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An ecosystem perspective on grasshopper control: possible advantages to no treatment

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Abstract

It has been hypothesized that some herbivores may increase the cycling of nutrients in ecosystems, thereby increasing plant production even after herbivore consumption is considered. Such herbivory could maintain the productivity of ecosystems and should not be curtailed. This contrasts with the traditional view whereby herbivory always reduces plant production. Two grasshoppers (*Melanoplus sanguinipes* and *Ageneotettix deorum*), considered pest species in Western US rangelands, are experimentally shown to enhance plant production under certain conditions and to diminish it under others. Plant production increased when grasshoppers' consumption increased nitrogen cycling, nitrogen being the limiting resource for plants at the study sites. This happened when grasshoppers consumed plant species with slowly decomposing litter, favoring plants whose litter decomposed rapidly, such that their store of nitrogen was more rapidly released to the soil. However, feeding preferences change between sites and with grasshopper species, creating a spatial mosaic in which grasshoppers can increase and decrease plant production. Because changes in plant species composition are the major reason for changes in nutrient cycling rate, plant communities are created that will persistently exhibit enhanced or diminished production. Therefore, grasshoppers cannot be generally viewed as detrimental to rangeland productivity and grasshopper control may need to be more judiciously applied.

Keywords

Grasshoppers, nutrient cycling, ecosystem management, nitrogen

Introduction

Traditionally, annual consumption of plants by grasshoppers has been thought to reduce forage for livestock, thereby justifying grasshopper control in rangelands. Control has been advocated and often applied when the short-term economic and political benefits of grasshopper control appear to exceed costs. Recently, a longer term perspective on natural resource management actions, called ecosystem management (Grumbine 1994), has been advocated and adopted by many government agencies. Ecosystem management addresses the long term impacts of management actions on ecosystem functioning and the value of the services that an ecosystem provides to society (Costanza & Folke 1997, Daly *et al.* 1997); this can provide a very different perspective from management decisions based on short-term costs and benefits. We address here how grasshoppers may affect the functioning of rangeland ecosystems and whether this should influence attitudes toward rangeland grasshopper control.

Ecologists and natural resource managers have traditionally held the view that when a herbivore consumes a unit of plant biomass,

there is now less food for other herbivores, and the plant whose part was consumed is now less able to survive, grow and reproduce. This population perspective has been the primary focus of most natural resource management (*e.g.*, fishery, wildlife and pest management: Caughley & Lawton 1976). More recent perspectives on herbivory do not deny these population processes, but argue that the response of a single population may not translate into a simple ecosystem change (*e.g.*, herbivory on a plant population may not lead to reduced ecosystem primary production), because ecosystem functions respond to population changes and may modify population effects (DeAngelis 1992).

For example, even if herbivory by one herbivore species reduces a plant species' biomass and this lost biomass makes less food available to another herbivore species, it is possible that the ecosystem's overall plant biomass or primary production may increase. This might occur if the herbivore's consumption increases the rate of nutrient cycling, cycling which limits plant growth, and thereby enhances ecosystem productivity (Hutchinson & Deevey 1949, McNaughton *et al.* 1988). On the other hand, if the herbivore decreases the rate of nutrient cycling, then the herbivore's reduction of plant biomass and food for other herbivores might be amplified (Pastor *et al.* 1988, Pastor & Naiman 1992). Examples of both processes have been demonstrated in the field (*viz.* Pastor *et al.* 1988 vs McNaughton *et al.* 1988). The question now is not whether herbivores increase or decrease rates of nutrient cycling and productivity, but under what conditions either of these effects occur.

Herbivory's effects on nutrient cycling are summarized in Fig. 1. Nutrient release from excrement and dead herbivores has been termed the **fast cycle** (McNaughton *et al.* 1988) because this detritus *rapidly* decomposes and releases nutrients for plant uptake. Release of nutrients from plant litter has been termed the **slow cycle** (McNaughton *et al.* 1988) because this detritus *slowly* decomposes and releases nutrients for plant uptake. Herbivory affects the **slow cycle** by changing the quantity of plant litter and its quality when herbivores preferentially feed on plants that differ in how rapidly their litter decomposes (Pastor *et al.* 1988, Pastor & Naiman 1992). Preferential feeding on plants that produce slower decomposing litter reduces their relative abundance, speeding up the **slow cycle**, whereas preferential feeding on plants that produce faster decomposing litter slows down the **slow cycle**.

Shifts in proportion of nutrients released by **Fast** versus **slow cycles** may change nutrient availability to plants, which may, in turn, modify plant production and plant species composition. If

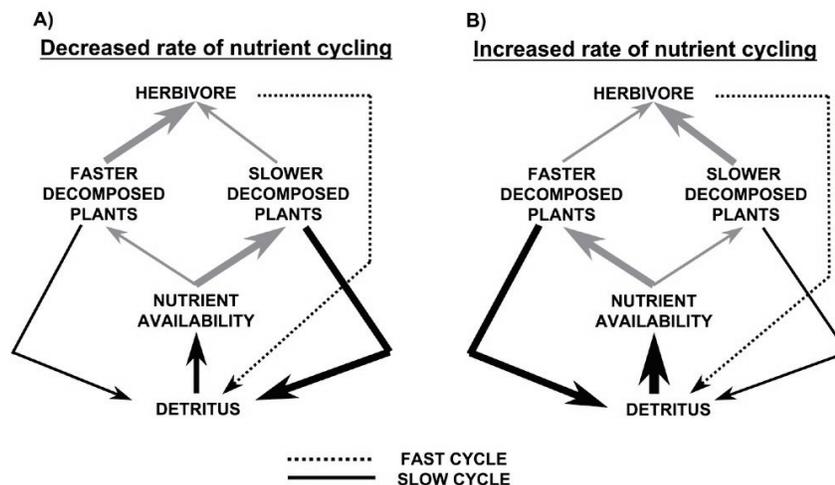


Fig. 1. The conditions for herbivores to modify nutrient cycling and NPP are presented: A) nutrient cycling slows down and NPP decreases and B) nutrient cycling speeds up and NPP increases. Black lines represent the slow cycle, dotted black lines represent the fast cycle, and solid gray lines represent consumption. Line thickness reflects the relative magnitude of consumption and nutrient cycling.

preferential feeding on slower decomposing plants overshadows deleterious effects of consumption on plants, it may accelerate nutrient cycling and increase plant production (Pastor & Naiman 1992). However, preferential feeding on fast-decomposing plants may decelerate nutrient cycling and decrease plant production (Pastor & Naiman 1992). Changes in nutrient cycling rates are one class of several factors that affect plant species composition. For example, if slowly decomposing plants are better competitors for nutrients when nutrients are less available, and rapidly decomposing plants are better competitors when nutrients are more available, herbivore-induced changes in nutrient cycling may affect plant competition and thereby change vegetation communities (Pastor & Naiman 1992). Therefore, changes in nutrient cycling, with resulting changes in plant species composition, may further accentuate changes in nutrient

cycling, plant species composition and plant production, thereby creating a self-enhancing or positive feedback.

We previously examined how a grasshopper (*Melanoplus sanguinipes* (Fabricius), which is abundant at a site in western Montana USA (4 to 36 adults/m²), and considered a pest in western US rangelands, can affect the rangeland ecosystem (Belovsky 2000, Belovsky & Slade 2000). We found that at the end of the growing season (Fall), grasshoppers diminished plant biomass within a year, compared with sites without grasshoppers (Fig. 2, Belovsky 2000). These results are in accord with the traditional perspective that control is warranted to provide more food for livestock.

However, an experiment was conducted to examine the grasshopper's effect on long-term (5 y, 1994 – 1999) ecosystem functioning (Belovsky 2000, Belovsky & Slade 2000): 1) grasshopper effects on the fast cycle were examined by manipulating grasshopper density, but maintaining plant litter production (125% or 50% of natural density in each year with litter produced by the natural density of grasshoppers in each year); 2) grasshopper effects on the slow cycle were examined by manipulating plant litter production, but maintaining grasshopper density (natural grasshopper density in each year with litter produced by 125% or 50% of natural density in each year); 3) grasshopper cumulative effects on fast and slow cycles were examined by manipulating grasshopper density and leaving plant litter *in situ*. Increasing grasshopper density increased plant production in every year through fast cycle, slow cycle, and cumulative effects (Fig. 3, Belovsky 2000, Belovsky & Slade 2000).

Several additional ecosystem characteristics were measured in these experiments (soil nitrogen, litter quantity, litter nitrogen content, soil moisture and decomposition rate of a common litter source: Fig. 4, Belovsky & Slade 2000). Grasshoppers increased the inorganic soil nitrogen availability (NH₄, NO₂ and NO₃). The increased sizes of these pools were not caused by increased plant litter production or by enhanced decomposition processes, because litter quantity declined and decomposition rates for common litter sources were unchanged with more grasshoppers. Rather, the grasshoppers increased the quality of plant litter (higher nitrogen content), which then decomposed faster (Fig. 4). This increase in litter quality occurs because consumption changes the relative

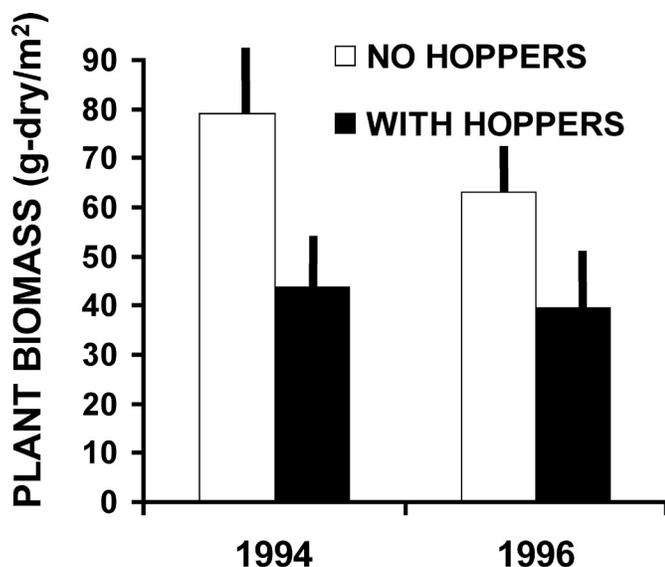


Fig. 2. In two years at our original study site (Site 1), natural grasshopper densities are seen to reduce the end of growing season (Fall) plant biomass (modified from Belovsky 2000) as measured in g/m² of dry biomass.

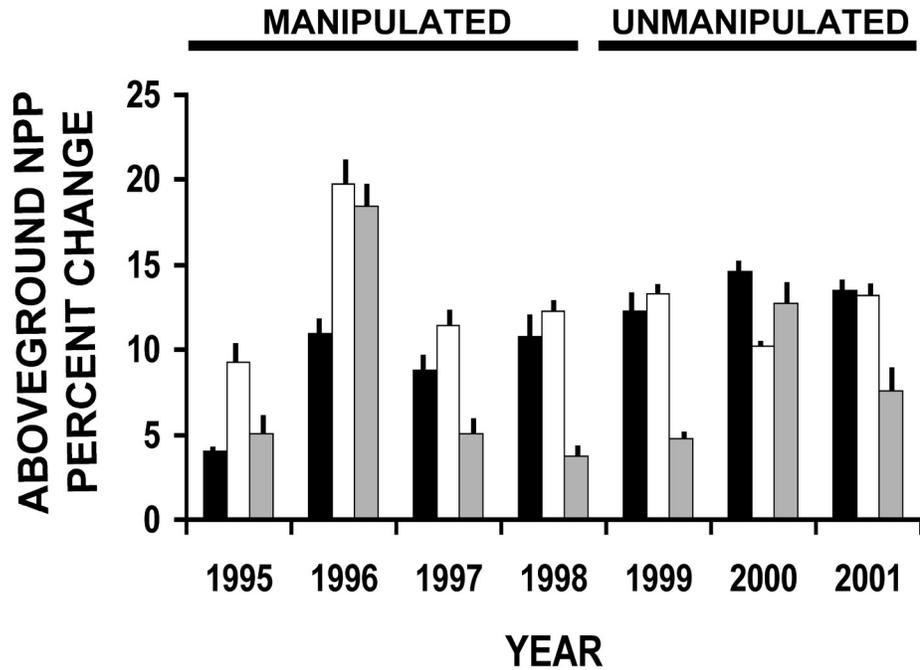


Fig. 3. Percent increase ($\pm s_{\bar{x}}$) in above-ground plant production (NPP) with increased (125%) compared to decreased (50%) grasshopper density for fast (black), slow (white) and combined fast and slow cycle (gray) effects. Unmanipulated (1999-2001) shows experimental areas when these were opened to field densities of grasshoppers.

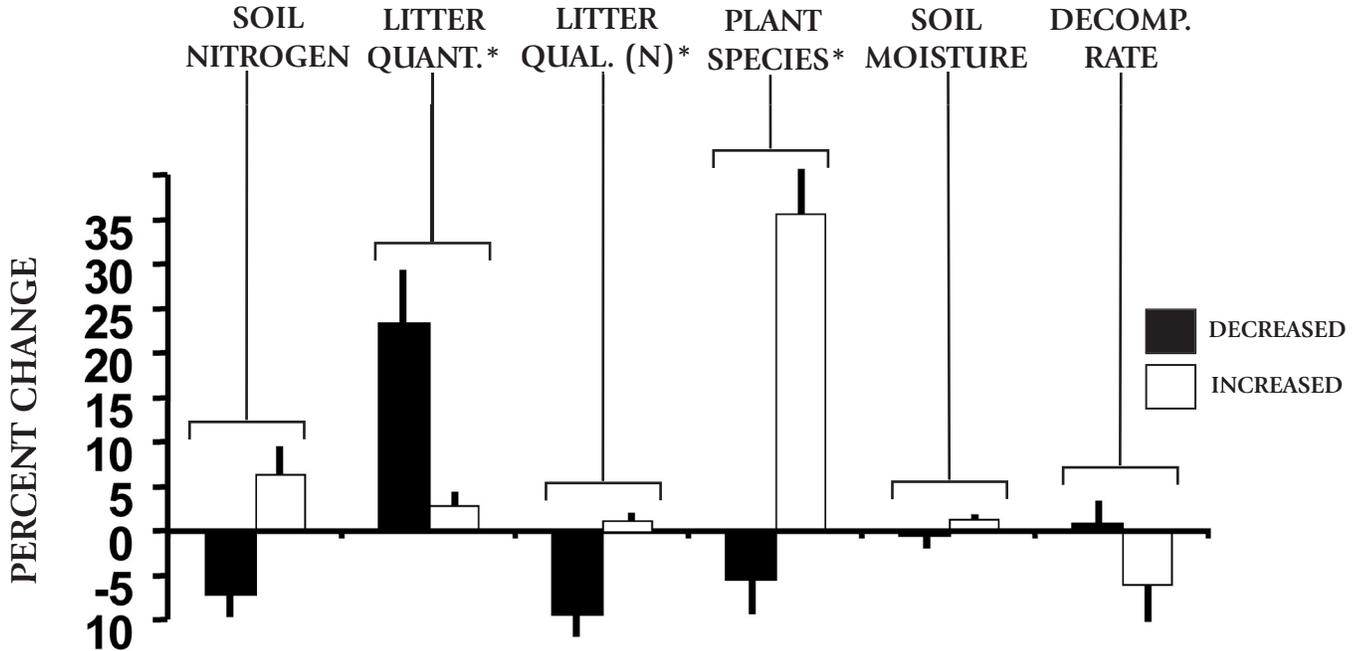


Fig. 4. Average percent changes ($\pm s_{\bar{x}}$) in ecosystem characteristics with decreased (black) and increased (white) grasshopper densities. An asterisk indicates statistical significance. For each ecosystem characteristic, the statistical information is: soil nitrogen, $p < 0.02$, $t = 3.10$, $df = 6$; litter quantity, $p < 0.04$, $t = 2.91$, $df = 6$; litter quality (nitrogen), $p < 0.009$, $t = 4.69$, $df = 6$; plant species (ratio of *Poa* to *Elymus*), $p < 0.0005$, $t = 48.18$, $df = 6$; soil moisture, $p < 0.70$, $t = 0.59$, $df = 4$; decomposition rate, $p < 0.62$, $t = 0.59$, $df = 4$.

abundance of the two dominant plant species (>90% total biomass) so that the slowly decomposing litter (*Elymus smithii*) decreases relative to the litter that decomposes rapidly (*Poa pratensis*) (Fig. 4). The shift in plant species' relative composition emerges because the grasshoppers preferentially feed on the slower decomposing plant species, *Elymus smithii* (Belovsky & Slade 2000). Finally, because plant growth at the study site increases with soil nitrogen availability ($r = 0.64$, $N = 21$, $p < 0.002$; Belovsky & Slade 2000), the observed increase in soil inorganic nitrogen availability explained the resultant increase in plant production with greater grasshopper density.

The findings support the theorized necessary conditions (see above) for a herbivore to increase plant production by increasing nutrient cycling rates. Whether this herbivory also created a positive feedback or self-enhancement so that ecosystem influences would be long lasting after the increased herbivory was removed, could not be determined at the time (see below). However, the observation that the plant community was changed by the herbivore is a necessary condition for a positive feedback or self-enhancement to occur. Furthermore, whether grasshoppers could have a long term detrimental effect on plant production by preferentially feeding on the fast-decomposing plants was not investigated; but *M. sanguinipes* is known to preferentially feed on *P. pratensis* rather than *E. smithii* at a nearby site (within 5 km). Finally, whether other grasshopper species exert similar influences to *M. sanguinipes* on the ecosystem is unknown. Preliminary results from investigations of these additional issues are presented here and grasshopper control in rangelands is discussed in light of these results.

Study sites and methods

Ecosystem manipulations.—We described the experimental design and measurements in detail elsewhere (Belovsky 2000, Belovsky & Slade 2000). In summary, the design employed 1-m² plots enclosed by insect netting in areas selected for their uniformity of vegetation. Within each plot, we manipulated grasshopper density (50%, 100% and 125% of natural density for each year) and plant litter (production from 50%, 100% and 125% of natural grasshopper density for each year). We established 24 plots in which these treatment levels were crossed in a factorial design (3 areas — 50% density and litter from 50% density; 3 areas — 50% density and litter from 100% density; 6 control areas — 100% density and litter from 100% density; 3 areas — 100% density and litter from 50% density; 3 areas — 100% density and litter from 125% density; 3 areas — 125% density and litter from 100% density; 3 areas — 125% density and litter from 125% density).

In each plot, we measured the following parameters. Above-ground living plant biomass was measured every 2 w using a radiometer to estimate primary production after consumption. We measured soil nitrogen availability (NH₄⁺, NO₂⁻ and NO₃⁻) for the periods May to October and October to May, using one resin bag for each period (Binkley & Mattson 1983, Binkley 1984). We measured soil moisture gravimetrically in May and October. We measured plant litter biomass in October and its nitrogen content by micro-Kjeldahl methods. We measured litter decomposition using 4-l bags of the two most common grasses (*P. pratensis* and *E. smithii*), placed in the plots each October: one bag of each species was removed each May and October. We measured grasshopper feeding on the common grasses as the percentage of 25 blades exhibiting damage in October.

We examined two sites where *P. pratensis* and *E. smithii* were the dominant grasses (>90% of plant biomass). One site was the original study site (Site 1) reported in Belovsky (2000) and Belovsky and Slade (2000), while the other site was <5km away (Site 2) and was described in Belovsky and Slade (1995). As at Site 1, Site 2's plant production was limited by the availability of soil nitrogen ($r = 0.48$, $N = 18$, $p < 0.023$). At Site 1, *M. sanguinipes* preferentially feeds on *E. smithii*, but at Site 2 it preferentially consumes *P. pratensis*. While the N content of these two grasses differs between the two sites, *P. pratensis* is always higher in N.

Since 1998 in the 1-m² plots at Site 1, we discontinued (relaxed) the previously described treatments so that all areas experienced natural grasshopper densities and litter production. We continued the ecosystem measurements to assess how resistant (long term) the previously observed ecosystem changes were to a return to natural densities and litter production. Since May 2000 at Site 2, we conducted the original experimental manipulations separately with two grasshopper species [*M. sanguinipes* and *Ageneotettix deorum* (Scudder)]. *A. deorum* is another common grasshopper in western US rangelands that often is considered a pest. These experiments examine whether grasshopper feeding preference and species of grasshopper affect the findings observed at the original study site.

We expressed measurements from manipulated plots as percent change relative to control areas since the start of the experiment (May 1994 at Site 1 and May 2000 at Site 2):

$$\% \text{ Change} = 100 \times \left(\frac{S_i/S_0}{C_i/C_0} - 1 \right)$$

where S_i is the measure in year i from the plots; S_0 is the initial measure from those plots (start of experiment: 1994 at Site 1 and 2000 at Site 2), C_i is the average measure in year i for 1-m² control plots, and C_0 is the initial average measure for 1-m² control plots (start of experiment: 1994 at Site 1 and 2000 at Site 2).

We normalized percent change by logit transformation for statistical tests (ANOVA, ANCOVA and t-tests). The percent change values were used to examine for **fast cycle**, **slow cycle** and **cumulative** effects. **Fast cycle** effects were measured by comparing areas receiving a constant litter treatment, but different grasshopper densities; **slow cycle** effects were measured by comparing areas with a constant grasshopper density, but different litter treatments; **cumulative** effects were measured by comparing areas that received litter produced by the grasshopper density in the areas.

Feeding trials.—Feeding preferences for the two dominant grasshopper species (*M. sanguinipes* and *A. deorum*) on the two dominant plants (*P. pratensis* and *E. smithii*) at Site 2 were measured by providing an individual of either grasshopper in a 0.5-l jar with equal amounts of each plant (5 cm²) collected from Site 2. Twenty individuals of each grasshopper species were tested (equal sex ratio) and for each individual we recorded whether a greater amount (cm²) of *P. pratensis* or *E. smithii* was consumed in 20 min. We then tested, using a χ^2 test, whether the number of individuals of each species consuming more *P. pratensis* or *E. smithii* differed.

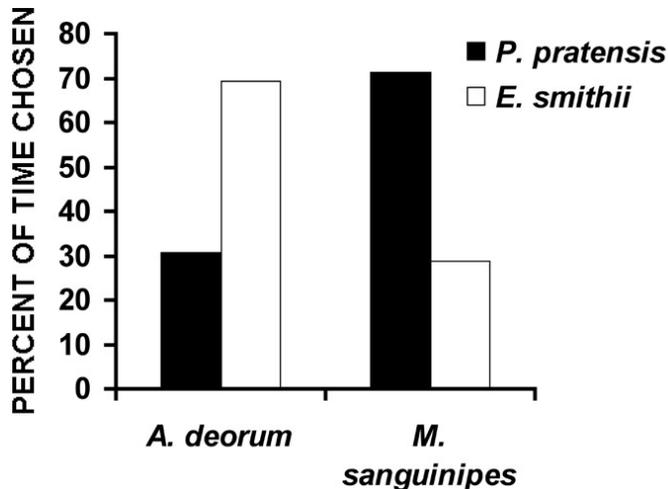


Fig. 5. The feeding preferences of *M. sanguinipes* and *A. deorum* on the two dominant grasses at Site 2 presented as the percentage of time that the grasshopper chose one species of grass more than the other.

Results

Persistence of observed changes at Site 1.—The previously observed increases in plant production at Site 1 (resulting from greater densities of *M. sanguinipes*) continued for 3 y after the density/litter manipulations were terminated (Fig. 3) in the **fast cycle** areas ($F = 14.56$; $df = 1, 14$; $p < 0.0001$), **slow cycle** areas ($F = 31.47$; $df = 1, 14$; $p < 0.0001$), and **cumulative** effect areas ($F = 7.99$; $df = 1, 14$; $p < 0.007$). These results did not vary from year to year ($p < 0.21 - 0.88$), demonstrating positive feedback or self-enhancement, *i.e.*, herbivory-created changes in primary production persisted after differences in herbivory were eliminated.

***M. sanguinipes*' and *A. deorum*'s effects at Site 2.**—Based on amount consumed in the feeding trials (Fig. 5: $\chi^2 = 6.08$, $df = 1$, $p < 0.02$), *M. sanguinipes* and *A. deorum* differ in their preference of the two dominant plant species, *P. pratensis* and *E. smithii*.

After one year at Site 2, plant production significantly decreased with *M. sanguinipes*' effect on the **fast cycle** (Fig. 6: $t = 6.24$, $df = 4$, $p < 0.001$) and the **cumulative** response (Fig. 6: $t = 9.96$, $df = 4$, $p < 0.001$). While plant production was measured to decrease with *M. sanguinipes*' effect on the **slow cycle**, the decrease was not statistically significant (Fig. 6: $t = 2.63$, $df = 4$, $p < 0.05$). Declines in plant production were expected at this site because *M. sanguinipes* preferentially feeds on *P. pratensis*, the faster decomposing plant species (Fig. 5).

After one year at Site 2, plant production increased with *A. deorum*'s effect on the **fast cycle** (Fig. 6: $t = 7.43$, $df = 4$, $p < 0.01$) and the **cumulative** response (Fig. 6: $t = 6.49$, $df = 4$, $p < 0.01$). No change was measured with *A. deorum*'s effect on the **slow cycle** (Fig. 6: $t = 1.08$, $df = 4$, $p < 0.50$). At this site, *A. deorum* preferentially feeds on *E. smithii*, the slower decomposing plant species (Fig. 5).

We were not surprised that **slow cycle** effects were not statistically significant, because the results were from a single year and per its name, the **slow cycle** will not respond rapidly. Nonetheless, *A. deorum*'s effects on plant production were significantly different and opposite from *M. sanguinipes*' effects (Fig. 6) for the **fast cycle** ($t = 6.59$, $df = 4$, $p < 0.01$), **slow cycle** ($t = 4.84$, $df = 4$, $p < 0.01$) and

cumulative effects ($t = 4.96$, $df = 4$, $p < 0.01$). This was expected, given the two grasshoppers' opposite feeding preferences.

Discussion

Grasshopper ecology and its influence on ecosystems.—As stated in the introduction, these are preliminary results. However, it is apparent from these two study sites that grasshoppers do not affect ecosystem functioning in the same way everywhere. *M. sanguinipes* is the most abundant grasshopper at both sites, but at one site it increases plant production and at the other it decreases it (Figs 3 and 6). As hypothesized from models that address the role of herbivores on the rate of nutrient cycling (Fig. 1), the observed difference appears to arise because *M. sanguinipes* preferentially fed upon the slower decomposing plant (*E. smithii*) at Site 1, where it increased plant production, and the faster decomposing plant (*P. pratensis*) at Site 2, where it decreased plant production. This conclusion is further supported by the experiment at Site 2 with *A. deorum*, where this grasshopper preferentially fed on the slower decomposing *E. smithii* and increased plant production, unlike *M. sanguinipes* at this site.

At Site 1 the observed increase in plant production due to greater grasshopper density was maintained long after the grasshopper density was decreased. This occurs because the grasshoppers changed the plant composition in favor of the faster decomposing grass (*P. pratensis*), which leads to a greater availability of soil N (NH_4 , NO_2 and NO_3). This plant species composition was maintained because *P. pratensis* is competitively superior to *E. smithii* (slower decomposing) when soil N is more available (Smika et al. 1965, Tilman 1988). Therefore, *M. sanguinipes*' consumption at Site 1 created a positive feedback through plant composition that led to a self-maintaining alternate ecosystem.

Given that *M. sanguinipes* and *A. deorum* were common at Site 2, but with *M. sanguinipes* dominant, the net effect of consumption by grasshoppers at this site was to decrease plant production. *M. sanguinipes* is more abundant than *A. deorum* at this site because *M. sanguinipes* competitively reduces *A. deorum* numbers, much more than *A. deorum* reduces *M. sanguinipes* numbers (Chase and

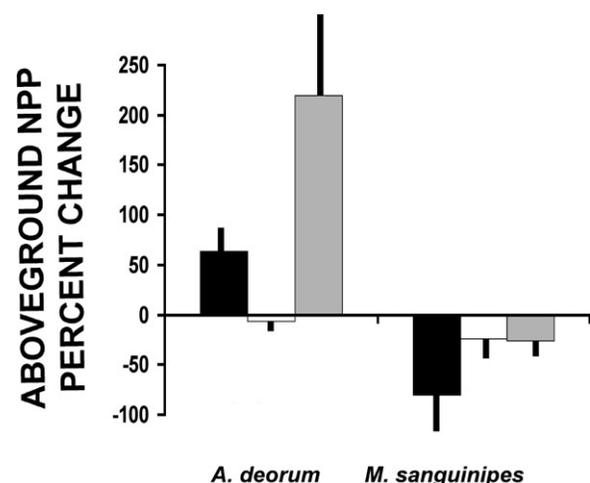


Fig. 6. Percent change ($\pm s_{\bar{x}}$) in above-ground plant production (NPP) with increased (125%) compared to decreased (50%) grasshopper density for fast (black), slow (white) and combined fast and slow cycle (gray) effects at the new study site with *M. sanguinipes* or *A. deorum*.

Belovsky 1994, Chase 1996). One might expect that if *A. deorum* could become temporarily more abundant than *M. sanguinipes*, *A. deorum* might be able to increase plant production and increase even more in numbers, thereby competitively overcoming *M. sanguinipes*. However, this is unlikely. First, how could *A. deorum* become initially more abundant? One possibility is if predators preferentially killed *M. sanguinipes*, but this is unlikely because predation rates on the two grasshoppers are very similar (Belovsky *et al.* 1990, Belovsky and Slade 1993). Second, even if *A. deorum* did increase plant production, this would not be self-sustaining because the faster decomposing grass, *P. pratensis*, would then become relatively more abundant and this grass is preferentially consumed by *M. sanguinipes* (unlike *A. deorum's* preference). Therefore, at Site 2, the self-sustaining condition should be a less productive ecosystem, with *M. sanguinipes* remaining the dominant grasshopper.

Why *M. sanguinipes* shifts its feeding preference between the slow decomposing grass (*E. smithii*) and the fast decomposing grass (*P. pratensis*) at the two sites is unknown at this time, but under investigation. Understanding this shift in preference may be the key to understanding when this and other common grasshoppers may function to enhance or diminish primary productivity in different ecosystems.

Implications for grasshopper control.—Grasshopper control programs whose goal is to increase forage for livestock in rangelands should be re-evaluated in light of our findings. Our findings support grasshopper control programs at locations where grasshoppers diminish nutrient cycling rates, and thereby decrease plant production, assuming that the economic costs and benefits make it feasible. However, at locations where grasshoppers increase nutrient cycling rates, and thereby increase plant production, grasshopper control programs cannot be ecologically or economically supported.

Assessing whether grasshoppers are likely to decrease or increase plant production at a site depends on the grasshoppers' feeding preferences and the decomposition rates of the food plants. This is not easy to assess and such information is seldom available to managers of control programs. Furthermore, the finding that *M. sanguinipes'* effect on plant production could reverse between sites only 5 km apart, sites with the same dominant plant species, indicates that a much finer scale of ecological knowledge and application of control programs is required. Often grasshopper feeding preferences are viewed as constant, not demonstrating the plasticity found in this study, nor are they examined over a range of small areas within a larger area. In addition, plant decomposition rates are seldom known. Finally, if herbivory-induced ecosystem changes in plant production are self-sustaining (*i.e.*, if there is positive feedback), when the intensity of herbivory changes, particular plant competitive relationships must be operating and these are seldom addressed. Past control programs have ignored ecosystem effects, and the necessary information to make even a crude assessment of them is usually unavailable.

Even if ecosystem effects are considered in a control program, their spatial scale needs to be assessed. Ideally from an ecological perspective, control programs would only be applied to specific areas where grasshoppers decrease plant production. However, such areas may comprise so small a patchwork that control could be economically or logistically impossible. If this is the case, then the pest manager must assess whether the average effect of grasshoppers

over the larger area increases or decreases plant production. This might be accomplished using a geographic information system, in which specific habitat (ecosystem) categories are identified as having increased or decreased plant production due to grasshoppers. If the average over the landscape indicates that grasshoppers are increasing production, then control is not warranted.

Finally, an even more vexing control problem is posed by our results. For a given site, how might a control program reduce the abundance of grasshopper species that decrease plant production (*e.g.*, *M. sanguinipes* at the one site), while increasing the abundance of species that increase plant production (*e.g.*, *A. deorum* at the same site)? Such will require an even greater ecological knowledge of grasshoppers and ecosystem effects than is currently available.

Taking an ecosystem perspective on grasshoppers in rangelands indicates that the universal application of control programs is unwarranted. Furthermore, the ecological information necessary to justify grasshopper control and its proper implementation exceeds what is currently available or employed.

Conclusion

Traditionally, grasshopper consumption in rangelands has been viewed as detrimental to plant production and forage resources for livestock. The studies presented here indicate that under certain conditions, grasshopper consumption increases the rate of nutrient cycling in an ecosystem, thereby increasing plant production. In such areas grasshoppers should be viewed as beneficial and not warranting control. Under other conditions, grasshopper consumption decreases the rate of nutrient cycling in an ecosystem, thereby decreasing plant production. In these areas grasshoppers can be considered detrimental in an economic sense and control efforts may be warranted. The task for ecologists and pest managers is to identify the conditions under which grasshoppers are beneficial *vs* detrimental to societal goals for ecosystems and properly employ this information to design control programs. Such an approach to ecosystem management is not easy: it requires new and more information than is typically available.

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