

Research Article

Relationships between Plant Diversity and Grasshopper Diversity and Abundance in the Little Missouri National Grassland

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A continuing challenge in orthopteran ecology is to understand what determines grasshopper species diversity at a given site. In this study, the objective was to determine if variation in grasshopper abundance and diversity between 23 sites in western North Dakota (USA) could be explained by variation in plant species richness and diversity. In this system with relatively low plant diversity, grasshopper species richness and abundance were not significantly associated with plant species richness in either year. Although a number of significant associations between plant diversity and grasshopper diversity were found through regression analyses, results differed greatly between years indicating that plant species richness and diversity did not lead to strong effects on grasshopper diversity metrics. Plant species richness appears to be too coarse grained to lead to accurate predictions of grasshopper species richness in this system dominated by generalist grasshopper species.

1. Introduction

Grassland insect diversity is often linked to plant species composition and habitat structure [1–4]. Several general hypotheses have been proposed to explain relationships between plant and herbivore species richness [5, 6], with insect herbivore diversity often thought to generally increase with increased plant species richness due to increased resource diversity [3, 5]. Although habitat associations with grasshoppers have been studied since the early 1900s [7], it remains a continuing challenge in grasshopper ecology to understand patterns of species diversity [4, 8]. Numerous factors could influence grasshopper species diversity including resource availability, habitat structure, escape space, and predators [4, 9, 10]. Furthermore, management practices such as livestock grazing and fire impact plant species composition and subsequently affect grasshopper species composition [4, 11]. Many studies have examined relationships between grasshopper community composition and vegetation patterns in grassland ecosystems worldwide (e.g., [2, 4, 8, 12–14]). Plant diversity often positively affects grasshopper species diversity, but relationships are not consistent. Additionally, grasshopper feeding patterns

can have important impacts on local plant abundance and community structure [15–17]. In most grassland ecosystems the nature of relationships between plant species richness and grasshopper abundance and diversity remains unclear [3, 4].

Grasshoppers are often the dominant native herbivore in grassland ecosystems worldwide, with widespread economically damaging grasshopper outbreaks occurring frequently in western North America [11, 15]. Despite the economic importance of grasshoppers in the area of this study, the northern Great Plains [18, 19], relationships between plant diversity and grasshopper diversity and abundance are not clearly defined. In contrast to the majority of herbivorous insects, most grasshopper species tend to be generalist feeders that consume a variety of unrelated plant species [20, 21]. As a result, relationships between plant species richness and grasshopper species richness could be weaker in grass dominated ecosystems with numerous grass or mixed feeding generalist grasshoppers. The objective of this study was to determine if variation in grasshopper abundance and diversity between 23 sites in western North Dakota (US) could be explained by variation in plant species richness and diversity.

TABLE 1: Characteristics of each site in western North Dakota.

Site	Elevation (m)	Coordinates	Plant species		Grasshopper species	
			2001	2002	2001	2002
Charbonneau	689	47°46'33N 103°49'30 W	11	6	19	19
Cheney	603	47°44'29N 104°01'35 W	5	8	*	16
Devitt	600	47°38'37N 104°01'53 W	12	7	18	14
East	710	47°36'35 N 103°56'09 W	8	7	13	18
Plant	609	47°38'05 N 104°01'08 W	8	5	17	16
Jacobson5A	690	47°48'04 N 103°48'31 W	6	5	19	24
Klandl	667	47°38'27 N 103°57'24 W	5	6	19	27
IndergardN	675	47°35'14 N 103°49'39 W	8	7	15	13
IndergardS	730	47°34'43 N 103°50'46 W	7	6	23	22
Rau	757	47°42'08 N 103°57'15 W	11	9	14	20
Saltwell	751	47°36'32 N 103°56'05 W	5	8	15	24
SD101	700	47°33'23 N 104°00'21 W	8	5	17	18
101 Creek	654	47°33'44 N 104°00'30 W	9	8	11	18
SM02	686	47°39'28 N 103°51'18 W	5	4	19	20
SM05B	740	47°37'42 N 103°45'45 W	10	7	20	21
SM05NB	747	47°37'03 N 103°45'58 W	10	8	21	20
SM07B	655	47°36'54 N 103°48'54 W	8	9	13	19
SM11	708	47°43'37 N 103°52'24 W	8	9	21	20
SM12	719	47°43'55 N 103°50'46 W	7	5	13	19
SM13	704	47°43'11 N 103°49'05 W	7	9	17	18
Shadwell	717	47°26'03 N 104°02'30 W	8	5	18	19
Whited	703	47°28'36 N 104°04'21 W	8	7	15	16
Windmill	658	47°39'07 N 104°00'11 W	3	4	15	20

2. Materials and Methods

The study was conducted on the Little Missouri National Grasslands in western North Dakota (USA), managed as part of the United States Forest Service Dakota Prairie Grasslands. The area of the study is characterized by wide summits and networks of gullies [22]. The historic plant community is a mixed grass prairie dominated by grasses including western wheatgrass (*Pascopyrum smithii*), blue gramma (*Bouteloua gracilis*), needle and thread (*Hesperostipa comata*), and green needlegrass (*Nassella viridula*). The region is semiarid and receives approximately 355 mm to 400 mm of precipitation annually; most of which occurs during the growing season. Mean daily temperatures range from -17.2°C in winter to 29.4°C in summer. Precipitation measured at a nearby weather station during the growing season of 2001 was slightly above, while precipitation during 2002 was slightly below the long-term average.

During the spring and early summer of 2001, 23 sites were established in the Little Missouri National Grassland. The sites were located within 35 km of each other, ranged in elevation from 600 to 751 m, and were randomly chosen to include a range of grassland habitat types (Table 1). Nearly all sites were dominated by native vegetation. At each site, a 10 m by 10 m subplot was established for sampling vegetation species composition and grasshopper densities. Grasshopper population densities were determined by counting the number of grasshoppers that flushed from within 20, 0.1 m²

aluminum wire rings, following the methods of Onsager and Henry [23]. Rings were arranged in a grid of four rows, with 5 rings per row, and held in place by landscape staples. Sites were sampled for grasshopper population densities and species composition four times in 2001 and six times in 2002, between the last week of June and the first week of September. Sampling took place when air temperature was greater than 23°C . A sweep net sample was taken, using an insect aerial net with a four foot handle, in the vegetation surrounding the 10 m by 10 m sampling plot to establish grasshopper community composition. Vegetation structure was dominated by grasses and forbs, with few shrubs. An equal number of 150 sweeps were taken while walking slowly that rubbed on the soil surface and that passed through the vegetation canopy while walking rapidly [24]. Sweep net samples were frozen, and grasshoppers were later identified to species in the laboratory. To adjust for differences in sweep net sample sizes between sites, individual species densities were estimated by combining the percentage composition in sweep samples with grasshopper densities from ring counts.

Vegetation species composition was examined in early July 2001 and 2002. Each side of the sampling site served as a 10 m transect with a fifth transect in the middle of the plot, with 500 sampling points per site. Along each transect, every one meter a standard 10-pin frame was used to determine vegetation composition based on the total number of contacts by a pin. A contact was considered as the pin point coming into contact with the basal area of a

plant, bare ground, or litter. Across both years of sampling, western wheatgrass was a dominant or codominant grass at 14 sites, blue grama at 13 sites, junegrass at eight sites, threadleaf sedge at three sites, needle and thread at two sites, crested wheatgrass (*Agropyron cristatum*) at two sites, green needlegrass at one site, and Kentucky bluegrass (*Poa pratensis*) at one site. For each site, total plant species richness, proportional coverage of live vegetation, and plant diversity were calculated.

Relationships between insect species diversity and plant diversity could differ seasonally but were not assessed in this study. As grasshopper sample sizes were low in some sweep net samples from sites with low population densities, all sweep samples were pooled prior to analysis to reduce error [24], increase the probability that rare grasshopper species would be incorporated [5], and better account for varying grasshopper phenologies [2]. Grasshopper abundance data was also averaged across sample periods within a year to reduce the influence of random sampling variation when few individuals are detected in density subsamples [25]. Data was transformed as needed. The majority of grasshopper species present at the sites overwinter as eggs and hatch in late spring or early summer; however four nymph-overwintering grasshopper species that hatch in late summer and become adults in the spring were caught in sweep samples. Only egg-overwintering grasshopper species were included in the analysis, as plant-grasshopper relationships would be expected to differ due to the divergent phenologies of these two groups. Patterns of grasshopper species diversity were examined using numerical species richness, Shannon index of species diversity, and Simpson evenness index [26]. Regression analyses were conducted to examine habitat variables responsible for grasshopper abundance and diversity. Systat 12 (Systat Software Inc.) was used for all analyses.

3. Results and Discussion

Cumulative plant species richness was relatively low, with a total of 31 species detected across all sites. Mean plant species richness was 7.24, with a maximum species richness of 12 species at a site (Table 1). Forb species richness ranged from zero to six species, while grass species richness ranged from two to seven. Vegetation was dominated by grass and sedge species, as is typical in this northern mixed grass prairie [22, 27, 28]. An average of ~88% of live vegetation hits were grasses and sedges. Abundant grasses and sedges were blue grama (*Buteloua gracilis*), western wheatgrass (*Agropyron smithii*), junegrass (*Koeleria macrantha*), and threadleaf sedge (*Carex filifolia*). The most abundant forb was the relatively ephemeral exotic common dandelion (*Taraxacum officinale*), which is frequently present in native dominated grasslands throughout the United States. Fringed sage (*Artemisia frigida*), scarlet globemallow (*Sphaeralcea coccinea*), and phlox (*Phlox* spp.) were other relatively common forbs.

Egg-overwintering grasshopper species richness ranged from 11 to 27 across sampling sites in a given year, with a mean species richness of 18 (Table 1). A total of

TABLE 2: Egg-overwintering grasshopper species caught in sweep samples in 2001 and 2002.

Species	2001	2002
<i>Ageneotettix deorum</i>	1,553	2,374
<i>Melanoplus sanguinipes</i>	1,162	1,631
<i>Phoetaliotes nebrascensis</i>	863	1,084
<i>Opeia obscura</i>	575	668
<i>Encoptolophus costalis</i>	490	590
<i>Philbostroma quadrimaculatum</i>	487	720
<i>Melanoplus gladstoni</i>	411	314
<i>Melanoplus femurrubrum</i>	343	490
<i>Melanoplus infantilis</i>	273	387
<i>Orphulella speciosa</i>	206	277
<i>Trachyrhachys kiowa</i>	165	281
<i>Amphitornus coloradus</i>	140	185
<i>Melanoplus dawsoni</i>	128	350
<i>Aulocara femoratum</i>	126	176
<i>Hypochlora alba</i>	115	152
<i>Melanoplus packardii</i>	111	185
<i>Melanoplus keeleri</i>	109	205
<i>Aeropedellus clavatus</i>	92	197
<i>Spharagemon equale</i>	36	64
<i>Arphia pseudonietana</i>	33	68
<i>Aulocara ellioti</i>	31	64
<i>Melanoplus confusus</i>	24	39
<i>Mermiria bivittata</i>	16	19
<i>Hadrotettix trifasciatus</i>	16	24
<i>Melanoplus bivittatus</i>	14	51
<i>Hesperotettix viridis</i>	12	17
<i>Melanoplus differentialis</i>	10	0
<i>Dissosteira carolina</i>	8	2
<i>Metator pardalinus</i>	7	36
<i>Dactylotum bicolor</i>	1	1
Total caught	9,236	13,590

34 egg-overwintering grasshopper species were collected (Table 2). Mean grasshopper species richness per site was slightly higher than Kemp [29] and Joern [4], while total species richness was within the range observed in other similar studies in the western US (e.g., [4, 29–31]). Average grasshopper density across sites was 7.4 per m², with a low of 1.9 and a maximum of 20.8 per m² at a given site. Relative to long-term grasshopper densities in the area, the densities were not exceptionally high. Just prior to this study, grasshopper densities were documented at 40 and 130 per square meter [18, 19]. However, grasshopper densities were much lower during a five-year period immediately following this study [17].

Common grasshopper species are presented in Table 2. Plant diversity did not affect grasshopper abundance (Table 3), similar to the findings of Joern [10] in tallgrass prairie. There was no effect of plant species richness on grasshopper species richness in either year (Figure 1, Table 3). Although several significant associations were

TABLE 3: Results from regression analyses of plant species richness, live cover percentage, Shannon diversity, and Simpson evenness on grasshopper abundance and diversity. Regression equations are provided for results with a P value less than .1.

Independent (plant)	Dependent (grasshopper)	Statistical data
A. 2001		
Species richness	Species richness	$R^2 = 0.002, P = .84$
	Shannon diversity	$Y = 1.70 + 0.055X; R^2 = 0.17, P = .057$
	Simpson evenness	$Y = 0.215 + 0.024X, R^2 = 0.19, P = .045$
	Abundance	$Y = 8.6 - 0.32X; R^2 = 0.02, P = .5$
Shannon diversity	Species richness	$R^2 < 0.001, P = .99$
	Shannon diversity	$R^2 = 0.1, P = .16$
	Simpson evenness	$R^2 = 0.06, P = .26$
	Abundance	$R^2 = 0.03, P = .43$
Live cover	Species richness	$Y = 8.23 + 0.292X; R^2 = 0.4; P = .001$
	Shannon diversity	$R^2 = 0.1, P = .15$
	Simpson evenness	$R^2 = 0.016, P = .6$
	Abundance	$Y = -3.37 + 0.329X; R^2 = 0.2, P = .036$
Evenness	Species richness	$R^2 = 0.003, P = .8$
	Shannon diversity	$R^2 = 0.11, P = .12$
	Simpson evenness	$R^2 = 0.05, P = .33$
	Abundance	$R^2 = 0.024, P = .5$
B. 2002		
Species richness	Species richness	$R^2 = 0.01, P = .6$
	Shannon diversity	$R^2 = 0.08, P = .2$
	Simpson evenness	$R^2 = 0.09, P = .15$
	Abundance	$R^2 = 0.06, P = .25$
Shannon diversity	Species richness	$Y = 24.01 - 3.882X, R^2 = 0.19, P = .04$
	Shannon diversity	$R^2 = 0.05, P = .32$
	Simpson evenness	$Y = 0.168 + 157X, R^2 = 0.21, P = .03$
	Abundance	$Y = 15.0 - 6.96X, R^2 = 0.24, P = .015$
Live cover	Species richness	$R^2 = 0.02, P = .53$
	Shannon diversity	$Y = 1.8 + 0.014X, R^2 = 0.2, P = .03$
	Simpson evenness	$Y = 0.158 + 0.008X, R^2 = 0.212, P = .027$
	Abundance	$R^2 = 0.003, P = .8$
Evenness	Species richness	$Y = 15.4 - 9.6X, R^2 = 0.25, P = .016$
	Shannon diversity	$R^2 = 0.035, P = .39$
	Simpson Evenness	$Y = 0.151 + 0.348X, R^2 = 0.22, P = .025$
	Abundance	$Y = 15.7 - 15.36X, R^2 = 0.26, P = .014$

found through the regression analyses, results differed greatly between years (Figure 1, Table 3). Grasshopper community Shannon diversity and Simpson evenness were positively associated with plant species richness in 2001, indicating that sites with increased plant diversity had a more evenly distributed grasshopper community assemblage. By contrast, grasshopper species richness, evenness, and abundance were all positively associated with Shannon diversity of plants in 2002. Grasshopper species richness and abundance were positively associated with the percentage of live plant cover in 2001, while diversity and evenness of the grasshopper community were positively associated with live cover in 2002. Grasshopper species richness, evenness, and abundance were

all positively associated with plant species evenness in 2002. As significant relationships differed almost entirely between years, it appears unlikely that either plant species richness or diversity was a strong causative factor responsible for observed significant statistical results. However, a consistent result in both years was that grasshopper species richness was not positively associated with plant species richness (Figure 1). Although specialist grasshopper richness would be expected to increase with plant species richness, this is a highly grass dominated system with many generalist feeding grasshoppers [32].

Strong conclusions regarding the nature of the relationship between plant species diversity and grasshopper species

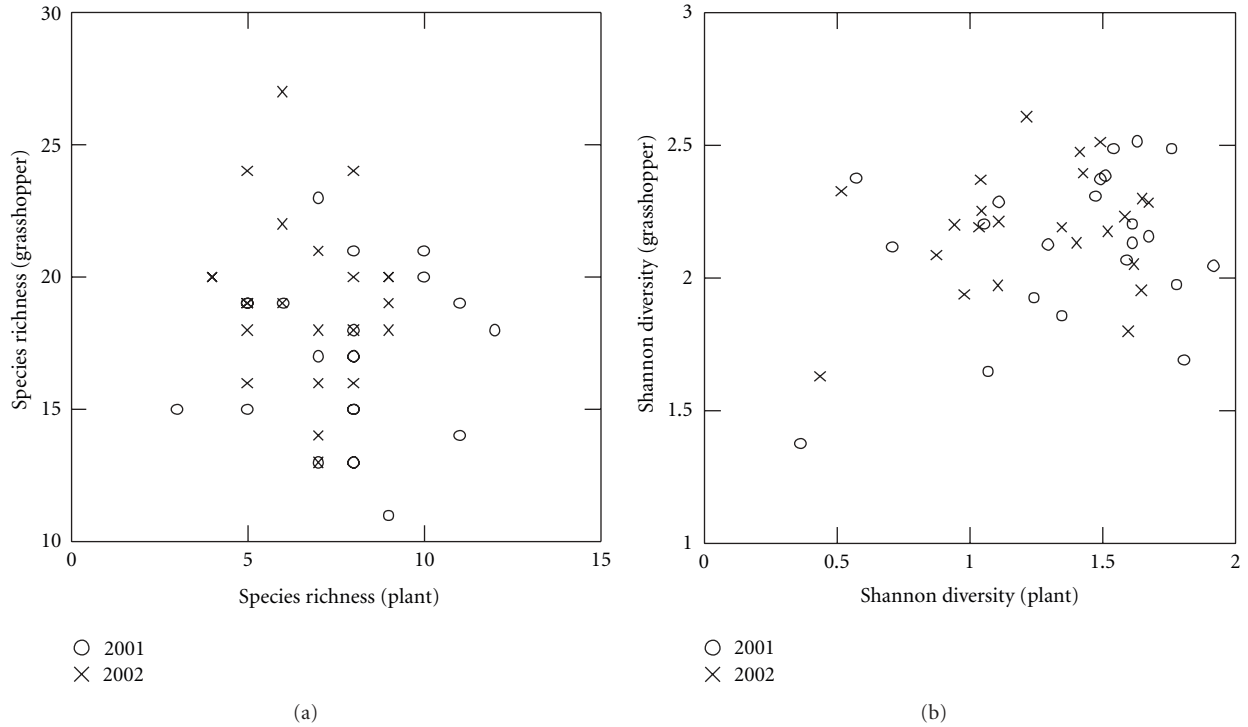


FIGURE 1: Relationship in 2001 and 2002 between (a) species richness of grasshoppers and plants and (b) Shannon diversity of grasshoppers and plants.

diversity in North America remain difficult. In a study across an elevational gradient in Montana, Wachter et al. [13] found no significant relationships between plant cover or species richness and grasshopper species richness, diversity, and abundance. By contrast, Fielding and Brusven [14] found a positive correlation between plant and grasshopper species richness in semiarid rangeland. In a more productive tallgrass prairie system, Evans [12] and Joern [4] also found grasshopper species richness was positively related with plant species richness. Plant species richness was similar in the study by Joern [4] and higher in the study by Fielding and Brusven [14]. In this study, as well as in Joern [4] and Fielding and Brusven [14] where positive relationships were found between grasshopper and plant species richness, the ratio of grasshopper species to plant species was typically greater than 1.0. In a desert environment in the southwestern US with low grasshopper species diversity but several specialist species, Otte [9] found a positive relationship between grasshopper and plant species diversity when the ratio of grasshopper species to plant species was always less than 0.43. As a result, the lack of a relationship between plant and grasshopper species richness does not appear a result of grasshopper or plant species richness varying by orders of magnitude from other studies. As pointed out by Fielding and Brusven [14], “grasshopper species richness is probably not a simple function of plant species richness.”

Grasshopper populations are highly cyclical in this area and respond to weather conditions [18, 19, 27]. Drought has been shown to reduce grasshopper species diversity at nearby sites in eastern Montana [33], while a late summer rainfall

event led to a three-fold increase in grasshopper densities in the following year [19]. Precipitation patterns during 2001 and 2002 were not extreme outliers relative to long-term averages. Given the variation in correlations between years, longer-term sampling would be required to determine if consistent patterns emerge and if patterns vary with precipitation or densities. Grasshoppers were relatively abundant during the period of the study and density dependent factors could have influenced grasshopper or plant species composition. Both intraspecific and intraspecific exploitative competition can play an important role in grasshopper population dynamics and plant composition [19, 34, 35]. In addition, preferential grasshopper herbivory has been shown to influence plant species diversity in study area when abundant [17]. Although grasshopper herbivory could have removed all visible plant material prior to plant sampling, vegetation sampling occurred relatively early in the summer.

Many of the hypotheses proposed to explain positive relationships between plant and herbivorous insect diversity are based on the fact that many insects are relatively specialized [5]. However, many grasshopper species are generalists [17, 32]. As a result, inconsistent and weak relationships could be reflective of the ability of generalist grasshoppers to feed on numerous plant species or could be an artifact of difficulties in sampling rare species [5]. Haddad et al. [5] conducted an 11-year experiment manipulating plant diversity and examining effects on arthropod herbivores and predators and found herbivore arthropod species richness was strongly positively related to plant species richness only when examining cumulative species richness across the

11 year time period. This illustrates the potential importance of longer term sampling when examining relationships between plant and grasshopper species richness.

The results from this study also support Kemp et al. [36], who argued that plant species richness is too coarse grained a measure to lead to accurate predictions of grasshopper species richness. Although plant community associations are likely to be a better predictor of grasshopper species richness than plant species richness in a variety of ecosystems [36, 37], a potential constraint is that ordination techniques may result in system specific conclusions regarding relationships between plant communities and grasshopper species.

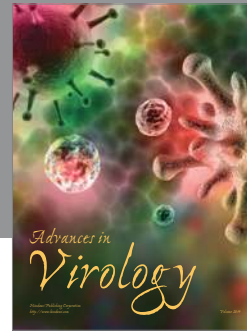
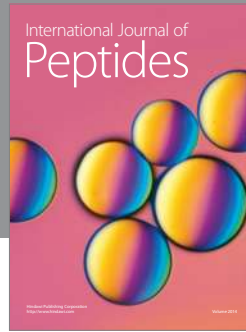
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