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Effects of nymph-overwintering grasshopper density on *Ageneotettix deorum* survival in a northern mixed grassland

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Abstract

Although most pest grasshopper species in North America overwinter as eggs and hatch in late spring or early summer, some species hatch in late summer, overwinter as nymphs, and become adults in late spring. It is not well understood how nymph-overwintering species impact densities of later-developing pest grasshopper species. In an earlier study examining temporally separated competition, nymphal survival of an egg-overwintering species *Ageneotettix deorum,* was reduced when high densities of adult nymph-overwintering grasshoppers strongly reduced grass biomass. However, in nature, early instar *A. deorum* nymphs overlap in time with declining densities of nymph-overwintering grasshoppers, and thus may experience direct competition from them. A field experiment was conducted to examine competitive effects from nymph-overwintering grasshoppers on the survival of *A. deorum* when phenologies overlapped. Precipitation and grass production during the experiment were well above the long term average. Although the maximum density of nymph-overwintering and egg-overwintering grasshoppers was 100 per m^2, interspecific exploitative competition was weak. This study suggests that in years with above-average precipitation, competition between nymph-overwintering adult grasshoppers and later-developing nymphal grasshoppers is likely to be weak, even when densities are high.

Keywords

grasshoppers, competition, Orthoptera, herbivory, phenology

Introduction

The complex biotic and climatic factors that influence grasshopper population densities remain poorly understood (Belovsky & Joern 1995, Joern 2000, Branson *et al*. 2006, Branson 2008). Although most abundant pest grasshopper species overwinter as eggs and hatch in early summer in the northern Great Plains of North America, others hatch in late summer, overwinter as nymphs, and are typically adults by late spring (Pfadt 2002). These species periodically reach high densities that are considered an economic concern (Pfadt 2002, Foster *et al*. 2006, Brust *et al*. 2008), with ~ 145,000 ha sprayed for nymph-overwintering grasshoppers in 2003 (USDA-APHIS-PPQ, unpub. data). However, the potential detrimental impacts of nymph-overwintering grasshopper species on population dynamics of egg-overwintering pest grasshopper species have not been fully examined.

Belovsky *et al*. (2000) hypothesized that competition from earlier hatching grasshoppers could reduce survival of later developing species and reduce outbreaks. In an experiment by Branson (2010) examining temporally separated competition, nymphal survival of an egg-overwintering species *Ageneotettix deorum* (Whitewhiskered Grasshopper) was reduced only when high densities of adult nymph-overwintering grasshoppers reduced grass biomass by 80%. In this case, the competing species were separated in time. However, early- and late-season grasshopper species also partially overlap in time and compete directly. For example, Belovsky *et al*. (2000) found an early hatching grasshopper species reduced survival of a later developing species only when phenologies overlapped. As early instar *A. deorum* nymphs overlap in time with adult nymph-overwintering grasshoppers, competitive effects could be stronger than observed by Branson (2010). Additional research is needed to examine the impact of competition from nymph-overwintering grasshoppers on survival of common egg-overwintering grasshopper species when phenologies overlap.

Materials and Methods

The experiment was conducted at the same northern mixed-grass prairie site in eastern Montana, USA, utilized by Branson (2010) (lat 47.47′N, long 104.08′W). Over 90% of vegetative biomass is grasses, with both cool (C$_3$) and warm-(C$_4$) season species (Branson 2005). Common grasses included western wheatgrass (*Pascopyrum smithii*), blue grama (*Bouteloua gracilis*), needle and thread (*Stipa comata*), prairie junegrass (*Koeleria pyramidata*) and threadleaf sedge (*Carex filifolia*). *Eritettix simplex* was the dominant nymph-overwintering species at the site. It feeds on sedges and cool-season grasses in the spring and later switches to warm-season grasses (Pfadt 2002). *Ageneotettix deorum*, the egg-overwintering species, is also gramnivorous (Mulkern 1967, Pfadt & Lavigne 1982) and is often abundant in outbreaks (Pfadt 2002). To reduce the potential of significant early instar handling mortality, experiments were initiated with 3rd instar *A. deorum*.

Avoiding areas of bare ground, 0.25 m^2 cages were placed over patches of similar vegetation. Cages were constructed of Lumite© (SI Corporation, Gainesville, GA) insect screening with horizontal 15-cm wide polyester flaps at the base. The cages were placed over a frame and sandbags placed around the cage on the horizontal flaps to prevent escapes. Similar cages have been used in numerous grasshopper experiments (Joern & Klucas 1993, Belovsky & Slade 1995, Branson 2010). Based on results from Branson (2010), high grasshopper densities were utilized in the experiment.

Cages were initiated with zero ("None"), 5 ("Low") and 15 ("High") adult *E. simplex* on June 16th, 2010. Additional cages served as a vegetation control treatment with no grasshoppers. As some cages were damaged, replication varied between five and seven cages. Cages with *E. simplex* were counted and restocked to the initial density within one week of initiating the experiment, to account for initial handling mortality. The cages for all three treatments (None, Low, High) were initiated with ten 3rd instar *A. deorum* nymphs on June 25th. Cage counts assessed *A. deorum* survival every 7 to 10 d, and

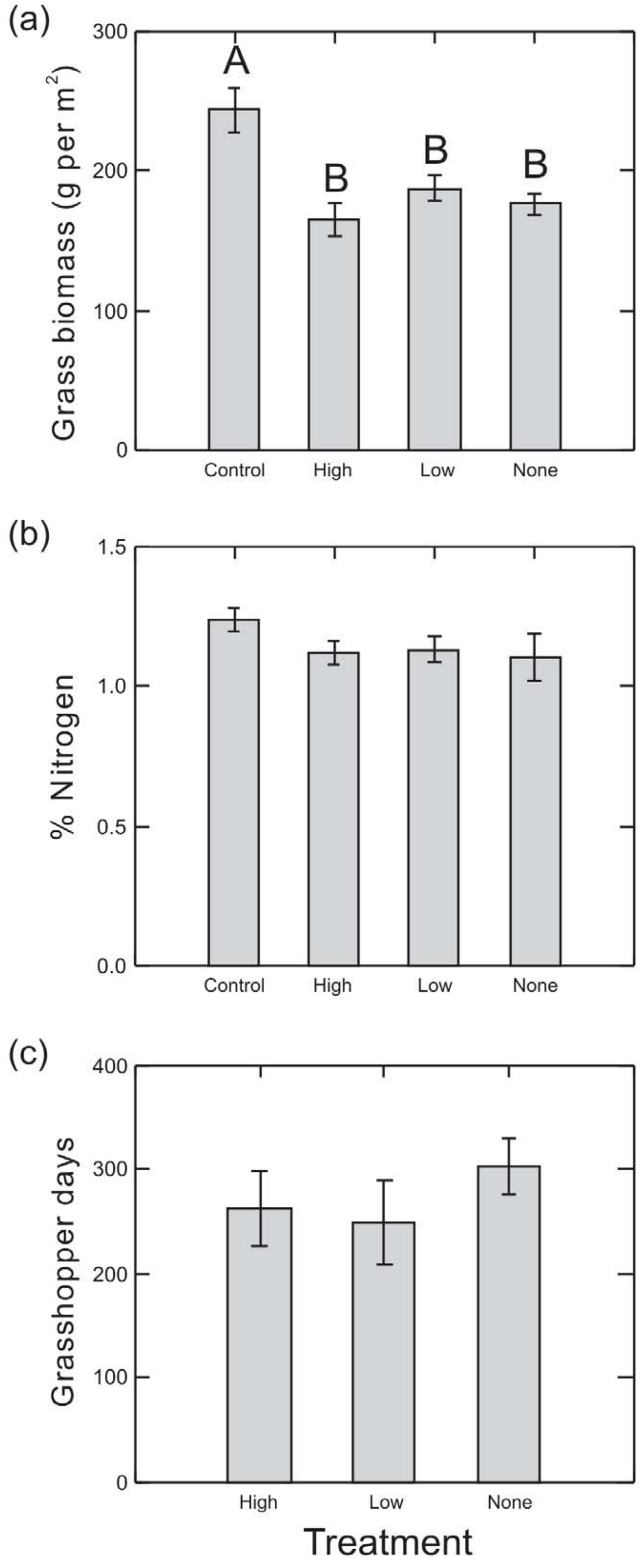

Fig. 1. A) Green-grass biomass (g dry per m^2); B) Percentage nitrogen content of green-grass biomass; C) Cumulative grasshopper survival days for *A. deorum* throughout the experiment. Cages were initiated at 0 (none) and 5 (low) and 15 (high) *E. simplex* nymph-overwintering grasshoppers per 0.25 m^2 cage. Vegetation control cages (control) had no grasshoppers. Letters, when shown, indicate treatment significant differences based on Tukey's HSD ($P < 0.05$).

the experiment ran two weeks after all *E. simplex* adults died.

At the end of the experiment in mid-August, the vegetation in each cage was clipped. Green vegetation was separated by grasses and forbs, dried, weighed and ground. The per cent nitrogen content of grass samples was assessed using a dry combustion C/N analyzer and this value used as a measure of plant quality. Forbs were not analyzed as they comprised less than 10% of biomass, and because both species of grasshoppers are primarily gramnivorous.

Statistics.—ANOVA models were used to assess treatment differences in survival, green grass biomass and percentage nitrogen content. Pairwise comparisons were assessed using Tukey's HSD test. Numbers of *A. deorum* surviving at a given count were multiplied by days since the last cage count and summed over the experiment to generate a measure of grasshopper survival days which was used to assess survival. Systat 13 (Systat Software 2009) was used for all analyses.

Results and Discussion

The presence of grasshoppers reduced peak grass biomass relative to control cages without grasshoppers (Fig. 1a, ANOVA: MS = 6195, $F_{3,13} = 9.2$, $P = 0.002$). Green grass biomass in cages with *A. deorum* did not significantly differ between the three nymph-overwintering density treatments (Fig. 1a). Although the per cent nitrogen content was low for all samples, there was no significant effect of the presence or density of *E. simplex* grasshoppers on grass nitrogen content (Fig. 1b, ANOVA: MS = 0.018, $F_{3,13} = 2.27$, $P = 0.13$). Combined herbivory by *E. simplex*, initiated at 60 per m^2, and *A. deorum*, initiated at 40 per m^2 (*i.e.*, the High Treatment) reduced grass biomass by ~32% relative to controls (Fig. 1a). In an earlier study under drier conditions, herbivory by nymph-overwintering grasshoppers alone reduced grass biomass by ~80% when initiated at 60 per m^2 relative to controls (Branson 2010). As there was no significant difference in grass biomass among the three *E. simplex* density treatments (Fig 1a), it appears that the primary driver of reduced grass biomass relative to the control cages was the presence of *A. deorum*. The influence of both early and late-season grasshopper herbivory on standing biomass has been shown to be highly dependent on precipitation and temperature patterns in the northern Great Plains (Branson 2008, 2010), with forage destruction significantly higher in years with lower production (Branson *et al.* 2006, Branson 2008).

Nymph-overwintering *E. simplex* initiated at densities of 20 and 60 per m^2 did not significantly affect *A. deorum* survival, as assessed by *A. deorum* survival days (Fig. 1c, ANOVA: MS = 5231, $F_{2,17} = 0.80$, $P = 0.47$). Although not significant, *A. deorum* grasshopper survival days were ~15% lower when *E. simplex* was present. As *A. deorum* survival and grass biomass did not differ between *E. simplex* density treatments, *E. simplex* did not lower the carrying capacity for *A. deorum*, as measured by survival. It is possible that fecundity was lowered, although this was not measured in this experiment.

Competition among grassland grasshoppers in North America is typically exploitative in nature (Belovsky & Slade 1995, Branson 2003), but the strength of exploitative competition would be reduced in years with abundant food availability (Branson 2003, 2008). Late spring precipitation in 2010 was above the long-term mean, with more than double the average May precipitation. As a result, green grass biomass in control cages without grasshopper herbivory was much higher than in the previous experiment by Branson (2010). This higher precipitation likely also contributed to higher regrowth following herbivory. Although the maximum combined density of nymph-overwintering and egg-overwintering grasshoppers was 100 per m^2, strong interspecific exploitative competition was not apparent.

The relatively high densities used in the experiment are within the range observed in the northern Great Plains (Branson 2010), with recent studies documenting maximum fall densities of nymph-overwintering species at 140 per m^2 (Foster *et al.* 2006) and maximum summer nymphal densities of egg-overwintering species at ~130 per m^2 (Branson 2008). Simultaneous high densities of nymph-overwintering and egg-overwintering species are likely an infrequent occurrence. Competition from early season species could result in delayed development and reduced reproduction for *A. deorum* when food availability was more limiting than occurred in this study (Danner & Joern 2004).

These results indicate that in years with above average precipitation, competition between phenologically overlapping nymph-overwintering adult grasshoppers and later developing nymphal grasshoppers is likely to have weak effects on survival, even when densities reach outbreak conditions. The results match the findings of Branson (2010) who found high reductions in grass biomass from temporally separated early season herbivory is required to reduce nymphal survival in *A. deorum*.

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