Grasshopper abundance and offtake increase after prescribed fire in semi-arid grassland

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ABSTRACT

Background. Fire modulates herbivore dynamics in open ecosystems. While extensive work demonstrates the interaction between fire and vertebrate grazers, less research describes how grasshopper herbivory dynamics respond to fire. **Aim.** We examined how fire increased grass crude protein content and increased the density of and offtake by grasshoppers relative to unburned mixed-grass prairie. **Methods.** We deployed grasshopper exclusion cages to determine grasshopper offtake of aboveground plant biomass, counted grasshopper abundance throughout the study period, and measured crude protein content of aboveground grass biomass. **Key results.** Offtake and density were higher in burned versus unburned plots. Burned plot grasshopper density increased over time, with greater rates of increase in recently burned plots, while density remained constant in unburned locations. **Conclusions.** We present a potential mechanism by which fire interacts with grasshoppers in open ecosystems. It is likely that greater grasshopper offtake and density in recently-burned plots is at least partially attributable to higher crude protein content, as grass in these plots has a much higher proportion of recent growth after fire removed senesced material. **Implications.** Grasshopper herbivory likely acts as a multiplier of livestock herbivory in burned rangeland. Restoring fire regimes can balance direct negative effects of heating against nutritional benefits.

Keywords: fire-grazing interaction, magnet effect, Orthoptera: Acrididae, prescribed fire, pyric herbivory, rangeland forage quality, rangeland pest management.

Introduction

As globally ubiquitous herbivores, grasshoppers (Orthoptera: Acrididae) contribute to ecosystem function around the world. Grasshoppers are particularly important in open ecosystems–rangeland biomes such as grasslands and savannas in which plant communities are regulated by interactive disturbances including fire and herbivory (Bond 2021).

Historically, interest in grasshoppers has generally increased with their local density, as grasshopper outbreaks and locust swarms have wrought economic damage for centuries (Cease *et al.* 2015). While such outbreaks were long considered to be primarily driven by environmental conditions beyond human control, research has described close interactions between land management and grasshopper dynamics (Le Gall *et al.* 2019). Although the utility of this broader understanding of grasshoppers and human land use has mostly been realised within the context of pest control (Branson *et al.* 2006), grasshoppers also contribute to nutrient cycling and plant community composition (Belovsky and Slade 2000; Meyer *et al.* 2002; Zhang *et al.* 2011; Kietzka *et al.* 2021).

Because the nutritive value of vegetation in open ecosystems often varies depending on the time since it last burned, fire likely also affects grasshoppers by modulating their food resources. Perennial, fire-adapted plants resprout using energy stored in organs protected from heat damage, and post-fire plant tissue is typically higher in crude protein and lower in structural carbohydrates than the mature or senescent tissue that was consumed by the fire (McGranahan and Wonkka 2021). Thus, despite overall lower plant biomass on account of the fire, grasshopper abundance on recently-burned areas

is often higher than unburned areas, especially for graminivorous (grass-eating) species (Meyer *et al.* 2002). More broadly, post-disturbance succession and plant nutritive value have been identified as important drivers of grasshopper abundance (Fartmann *et al.* 2012; Schirmel *et al.* 2019). Yet explicit examination of the relationships between time-since-fire, plant nutritive value, and grasshopper abundance have not been conducted.

We measured grasshopper abundance and forage consumption, along with grass protein content, in a replicated experiment that created a time-since-fire gradient in temperate grassland. We predicted that more recently burned plots would have both higher protein content, especially in leaves, and greater grasshopper abundance. As such, we predicted a greater degree of vegetation removal by grasshoppers from recently-burned plots, as determined by comparing aboveground plant biomass against that from within grasshopper exclosures.

Materials and methods

Study location & design

Our study was conducted at the USDA Agricultural Research Service (USDA-ARS) Livestock and Range Research Laboratory in Miles City, Montana, USA (46.40 N, 105.95 W). Vegetation is typical mixed-grass prairie, and the study site was dominated by western wheatgrass *Pascopyrum smithii*. During the study period, the overwhelming majority of grasshoppers on the study site, as determined by mid-season sweep netting and identification at the USDA-ARS Pest Management Research Unit in Sidney, Montana, consisted of the migratory grasshopper *Melanoplus sanguinipes*, a native species of spur-throated grasshopper in the family Acrididae.

Within a larger prescribed fire experiment, we selected nine rectangular, 300-m² plots to test three different time-since-fire treatments ($n = 3$ each): (1) fire the previous autumn; (2) fire the previous spring; and (3) a control treatment left unburned for several years. Livestock were excluded from the entire study area and had been for several years. While the study area was open to wildlife such as deer (*Odocoileus* spp.), pronghorn *Antilocapra americana*, and lagomorphs including *Sylvilagus floridanus* and *Lepus* spp., we observed no evidence of their presence on any plots during the sampling period. Nor were we aware of other substantial invertebrate herbivores.

Sample collection

To measure the amount of vegetation removed by foraging grasshoppers, we established two pairs of sample points within each plot. Each pair of 0.25-m² sample points consisted of one full mesh grasshopper exclosure alongside another structure with a similar footprint and shade factor that was open to grasshopper herbivory. Each type of structure consisted of a polyvinyl chloride tube frame with heavy nylon netting, which when fully wrapped and zipped around the frame and weighted down with sand-filled tubes, effectively kept grasshoppers out (Parker and Salzman 1985). Because the mesh reduced sunlight intensity by $400 \, \text{w m}^{-2}$ compared to the surrounding area, we designed control structures that remain open on the north and south faces to allow grasshoppers to enter while still producing shade conditions that matched the exclosures during peak photosynthetic activity. These paired structures ensured that shade would not influence grass development, skewing offtake measurements. Structures were monitored at least every 48 h and after any substantial weather event to ensure they remained intact; in the few instances grasshoppers had crawled under the exclosures, they were removed upon discovery.

On all plots, the first pair of structures was established 1 July 2021, and the second pair 1 week later. On 9 August (40 days after the first pair of structures were erected), all aboveground biomass, standing dead and current year's growth, within each 0.25 m² frame footprint was clipped to ground level. Within the recently-burned plots, individual grass tiller counts were recorded – because structures were placed randomly and tiller density was observed to be variable, we examined biomass on both a per-tiller basis as well as by area. Clipped biomass was dried at 60°C for 48 h and weighed to the nearest 0.001 g.

We collected forage quality samples on the 26th day of the study, roughly halfway through the study period. For each plot, samples were comprised of 40 western wheatgrass tillers randomly selected by tossing a marker flag in the air and clipping, to ground level, the tiller nearest to where it landed, regardless of phenology or live/dead status. Tillers were separated into leaf blades and stems (which included leaf sheaths) prior to drying at 60°C for 48 h and grinding into fine powder. Protein content was determined with a Thermo Scientific Flash 2000 combustion analyser.

To determine grasshopper density, we employed a standard ring count methodology (Onsager 1977; Joern and Laws 2013). One week after the initial pairs of structures were established, we placed 5, 0.1 m² rings on the ground in a ×pattern centred on each plot, with rings approximately 1.5 m apart and at least 2 m from plot edges. Nineteen observations were made over the course of the study period, between 9 July and 6 August. All plots were sampled in each round of observations by a single observer (the first author), and all observations were conducted between 10:00 hours and 12:00 hours for consistent solar conditions. Sampling consisted of walking slowly through the plot and agitating the area near each ring with a long stick, and recording the number of grasshoppers that jumped from the ring.

Data analysis

To determine whether accessibility to grasshoppers affected the amount of aboveground vegetation, we subtracted the

dried biomass values from control structures from that of their paired grasshopper exclosures and calculated the mean of these two differences for each plot ($n = 3$ experimental units per treatment). To account for the different lengths of deployments among the two pairs of structures, offtake was expressed as daily rate of removal by dividing the difference in biomass between paired structures by the number of days each structure pair was deployed. We used a linear model with the intercept term removed to test each of the three difference values against 0 (null hypothesis: no difference in standing crop between grasshopper exclosures and control frames) using the `lm` function in the R statistical environment (R Core Team 2020). We tested pairwise contrasts in standing crop differences across each treatment with a *post hoc* Tukey test using `TukeyHSD`.

We determined whether crude protein content varied with fire treatment and plant organs (leaf blades vs stems) by fitting each term and their interaction in an ANOVA. Pairwise contrasts among fire treatments were again tested with `TukeyHSD`.

To determine if there were general linear trends in grasshopper abundance patterns over the course of the study, we conducted a non-parametric test of the Kendall's tau (τ) statistic fit to the grasshopper count data within each burn treatment using the `kendallTrendTest` function in the EnvStats package for R (Millard 2013). To compare the relative rates of change over the study period, we plotted the estimated eight slope of the trend for each burn treatment and the associated 95% confidence intervals as returned by `kendallTrendTest`.

Results

Overall, aboveground plant biomass was lower outside of exclosures in both fire treatments ($64 \pm 4\%$ less in fall burn plots and $55 \pm 9\%$ less in spring burn plots), but did not differ between exclosures and accessible unburned plots ($1 \pm 8\%$). Biomass removal by grasshoppers accounted for statistically-significantly lower biomass outside of grasshopper exclosures in both fall and spring burns ($t = -7.4$, $P < 0.001$ and $t = -5.8$, $P < 0.001$, respectively; Fig. 1). Aboveground biomass was not different between grasshopper exclosures and areas accessible to grasshoppers in unburned plots ($t = -0.16$, $P > 0.05$). Offtake was significantly lower in unburned plots than plots burned in both the previous fall and spring ($P < 0.01$ and $P = 0.01$, respectively). Over the course of the study period, daily offtake rates averaged $3.9 \pm 0.5 \, \text{kg ha}^{-1} \, \text{day}^{-1}$ in fall burns and $2.4 \pm 1.3 \, \text{kg}$ $\text{ha}^{-1} \, \text{day}^{-1}$ in spring burns, while offtake in unburned plots was not different from 0 ($-0.4 \pm 1.9 \, \text{kg ha}^{-1} \, \text{day}^{-1}$).

Crude protein content of western wheatgrass tillers varied among the fire treatments ($t = 57$, $P < 0.001$; Fig. 2). Crude protein content in fall and spring burns averaged $6.4\% \pm 0.2$ s.e. and did not differ from one another
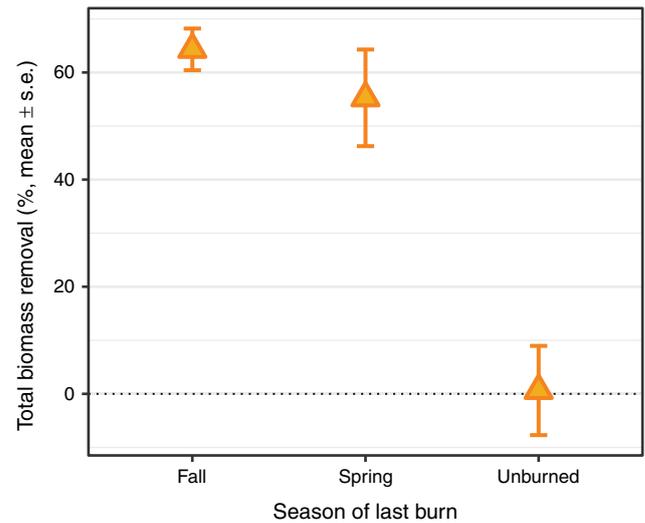

Fig. 1. Biomass removal by grasshoppers in control (shaded, unenclosed) frames relative to paired exclosures in plots with three different fire treatments. Standing crop (kg ha^{-1}) was determined by clipping at the end of the 4-week study period and differences attributable to grasshopper removal from control frames are expressed as a percentage of total standing crop in paired exclosures.
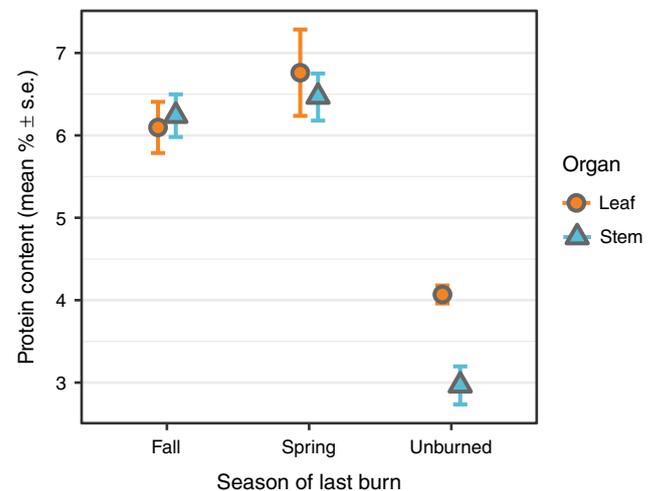

Fig. 2. Mean protein content of western wheatgrass *Pascopyrum smithii* sampled from three burn treatments as a percentage of total dry matter. Orange circles indicate the protein content of leaf blades; blue triangles are stems (including leaf sheaths).

($P > 0.05$). But crude protein content in unburned plots, which included a substantial amount of senesced material from previous growing seasons was lower than in both fall and spring burns plots ($t = -2.7$, $P < 0.001$ and $t = -3.1$, $P < 0.001$, respectively).

Across all samples, crude protein content did not vary among leaves and stems ($t = 2.7$, $P > 0.05$). Despite a trend towards higher crude protein in leaf tissue in unburned plots (Fig. 2), the pattern was not influential enough to create a significant fire treatment $\times$ organ interaction ($t = 2.1$, $P > 0.05$).
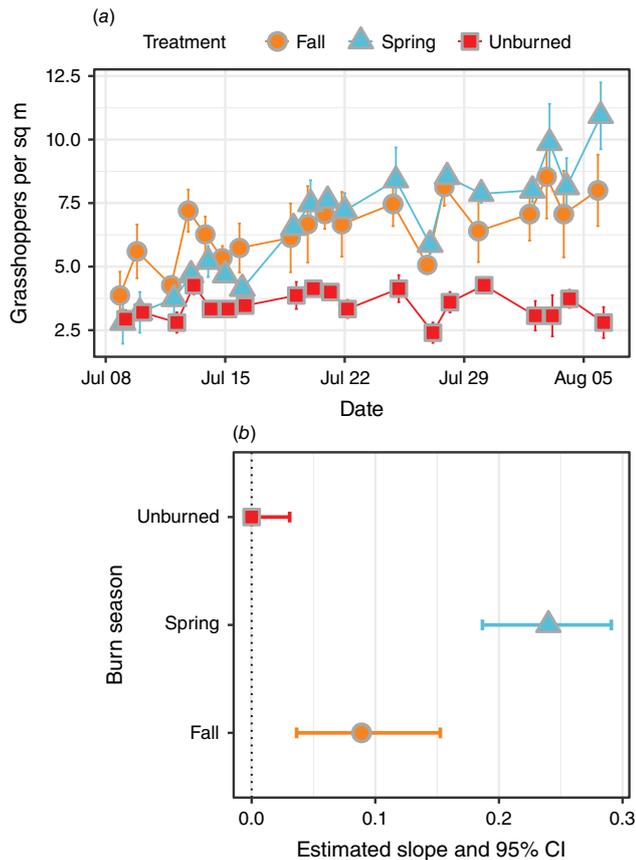
Fig. 3. (*a*) Observed grasshopper counts per square metre. Orange circles indicate data taken from fall burn treatments, blue triangles from spring burn treatments, and red squares from unburned (control) plots. (*b*) Data from Kendall's Tau statistic, which assessed the observed count trendline consistency over time. Tau values were compared against the null hypothesis that there was no trend (slope = 0). 95% confidence intervals show the possible variance in slope for the data over time. Most grasshoppers observed were the migratory grasshopper *Melanoplus sanguinipes*.

Grasshopper abundance was similar across plots at the beginning of the study period (early July) but increased significantly over the next month in fall and spring burn plots ($\tau = 0.29$, $P < 0.01$ and $\tau = 0.62$, $P < 0.001$; Fig. 3*a*). Grasshopper abundance remained constant over the study period in unburned plots ($\tau = 0.039$, $P > 0.05$). While grasshopper abundance increased in both burn treatments, the rate of increase was approximately three times greater in plots that had been most recently burned in the spring than those that had been burned in the previous fall (Fig. 3*b*), which represented more than a four-fold increase in density from less than 3–12 grasshoppers m^{-2} (Fig. 3*a*).

Discussion

Interactions between fire and herbivores drive plant and nutrient dynamics and affect ecosystem service delivery in open ecosystems. Grasshoppers are widely seen as pests in competition with economically-valuable livestock for herbaceous primary productivity (Zhang *et al.* 2019). Hewitt and Onsager (1983) estimated grasshoppers consume nearly USD400 million (USD1.7 billion, adjusted for inflation) worth of livestock forage per year in the western United States. Fire interacts with grasshoppers via direct and indirect effects, which are variable among species depending on their biology (e.g. Vermeire *et al.* 2004). In our study of indirect grasshopper responses to fire, grasshoppers removed over half of available aboveground plant biomass in burned plots but had no detectable effect in unburned plots, consistent with other ecosystems in which grasshoppers select burned vegetation (Stein *et al.* 1992; Lopes and Vasconcelos 2011).

Time since last fire drives spatial and temporal variability in the distribution of plant nutritional quality, which can be a strong determinant of grasshopper abundance and distribution (Joern *et al.* 2012; White 2012; Ozment *et al.* 2021). While the effect on grasshopper responses of differing phenological stages when burning occurs have not been specifically evaluated, plant tissues that resprout after fire generally have higher protein content than their mature counterparts on account of having a lower proportion of structural carbohydrates (McGranahan and Wonkka 2021). At the stand level, fire removes low quality, senesced material from previous seasons' growth, allowing high quality regrowth to dominate the sward. This elevated protein content in burned areas can be maintained over longer periods by repeated grazing (Wanchuk *et al.* 2021), even during drought (Spiess *et al.* 2020). Higher post-fire nutritional quality attracts herbivores, whose repeated defoliation maintain the high nutritional quality (Archibald *et al.* 2005; Sensenig *et al.* 2010; Allred *et al.* 2011). Previous work shows that the dominant grasshopper species in our plots, *M. sanguinipes*, prefers current year's growth and standing dead material makes up only a small proportion of its diet (Anderson and Wright 1952; Mulkern *et al.* 1962). We suggest that in our study, burned plots with overall higher crude protein content as a result of higher proportions of green, resprouting tissue likely attracted *M. sanguinipes*.

Other sources of variability likely modulate the ubiquity of the fire–crude protein–grasshopper interaction. Firstly, grasshopper community composition can vary, with variable effects on food resources. While we observed *M. sanguinipes* to be the dominant species in our single-season study, other work from our research station has shown variability in dominant species. For example, Branson and Vermeire (2016) reported *Ageneotettix deorum* and *Opeia obscura* were the two most common species, while Branson and Haferkamp (2014) reported dominance by *Phoetaliotes nebrascensis*. Further research ought to determine how general the attraction to burned areas is among rangeland grasshopper species; previous fire ecology work has focused

on direct effects of heating during fire, not indirect effects of post-fire resource alteration.

Secondly, crude protein is but one component of herbivore nutrition and is therefore not the sole determinant of use, despite being commonly used as a proxy for forage nutritive quality, more broadly. Certainly, diet selection among *M. sanguinipes* populations varies considerably, especially within temperate regions (Fielding and Defoliart 2008). At the same time, *M. sanguinipes* responds positively to plant nitrogen content (Branson 2003) and demonstrates higher physiological performance under high-protein diets and their relative diet selection tends to mirror that of what is available on the landscape (Zembrzuski *et al.* 2021). Furthermore, the pattern of fire and forage extends from crude protein to a broad suite of forage quality components including mineral content (Wanchuk 2022). Thus, it is reasonable to infer that crude protein content likely had a substantial contribution to the correlation between grasshopper density and time-since-fire reported here.

Thirdly, fire altered both vegetation nutritional status and structure in our study plots, making it difficult to parse the relative effect of either. For example, Schirmel *et al.* (2019) identified vegetation structure as the primary driver of grassland Orthoptera community composition, but found strong evidence for plant nutritive quality as driver as well. Fortunately, Ozment *et al.* (2021) provided some insight into the relative effects of vegetation structure and nutrient content: not only did they find grasshoppers are generally attracted to high-nutrient grazed areas, but they found the attraction weakened when the nutritional contrast between grazing lawns and surrounding areas lessened during drought. But the structural difference remained, which supports nutritional quality as an important driver.

Regardless of the mechanism, recently burned plots clearly attracted more grasshoppers and subsequently had more aboveground biomass removal than unburned plots, which has potential implications for management.

In terms of fire management, we suggest restoring fire regimes with frequent, spatially-discrete prescribed fire might leverage the direct, negative effects of heating to reduce overall grasshopper populations against the potential nutritional gains post-fire vegetation provides for individual grasshoppers that survive or migrate into recently-burned areas. Improved survival and reproduction resulting from nutrient enhancement in burned vegetation (Branson 2003) could intensify competition between livestock and grasshoppers in burned areas. In contrast, benefits of nutritive enhancement could be offset by negative fire effects, as fire alone can result in short-term reductions in grasshopper abundance by up to 75% (Branson and Vermeire 2016). Direct effects of fire include adult and nymphal mortality (Bock and Bock 1991), and egg mortality due to soil heating (Vermeire *et al.* 2004; Branson and Vermeire 2013, 2016). Thus, even despite positive nutritional benefits, fire could remain a sustainable low-cost alternative to conventional (chemical) control of economically-damaging grasshopper outbreaks (Branson *et al.* 2006), which are expensive, unreliable, and have off-target effects on non-pest species (Joern 2000).

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