

# Effects of Fire on Grasshopper Assemblages in a Northern Mixed-grass Prairie

DAVID H. BRANSON<sup>1</sup>

Northern Plains Agricultural Research Laboratory, USDA-ARS, 1500 N. Central Ave., Sidney, MT 59270

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**ABSTRACT** Grassland fires have been shown to influence grasshopper community composition and population dynamics, but studies of their effects on rangeland grasshopper assemblages in the northern Great Plains are lacking. This study was designed to examine the effect of a grassland wildfire on grasshopper community composition and population densities of three grasshopper subfamilies in western North Dakota northern mixed-grass prairie with sampling in paired burned and unburned plots. A rapidly moving fire occurred in late October 1999, after egg-overwintering grasshoppers had died. Vegetation biomass and nitrogen content of grasses did not differ statistically between burned and unburned plots in 2000. The fire negatively affected grasshopper population densities the year after the fire, but species diversity was not affected by the fire. Much of the reduction in grasshopper population densities was caused by a decline in densities of Gomphocerinae species. Grasshopper subfamily densities did not differ statistically between burned and unburned plots in 2001. Additional research is needed to determine the mechanisms leading to the reduction in Gomphocerinae species densities.

**KEY WORDS** grasshopper, fire, mixed-grass prairie, Acrididae, Gomphocerinae

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GRASSLAND FIRES CAN INFLUENCE grasshopper population dynamics and community composition, but studies of their effects on grasshopper assemblages in the northern mixed-grass prairie are lacking (Bock and Bock 1991). Grassland fires seem capable of having positive or negative effects on grasshopper population densities, with the timing and intensity playing important roles. Grasshopper population densities often increase with burning in the tallgrass prairie (Knutson and Campbell 1976, Meyer et al. 2002), although the effects vary with the timing and frequency of burning (Evans 1988). In contrast, grasshopper densities declined after a spring burn in a California grassland (Porter and Redak 1996) and a summer wildfire in a semiarid Arizona grassland (Bock and Bock 1991).

Burning in the tallgrass prairie typically increases nutrient availability and primary production (Collins and Steinauer 1998), which could explain increased grasshopper populations after a fire (Meyer et al. 2002). However, the effects of burning on vegetation have received less attention in the northern mixed-grass prairie (Redman et al. 1993, Shay et al. 2001). The combined effects of frequent drought and low annual precipitation lead to relatively low fuel loads and fire intensities in northern mixed-grass prairies. In separate studies in northern mixed-grass prairies, Redman et al. (1993), in central Saskatchewan, and White and Currie (1983), in eastern Montana, found little effect of fall burning on peak green biomass the following year. Although fire frequency in the northern

Great Plains has declined since European settlement (Umbanhowar 1996), wildfires remain fairly common and occur most frequently in summer (Higgins 1984).

The objective of this study was to examine the effects of a late fall wildfire, which occurred after all egg-overwintering adults had died, on grasshopper population densities and community composition in a northern mixed-grass prairie. A late season fire in the northern mixed-grass prairie could affect grasshopper populations through direct or indirect mechanisms. The effects of a fire on grasshopper assemblages could be mediated by fire-induced changes in host plant quality and plant community composition as proposed by Porter and Redak (1996) and Meyer et al. (2002). Although most grasshopper species in the northern Great Plains overwinter as eggs, several nymph-overwintering species hatch in late summer and were nymphs at the time of the fire (Pfadt 2002). Grassland fires can kill grasshoppers alive at the time of a fire (Bock and Bock 1991), and nymph-overwintering grasshoppers would seem to be less likely to survive a fire compared with eggs in the soil. However, elevated soil temperatures during a fire could increase mortality rates of overwintering eggs. Increased light penetration after a fire can result in higher soil temperatures in burned areas (Hulbert 1988). Differences in soil moisture or temperature during the fall, winter, or spring after a fall fire could increase egg mortality or accelerate hatching phenology. Additional research is needed to examine the effects of rangeland fires on

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<sup>1</sup> Corresponding author, e-mail: dbranson@sidney.ars.usda.gov.

grasshopper species and population dynamics under a range of climatic conditions.

### Materials and Methods

A late fall wildfire in western North Dakota partially burned three sites that had been sampled for grasshopper population densities and species composition since 1993 (Onsager 2000; unpublished data). The fire occurred on 31 October 1999, after all egg-overwintering grasshoppers had died. The three sites were located in separate pastures of a grazing allotment on the Little Missouri National Grassland (U.S. Forest Service) in McKenzie County, ND, within 4.5 km of each other. The twice-over rotational grazing system used in the allotment consisted of two sequential rotations of a herd of livestock through four pastures in a given season, with the exit pasture serving as the entry pasture in the next season (Biondini and Manske 1996, Onsager 2000). No livestock grazing occurred during the summer after the fire. Paired sampling sites were established at each of the three locations, with each sampling site located at least 50 m from the edge of the burn. The study sites consisted of a northern mixed-grass prairie with >90% of the biomass comprised of grass. Common grasses included *Bouteloua gracilis*, *Pascopyrum smithii* (syn. *Agropyron smithii* Rydberg), *Hesperostipa comata* (Trinius and Ruprecht) Barkworth (syn. *Stipa comata* Trinius and Ruprecht), *Nassella viridula* (Trinius) Barkworth (syn. *Stipa viridula* Trinius), *Koeleria macrantha* (Ledebour) Schultes, and *Poa pratensis* L. Common forbs included *Artemisia frigida* Willdenow and *Spharalcea coccinea* (Nuttall) Rydberg. From 1992 to 2003, yearly precipitation averaged 39 cm, with 33.6 cm between April and October. Average daily high temperatures over the 10-yr period were 26°C in June and 30°C in July. Precipitation between April and October 1999 was 30 cm. Precipitation between April and October 2000 was 28.8 cm, with average high temperatures of 22.5°C in June and 29.5°C in July.

Grasshopper population density and species composition were sampled on 28 June, 20 July, 7 August, and 11 September 2000 and on 23 July and 24 August 2001. Sampling took place on sunny days when air temperature was >23°C. Total grasshopper population densities were estimated by counting the number of grasshoppers within 40, 0.1-m<sup>2</sup> aluminum wire rings in each of the six plots, following the methods of Onsager and Henry (1977). Rings were permanently placed in four transects in each replicate, located ≈5 m from each other and held in place with landscape staples. A sweep net sample, consisting of at least 150 fast and 150 slow sweeps, was taken to establish grasshopper community composition and developmental stage of individual grasshoppers (Berry et al. 2000). Sweep net samples were frozen, and grasshoppers were identified to species and developmental instar. Common Gomphocerinae (slantfaced) species were *Ageneotettix deorum* Scudder, *Eretettix simplex* Scudder and *Opeia obscura* Thomas; common Oedipodinae (bandwinged) species included *Encoptolophus costalis*

Scudder and *Trachyrhachys kiowa* Thomas; and common Melanoplinae (spurthroated) species were *Melanoplus sanguinipes* Fabricius, *M. gladstoni* Scudder, *M. infantilis* Scudder, *M. femurrubrum* DeGeer, and *Phoetaliotes nebrascensis* Thomas. Relative abundance of grasshopper species was estimated as the proportion of a sweep sample composed of a given species. Grasshopper subfamily and species densities for a given sample date were calculated by multiplying the total grasshopper population density by the relative abundance of a particular grasshopper subfamily or species (Onsager 2000, Danner and Joern 2004). Because larger grasshopper sample sizes than were caught in a typical sweep sample were needed to accurately assess grasshopper community composition (Onsager 1981, Berry et al. 2000), cumulative densities were calculated by summing grasshopper subfamily or species densities over a season.

Vegetation was sampled in June and July during the summers of 2000 and 2001 to assess green biomass and percentage nitrogen content of grasses. Grass biomass and nitrogen content are often positively correlated with survival and reproduction in grasshoppers (Joern and Behmer 1998, Branson 2003). On a given date, five 0.1-m<sup>2</sup> plots were clipped at each of the six treatment combination locations by randomly tossing a 0.1-m<sup>2</sup> ring and clipping only the green vegetation inside the ring. Vegetation was separated by grasses and forbs and dried, weighed, and ground with a Wiley mill. Total nitrogen content of grass samples was determined using a dry combustion C/N analyzer (Mastajovic 1997) (FP-2000; LECO, St. Joseph, MI). Total nitrogen content of forb biomass was not examined, because >75% of the 0.1-m<sup>2</sup> plots clipped had less than the 0.5 g dry of forb biomass needed for analysis. Plant species composition was not examined. Yearly mean biomass and nitrogen values were used for statistical analyses.

Patterns of grasshopper community diversity were examined using numerical species richness and Shannon index of species diversity (Magurran 2004). Paired *t*-tests were used to examine differences in Shannon index and numerical species richness between burned and unburned plots. Two methods were used to test the significance of differences in grasshopper abundance between burned and unburned plots. First, analysis of variance (ANOVA) was used to assess differences in cumulative grasshopper densities and to determine which grasshopper subfamilies contributed to the overall result (Quinn and Keough 2002). A multivariate ANOVA (MANOVA) was used to assess effects of the fire on population densities of the three grasshopper subfamilies (Warton and Hudson 2004). If the MANOVA model was significant, univariate ANOVAs were used to assess treatment differences in population densities for each of the subfamilies (Quinn and Keough 2002). Second, a permutational distance-based MANOVA (PERMANOVA\_2factor), using a Bray-Curtis distance measure, was used to assess differences in community structure resulting from the fire (Anderson 2001, 2004). Cumulative densities for the 27 species

**Table 1.** Paired *t*-test results for mean grass biomass (g dry/m<sup>2</sup>), for biomass (g dry/m<sup>2</sup>), and percentage nitrogen content of grass (%N) in burned and unburned plots in 2000 and 2001

	Burned	Unburned	SD	<i>T</i>	df	<i>P</i>
<b>2000</b>						
Grass	91.2	85.5	10.8	0.88	2	0.47
Forb	9.6	5.1	5.6	-1.42	2	0.29
%N of grass	1.58	1.40	0.24	1.28	2	0.33
<b>2001</b>						
Grass	115.2	87.9	21.4	2.22	2	0.16
%N of grass	1.18	1.20	0.09	-0.27	2	0.81

**Table 2.** Results of permutational MANOVA based on Bray-Curtis distances for community assemblages of grasshoppers in burned and unburned plots

Source	df	SS	<i>F</i>	<i>P</i>
Burn	1	485.03	0.869	0.6
Residual	4	2,259.68		
Total	5	2,744.71		

present in sweep samples during 2000 were fourth root-transformed before analysis (Quinn and Keough 2002). Mean biomass and percentage nitrogen content values from vegetation samples for a given site-day combination were combined to generate a yearly mean value. Paired *t*-tests were used to examine differences in biomass and percentage nitrogen between paired burned and unburned plots. Systat 10.2 (Systat Software 2002) was used for all statistical analyses other than the permutational distance-based MANOVA.

**Results and Discussion**

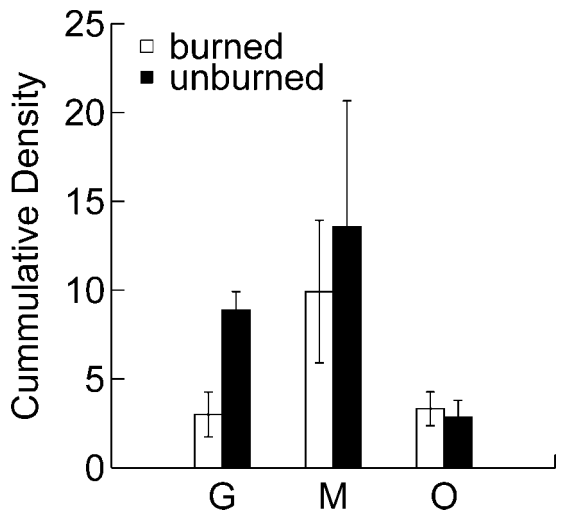
**Effects of Fire on Vegetation.** There was no statistically significant effect of the fire on green grass and forb biomass in 2000 (Table 1). Although percentage nitrogen content of grasses was higher in burned plots in 2000, there was no statistically significant difference in percentage nitrogen content between burned and unburned plots in either 2000 or 2001 (Table 1). Grass biomass was higher in burned plots in 2001, but there was no statistically significant effect (Table 1). Given the replication, statistical power was low, limiting generalizations. Similar to these findings, however, Redman et al. (1993) and White and Currie (1983) found little effect of fall burning on peak green biomass in the year after a fire, and Redman et al. (1993) found no effect of fall burning on nitrogen content of *Festuca* in central Saskatchewan.

**Effects of Fire on Grasshoppers.** Shannon diversity was lower in all burned sites in 2000, but there was no statistically significant effect (paired *t*-test, mean burned = 2.46; mean unburned = 2.69; SD = 0.18; *T* = -2.23; df = 2; *P* = 0.156). There was also no statistically significant effect of the fire on numerical species richness in 2000 (paired *t*-test, mean burned = 8.38; mean unburned = 10.20; SD = 2.60; *T* = -1.21; df = 2; *P* = 0.35). Grasshopper community structure, as examined with a permutational distance-based MANOVA (Anderson 2001), did not differ significantly as a result of the fire (Table 2). The low power and the variability in species composition between the three sites may have contributed to the lack of a significant effect of the fire on grasshopper community composition.

Cumulative grasshopper densities were lower in burned plots in 2000, as assessed by a MANOVA on grasshopper subfamilies (Fig. 1; Table 3). The negative effect of the grassland fire on grasshopper population densities was short-lived, because densities did

not differ in a statistically significant manner between burned and unburned plots in 2001 (Table 3). Mean grasshopper density in 2001 was 5.2/m<sup>2</sup> in burned plots and 5.4/m<sup>2</sup> in unburned plots. A short-term negative effect of fire on grasshopper populations was also found by Porter and Redak (1996) after a spring burn that occurred before grasshoppers hatched, but after grasses had sprouted. The population reductions were linked to fire induced changes in plant community composition resulting from a decrease in exotic annual grasses (Porter and Redak 1996).

Based on univariate *F* tests, no statistically significant differences were apparent in densities of Oedipodinae species in 2000 (Table 3). Oedipodinae species were not numerically abundant in either treatment (Fig. 1). There was no statistically significant effect of the fire on cumulative densities of Melanopliinae species in 2000 (Table 3). Melanopliinae species densities were highly variable between the three sites (Fig. 1). Much of the overall reduction in grasshopper population densities in 2000 resulted from a decline in the Gomphocerinae subfamily (Fig. 1; Table 3). Vermeire et al. (2004) found reduced densities of a common Gomphocerinae species, *A. deorum*, after a prescribed fire in Oklahoma. Qualitatively, it seems the response of Gomphocerinae species to fire resulted from reductions in densities of both egg-overwintering and nymph-overwintering species. In 2000, cumulative density of nymph-overwintering Gomphoceri-



**Fig. 1.** Cumulative densities per square meter (±SE) in 2000 for Gomphocerinae (G), Melanopliinae (M), and Oedipodinae (O) subfamilies in burned and unburned plots.

**Table 3.** MANOVA results for cumulative grasshopper densities from burned and unburned plots in 2000 and 2001 and univariate *F* tests by cumulative grasshopper subfamily densities in 2000

MANOVA	Pillai trace	df	<i>F</i>	<i>P</i>
Burn (2000)	0.991	3,2	70.65	0.014
Burn (2001)	0.418	3,2	0.48	0.73
Univariate <i>F</i> test	MS	df	<i>F</i>	<i>P</i>
Gomphocerinae	52.8	1	24.1	<0.01
Oedipodinae	2.2	1	0.002	0.9
Melanoplinae	19.9	1	0.35	0.59

nae species averaged  $0.2/m^2$  in burned plots compared with  $2.6/m^2$  in unburned plots, whereas cumulative density of egg-overwintering Gomphocerinae species averaged  $1.6/m^2$  in burned plots and  $3.3/m^2$  in unburned plots. Although additional experiments are needed to quantitatively determine if both egg-overwintering and nymph-overwintering Gomphocerinae species are negatively affected by late season fires, the qualitative results support the hypothesis that multiple mechanisms may play a role in the response of Gomphocerinae species to the fire.

The late fall wildfire was likely a direct source of mortality for the two species, *E. simplex* and *Psoloessa delicatula* (Scudder), which overwinter as fourth- or fifth-instar nymphs in the ground litter (Pfadt 2002), given the qualitative reduction in densities of nymph-overwintering grasshoppers in burned plots. Direct mortality from a summer fire in a semiarid Arizona grassland was thought to cause a reduction in grasshopper densities after the fire, because most grasshoppers were alive at the time of the fire (Bock and Bock 1991), as was the case with nymph-overwintering species in this study.

Temperatures eggs are exposed to during a fire likely vary between species and with fire intensity, because wide variation exists between species in the size, orientation, and below surface depth of egg pods (Onsager and Mulkern 1963, Pfadt 2002). Several common Gomphocerinae species lay small egg pods near the soil surface or in the crown of grasses (Onsager and Mulkern 1963, Pfadt 2002). For example, *A. deorum* lays egg pods parallel to the surface in the top 0.6 cm of soil (Shotwell 1941, Onsager and Mulkern 1963). In contrast, many Melanoplinae and Oedipodinae species lay larger, vertically oriented egg pods deeper in the soil with a foam plug near the soil surface (Pfadt 2002). These characteristics would reduce the vulnerability of eggs to elevated soil temperatures during a fire. Eggs of Gomphocerinae species laying shallow egg pods were likely exposed to higher temperatures during the fire, which could have increased egg mortality rates. Although the effects of temperature regimes occurring during grassland fires on egg mortality have not been examined, high egg mortality occurred when unburied egg pods were exposed to high temperatures for short time periods (Parker 1930).

In addition, overwintering survival of eggs or hatching phenology could be affected by differences in soil moisture or temperature after the fire. Prolonged dry

soil conditions have been hypothesized to increase egg-overwintering mortality (Pickford 1966), but soil moisture content was not affected by fall burning in a northern mixed-grass prairie (White and Currie 1983). Reduced surface litter after the fire could have led to colder soil temperatures during winter and increased egg mortality for egg pods closer to the surface, as hypothesized by Pickford (1966). Summer soil temperatures are typically higher after fire or the removal of surface litter in mixed-grass prairie (Willms et al. 1993, Shay et al. 2001), which could accelerate egg hatching patterns as found by Evans (1988). Treatment differences in grasshopper phenology could not be examined given the frequency of grasshopper sampling (Onsager 2000).

Even though differences in vegetation biomass or quality were not detected in 2000 with the relatively coarse-grained vegetative analyses, the fire could have altered numerous characteristics of grasses. Most Gomphocerinae species are highly selective grass specialists, with some species feeding on litter (Pfadt 2002). Consequently, resource availability for nymphal Gomphocerinae species could change as a result of the fire and lead to reduced survival. A phenological shift in plant growth patterns after a fire, as found by Redman et al. (1993), would also likely negatively impact the quality of vegetation available for some nymphal Gomphocerinae species, because plant quality declines through the growing season.

**Conclusions.** Fire negatively affected grasshopper population densities in the year after a late fall wildfire but did not significantly affect green plant biomass or nitrogen content of grasses. A decline in densities of the Gomphocerinae subfamily was responsible for much of the overall reduction. Additional research is required to determine the relative contributions of direct mortality from a fire, increased egg-overwintering mortality, and reduced nymphal survival to the reductions in Gomphocerinae populations after a fire. As found in other studies, the effects of rangeland fire on grasshopper populations were short-lived. Although the late fall fire negatively affected grasshopper population densities at the northern mixed-grass prairie site in western North Dakota, the effects of precipitation patterns both before and after a fire could affect the results. The northern Great Plains have high climatic variability with periodic droughts (Coupland 1992), and the effects of fire on vegetation in semiarid grasslands are likely to be strongly dependent on climatic conditions (Lesica and Martin 2003). Little is known of the potential role of burning in managing insect populations in grasslands (Watts et al. 1989). Additional experiments using prescribed fire are needed to examine the mechanisms leading to the reduction in grasshopper population densities and determine whether burning can be used to control grasshopper populations in the northern Great Plains.

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