

Interspecific competition among grasshoppers and their effect on plant abundance in experimental field environments

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Summary. We tested whether grasshoppers in experimental field environments, i.e. cages (40 × 40 cm) placed on existing old field vegetation, (1) were limited in density by plant abundance and/or nitrogen content, (2) exhibited interspecific competition, and (3) altered the relative abundance of different plant species. We examined interactions among a pair of early season grasshopper species (May–June; *Arphia conspersa* and *Pardalophora apiculata*) and a late season pair (July–August; *Melanoplus femur-rubrum* and *Melanoplus bivittatus*). Each grasshopper species was placed in cages by itself and with another grasshopper species. Grasshoppers generally survived at higher density in fertilized cages and they reduced plant abundance relative to empty cages, suggesting that grasshoppers may be food limited at these densities. In unfertilized plots, early season grasshoppers preferred grasses (*Schizachyrium scoparium* and *Poa pratensis*) and favored the growth of forbs (especially *Solidago* spp.). However, late in summer, *Melanoplus* spp. preferred *Solidago* spp. and favored the growth of grasses.

The pattern of grasshopper survivorship and plant reduction within these experimental environments provide preliminary support for some of the predictions of resource competition theory. Grasshoppers exhibited interspecific competition only if they significantly reduced plant biomass. If two species competed, a grasshopper species was eliminated only if the superior competitor, when living by itself, could reduce plant biomass to a significantly lower level than the inferior competitor. Competitors persisted only if they did not differ in their ability to reduce plant biomass or reduced the abundance of different plant species.

Key words: Grasshoppers – Interspecific competition – Food limitation – Nitrogen – Indirect mutualism

If insect herbivores are food limited, they should reduce the abundance of their plant food resource (Lawton and

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Strong 1981; Strong 1984). Indeed, when herbivores compete, resource reduction may be a major mechanism of competition. Thus, the outcome of interspecific competition among herbivores may reflect the ability of each herbivore species to reduce the abundance of different plant species (Schoener 1976; Tilman 1980, 1982). If two herbivore species compete exploitatively for a single resource (e.g., for a single species or growth form of plant), then the species that can reduce this resource to the lowest level should competitively displace the other (Tilman 1976, 1980; Hsu et al. 1977; Rothhaupt 1988). On the other hand, if two herbivore species compete for more than one resource and partition resources, the herbivores should coexist (Schoener 1976, 1978; Tilman 1976, 1980; Belovsky 1986). In addition, consumption of some plant species indirectly favors unpreferred plant species that compete with preferred plant species (Levine 1976; Vandermeer 1980; Holt 1977; Lawlor 1979; Louda et al. 1989), thereby producing an indirect mutualism. These outcomes are expected regardless of the proximate factors that affect herbivore diet choice, e.g. plant dry matter digestibility, nitrogen content, secondary chemicals, or physical properties (Mulkern et al. 1969; Campbell et al. 1974; Cook 1977; Joern 1979; Bernays and Barbehenn 1987). Consequently, examining the effects of insect herbivores on plant abundance is important in testing for both the phenomenon and mechanisms of competition.

We conducted experiments in contrived field environments to explore the relationships between resource reduction and competition among grasshoppers. Instead of examining interactions in natural populations (Evans 1989; Joern and Lawlor 1980, 1981), we addressed four questions about the potential mechanisms of competition among grasshoppers. (1) Does exploitative interspecific competition occur only if each grasshopper species can reduce food resources (plant biomass) when living by itself? (2) Does competitive displacement of one herbivore by another occur only if, when each species lives by itself, the superior competitor can reduce the food resource to a lower level than the inferior competitor? (3)

Do competing herbivores persist together only if they either are each specialized on different resources (e.g., plant species) or do not differ in their abilities to reduce resources? (4) Does preferential feeding by herbivores on one or more plant species increase the biomass of unpreferred plant species?

We established a series of caged field plots to which we added either no grasshoppers, a grasshopper species by itself, or a pair of species. Separate experiments were conducted early and late in summer in 1989 and early in summer of 1990. Each experiment was performed on (1) the natural, prairie-like multi-species vegetation of a thirty year-old field, (2) the virtual monocultures of *Agropyron repens* that resulted from long-term nitrogen fertilization of large replicate sections in this field (in 1989), or (3) natural vegetation fertilized with nitrogen one week before the experiment (in 1990). We tested for competition by comparing the final density and mortality rates of species stocked in replicated cages by themselves vs. with another species. We determined grasshopper effects on plant biomass and species composition by comparing the biomass of abundant plant species in cages with and without grasshoppers.

Methods

Study area

The study was conducted in a 30 year-old field during May–September, 1989, and in May and June of 1990 at Cedar Creek Natural History Area (CCNHA) in east central Minnesota, 45 km north of Minneapolis. A portion of this field was divided into nine 20 × 50 m sections that had received different fertilizer treatments twice per year since 1983 (Huntly and Inouye 1988). In 1989 we used the six sections receiving (1) no added fertilizer (*unfertilized*, three replicates) and (2) a high level of nitrogen (26 g/m² of NH₄NO₃) and sufficient amounts of P, K, Ca, and Mg to assure that they were not limiting (*fertilized*, three replicates) (Tilman 1987). In 1990, we established cages on a single unfertilized section using a completely randomized design. These cages were either unfertilized or fertilized with 26 g/m² of NH₄NO₃ one week before the experiment began.

Vegetation in sections fertilized since 1983 was almost entirely (99%) *Agropyron repens*, a perennial grass (see Tilman 1987, 1988). In unfertilized sections, vegetation was dominated by the grasses *Schizachyrium scoparium* and *Poa pratensis* and various prairie forbs, especially *Solidago rigida*, *Solidago nemoralis*, *Liatris aspera*, *Lespedeza capitata*, and *Hieracium longipilum*. Short-term fertilization in 1990 was intended to change the nutritional quality and the nitrogen available to plants while retaining the plant species present in the unfertilized old field.

We used four different grasshopper species in the experiments. Early in the summer of both years, we used two species of nymph-overwintering grasshoppers: *Arphia conspersa* (average mass (g) = 0.487 ± 0.179 (SD), N = 20) and *Pardalophora apiculata* (average mass (g) = 1.336 ± 0.483, N = 20). Late in summer, we used two species that overwinter as eggs and do not develop into adults until mid-July: *Melanoplus femur-rubrum* (average mass (g) = 0.374 ± 0.076, N = 35) and *Melanoplus bivittatus* (average mass (g) = 1.194 ± 0.55, N = 22). All four grasshoppers are generalist feeders (i.e. eat many species of plants), but the two early season species prefer grasses while the two *Melanoplus* species prefer forbs (Mulkern et al. 1969; Campbell et al. 1974).

Cages and Grasshopper Dynamics

We used window screen cages (220 cm tall, 40 × 40 cm at the base, and 1.5 mm mesh size) to contain grasshoppers, similar to methods used by Belovsky (1986) and A. Joern (*personal communication*). Cages were inserted 4 cm into the soil over existing vegetation and anchored with steel bars at each corner. All large arthropods (e.g., grasshoppers, spiders, beetles, etc.) were removed from each cage by hand. The desired number of each grasshopper species was added to each cage, which was then folded shut at the top.

Grasshoppers were stocked at a high density and allowed to die off to the density that the vegetation could support, which, in most cases, was constant for the last 14 days of the experiment. Grasshopper densities were determined by direct counts every 3–7 days. Therefore, these experiments examine the effect of treatments on survivorship but not reproduction. The high initial densities may cause some competition to occur even though competition might not occur at natural densities. However, we were interested only whether the predictions of resource competition theory were met *if* competition occurred and not whether competition occurred at natural densities. Consequently, the high densities are necessary to test our hypotheses because grasshoppers must be dense enough to decrease to the level that the vegetation can support.

Experimental design

Three separate experiments were performed, two in 1989 and one in 1990. From 25 May–26 June of 1989, we used adults of *Arphia conspersa* and *Pardalophora apiculata*. After this experiment, cages were moved to nearby but previously undisturbed locations. From 25 July–2 September of 1989, we used adults of *Melanoplus femur-rubrum* and *Melanoplus bivittatus*. We placed cages 2 m apart in a 20 m transect along a short side of each section, 2 m from the edge for the early experiment and 4 m from the edge for the late experiment. Each section received eight cages. There were three replicate sections for each fertilizer treatment and two fertilizer treatments, giving a total of 48 cages. Within each fertilizer treatment, we examined grasshopper density and plant biomass in four different treatments: each grasshopper species by itself (two treatments), the two grasshopper species combined, and no grasshoppers (empty cage). Each of the four treatments was randomly assigned to two of the eight cages within each replicate section.

In early summer of 1990, the experiment was conducted by randomly assigning treatments to eighty 0.16 m² plots 1.5 m apart placed in several rows 2 m apart, all within a single fertilized section. Half of these plots (40) were fertilized with 26 g/m² NH₄NO₃ one week before the experiment and the other half left unfertilized. Within each fertilizer treatment, there were eight replicates of each grasshopper treatment (no cage, empty cage, cage with *A. conspersa* or *P. apiculata* by itself, and cage with both species together).

We chose initial grasshopper densities as a compromise between equalizing total grasshopper biomass in all cages within an experiment and ensuring enough individuals to prevent bias caused by random death within a cage. For the early season experiments, initial densities on both fertilized and unfertilized sections were: *A. conspersa*, 5 per cage when by itself, 4 per cage when combined with *P. apiculata*; *P. apiculata*, 4 per cage when by itself, 3 per cage when combined with *A. conspersa*. In the late experiment in 1989, we added *M. femur-rubrum*, 6 per cage when by itself, 4 per cage when combined with *M. bivittatus*; *M. bivittatus*, 4 per cage when by itself, 3 per cage when combined with *M. femur-rubrum*.

Interspecific competition can be inferred if a species' final density is significantly lower and its mortality rate significantly higher in the presence of the other species than when by itself. However, intraspecific competition cannot be detected with our design. All comparisons were analyzed using ANOVA followed by multiple comparisons with Duncan's Multiple Range test on Number Cruncher (NCSS) statistical package.

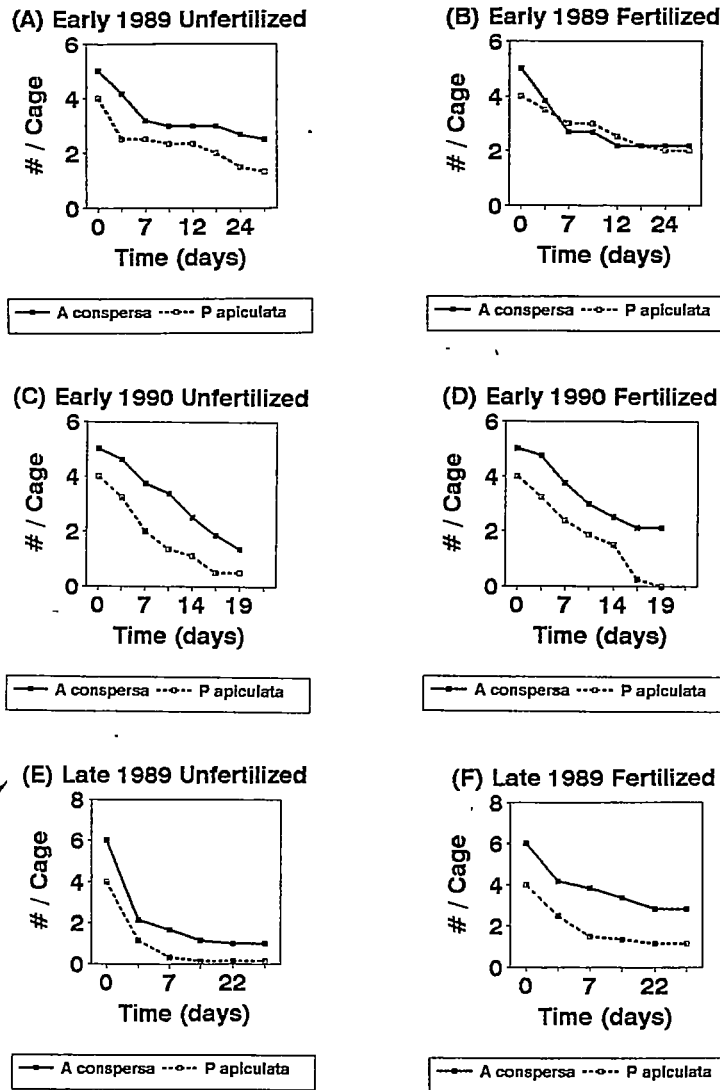


Fig. 1A-F. Time series of mean (\pm SE) grasshopper densities for each species stocked in cages by themselves for early 1989 (A unfertilized, B fertilized), early 1990 (C unfertilized, D fertilized), and late 1989 (E unfertilized, F fertilized). These time series show the typical pattern of decline in grasshopper densities within cages

Vegetation sampling

We sampled vegetation at the beginning and end of each experiment. Two days before the early experiment in 1989, we clipped 36 strips (each 1×0.1 m, six in each 20×50 m section) of vegetation adjacent to grasshopper cages on both fertilized and control sections, yielding 18 per fertilizer treatment. Prior to the late experiment in 1989, we clipped 12 strips, 2 in each section, yielding 6 per fertilizer treatment. In 1990, we clipped twelve strips between plots at the beginning of the experiment. After counting final grasshopper densities, we removed grasshoppers from all cages. We then clipped above-ground vegetation from each entire 40×40 cm plot and sorted it to live vs. dead plant material. Live plant material was sorted to species, dried at 45°C for seven days, and weighed. Plant biomass data were logtransformed before analysis to help correct for non-normal distributions.

Grasshopper diets were measured in 1990 from individuals remaining alive in each cage at the end of the experiment. These individuals were preserved in 70% ethanol and later dissected. The gut contents of each individual were removed and plant fragments were identified as either monocot or dicot using microhistological techniques (Sparks and Malechek 1968; Belovsky 1986; Ritchie 1988).

Results

Grasshopper dynamics within a cage

Grasshopper density in a cage typically declined most strongly during the first 3–10 days of an experiment (Fig. 1). Of our 120 time series of grasshopper density, 97 contained the same densities of a species over the last 14 days. Of the others, 13 were species that went extinct during the last 7 days and the other ten were constant over the last 7 days of the experiment. Consequently, we used density at the end of the experiment (final density) as our estimate of the density of grasshoppers that could survive in a treatment.

We also estimated the average mortality rate for different species for different grasshopper treatments. A negative exponential function, $y = ae^{-bt}$, was fit to the time series of average density for each species by linear regression of average density (y) against the logarithm of t , the number of days since grasshoppers were stocked. This function fit the time series well in all cases ($0.69 < r^2 < 0.98$). Mortality rate was assumed to be the

parameter b obtained from the regression equation. A higher value of b indicates a greater mortality rate. Mortality rate of a grasshopper species in cages by itself was compared with that in cages with the other species using t -tests, based on the estimate and standard error of b .

Final grasshopper densities

Because grasshopper treatments were randomized within sections (blocks) in 1989, the separate effects of fertilizer treatment, block, and grasshopper treatment were analyzed for both the early and the late experiments using three-way ANOVA. However, block effects were not significant for any species (Range in F -values, 0.17–0.89, $df=6,23$, $P>0.20$). Consequently, block effects were removed from the analysis for 1989 data, so that mean densities for particular fertilizer \times grasshopper treatments (six replicates pooled) could be compared more simply.

Competition among grasshoppers early in summer depended on the fertilizer treatment applied (Table 1). In 1989, *P. apiculata* (PA), when living by itself, persisted

at significantly higher densities on fertilized than unfertilized sections ($F=19.06$, $df=1,23$, $P<0.01$), but *A. conspersa* (AC) did not ($F=0.86$, $df=1,23$, $P=0.54$). In 1990, neither PA nor AC persisted at higher densities on fertilized plots ($F=0.19$, $df=1,31$, $P=0.58$; $F=0.20$, $df=1,31$, $P=0.57$). In unfertilized sections, each species significantly reduced the abundance of the other when living together and AC eliminated PA in all cages where they were together in both 1989 and 1990 (see contrasts in Table 1). In fertilized sections, neither species significantly reduced the abundance of the other in 1989, but in 1990, PA reduced the abundance of AC (see contrasts in Table 1). In fertilized plots in 1990, PA did not persist when by itself, but did persist when in the presence of AC, although PA density with AC present was not significantly greater than zero ($F=2.36$, $df=1,15$, $P=0.16$).

In the late experiment in 1989, the densities of both *M. bivittatus* (MB) and *M. femur-rubrum* (MF) were significantly greater in fertilized sections (MB: $F=12.00$, $df=1,23$, $P<0.001$; MF: $F=48.17$, $P<0.001$). MB reduced the density of MF significantly in both unfertilized and fertilized sections (Table 1) and the effect was

Table 1. Densities ($\#/m^2$) and mortality rates for each grasshopper species in both fertilized and control sections at the end of the cage experiments (A) early in summer, 1989, (B) early in 1990, and (C)

late in 1989. Data are shown for each species alone ($N=6$ cages in 1989, $N=8$ in 1990) and with the other species. Significant contrasts between Alone and With Other are indicated by different letters

Fertilizer Treatment	Species	Density (\pm SE)		Mortality Rate ¹ (\pm SE)	
		Alone	With Other	Alone	With Other
A. Early experiment 1989					
Unfertilized	<i>Arphia</i>	a	b	a	b
	<i>conspersa</i>	16.7 \pm 2.8	5.5 \pm 2.0	0.018 \pm 0.004	0.038 \pm 0.003
	<i>Pardalophora</i>	a	b	a	b
	<i>apiculata</i>	8.8 \pm 2.0	0 \pm 0	0.029 \pm 0.004	0.114 \pm 0.020
	<i>Arphia</i>	a	a	a	a
	<i>conspersa</i>	14.4 \pm 2.0	12.2 \pm 2.0	0.023 \pm 0.003	0.015 \pm 0.002
Fertilized	<i>Pardalophora</i>	a	a	a	a
	<i>apiculata</i>	12.2 \pm 2.0	10.0 \pm 1.5	0.023 \pm 0.003	0.024 \pm 0.003
	<i>Arphia</i>	a	b	a	a
Unfertilized	<i>conspersa</i>	10.0 \pm 1.4	5.0 \pm 1.3	0.065 \pm 0.007	0.067 \pm 0.007
	<i>Pardalophora</i>	a	b	a	b
	<i>apiculata</i>	2.5 \pm 1.2	0 \pm 0	0.114 \pm 0.009	0.188 \pm 0.017
	<i>Arphia</i>	a	b	a	a
	<i>conspersa</i>	12.5 \pm 1.5	5.0 \pm 2.1	0.056 \pm 0.003	0.063 \pm 0.012
	<i>Pardalophora</i>	a	a	a	a
Fertilized	<i>apiculata</i>	0 \pm 0	1.7 \pm 1.3	0.134 \pm 0.037	0.127 \pm 0.013
	<i>Melanoplus</i>	a	b	a	b
	<i>femur-rubrum</i>	5.5 \pm 1.1	3.3 \pm 1.4	0.041 \pm 0.002	0.052 \pm 0.002
Unfertilized	<i>Melanoplus</i>	a	a	a	b
	<i>bivittatus</i>	1.1 \pm 1.1	3.3 \pm 1.4	0.077 \pm 0.003	0.042 \pm 0.002
	<i>Melanoplus</i>	a	b	a	b
	<i>femur-rubrum</i>	18.8 \pm 1.1	8.8 \pm 1.4	0.019 \pm 0.002	0.028 \pm 0.003
	<i>Melanoplus</i>	a	a	a	a
	<i>bivittatus</i>	7.8 \pm 1.1	5.5 \pm 1.1	0.030 \pm 0.002	0.031 \pm 0.001

¹ the regression coefficient of linear regression of average density vs. the log of number of days since grasshoppers were stocked (see text)

stronger in fertilized sections (i.e. the interaction term was significant, $F=4.08$, $df=2,23$, $P=0.03$). However, MF had no significant effect on the density of MB in either fertilizer treatment (Table 1).

Mortality rates generally reflected the results for final densities. In the presence of another species, a species' mortality rate was significantly greater whenever the species' final density was significantly lower (Table 1). Otherwise, there was no difference in mortality rate if there was no difference in final density. The exceptions were (1) *M. bivittatus* on unfertilized plots in 1989 had a significantly lower mortality rate in the presence of *M. femur-rubrum* even though there was no significant difference in its final density, and (2) *A. conspersa* in 1990 did not have a significantly higher mortality rate in the presence of *P. apiculata* on either fertilized or unfertilized plots even though its final densities were significantly lower.

Plant biomass

We analyzed fertilized sections only for the abundance of *Agropyron repens* because it represented 99% of above-

ground biomass (see Tilman 1987, 1988). For the unfertilized sections in 1989 and all plots in 1990, we analyzed biomass of *Schizachyrium scoparium*, *Poa pratensis*, and *Solidago rigida* and *S. nemoralis* combined. Other species were too infrequent for meaningful analysis. We compared plant species biomass using one-way ANOVA for: (1) cages with grasshoppers vs. empty cages, (2) cages with grasshoppers vs. plots outside the cages before the experiment, and (3) empty cages vs. plots outside cages before the experiment. Block (section) effects were not significant (F -values were all < 1.13 , $df=2,23$, $P>0.20$), so replicates were pooled.

In 1989, plant biomass in fertilized sections was significantly greater than in unfertilized sections in both experiments (early, Fig. 2: $F=90.4$, $df=1,23$, $P<0.001$; late, Fig. 3: $F=25.7$, $P<0.001$). In 1990, however, short-term fertilization did not increase above-ground plant biomass (Fig. 3: $F=1.02$, $df=1,15$, $P>0.20$).

Early season 1989

In the early experiment on unfertilized sections, cages with grasshoppers had a significantly lower biomass

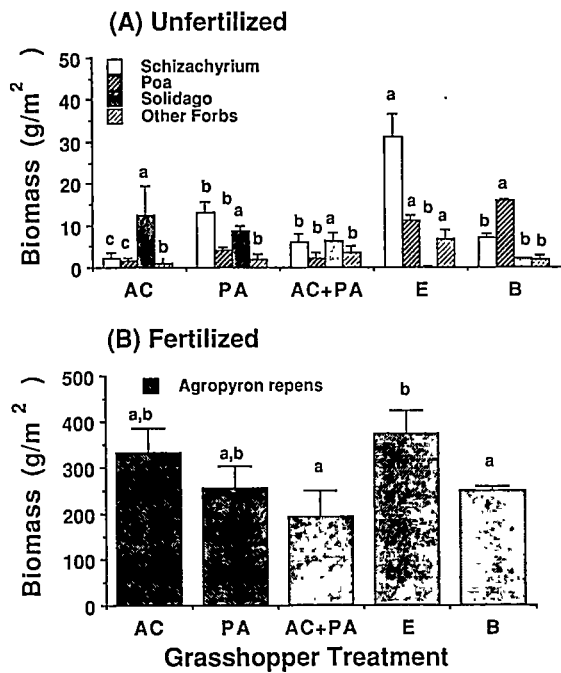


Fig. 2. Mean plant biomass (\pm SE) inside grasshopper cages on early in 1989. Grasshopper treatments (6 replicates) are AC, *Arphia conspersa* by itself, PA, *Pardalophora apiculata* by itself, and AC+PA, both species together. Treatments E, empty cage, and B, plots clipped before the experiment began, served as controls. In unfertilized sections (A), clear bars indicate *Schizachyrium scoparium*, heavily hatched bars indicate *Poa pratensis*, lightly shaded bars indicate all *Solidago* species, and lightly hatched bars indicate other forbs. In fertilized (for previous 7 years) sections (B), all data is for *Agropyron repens*, which represented 99% of the plant biomass. Differences in small letters indicate significant contrasts among treatments within a plant group obtained from Duncan's Multiple Range Test ($P<0.05$)

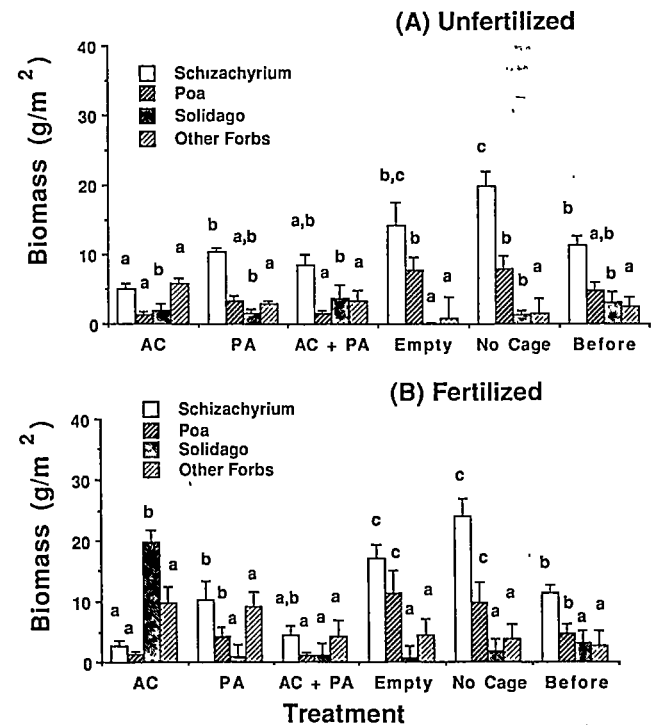


Fig. 3. Mean plant biomass (\pm SE) inside grasshopper cages on a 30 year-old field early in 1990 in both (A) unfertilized and (B) fertilized (1 week before the experiment) plots. Grasshopper treatments (8 replicates) are AC, *Arphia conspersa* by itself, PA, *Pardalophora apiculata* by itself, and AC+PA, both species together. Treatments EMPTY, empty cage, BEFORE, plots clipped before the experiment began, and NO CAGE, plots without a cage, served as controls. Clear bars indicate *Schizachyrium scoparium*, heavily hatched bars indicate *Poa pratensis*, lightly shaded bars indicate all *Solidago* species, and lightly hatched bars indicate other forbs. Differences in small letters indicate significant contrasts among treatments within a plant group obtained from Duncan's Multiple Range Test ($P<0.05$)

of *Schizachyrium* ($F=10.37$, $df=1,23$, $P=0.01$), *Poa* ($F=10.20$, $P=0.01$), and forbs other than *Solidago* ($F=3.89$, $P=0.06$) but a higher biomass of *Solidago* ($F=5.29$, $P=0.03$) than cages without grasshoppers (see contrasts in Fig. 2). Compared to initial conditions, the biomass of *Schizachyrium* ($F=30.67$, $df=1,23$, $P<0.001$) and of forbs other than *Solidago* was significantly higher in cages without grasshoppers, while biomass of *Solidago* was lower ($F=4.38$, $P=0.05$). Biomass of *Poa* in empty cages was not different from that observed before the experiment ($F=0.42$, $P=0.50$), but cages with grasshoppers had significantly less *Poa* biomass than before the experiment ($F=7.90$, $P=0.01$). In unfertilized sections, *Arphia conspersa* in cages by itself reduced *Schizachyrium* and *Poa* to a lower biomass than did *Pardalophora apiculata*, but this pattern was not observed for *Solidago*, or forbs other than *Solidago*.

In the early experiment on fertilized sections, each grasshopper species by itself did not significantly reduce *Agropyron* biomass relative to empty cages (see contrasts in Fig. 2). However a significant reduction did occur when both species were together ($F=4.03$, $df=1,23$, $P=0.03$). *Agropyron* biomass in empty cages was significantly greater than before the experiment ($F=6.55$, $df=1,11$, $P=0.02$).

Early season 1990

The proportion of monocots in the diets (Table 2) of the two grasshopper species, when alone, was not significantly different on unfertilized plots ($F=1.25$, $df=1,10$, $P>0.20$). However, the proportion of monocots in the diet of *A. conspersa* increased significantly in the presence of *P. apiculata* on both unfertilized and fertilized plots ($F=5.97$, $P=0.045$; $F=249.5$, $P<0.001$, respectively; $df=1,6$). In the presence of *A. conspersa* on fertilized plots, *P. apiculata* consumed a much lower proportion of monocots than *A. conspersa* ($F=89.12$, $df=1,5$, $P<0.001$). Diets for *P. apiculata* with *A. conspersa* on unfertilized plots and alone on fertilized plots were unavailable because no *P. apiculata* individuals survived to the end of the experiment.

In 1990 on unfertilized plots, early season grasshoppers had effects similar to 1989 (see contrasts in Fig. 3). *A. conspersa* significantly reduced the biomass of

Schizachyrium and *Poa* relative to empty cages and plots with no cage, as did *P. apiculata*. In addition, *A. conspersa* reduced *Poa* and *Schizachyrium* to significantly lower levels than *P. apiculata*. The biomass of *Solidago* spp. was significantly higher in cages with *A. conspersa* and *P. apiculata*, both by themselves and together, relative to empty cages. *Solidago* spp. biomass in plots without cages was not different than that in cages with grasshoppers. Biomass of forbs other than *Solidago* was not different among treatments.

In fertilized plots in early summer 1990, the two grasshopper species had very different effects on plant biomass (see contrasts in Fig. 3). *Schizachyrium* and *Poa* biomass was significantly lower in cages with *A. conspersa* than in cages with *P. apiculata* by itself, empty cages, and plots without cages, while *Solidago* spp. biomass was significantly higher in cages with *A. conspersa* by itself than in cages with *P. apiculata*, empty cages, or plots without cages. Biomass of forbs other than *Solidago* was not different among treatments.

In 1990, the experimental treatments changed the biomass of plant species relative to before the experiment. *Schizachyrium*, *Poa*, and forbs other than *Solidago* increased in empty fertilized cages ($F=4.68$, $P=0.05$; $F=4.39$, $P=0.07$; $F=7.58$, $P=0.012$; respectively; $df=1,15$), but biomass of *Solidago* spp. did not ($F=2.12$, $df=1,15$, $P>0.20$). In unfertilized empty cages, none of the plant groups changed significantly relative to the beginning of the experiment (range in F : 1.82–3.59, $df=1,15$, $P>0.15$). Relative to initial conditions, *A. conspersa* increased the biomass of *Solidago* spp. ($F=6.62$, $df=1,15$, $P=0.018$) and decreased the biomass of *Schizachyrium* and *Poa* ($F=7.75$, $P=0.011$; $F=5.68$, $P=0.03$; respectively; $df=1,15$) on fertilized plots. On unfertilized plots, *A. conspersa* only reduced the biomass of *Schizachyrium* relative to initial conditions ($F=6.91$, $df=1,15$, $P=0.014$). Grasshoppers had no significant effects on the biomass of other plant groups in either fertilizer treatment relative to before the experiment (range in F : 0.78–1.76, $df=1,15$, $P>0.20$).

Late season 1989

In the late experiment on unfertilized sections, cages with grasshoppers had a significantly higher biomass of *Schizachyrium* ($F=3.72$, $df=1,23$, $P=0.03$) but lower biomass of *Solidago* spp. ($F=7.03$, $P=0.01$) than empty cages. However, grasshoppers had no effect on biomass of *Poa* ($F=0.81$, $P=0.57$) or forbs other than *Solidago* ($F=0.63$, $P=0.51$). Relative to before the experiment, the biomass of all four groups was not different in empty cages (range in F : 0.03–1.78, $df=1, 11$, $P>0.21$), but biomass of both *Solidago* ($F=10.75$, $df=1,23$, $P<0.001$) and forbs other than *Solidago* ($F=6.50$, $P=0.02$) was lower in cages with grasshoppers. Cages with *M. bivittatus* and *M. femur-rubrum* did not differ in the biomass of any plant species (see contrasts in Fig. 4).

In the late experiment on fertilized sections, all cage treatments had significantly lower *Agropyron* biomass than before the experiment ($F=25.5$, $df=1,29$,

Table 2. The mean proportion of monocots (\pm SE) in the guts of grasshoppers surviving to the end of the experiment in early 1990 (sample size in parentheses). Significance of differences is provided in text

Grasshopper Species	Treatment	% Monocots in Diet	
		Unfertilized	Fertilized
<i>P. apiculata</i>	Alone	77.0 \pm 3.0 (5)	NA
	with <i>A. conspersa</i>	NA	40.0 \pm 9.5
<i>A. conspersa</i>	Alone	73.0 \pm 5.1 (5)	75.2 \pm 0.8
	with <i>P. apiculata</i>	81.3 \pm 3.5 (3)	86.6 \pm 1.3

NA: None surviving at end of experiment

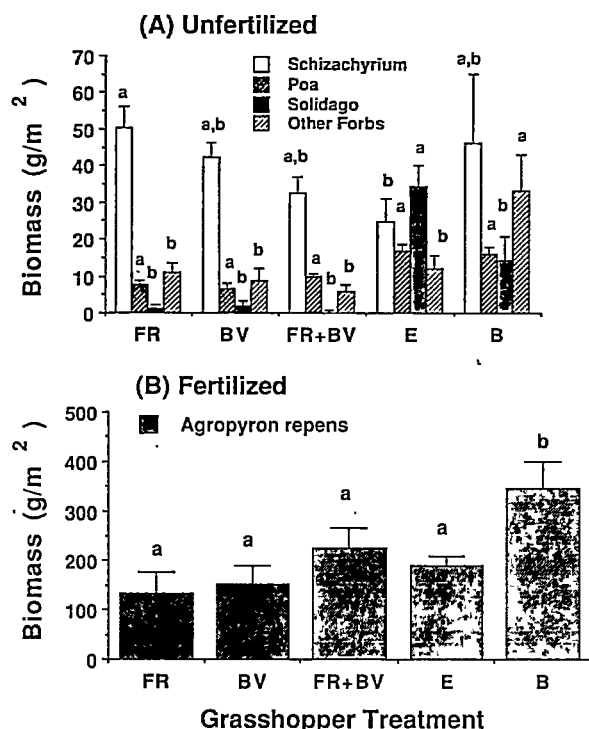


Fig. 4. Mean plant biomass (\pm SE) inside grasshopper cages on a 30 year-old field late in 1989. Grasshopper treatments (6 replicates) are FR, *Melanoplus femur-rubrum* by itself, BV, *Melanoplus bivittatus* by itself, and FR + BV, both species together. Treatments E, empty cage, and B, plots clipped before the experiment began, served as controls. In unfertilized sections (A), clear bars indicate *Schizachyrium scoparium*, heavily hatched bars indicate *Poa pratensis*, lightly shaded bars indicate all *Solidago* species, and lightly hatched bars indicate other forbs. In fertilized (for previous 7 years) sections (B), all data is for *Agropyron repens*, which represented 99% of the plant biomass. Differences in small letters indicate significant contrasts among treatments within a plant group obtained from Duncan's Multiple Range Test ($P < 0.05$)

$P < 0.001$) but grasshoppers had no effect relative to an empty cage ($F = 1.77$, $P = 0.20$). *M. bivittatus* and *M. femur-rubrum* did not differ in their effects on vegetation (see Fig. 4 for contrasts).

Discussion

Our experiments allow us to address some questions about the potential mechanisms of interaction among grasshoppers, among plants, and between grasshoppers and plants. These experiments do not reflect the importance of the interactions under natural conditions and field densities of grasshoppers. Our experiments, however, do provide insight into the way in which resource use by consumers influences the outcome of interactions within and between trophic levels as well as the ability of resource competition theory to predict the outcome of the interactions.

Resource reduction and grasshopper competition

Agropyron repens constitutes both a more abundant (Figs. 2 and 4) and probably higher quality food resource for grasshoppers than the vegetation in unfertilized plots (Inouye et al. 1987; Tilman and Wedin 1991). Thus, our

results in 1989 suggest that final grasshopper densities in our cages were food limited because grasshopper densities were higher in cages on fertilized vegetation both early and late in summer (Table 1). However, this effect could be caused by a difference in the species of available food plants because *Agropyron* did not occur on unfertilized sections. Our 1990 results suggest this possibility, because there was no difference in grasshopper densities between fertilized and unfertilized plots when fertilizer was applied to previously unfertilized vegetation (Table 1). Short-term addition of fertilizer had little effect on the species composition of plots (Fig. 3), so the lack of increase in above-ground plant biomass with fertilization may be due to low allocation of nitrogen or other nutrients to leaves by the existing plant species (Tilman 1988; Tilman and Wedin 1991). However, short term fertilization may have changed plant quality and consequently grasshopper diet choice. For example, *P. apiculata* consumed less monocots on fertilized plots than on unfertilized plots.

Our results provide several insights about grasshopper interactions. First, stocking grasshoppers at high densities in cages does not always lead to interspecific competition (Table 1). In the early experiment in fertilized sections in 1989 (Table 1), competition did not occur even when both species consumed a single plant species. Interestingly, neither species significantly reduced *Agropyron* biomass when living alone in this experiment (Fig. 2). In early season 1990 on fertilized plots, the two grasshopper species reduced the biomass of different plant groups. Although *P. apiculata* significantly reduced the final density of *A. conspersa*, the mortality rate of *A. conspersa* was not significantly higher in the presence of *P. apiculata*. We chose not to interpret this as competition since equal density independent mortality rates of *A. conspersa* stocked at different densities could account for the difference in final density.

Interspecific competition occurred in the other four cases (Table 1). These cases are not completely consistent with resource competition theory, but they suggest that competition may be linked with resource reduction. Both grasshopper species, when living by themselves, significantly reduced the biomass of plant food in three cases (early and late unfertilized sections 1989, Figs. 2 and 4; early 1990 fertilized, Fig. 3). Thus, competition was detected in all cases in which both species significantly reduced food resources and was not detected when each species, living alone, did not reduce plant biomass. As might be expected, competition was more likely to occur, for the grasshopper densities we used, on the lower biomass, lower nitrogen (protein), unfertilized sections.

In the late fertilized experiment in 1989, vegetation declined in the absence of grasshoppers (Fig. 3). Grasshopper herbivory may have been compensatory in this case, i.e., grasshoppers ate plant parts that would have senesced in the absence of herbivory. This result may explain why grasshopper species competed even though they did not reduce *Agropyron* biomass when living by themselves.

If grasshoppers compete for plant food by reducing its biomass, the ability of each grasshopper species, when living by itself, to reduce food resource abundance may predict the outcome of competition. If two species com-

pete for a single resource, the species that can reduce the resource to a lower abundance should displace the other (Tilman 1980, 1982; Schoener 1976). If two species compete but do not differ in their ability to reduce the abundance of two or more resources, they can coexist. Finally, if two species reduce different resources to different levels, they may either compete and coexist, not compete, or act as indirect mutualists.

The results from the unfertilized sections support these hypotheses. In the early season of both 1989 and 1990, *A. conspersa* competitively displaced *P. apiculata* (Table 1), and *A. conspersa*, when living by itself, also reduced the biomass of the two most abundant plant species (*Schizachyrium* and *Poa*) to a lower biomass than *P. apiculata* (Fig. 2). In the late season of 1989, the two grasshopper species competed but persisted (Table 1), and neither grasshopper species, when living by itself, reduced the biomass of any plant species to a lower level than the other (Fig. 3). In early season 1990 fertilized plots, *A. conspersa* and *P. apiculata* reduced different plant groups and did not compete. Therefore, we cannot reject the resource competition hypothesis. However, these are only four cases, and the possibility that competitive ability is associated with the ability to reduce food resources needs to be explored for many other combinations of species and at other herbivore and plant densities before its generality is known.

Our results are clearly open to alternative explanations. For example, in our analysis, we have made the simplifying assumption that each plant species is a distinct grasshopper resource. However, grasshoppers are likely to differentiate between different parts of a plant, and may respond to several plant species as a group (Belovsky 1986). Previous studies (Gwynne and Bell 1968; Jarman 1974; McNaughton 1983; Belovsky 1981, 1984, 1986) suggest that competing herbivores may partition plant parts according to quality (digestibility) and abundance. From this perspective, plant species would have different proportions of their parts within acceptable limits of quality and abundance to a particular herbivore species. Such a hypothesis might explain our results, but we do not have the data to test it.

Plant dynamics and grasshopper herbivory

Grasshoppers had significant effects on the biomass and relative abundance of the dominant plant species on unfertilized sections (Figs. 2, 3, 4). These effects were due in part to reduction of plant species preferred as food by grasshoppers, but also to apparent indirect effects of grasshopper herbivory on non-preferred species. Diet analysis (Table 2) suggests that early in summer, both species of grasshoppers fed heavily on the two dominant grass species *Schizachyrium* and *Poa*. *Solidago*, which was not eaten early in summer, increased seasonally in biomass in both 1989 and 1990 (Fig. 2, 3). In contrast, the two late season grasshopper species fed more heavily upon forbs (as determined by inspection of damaged plants). *Schizachyrium*, which they did not prefer, increased significantly, even though, in the absence of grasshopper herbivory, it declined relative to before the experiment (Fig. 3). Consequently, in both the early and late unfertilized sections, plant species preferred as food

declined in biomass, and unpreferred plant species increased in biomass in the presence of grasshoppers.

Indirect effects of consumers on non-preferred food species have been hypothesized to occur by Lawlor (1979), Holt (1977), and Vandermeer (1980). For herbivores, these effects are probably mediated through plant competition. Previous data from CCNHA suggest that plants on unfertilized sections may compete for nitrogen (Tilman 1984, 1987; Inouye and Tilman 1987; Wilson and Tilman 1991). Consequently, herbivory on one plant species should reduce its consumption of soil nitrogen and may also increase available soil nitrogen concentration through recycling. Both of these effects would increase the abundance of unpreferred plant species. In our study, herbivory on *Schizachyrium* and *Poa* in early summer facilitates the growth of *Solidago* species, which in turn reduces the biomass of other forbs. Likewise, herbivory on *Solidago* and other forbs late in summer facilitates the growth of *Schizachyrium*.

Our early season 1990 fertilized plots illustrate how such indirect effects might affect herbivore interactions (Fig. 3). In this case, *A. conspersa* reduced both grass species to a lower level than did *P. apiculata*, but *A. conspersa* increased the biomass of *Solidago* relative to empty cages or cages with *P. apiculata*. This apparent difference in food preference is corroborated by the proportion of monocots and dicots in the diets of each species (Table 2). If herbivory of grasses by *A. conspersa* facilitates the growth of forbs, then *A. conspersa* may act as a mutualist to *P. apiculata* rather than a competitor, allowing *P. apiculata* to persist at higher densities than it would if living alone. The final densities and mortality rates of the two species (Table 1) suggest that these two species do not compete in this case and that *A. conspersa* may increase *P. apiculata* density, although the trend is not significant. These results suggest the potential for the opposite pattern to occur among grasshopper species in late summer: reduction in forbs by the two *Melanoplus* spp. increases the biomass of grasses and this may increase the density of grasshopper species that prefer grasses.

The seasonal change in the plant species preferred by grasshoppers may be caused by differences in food preferences among early and late grasshopper species (Mulkern et al. 1969; Campbell 1974) or by phenological changes in plant nutrient content. Plants in seasonal environments typically change in N concentration over the growing season (Chapin 1980; Jonasson and Chapin 1985; Faeth 1986). Grasshoppers may switch from preferring *Schizachyrium* and *Poa* to preferring forbs and *Poa* as the summer progresses (Bernays and Chapman 1970; Belovsky 1986). Consequently, the early (nymph-overwintering) grasshopper species may prefer grasses, while late season (egg overwintering) species may prefer forbs. Data from CCNHA (Tilman and Wedin 1991) show that *Schizachyrium* and *Poa* have similar above-ground tissue N content early in summer. However, tissue N in *Schizachyrium* declines to very low and potentially unacceptable levels (Bernays and Chapman 1970; Robbins 1983; Tilman and Wedin 1990) in late summer. Such changes in N concentration may explain how phenology affects grasshopper herbivory and its effect on plant-plant interactions.

Conclusion

We demonstrate that grasshopper species are potentially food limited and can compete. Furthermore, competition appears to be for food and the outcome of competition can, in some cases, be predicted from the ability of different grasshopper species to reduce plant biomass. However, when grasshopper species coexist, they do not appear to differ in their ability to reduce different plant species. Consequently, plant species may not be the "resources" for which grasshoppers compete.

In reducing plant biomass, grasshoppers may affect the relative abundance of different plant species in two ways: (1) directly, by depleting species used as food, and (2) indirectly, perhaps by affecting the outcome of competition among plant species for a soil resource. The effect of grasshoppers on the abundance of plant species changes because species preferred by grasshoppers early in summer are different than those preferred later in summer. Differing phenology in leaf nutrient content among plant species may be responsible for these dietary shifts.

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