPIRO, AND X. WALKER. 2000. Edaphic prairie arthropods, with the exception of Diptera, show no reaction to seasonal burns. Tillers 2:47–57.

KNAPP, A. K., J. M. BLAIR, J. M. BRIGGS, S. L. COLLINS, D. C. HARTNETT, L. C. JOHNSON, AND E. G. TOWNE. 1999. The keystone role of bison in North American tallgrass prairie–bison increase habitat heterogeneity and alter a broad array of plant, community, and ecosystem processes. BioScience 49:39–50.

KNIGHT, T. M., AND R. D. HOLT. 2005. Fire generates spatial gradients in herbivory: an example from a Florida sandhill ecosystem. Ecology 86:587–593.

LEACH, M. K., AND T. J. GIVNISH. 1996. Ecological determinants of species loss in remnant prairies. Science 273:1555–1558.

LOSEY, J. E., AND M. VAUGHAN. 2006. The economic value of ecological services provided by insects. BioScience 56:311–323.

MARSHALL, S. A. 2006. Insects: their natural history and diversity: with a photographic guide to insects of eastern North America. Firefly Books, Buffalo, New York.

PANZER, R. 1988. Managing prairie remnants for insect conservation. Natural Areas Journal 8:83–90.

PANZER, R. 2002. Compatibility of prescribed burning with the conservation of insects in small, isolated prairie reserves. Conservation Biology 16:1296–1307.

PANZER, R. 2003. Importance of in situ survival, recolonization, and habitat gaps in the postfire recovery of fire-sensitive prairie insect species. Natural Areas Journal 23:14–21.

PARTON, W. J., AND P. G. RISSER. 1980. Impact of management practices on the tallgrass prairie. Oecologia (Berlin) 46:223–234.

PENDERGRASS, K. L., P. M. MILLER, AND J. B. KAUFFMAN. 1998. Prescribed fire and the response of woody species in Willamette Valley wetland prairies. Restoration Ecology 6:303–311.

RADELOFF, V. C., D. J. MLADENOFF, AND M. S. BOYCE. 2000. A historical perspective and future outlook on landscape scale restoration in the Northwest Wisconsin pine barrens. Restoration Ecology 8:119–126.

RISSER, P. G., AND W. J. PARTON. 1982. Ecosystem analysis of the tallgrass prairie: nitrogen cycle. Ecology 63: 1342–1351.

Robinson, J. V. 1981. The effect of architectural variation in habitat on a spider community: an experimental field study. Ecology 62:73–80.

Schwartz, M. W. 1994. Conflicting goals for conserving biodiversity–issues of scale and value. Natural Areas Journal 14:213–216.

Seastedt, T. R. 1984. Belowground macroarthropods of annual burned and unburned tallgrass prairie. American Midland Naturalist 111:405–408.

Siemann, E., J. Haarstad, and D. Tilman. 1997. Short-term and long-term effects of burning on oak savanna arthropods. American Midland Naturalist 137:349–361.

Siemann, E., D. Tilman, J. Haarstad, and M. Ritchie. 1998. Experimental tests of the dependence of arthropod diversity on plant diversity. American Naturalist 152:738–750.

Simmons, M. T., S. Windhager, S. P. Power, J. Lott, R. Lyons, and C. Schwope. 2007. Selective and non-selective control of invasive plants: the effects of growing-season prescribed fire, herbicide, and mowing in two invaded Texas prairies. Restoration Ecology 15:662–669.

Smeins, F. E. 1982. Natural role of fire in central Texas. Pages 1–15 in Prescribed range burning in central Texas (T. G. Welch, editor). Texas Agricultural Extension Service, Goldthwaite.

Smeins, F. E. 1997. Environmental and land use changes: a long-term perspective, juniper symposium. Texas Agricultural Experiment Station, San Angelo.

Steinauer, E. M., and S. L. Collins. 2001. Feedback loops in ecological hierarchies following urine deposition in tallgrass prairie. Ecology 82:1319–1329.

Swengel, A. B. 1996. Effects of fire and hay management on abundance of prairie butterflies. Biological Conservation 76:73–85.

Swengel, A. B. 2001. A literature review of insect responses to fire, compared to other conservation managements of open habitat. Biodiversity and Conservation 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.

Towne, G., and C. Owensby. 1984. Long-term effects of annual burning at different dates in ungrazed Kansas tallgrass prairie. Journal of Range Management 37:392–397.

Triplehorn, C. A., and N. F. Johnson. 2005. Borror and DeLong's introduction to the study of insects. Thomson Brooks/Cole, Belmont, California.

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