Part 1. GRASSHOPPERS AS INTEGRAL ELEMENTS OF GRASSLANDS

1. DO GRASSHOPPERS DIMINISH GRASSLAND PRODUCTIVITY?

A New Perspective For Control Based on Conservation

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Abstract

Experimental studies of the effects of grasshopper consumption on plant production are presented. The long held claim that grasshopper consumption of plants in some years can reduce forage for livestock and wildlife is supported. However, examining grasshopper consumption over a longer term (multiple years), I find that grasshoppers enhance plant production. This emerges because grasshoppers accelerate nutrient cycling primarily by increasing the proportion of litter provided by faster decomposing plants. The greater availability of nutrients further increases the abundance of faster decomposing plants because they are competitively favored under these conditions and this further enhances nutrient availability and plant production. Therefore, the short-term loss of forage for livestock and wildlife is outweighed by the long-term enhancement of forage production. The rangeland conditions which lead to grasshoppers producing beneficial production effects are reviewed.

1. Problem

1.1. INTRODUCTION

E.O. Wilson [1] claims that biodiversity provides economic, cultural and biological wealth to mankind. Economic wealth arises from the products that biodiversity provides; cultural wealth emerges because biodiversity is part of every nation's history and art, and biological wealth refers to the aesthetic pleasure and environmental health provided by biodiversity.

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As ecologists have become increasingly concerned with the global loss of biodiversity, they have begun to stress the biological wealth provided by biodiversity. In particular, the idea that endemic species and native ecosystems may provide ecological services that benefit humanity has emerged as a major motive for conservation [2, 3]. However, it is a difficult and contentious task to decide how these ecological services should be economically valued for comparison with the economic gains provided by their destruction [4].

Valuation of ecological services is not always problematic. For example, if products from an ecosystem are being exploited and current management practices for the system reduce biodiversity and this diminished biodiversity decreases ecological services that diminish production, then biodiversity needs to be restored to rejuvenate production. I present in this chapter an example based on grasshoppers (Orthoptera: Acrididae) and rangeland production of forage plants in the western USA, where grasshoppers enhance the production of forage for mammalian herbivores.

I will show that grasshoppers can reduce the forage for livestock within a year as commonly assumed; however, I will also show that grasshoppers actually stimulate forage production between years and this long-term enhancement exceeds annual losses. The stimulation of production occurs because grasshoppers can accelerate nutrient cycling in the grassland ecosystem, more effectively than mammalian herbivores can. This means those commonly accepted rangeland management practices that try to control grasshopper consumption may actually reduce the ecosystem's long-term productivity, rather than making more forage available to mammalian herbivores. Consequently, grasshopper control may reduce ecological services provided by grasshoppers and this may be detrimental to the economic wealth provided by rangelands.

To reach the above conclusions, I conducted long term (six years) experiments in grassland that manipulated grasshopper herbivory to assess how this herbivory changes 1) nutrient cycling, 2) plant production and 3) plant species composition within and between years.

1.2. STUDY SYSTEM

The study was conducted at the National Bison Range in Montana, USA. This site is Palouse Prairie, which is the ecosystem of the intermountain region of western North America bounded by the Rocky Mountains on the east, the Cascade Mountains on the west, southern Alberta and British Columbia in Canada on the north, and northern Utah and Nevada in the US on the south. This grassland averages 35 cm/yr of precipitation, which primarily falls as rain in spring (May – June). I chose a 4 ha site at ~750 m elevation for its uniformity in slope and aspect (very flat) and homogeneity in vegetation (plant biomass and species composition) for conducting the experiments. More than 90% of the plant biomass at this site was represented by three monocot species (*Elymus smithii*, *Poa pratensis* and *P. compresa*), with a variety of non-woody dicots comprising the remainder of the plants. During the study period (May, 1994 – July, 1999), aboveground net plant production (NPP) was measured with a radiometer and it varied between 108 and 237 g/m^2 or approximately 2.2 fold.

NPP at this site is a function of precipitation and soil N availability. First, over six years at the National Bison Range, monocot NPP is positively correlated with May – September precipitation ($P < 0.02$) and soil nitrogen availability during May – September ($P < 0.03$), not annual nitrogen availability, as indicated by N absorbed by buried resin bags (see below). Over this same period, dicot NPP was not correlated with precipitation and was negatively correlated with annual N absorbed by resin bags ($P < 0.02$), not nitrogen availability only from May - September. Second, at the 4 ha study site during 1994, 21 resin bags were buried in early May and removed in early October to indicate soil N availability during the plant growing season, and plant biomass was measured by clipping a 0.1 m^2 area around each resin bag. Plant biomass was positively correlated with N absorbed by resin bags ($r^2 = 0.41$, $N = 21$, $P < 0.02$). Finally, at the study site, nitrogen fertilization from June – August increased plant biomass [5, 6].

The common (>90%) grasshoppers at this site were represented by Gomphocerinae (*Chorthippus curtipennis*), Oedipodinae (*Camnula pellucida*) and Melanoplinae (*Melanoplus sanguinipes*, *M. femurrubrum*, *M. dawsoni*, *M. bivittatus*). *M. sanguinipes* comprised more than 50 - 70% of the grasshoppers in a year. During the study period, grasshopper hatchling densities varied between 11 and 91/m^2 among the six years or more than 8 fold, and peak adult densities varied between 4 and 36/m^2 or more than 9 fold. During the study grasshopper density exhibited a build-up and then decline (Fig. 1). High grasshopper densities are typical for Palouse Prairie [7 - 9].

The range of plant and grasshopper abundances at this site is not atypical for arid grasslands in which grasshopper control has been a management concern. Therefore, the patterns reported here may also apply to other areas throughout the world.

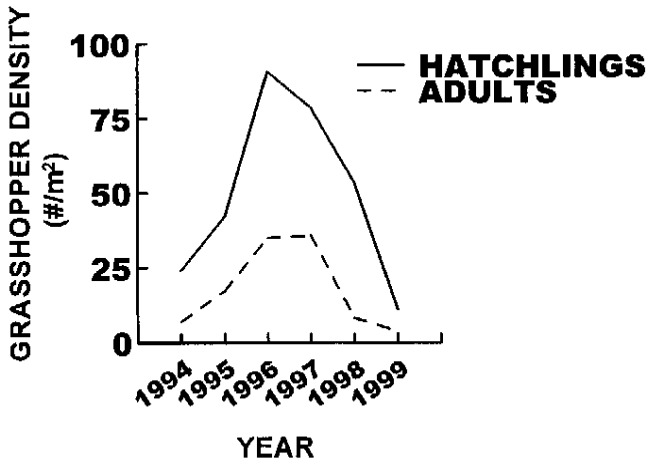

Figure 1. Field grasshopper populations during the study

1.3. ANNUAL (SHORT TERM) STUDIES

Claims that grasshoppers reduce plant abundance so that mammalian herbivores, especially livestock, have less forage are based upon annual measures or calculations of grasshopper consumption. Experiments were conducted to directly measure the impact of grasshopper consumption on forage availability in my study area.

1.3.1. *Experimental Design*

In 1994 and 1996, 40 cages were placed in an 8 x 5 grid over vegetation in May at the 4 ha study site with at least 1 m between cages. In 1994, 0.1m^2 cages were used and these cages were replaced with larger ones, 0.35 m^2, in 1996. The cages were constructed of aluminum window screens [10]. Half of the cages received natural precipitation, while the other half received supplemental water every other day, which in total equaled 50% of the average amount of precipitation from May – Sept. Cages in each water treatment contained either grasshoppers at the field density (5 cages) or no grasshoppers (15 cages). Grasshopper field density at the site was measured weekly by counting the number of grasshoppers in 24 – 0.1 m^2 rings [11] at ~11a.m. and ~4 p.m.. The cages were stocked in mid-June with *M. sanguinipes* nymphs ($\leq 3^{rd}$ instar), because these were the most common grasshoppers at the site in mid-June. The number used to stock the cages approximated the current field density. Individuals in each cage were counted weekly [10] and *M. sanguinipes* individuals were added or removed from each cage weekly to maintain field density. The individuals added were selected from the current most common developmental stage and removed individuals were killed and their corpses were left in the cage.

The 15 cages in each water treatment containing no grasshoppers received one of three additional treatments: no further manipulation, grasshopper frass added, or grasshopper corpses added. Frass was collected from *M. sanguinipes* individuals of the current most common developmental stage in the field. These individuals were kept at field temperature and light/dark cycles in 20 liter aquaria and fed an assortment of plant species from the site at the current field plant biomass per grasshopper. Once a week, the frass in each aquarium was collected and *per capita* frass production was determined by dividing total frass mass by the average number of grasshoppers in the aquarium ([individuals at start + individual at the end]/2). Given the observed field density of grasshoppers during a week, the appropriate mass of frass was added to a cage. Corpses were added by catching *M. sanguinipes* individuals, killing them and placing them in a cage, based on the decline in grasshopper density observed in the field during a week. Five cages represented each treatment. All treatment combinations (water/control/corpse/frass/grasshoppers) were represented in a row (5 rows), and these treatments were randomly assigned.

Living plant biomass in each cage was measured in early October by clipping plants in half of each cage's area, and litter was collected from the same area. In the following May, this was repeated. The living plant material was separated between grasses and forbs; living plants and litter were dried at 60° C and then were weighed.

An index of soil nitrogen availability was measured in each cage using an ion exchange resin bag [12, 13]. Resin bags were made using undyed nylon (pantyhose) containing 10g of Rexyn. The Rexyn absorbs nitrogen from the soil, which can be released using 2N KCl and the extractant can be analyzed colorimetrically for NO_3^- and NH_4^+ using an autoanalyzer [14 - 18]. A resin bag was buried at 15 cm in each cage in May and removed in early Oct. to indicate N availability during the plant-growing season; another bag was placed in each cage in early Oct. and removed the following May to indicate N availability for initiation of the next year's plant growth.

1.3.2. *Results*

Whether plant biomass by October was diminished by grasshopper consumption depended upon water availability, significantly decreasing with natural precipitation (Bonferroni contrast: $F = 3.99$; $df = 1, 32$; $P < 0.05$), but remaining unchanged with added water (Fig. 2). Both 1994 and 1996 were drought years, experiencing respectively 53% and 68% of average (18.9cm) precipitation during the plant-growing season (May – Sept), therefore, the added water treatment produced precipitation conditions that were approximately average. Even though grasshoppers decreased plant abundance by October under the drought conditions, the plant abundance in the following spring was unaffected by grasshopper consumption ($F = 0.25$; $df = 3, 64$; $P < 0.86$; data not shown) or by added water during the previous year's plant-growing season ($F = 0.78$; $df = 1, 64$; $P < 0.38$; data not shown). Therefore, when grasshopper consumption did reduce plant abundance, this was a transient, not a long-lasting effect.

Under approximately normal precipitation (added water), grasshopper consumption did not decrease plant abundance, because grasshoppers recycled N through their frass that could be readily absorbed by plants, and with the normal precipitation (added water) the plants exhibited compensatory growth (Fig. 2). Even with considerable between and within year variation, this was demonstrated by plants exhibiting the greatest abundance when grasshopper frass was added to cages along with water (Fig. 2: Bonferroni contrast: $F = 5.61$; $df = 1, 32$; $P < 0.02$). The N measured in fall-collected ion exchange resin bags indicated that cages containing grasshoppers or with added frass had the greatest N availability (Fig. 3: Bonferroni contrast: $F = 2.69$; $df = 3, 60$; $P < 0.05$). In accord with the absence of differences between treatments in the following spring's plant abundance, no differences in spring availability of N were observed ($F = 0.54$; $df = 3, 48$; $P < 0.68$; data not shown). Therefore, increased availability of N from grasshopper frass caused only short-term effects on plant growth.

1.3.3. *Implications for Long Term Studies*

These findings are not surprising in light of commonly held ideas that grasshoppers are most likely to reduce forage abundance for livestock in dry years [19, 20]. These results emerged regardless of grasshopper density relative to plant abundance. The years 1994 and 1996 had comparable plant abundances (86.6 ± 11.3 *vs.* 68.5 ± 6.7 g/m^2, SE, N = 5), but very different grasshopper densities (7 *vs.* 35 adults/m^2). Furthermore, under these conditions, grasshoppers substantially reduced fall plant abundance, but by comparable amounts (39.3 *vs.* 30.3%) in the two years. Similar results in other years have been

observed at the National Bison Range, where the fraction of plant biomass that is edible (nutritionally useable) to grasshoppers is far less variable than total plant biomass, which

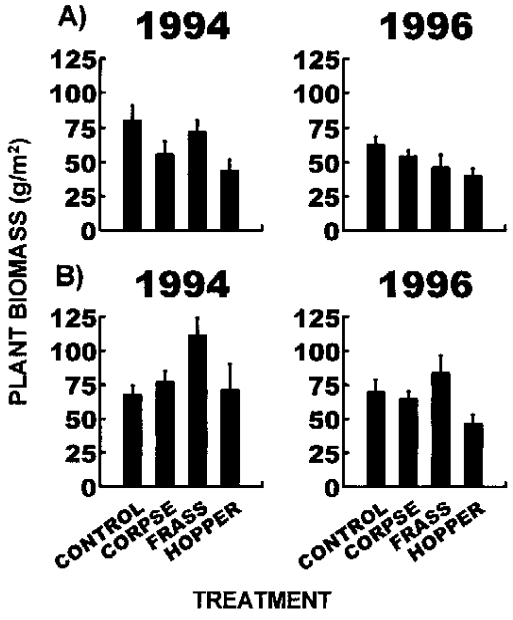

Figure 2. Annual results for plant biomass in October from 1994 and 1996 with natural precipitation (A) and added water (B)

is largely inedible [10]. With normal precipitation, grasshoppers reduced plant abundance by only 12.7%, which was not significant. Furthermore, grasshopper consumption did not carry over to reduce the next spring's plant abundance.

Regardless of precipitation, grasshoppers enhanced N availability in soil through the deposition of frass. However, even with greater availability of N, plants could not compensate for grasshopper consumption without normal precipitation. However, by next spring, differences in N availability disappeared and next spring's plant abundance was independent of grasshopper consumption.

Therefore, potential grasshopper damage to forage may be less dependent on grasshopper density than precipitation, and may not influence long-term plant abundance. However, this may suggest that droughts lead to grasshoppers creating economic damage that necessitates grasshopper control.

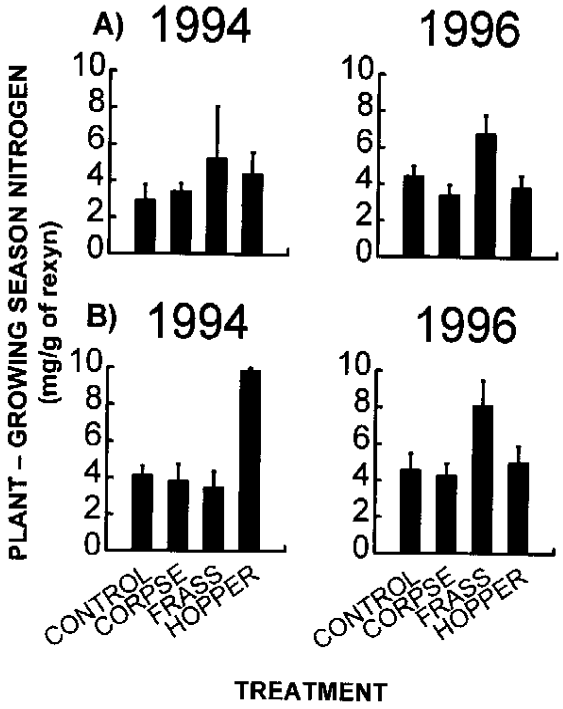

Figure 3. Annual results for N availability over the plant growing season in 1994 and 1996 with natural precipitation (A) and added water (B)

1.4. MULTIPLE YEAR (LONG TERM) STUDIES

The within year studies presented above are typical of how grasshopper economic damage has been assessed. However, grasshopper consumption might have longer lasting impacts on plant abundance. First, long-term grasshopper consumption might eventually weaken plants and lead to their death or reduced production. This effect is well established for grazing by livestock [21, 22]. Second, it has long been hypothesized that herbivory might modify nutrient cycles in ecosystems, which can either reduce or increase plant abundance depending on whether nutrient cycling is slowed down or speeded up [23]. Herbivory might change nutrient cycling by deposition of excrement, changing the quantity and quality (a nutrient content and decomposition rate) of plant litter, and by sequestering nutrients in herbivore bodies. These long-term effects may be far more important than the short-term perspective commonly taken towards grasshopper consumption.

Herbivory's hypothesized effects on nutrient cycling are summarized in Fig. 4.

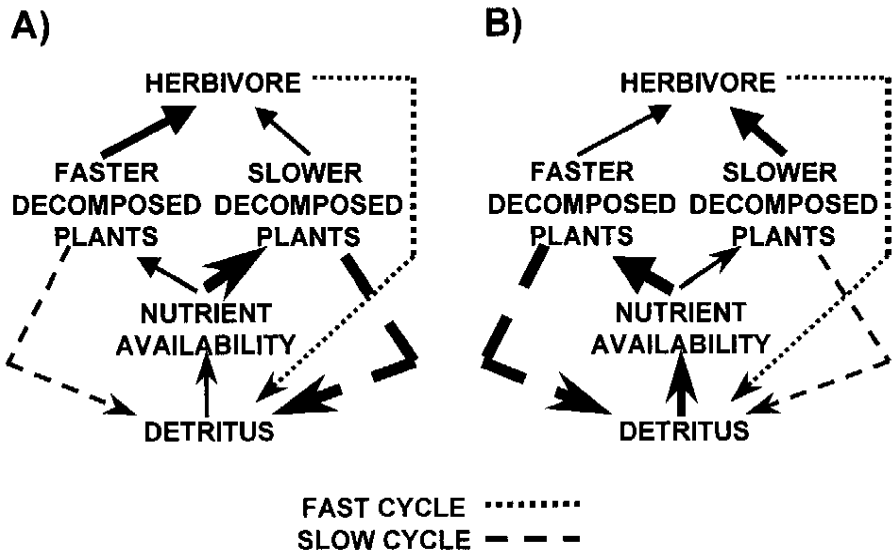

Figure 4. The conditions for herbivores to decrease nutrient cycling and primary productivity (A) and to increase nutrient cycling and primary productivity (B) are presented. The solid lines reflect the trophic transfers in the ecosystem. The broken lines reflect the pathways by which nutrients are recycled in the ecosystem. Line thickness reflects the relative magnitude of the trophic transfer or recycling pathway

The release of nutrients from excrement and the corpses of dead herbivores have been termed the Fast Cycle [24], because these sources of detritus are readily decomposed to make the nutrients rapidly available for plant uptake. The release of nutrients from plant litter has been termed the Slow Cycle [24], because this source of detritus slowly decomposes so that nutrients are slowly released for plant uptake. Furthermore, the Slow Cycle can be further affected by herbivory, if herbivores preferentially feed on different plant species which differ in how rapidly their litter is decomposed [25, 26]. Therefore, if the herbivore preferentially feeds on plants that produce slower decomposing litter, thus removing them from the litter pool, then the Slow Cycle may become faster, while preferential feeding on plants that produce faster decomposing litter may slow down the Slow Cycle.

The hypothesized net effect of this proportional shifting of nutrient cycling between Fast and Slow Cycles is for preferential feeding on slow decomposing plants to increase nutrient cycling, and preferential feeding on fast decomposing plants to decrease nutrient cycling [26]. It has been hypothesized that slow decomposing plants are competitively superior when nutrients are less available, and fast decomposing plants are competitively superior when nutrients are more available [26]. This would lead to herbivores changing the competitive outcome between the two types of plant species as herbivory speeds up or slows down nutrient cycling, which would produce different

cycling can lead to ecosystems that have more (faster nutrient cycling) or less (slower nutrient cycling) plant production. However, whether faster nutrient cycling enhances ecosystem primary production depends on whether the effects of accelerated nutrient cycling overshadow the deleterious effects of herbivory on plant growth and survival. In terrestrial ecosystems, this has largely been examined for mammalian herbivores [24 - 29], but may be more important for insect herbivores [30, 31].

1.4.1 *Experimental Design*

Starting in May 1994, 24 – 1 m^2 areas were established as replicated mesocosms of the study site's ecosystem and maintained for 6 years. Eighteen areas were covered by cages to contain grasshoppers so their densities could be manipulated and nine areas (6 – 1m^2 and 3 – 9m^2 areas) served as controls (field grasshopper densities). Garden edging was buried 15 cm in the soil to delineate areas. Cages were constructed of nylon insect screens, supported with a PVC frame, and attached to garden edging with plastic clips. Each cage had a sleeve that permitted access to the mesocosm.

The mesocosms were manipulated in three ways.

Experiment A. In six areas, grasshopper density was manipulated (50% or 125% of field density for each year: 3 replicates of each) and each area received plant litter produced in an area with field grasshopper density (control areas). This manipulation examined the Fast Cycle (variable grasshopper consumption/litter produced by a constant level of grasshopper consumption).

Experiment B. In six areas, grasshopper density was held constant (field density for each year) and litter was manipulated (litter produced in an area where grasshopper density was 50% or 125% of field density for each year – Exp. A, above: 3 replicates of each). This manipulation examined the Slow Cycle (constant grasshopper consumption/litter produced by a variable level of grasshopper consumption).

Experiment C. In six areas, grasshopper density and litter were manipulated (50% or 125% of field density for each year/litter produced in each: 3 replicates of each). This manipulation examined net effects of Slow and Fast Cycles.

Litter exchanges (Experiment A and B) were conducted in early October by collecting dead plant material and clipping live plant material at a height of 1.5 cm in each area, removing it, weighing it with a handheld Pescola spring balance and then spreading it on the appropriate area. To keep the litter in the appropriate area from October – May when the cages were removed to prevent winter damage, avian netting (2.54 cm mesh) was staked over each area. The six areas not receiving litter exchanges (Experiment C) had their litter manipulated in the same way to control for any disturbance due to litter collection and clipping.

Grasshopper field density at the site was measured weekly by counting the number of grasshoppers in 24 – 0.1 m^2 rings [11] at ~11a.m. and ~4 p.m.; individuals also were identified to a developmental stage: early (1^{st} –3^{rd} instar), late (4^{th} – 5^{th} instar) and adult. Cages were stocked with *M. sanguinipes* nymphs ($\leq 3^{rd}$ instar) in mid-June to 50, 100 or 125% of the current field density. *M. sanguinipes* was the most common grasshopper at the site. Individuals in each cage (Experiments A – C) were counted weekly [10] in 3 –

0.05 m^2 rings at ~11a.m. and ~4 p.m.. *M. sanguinipes* individuals were weekly added or removed from each cage (Experiments A – C) to maintain experimental densities. Added individuals were the current most common developmental stage and removed individuals were killed and their corpses were left in the cage.

The 6 - 1m^2 control areas (field grasshoppers), where litter was clipped, but not removed, were compared to the 3 - 9m^2 uncaged control areas (field grasshoppers), where litter was neither clipped nor removed, to assess the impact of small spatial scale, litter manipulation methods, and cages on ecosystem measurements.

The following measurements were made each year in each of the 27 areas.

1. An index of N availability to plants was obtained by measuring N absorbed by an ion exchange resin bag placed in the ground in May and removed in October to reflect the plant-growing season and another placed in the ground in October and removed in May to reflect the initiation of plant growth in the spring.
2. Total soil N content, inorganic soil N content and percent soil water content (1 - dry weight at 100°C for 48 h/fresh wet weight) were measured for soil taken from a core (15 cm) in May and October.
3. *In vitro* N mineralization was measured as the difference in inorganic N between the above soil core and soil maintained between sampling periods in an incubation tube (capped PVC tube: 2.54 cm diameter x 15 cm) that was buried to 15 cm in May and removed in October and another placed in the ground in October and removed in May [32, 33].
4. Plant N content was measured with a 5 g-dry sample (< 2% of plant biomass in area) collected in June.
5. Plant litter content was measured from a 5 g-dry sample (< 2% of litter biomass in area) collected in October.
6. Plant species composition and proportion of bare ground were assessed in July by point-sampling [34] at 100 points along 4 transects in each area.
7. Litter decomposition rate for common sources (field) of the two most abundant grasses (*P. pratensis* and *E. smithii*) was measured using decomposition bags. Four nylon mesh (1 mm) bags of each plant species (10 g collected in June from the field) were placed on the soil in May and collected in October and May over the next 2 years. Decomposition was measured as percent dry matter (60°C for 48 h) change and percent change in total N.
8. Plant aboveground production and living biomass were measured using radiometer readings taken every 2 weeks from May - October. The radiometer measures the ratio of far-red/infrared reflected radiation and this ratio can be converted into living plant biomass [35, 36]. The conversion into living plant biomass was based on a regression between green plant biomass measured by clipping and the radiometer readings for 10 - 0.10 m^2 areas at the study site at the start of the experiment and 3-4 areas (0.1 m^2) every 2 weeks from May – October. Annual plant production is computed as the

May plant biomass plus all positive differences between consecutive biomass measures made every 2 weeks from May – October.

9. Plant damage by grasshoppers was measured by examining 50 blades of *P. pratensis* and 50 blades of *E. smithii*, and recording whether they had been fed on by grasshoppers.

Plant and litter N measurements were made by extracting N using micro-Kjeldahl methods. Inorganic N in the soil and resin bags was extracted using 2N KCl [14, 15]. The N in extractants (g N/g dry of soil, plant or litter) was assessed colorimetrically with an autoanalyzer [14, 16 - 18].

Monthly precipitation values were available from a USFWS weather station located within 4 km of the study area and at the same elevation.

1.4.2. *Results*

Soil, plant composition and plant production measurements for the 6 – 1 m^2 control areas did not differ from the 3 – 9 m^2 control areas for each year over the six year study (Table 1), while values did significantly vary among years. This indicated that the small

TABLE 1. A comparison of the ecosystem characteristics for control areas where plant litter is clipped versus unclipped

Characteristic	Statistic	Degrees of freedom	P
Primary production	F = 0.21	1, 39	< 0.64
Annual soil nitrogen	F = 0.032	1, 28	< 0.86

spatial scale of the mesocosms, caging, and litter manipulation methods were unlikely to be responsible for any differences measured in the areas where grasshopper density and litter were experimentally manipulated. Therefore, the mesocosms are likely to reflect the processes of the larger ecosystem.

Annual effects of grasshopper consumption on forage availability measured in long-term experiments (Experiments A – C) were similar to annual effects in short-term experiments. The proportional reduction in fall (Oct.) plant biomass was positively correlated with early instar (hatchling) grasshopper density ($P < 0.0001$) and spring (May) plant biomass ($P < 0.0001$), but was negatively correlated with precipitation during the plant growing-season (May – Oct.: $P < 0.0001$) (Fig. 5a). Grasshoppers decreased fall (Oct.) plant biomass by up to 63%, averaging 26.1 $\pm$ 20.9% (SD). Grasshopper consumption had no effect on plant biomass for the next spring ($P < 0.20$) and spring plant biomass was positively correlated with the precipitation during the current (0.0001) and past growing-seasons ($P < 0.0001$)(Fig. 5b). Therefore, grasshopper consumption can reduce forage abundance within a year, especially in dry years, but this short-term reduction does not depress the next year's forage abundance.

Nonetheless, long-term effects of grasshopper consumption on forage availability were observed in the experimental mesocosms. Measurements for manipulated mesocosms

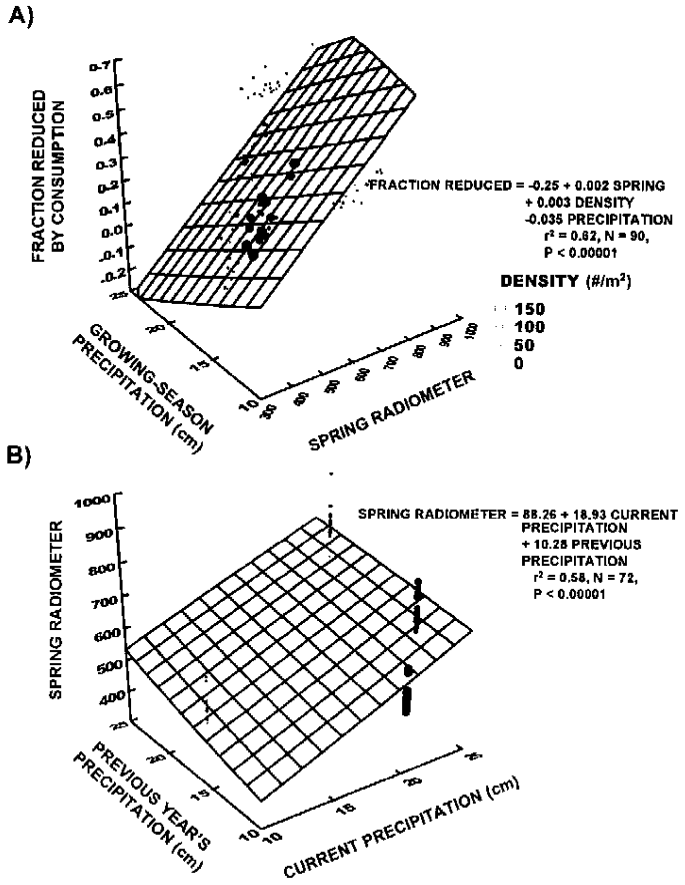

Figure 5. The within-year results from the long-term experimental mesocosms are presented. A) examines the factors controlling the fraction of plant biomass removed by grasshoppers by October, and B) examines the factors controlling the following year's spring (May) plant biomass

were expressed as percent change relative to control areas since the start of the experiment:

$$\% \text{ Change} = 100 \times \frac{S_i/S_0}{C_i/C_0} ,$$

where S_i is the mesocosm's spring plant biomass in a year i; S_0 is the mesocosm's spring plant biomass at the start of the experiment (May, 1994), C_i is the average spring plant biomass in a year i for the 6 - 1 m^2 control areas, and C_0 is the average spring plant biomass at the start of the experiment (May, 1994) for the 6 - 1 m^2 control areas.

With these measures of percent change, the following emerged:

Experiment A - Fast Cycle Experiments (varied grasshopper density/control-level litter). While values varied among years, spring (May) plant biomass increased relative to controls (field density) with increased grasshopper density (125% of field) and decreased compared with controls with decreased grasshopper density (50% of field) (Fig. 6a; ANOVA: $F = 7.0$; $df = 1, 28$; $P < 0.01$). This is expected because a greater grasshopper density produces more frass, which makes more N available to plants (increased Fast Cycle).

Experiment B - Slow Cycle Experiments (control grasshopper density/varied litter production). While values varied among years, spring (May) plant biomass increased relative to controls (field density) with litter produced by increased grasshopper densities (125% of field) and decreased compared with controls with litter produced by decreased grasshopper densities (50% of field) (Fig. 6b; ANOVA: $F = 22.05$; $df = 1, 28$; $P < 0.0001$). This means that grasshoppers are speeding up the Slow Cycle, so that more N is released by decomposition of plant litter.

Experiment C - Net Effect of Fast and Slow Cycles (varied grasshopper density and *in situ* produced litter). As would be expected from the above results, the net effect was that spring (May) plant biomass increased relative to controls (field density) with increased grasshopper densities and decreased compared with controls with decreased grasshopper densities (Fig. 7; ANOVA: $t = 4.25$, $df = 4$, $P < .02$). Furthermore, factoring in the measured reduction of forage by grasshopper consumption, forage availability in the fall was still greater with greater grasshopper densities. Therefore, grasshoppers enhanced the ecosystem's overall plant production.

Each year, experimentally increased grasshopper density led to greater plant production than experimentally reduced grasshopper density; however, the degree of change in productivity varied between years and will be discussed later. How increased grasshopper densities impacted the ecosystem's plant production is complicated and has many facets.

Fast and Slow Cycle effects were not additive, but antagonistic (Fig. 8), because Fast Cycle effects, rather than increasing the net effect, led to its decrease. Furthermore, Slow Cycle effects were twice as strong as Fast Cycle effects. Therefore, the Slow Cycle effects of increased grasshopper densities explained the increase in plant abundance relative to areas with control and decreased grasshopper densities. This is expected, because a greater relative reduction in plant biomass by grasshoppers will decrease the relative abundance of litter, which will make the Slow Cycle contributions to N availability for plant growth less important. Nonetheless, the net effects of the Fast and Slow cycles with increased grasshopper densities were to increase the availability of N for plant growth as measured by ion exchange resin bags (Fig. 9), which is expected given that plant growth at this site is N-limited.

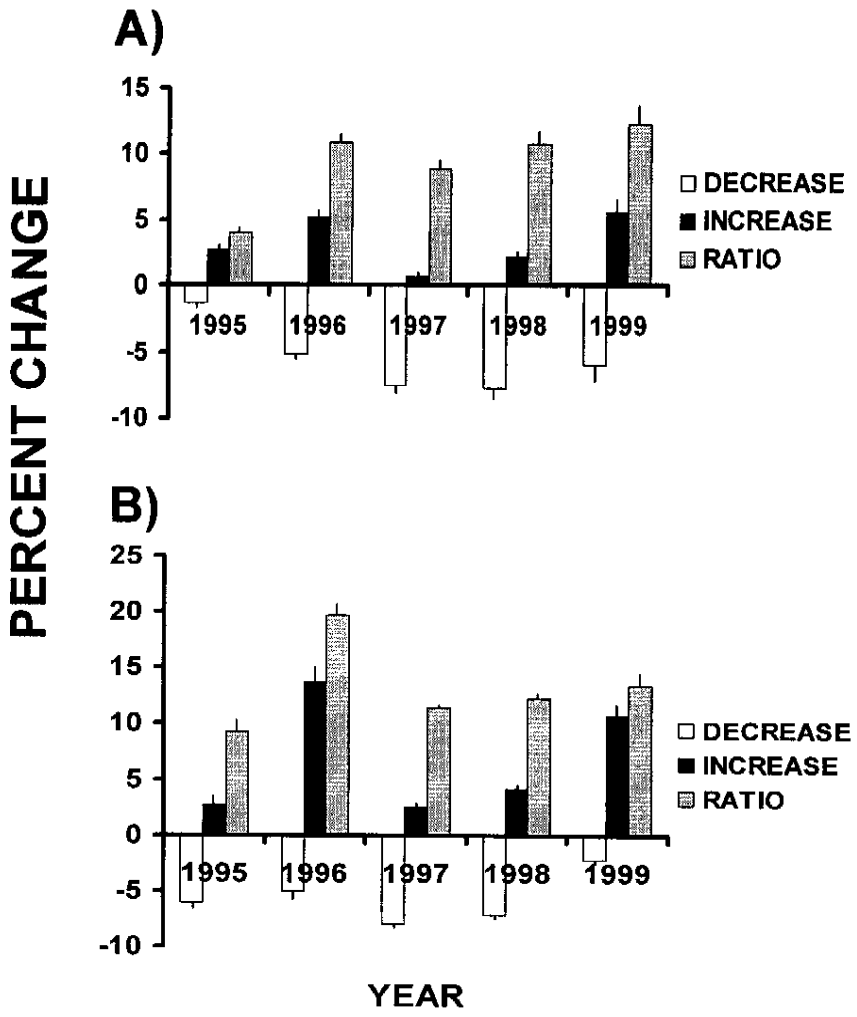

Figure 6. The effects of the Fast (A) and Slow (B) Cycles relative to control areas (± SE) by year in the long-term experimental mesocosms when grasshopper densities are decreased by 50% or increased by 25%. The ratio (± SE) refers to the net effect between the decreased and increased grasshopper densities

The possible mechanisms by which the Slow Cycle effects emerge are presented in Fig. 9. Litter quantity was lower in each year with increased grasshopper density as

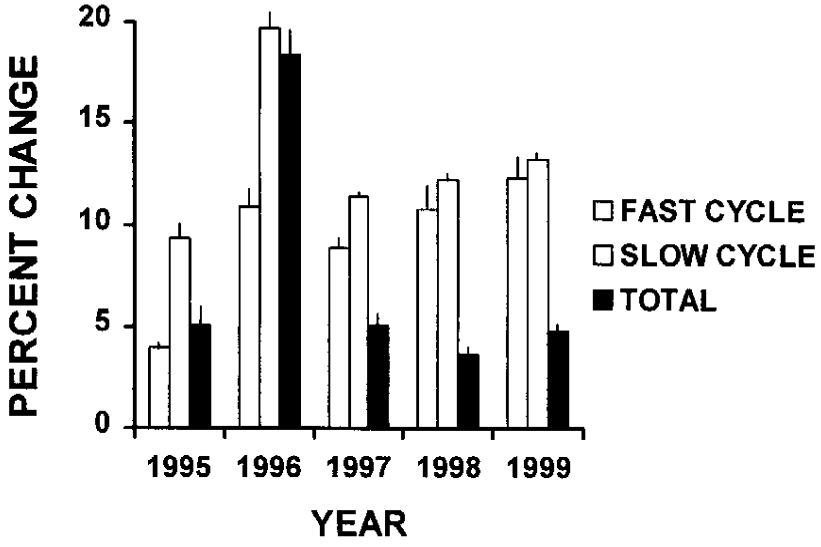

Figure 7. The cumulative effect of the Fast and Slow Cycles relative to control areas (± SE) in the long-term mesoscosms when grasshopper densities are decreased by 50% or increased by 25%. The total refers to the net effect (± SE) between the decreased and increased grasshopper densities

would be expected with greater consumption. However, the N content of the litter, which reflects how easily it can be decomposed, was greater with increased grasshopper

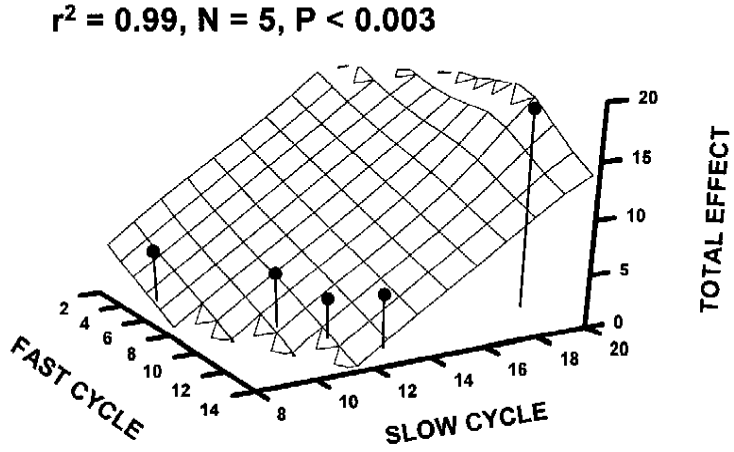

Figure 8. The combination of Fast and Slow Cycles to produce a cumulative or total effect

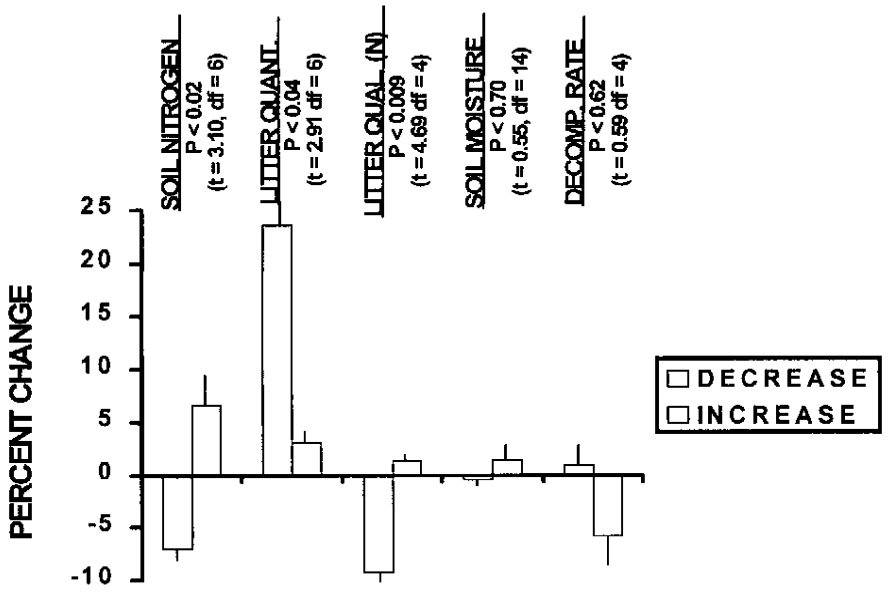

Figure 9. The average effects of decreasing grasshopper density by 50% and increasing grasshopper density by 25% in the long-term experimental mesocosms

densities. The increase in litter N content would be expected if the grasshoppers preferentially fed upon plant species of lower N content that decompose more slowly. This was observed because 1) a greater proportion of blades of *E. smithii* than *P. pratensis* had been fed on by grasshoppers by October in each year ($\chi^2 = 9.45$, df = 1, $P < 0.002$), *E. smithii* decomposed 11% more slowly than *P. pratensis* in litter bags ($t = 5.10$, df = 2, $P < 0.03$), and 3) *E. smithii* contained 28% less N than *P. pratensis* ($t = 13.76$, df = 8, $P < 0.0001$). Therefore, the conditions for herbivory to speed up the slow cycle and thereby, make more N available for plant growth and enhance ecosystem primary productivity (Fig. 4b) were observed. Why these grasshoppers should preferentially feed on a plant that is lower in N content is not known.

Concomitant with the observed changes in the Slow Cycle, *P. pratensis* and *P. compresa* were observed to increase in abundance relative to *E. smithii* as grasshopper density increased (Fig. 10). This would further speed up the Slow Cycle and enhance the ecosystem's primary production, because *P. pratensis* decomposes faster than *E. smithii*. *P. pratensis* is a better competitor at higher N availabilities [37, 38] and is less preferred by grashoppers, which should lead to its increase in abundance compared with *E. smithii*. Therefore, the grasshoppers change plant composition and create a more productive ecosystem.

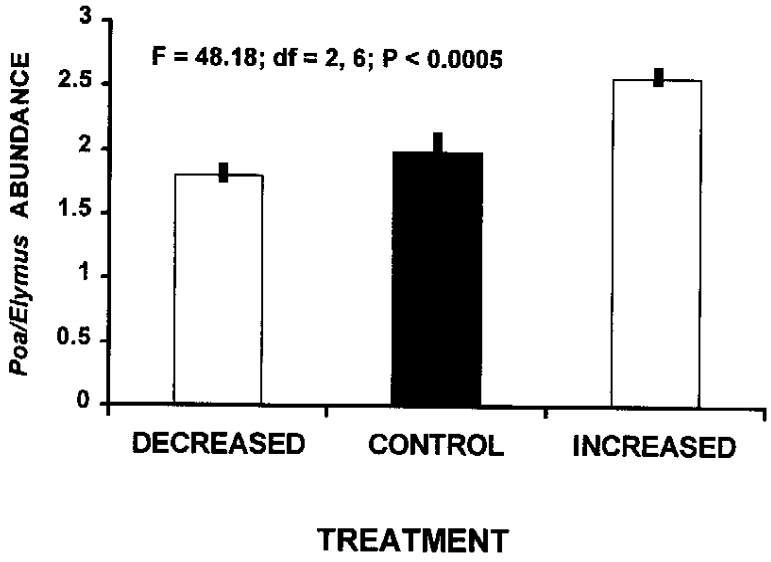

Figure 10. The average effect of decreasing grasshopper density by 50% and increasing grasshopper density by 25% in the long-term experimental mesocosms

The grasshoppers' influence on the Slow Cycle might counter the enhancement of ecosystem productivity in two ways. First, the decrease in litter quantity might lead to greater soil evaporation so that plants have less moisture available to them and become water-limited, but this was not observed (Fig. 9). Second, the decrease in litter quantity and increase in litter and soil N might make the soil microbes responsible for decomposition C-limited rather than N-limited and decrease decomposition rates [39, 40]. While the decomposition of a common litter source was slower with increased grasshopper densities, the difference was very small and statistically insignificant. Therefore, none of the counter-mechanisms to herbivory increasing the Slow Cycle and increasing ecosystem productivity were observed.

2. Tools

Very simply, grasshoppers enhance ecosystem productivity and forage availability to mammalian herbivores at this site. Therefore, consumption of plants by grasshoppers cannot be viewed as detrimental and would not warrant control, *i.e.*, there is no economic damage even though grasshoppers decrease fall plant abundance in a given year. This means that the standard measure of grasshopper economic damage is not valid at this site.

Enhancement of plant productivity by grasshoppers changes with adult grasshopper density (Fig. 11), even though enhancement was observed at all adult grasshopper densities observed in the study. At low adult densities, enhancement of primary production is not great, because low densities do not consume enough plant biomass to appreciably affect the Slow Cycle. At very high adult grasshopper densities, enhancement of primary production

is not great, because high densities consume so much plant biomass that plants are damaged and cannot take advantage of increased nitrogen availability. Therefore, greatest benefits emerge at an intermediate adult grasshopper density.

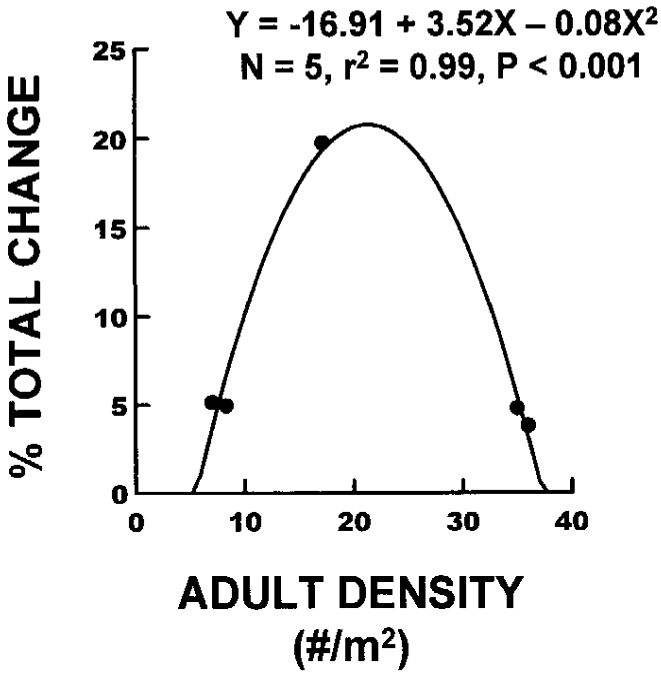

Figure 11. The effect of grasshopper density on primary productivity

3. Solutions

3.1. THIS ECOSYSTEM

One might argue that the grasshoppers' enhancement of ecosystem productivity might not emerge at lower or higher grasshopper densities than observed in the study and grasshoppers might need to be controlled at densities outside this range. Let us consider this. First, an enhancement was observed at densities of 7 adults/m^2 (1994), but would grasshopper control be warranted at lower densities, even if lower densities decreased ecosystem productivity? Second, an enhancement was observed at densities of 36 adults/m^2 (1997), but how often do densities become greater than this and perhaps diminish ecosystem productivity? Therefore, when would control be warranted?

These findings raise a new perspective on grasshopper control: might grasshoppers be controlled at an optimum level to maximize their enhancement of ecosystem

productivity? Before addressing this question, a caveat needs to be made: this is a very complex question to address and the limited range of grasshopper densities and precipitation observed in this study do not provide sufficient detail to adequately address this management possibility. Nonetheless, this study suggests that there may be an optimum grasshopper density that maximizes ecosystem productivity: 21.5 adults/m^2 increasing ecosystem production by 20.9% or 19.6% after grasshopper consumption (Fig. 11). Furthermore, grasshoppers would diminish ecosystem productivity when their densities fall below 5.5 adults/m^2 or increase above 37.4 adults/m^2. The above predictions would change with precipitation; drought would diminish the enhancement of ecosystem productivity by grasshoppers and reduce the range of grasshopper densities that lead to increased primary productivity, while greater precipitation would increase the enhancement of primary productivity and increase the range of grasshopper densities producing it. This is particularly important for the Slow Cycle, which is the dominant factor for enhancing the ecosystem's productivity.

To achieve this optimization, much more detailed monitoring of grasshopper densities and precipitation than is usually available would be needed and this may not be economically feasible. Managers might have to be content with letting grasshoppers provide whatever enhancement naturally emerges. This might not be so bad, because grasshoppers provided enhancement in every year over the six years of the study.

3.2. OTHER GRASSLAND ECOSYSTEMS

One might argue that the ecosystem studied here is not typical of grasshopper/rangeland conditions and grasshoppers might not enhance productivity in many other ecosystems. There are a number of ways that an ecosystem might differ from that studied here.

First, other ecosystems might not provide the conditions whereby grasshopper consumption increases ecosystem productivity, *i.e.*, preferential feeding on the slower decomposing plant species. Interestingly, grasshoppers at another site within 4 km preferentially fed on *P. pratensis* over *E. smithii*. At this second site, *P. pratensis* decomposed faster and was higher in N content. Therefore, the grasshoppers at this other site preferentially feed on the faster decomposing plant, which would tend to diminish ecosystem productivity. The second site has similar rainfall and elevation, but plant production is only 75% of my experimental study site. This raises several issues. Why would grasshoppers change their feeding preferences between the two sites? How often do grasshoppers preferentially feed on slower decomposing plants, and thereby, tend to enhance ecosystem productivity? What is the proper spatial scale to differentiate between areas where grasshoppers enhance and diminish ecosystem productivity? Obviously, the spatial scale employed in grasshopper control programs (thousands of hectares) is too large given my observations to discriminate between areas where grasshoppers potentially enhance vs. diminish ecosystem productivity.

Second, how similar is the study ecosystem to other rangeland ecosystems?

1. The range of plant productivity and precipitation values observed at my study site includes the values reported for many grasslands [41, 42].

2. Large non-domestic mammalian herbivores are very abundant at my study site (~2.5 g/m^2 or the equivalent of ~0.1 cattle/ha). The greatest density of large mammalian herbivores reported for the Great Plains of North America by early European explorers was ~5–9 g/m^2 [43, 44]; therefore, this site supports an abundance of large mammalian herbivores by North American standards. Furthermore, cattle grazing is one of the reasons why unprotected Palouse Prairie has been destroyed and the National Bison Range is the largest tract of undisturbed Palouse Prairie remaining.
3. Palouse Prairie sites generally are known to have historically supported large grasshopper densities [7 – 9]; therefore, grasshopper densities reported in my study are not unusual. In comparison to large mammals, the grasshoppers annually consume 1.25 – 2.25 times more plant biomass. However, grasshopper densities in other grasslands may not be as great, e.g., North American tall grass prairie [45, 46].
4. The incidence of lightning-caused wildfires is much lower in Palouse Prairie than other North American grasslands [47].

Consequently, without repeating my experiments in other grasslands, one cannot ascertain how general the results are, and if they do not hold in other ecosystems, why this is the case.

Third, could large mammalian herbivores be substituted for grasshoppers to provide the same enhancement of ecosystem productivity? This is not a simple substitution of consumption by one herbivore for another, because large mammalian herbivores impose damage to plants beyond consumption through trampling, soil compaction and uprooting of plants. These additional impacts will tend to diminish ecosystem productivity [48, 49]. Furthermore, at my study site, I added large mammal feces to cages in an amount (g-dry/m^2) comparable to the field deposition by mammals and monitored plant production. Even though the large mammals annually deposit a comparable amount of N in feces and urine as grasshoppers do in frass (0.47 g/m^2/yr vs. 0.5 g/m^2/yr), plant production was greater with frass than with mammalian feces in both fall (109%) and spring (28%) (repeated measure ANOVA: $F = 7.28$; $df = 1, 8$; $P < 0.03$). The main reason for this is that mammalian feces decompose slower than frass.

Fourth, grasshoppers at other locations may be more likely to enhance nutrient cycling by feeding on plant litter, which would speed up the Slow Cycle. The dominant grasshopper at my study site and the species employed in the experiments, *M. sanguinipes*, does not consume litter to any great extent, nor do any of the other Melanoplines [50]. However, other grasshopper species, especially Gomphocerines, often consume large quantities of plant litter [51, 52], which would lead to a more rapid release of nutrients from plant litter by shifting the mechanism from the Slow Cycle (litter decomposition) to the Fast Cycle (grasshopper frass).

Therefore, it is unclear how often grasshoppers increase ecosystem productivity as I observed in the experiments. Nonetheless, what is clear is that a reduction in plant biomass by grasshopper consumption does not necessarily imply that grasshoppers are making forage less abundant for mammalian herbivores and does not necessarily indicate the need for grasshopper control. I suspect that grasshoppers may frequently enhance primary production in grassland ecosystems, especially at locations where grasshoppers

consume considerable quantities of plant litter, and grasshoppers are certainly more likely to enhance primary production than large mammals with their uprooting of plants and soil compaction.

Finally, these results indicate that we cannot assess the impact of grasshoppers on rangeland ecosystems without a better understanding of grasshopper population dynamics [53, 54]. For example, if higher grasshopper densities enhance nutrient cycling and grasshopper populations are unable to attain these densities, the ecosystem will not exhibit higher productivity. This means that grassland ecosystem functioning may be dependent not only on the presence of grasshoppers, but their abundance.

3.3. CONCLUSION

The observations from the ecosystem studied here and the implications for grasshopper control typify the "state of the art" in our management of nature. As we conduct careful experimental studies of ecosystems and try to apply this knowledge, we find that what we firmly held as truths about how nature operates and how we should manage it may be wrong. Therefore, we should be humbled by how little we know and be very cautious in the application of our knowledge to management.

As we gain more knowledge about ecosystems, we are continually discovering that many of the component species are playing crucial roles in maintaining the ecosystem's sustained operation (*i.e.*, health). The functioning of ecosystems depends upon the component species and species may not easily be substituted and still maintain these functions [55]. Therefore, long-term sustainability of ecosystem productivity may be the essence of the biological wealth provided by biodiversity and we need to understand this value better and protect it.

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