Fall 12-2010

Is Orthoptera Abundance and Distribution Across a Small Grassland Area Affected by Plant Biomass, Plant Species Richness, and Plant Quality?

Caitlin Falcone
University of Nebraska-Lincoln

IS ORTHOPTERA ABUNDANCE AND DISTRIBUTION ACROSS A SMALL GRASSLAND AREA AFFECTED BY PLANT BIOMASS, PLANT SPECIES RICHNESS, AND PLANT QUALITY?

By:

Caitlin Falcone

AN UNDERGRADUATE THESIS

Presented to the Faculty of

The Environmental Studies Program at the University of Nebraska-Lincoln

In Partial Fulfillment of Requirements

For the Degree of Bachelor of Science

Major: Environmental Studies

Emphasis: Biological Sciences

Under the Supervision of Dr. Johannes Knops

Lincoln, Nebraska

December 2010

ABSTRACT

The choice of a specific microhabitat represents a compromise among a number of different factors organisms use to monitor habitat suitability. Grassland vegetation structure can vary widely along environmental gradients over a relatively small area. This vegetation structure can have a large influence on habitat selection by grasshoppers (Orthoptera). However, it is not clear which vegetation characteristics are most important in determining grasshopper abundance. We found that plant biomass, plant species richness, and plant quality all have an effect on grasshopper abundance and distribution. We observe that these affects vary both within and among the two years of data collection. The timing of rainfall within a year strongly affects plant productivity and a large difference in plant productivity among years may lead to different outcomes. In a year of lower plant productivity, plant biomass and plant species richness determine grasshopper abundance. In a year of higher plant productivity, plant quality and plant biomass determine grasshopper abundance.

There has been little work to examine how increased nutrient loads in today's environment affect grassland plant communities and in turn, insect herbivore communities. Grasshopper choice between two vegetation treatments, control and nutrient addition, can affect the outcome of interactions of soil nutrients, plant biomass, and grasshopper biomass. By modeling the effects of grasshopper choice for plant quality and quantity, I was able to predict an effect multiple levels of nutrients can have on the overall vegetation biomass in nitrogen enriched and control plots. I found that there is a threshold level of nitrogen addition at which the nitrogen enriched plots have the same value of plant biomass as the control plots mediated by grasshopper response to plant

quality and quantity. A comparison of two models, constant vs. variable (constant plant quality vs. variable plant quantity), revealed that the constant model predicts the biomass of grasshopper better.

TABLE OF CONTENTS

AKNOWLEDGEMENTS

I would like to thank my Dr. Johannes Knops and Dr. Bo Deng for their support and invaluable assistance with this paper, Sarah Bailey, Allison Mettler, Heather Buss, Trevor Hefley, and Steven Falcone for their help with conducting the research, Dr. Svata Louda and Natalie West for mentoring and guidance, and NSF-RUTE and Cedar Point Biological Station for funding.

INTRODUCTION

The choice of a specific microhabitat represents a compromise among a number of different factors organisms use to monitor habitat suitability (Joern 1982). Factors affecting the abundance of Orthoptera include microclimate variables (temperature, humidity, light intensity, etc.), availability of food, structural qualities, oviposition sites, suitable hiding places, and the presence of predators (Joern 1982). Grasshoppers do not inhabit microhabitats in a random fashion and very definite preferences are observed for most species (Joern 1982).

In particular, the vegetation structure within a grassland area has a large influence on habitat selection by grasshoppers (Anderson 1964). Vegetation determines the availability and distribution of all resources required by grasshoppers (Joern et al 2009). In grasslands the plant community composition and structure can vary widely along environmental gradients over a relatively small area. Typically these plant community differences can have a direct effect on insect herbivore abundance and species diversity. Kemp et al (1990) found that both plant and grasshopper species composition changed over observed environmental gradients suggesting that habitat type influenced species presence, as well as relative abundance. Despite species of grasshoppers having different food choices it has been observed that relative abundance of grasshoppers' increases with plant community diversity (Kemp et al 1990).

In addition, insect herbivores, such as grasshoppers, are often nitrogen limited (Heidorn and Joern 1987). Any environmental condition that increases plant quality will increase population growth in insect herbivores (Mattson and Haack 1987, Berryman 1987). If some plant patches are of a higher quality than others, local grasshopper densities may increase as individuals move into the patch and remain, especially if food is limiting (Heidorn and Joern 1987). Yet, grasshoppers may not be able to actively discriminate among leaves with different nitrogen levels (Heidorn and Joern 1987). Prior studies have revealed that the distribution patterns of graminivorous grasshoppers were congruent with the applications of increased levels of nitrogen fertilization, but no interaction between phosphorus and nitrogen was observed (Joern et al 2009).

Environmental heterogeneity, which creates differences in plant quality, can be caused by a variety of factors, including human. Humans have had a large impact on many ecosystems, especially in relation to the alteration of nutrient budgets (Nutrient Network 2009). Thus it is important to test the effects of changing nutrient budgets on grassland communities through nitrogen addition experiments.

Previous studies have shown that vegetation structure can have a large influence on habitat selection by grasshoppers (Orthoptera); however it is not clear which vegetation characteristics are most important in determining grasshopper abundance and how these are affected by changing nutrient budgets. Studies are needed to look at the micro-scale level of how grasshopper assemblies change as a plant community shift along environmental gradients (Joern et al 2009). A number of studies of mid- and large-scale communities have been conducted on species richness and diversity of both plants and grasshoppers. Smaller scale studies that attempt to relate vegetation type to grasshopper community complexity typically lack the sampling intensity within given plant communities required to make regional inferences (Joern et al 2009).

The aim of this study is to gain a better understanding of the community level interactions of nutrients, plant biomass, and plant species richness in relation to grasshopper abundance and distribution across a small-scale mixed grass prairie ecosystem. Our overall question was: "What parameters best describe the abundance and distribution of Orthoptera across the grassland?" We hypothesize that grasshopper abundance across the small grassland area is affected by plant biomass, plant species richness, and plant quality. Fig. 1 demonstrates the predicted relationships between these factors and nutrients (both added and previously present) in the soil. We also hypothesize that as most grasshopper species mature from egg to adult in a growing season, they require different microhabitat characteristics as they develop.

MATERIALS AND METHODS

Study Site

Our study site is located in western Nebraska at the University of Nebraska's Cedar Point Biological Station. This mixed grass prairie ecosystem was dominated by *Stipa Comata* and *Carex Filifolia* and was a previously grazed area. We set up the site following specific protocol as described on the Nutrient Network website (Nutrient Network 2008). A total of 60, 5m x 5m plots were measured and marked the summer prior to the study. The plots were organized into 6 blocks with 10 plots in each block. Each plot was randomly subdivided into 4 subplots of 2.5 m x 2.5 m. These subdivisions were used to designate what area of the plot was to be used for measurements for current and future years. We took various measurements within each plot in order to understand how grasshopper abundance and distribution over a small area is affected by variations in soil nutrients, plant biomass, plant species richness, and plant quality.

Grasshoppers

Grasshopper counts were conducted weekly in each plot during the months of June and July in 2008 (7 weeks total) and in early and late July 2009 (2 weeks total). Based on the recommendations of Gardiner et al. (2005) and Gardiner and Hill (2006) we chose to collect grasshoppers through a method combining sweep netting and box quadrat trapping. We constructed a box quadrat that was 1.5 m x 1.5 m on all sides and 1 m tall, making it easy to sweep net within the enclosure. We used the same counting technique for each plot. We held the box quadrat over the center of the Future 1 site and dropped it approximately 10-20 cm from the ground as to reduce disturbance to the grasshoppers present before they could be contained. Once the box quadrat was in place, the researcher would stand right outside and begin sweep netting low to the ground around the inside of the quadrat. Sweeping was first done in a circular motion close to the ground and around the outer part of the sample area in a square, which was followed by sweeping in the middle of the sample area in an arcing, back-and-forth motion. One full sweep took approximately 20-25 s to complete. We counted, recorded, and released the grasshoppers just outside the box quadrat after each sweep. We would continue to sweep, count, record, and release the grasshoppers until there was three consecutive sweeps where no individuals were caught. At this time we would stop and count the grasshoppers on the sides of the box quadrat and added the side count to the total.

Individuals that were not caught in the net were prevented from escaping and were contained to the sides of the quadrat where they were counted. The quadrat could easily be moved from plot to plot when conducting counts without much disturbance. In order to avoid sweep netting over an area that was being used for other plant based measurements it was determined that a specific subplot area in each plot was to be used for the grasshopper counts.

Grasshopper counts were conducted each week between June-July 2008. On the last week of grasshopper counts in 2008 (7/25/2008) grasshoppers were collected and frozen for future species identification. Using the data results from 2008, it was decided the following year to conduct grasshopper counts the specified weeks of July 3, 2009 and July 26, 2009.

Nutrient Additions/ Plant Quality

In order to determine percent soil nitrogen prior to the nutrient addition, soil samples were collected from each plot on May 28, 2008. Within each plot we ran a factorial experiment with four treatments: nutrient additions of nitrogen, phosphorus, and potassium and control. Nutrients were added to the plots on June 9, 2008. This was the first year in which nutrients had been added to the study site. The following year nutrients were added on June 2, 2009.

Plant tissue samples from each plot and each biomass category were analyzed for tissue quality. We calculated the carbon: nitrogen ratio for each. We also analyzed the tissue quality of phosphorous.

Plant Biomass

We clipped and collected plant biomass from the core area of the plots in 0.2 m^2 (two 10 x 100 cm) strips for each plot on July 9-10, 2008. Biomass was sorted into seven different categories. The categories were: 1. previous year's dead, 2. current year's bryophytes, 3. current year's graminoid (grasses, sedges, rushes), 4. current year's legumes, 5. current year's non-leguminous forbs, 6. current year's woody growth, 7. cacti (Nutrient Network, 2008). All biomass was dried and weighed.

Plant Species Diversity

We used a modified Daubenmier method to measure the diversity and abundance of plant species within each plot. Percent cover of each plant species, bare soil, and litter were determined for a 1 m x 1 m subplot within each plot. We used the number of plant species to represent plant species richness within each plot.

Data Analysis

We used multiple linear regressions with grasshopper abundance as the dependent variable and plant biomass, plant species richness, and plant quality as the independent variables for our analysis. We also examined differences in rainfall patterns, both between years and within each season. This was done in order to examine the influence of rainfall on vegetation characteristics.

RESULTS

We found that plant biomass, plant species richness, and plant quality all have an effect on grasshopper abundance and distribution; however, we observe that these affects vary both within and among the two years of data collection. Table 1 summarizes 2008 and 2009 results of a linear regression of grasshopper abundance as the dependent variable and plant biomass, plant species richness, and plant quality as the independent variables. The three weeks for 2008 included in the table depict the typical results from the three different seasons (early, middle, and late) in 2008. Table 1 also contains a summary of the results of the 2009 data.

In 2008 we found that early in the season (6/6/2008), grasshoppers tend to be randomly distributed across the study site; none of the measured factors were significant in affecting their distribution. Mid-season (6/27/2008), grasshopper abundance increases significantly where there is both greater plant biomass ($p=0.00$) and greater plant species richness ($p=0.011$). Fig. 2 illustrates that grasshopper abundance increases with plant biomass and shows that plant biomass accounts for 30% ($R= 0.300$) of the variance seen in grasshopper abundance for 6/26/2008; and 15.2% ($R= 0.152$) of the residual variance is accounted for significantly ($p=0.002$) by plant species richness. Late in the season of 2008 (7/25/2008), grasshopper abundance increases significantly ($p=0.000$) only where there is greater plant biomass.

In 2009 we found that mid-season (7/3/2009) grasshopper abundance increases significantly ($p= 0.003$) with a decreasing carbon: nitrogen ratio, which characterizes an increase in plant quality; however, plant quality of phosphorus was not significant for any period. Fig. 3 illustrates the relationship on 7/3/2009 of grasshopper abundance increasing with increasing plant quality. Fig. 3 also shows C:N (grams C: grams N) for control and nitrogen enriched plants for 2008 and 2009. In 2009 the nitrogen and control plots had higher plant quality than they contained within 2008. Late in the season of 2009 (7/26/2009) grasshopper abundances increases significantly (p=0.000) only where there is greater plant biomass.

Fig. 4 shows the annual plant biomass in the nitrogen and control plots and the monthly rainfall distribution for the study area for 2007, 2008, and 2009. Annual plant biomass for both the control and nitrogen enriched plots is significantly higher in 2009 than in both 2007 and 2008. Differences in total annual precipitation for 2007, 2008, and 2009 are negligible; however, Fig. 4 shows that the timing of the rain is variable for all the years.

DISCUSSION

Both years, 2008 and 2009, varied in the significance of the factors that affected grasshopper abundance within a season. This difference is due in large part to the timing of rainfall within a year strongly affects plant productivity. Fig. 4 shows that in June of 2009 there was a large peak of rainfall, this large peak of rainfall allowed plants to grow more than in previous years in which plants would begin undergoing desiccation. The large amount of rainfall the study site received in June of 2009 led to annual plant biomass of 2009 being greater than 2008. This large difference in plant productivity among years leads to different outcomes: (1) In a year of lower plant productivity, plant biomass and plant species richness determine grasshopper abundance. (2) In a year of higher plant productivity, plant quality and plant biomass determine grasshopper abundance.

Despite various species of grasshoppers having differing food preferences we found that the abundance of grasshoppers is dependent upon gradients in the plant community. These findings provide evidence that grasshoppers specifically seek out areas of higher plant biomass and likely mix their diets with a few forbs and other plants. Due to the fact that the majority of the grasshoppers in our study were univoltine we saw a change in preferences as they developed into different life stages.

These results suggest that generalizations about grasshopper abundance and distribution across a small grassland area cannot be made from only a couple years of data. Rather, patterns must be observed and analyzed over many years because different habitat characteristics are important in different years. We must have a solid understanding of the vegetation characteristics present and the impact that timing of rainfall events has on the plant community in order to understand grasshopper abundance dynamics. It is also important to note that grasshoppers respond differently at different life stages, which may explain why we see shifts in their habitat preferences throughout a season. Thus, these findings have important implications for grassland management and show how environmental variation, man-made or natural, affect the abundance and distribution of grasshoppers. Further research should be conducted to increase our understanding of the long term effects of increased nutrient budgets on the plant community and ultimately the grasshopper and insect herbivore communities. Future research is essential for understanding how increased nutrient budgets impact the plant community and ultimately grasshopper and insect herbivore communities.

INTRODUCTION

Grasshoppers are an abundant and important generalist herbivore group in temperate grasslands (Pfisterer, Diemer, Schmid 2001). Plant productivity can be affected by the abundance and clumped distributed aggregation of grasshoppers. Despite various species of grasshoppers having differing food preferences, it has been observed that the abundance of grasshoppers tends to increase across various environmental gradients (Kemp et al. 1990). Choice of a specific microhabitat by a grasshopper represents a compromise among multiple factors used in evaluating habitat suitability. Factors determining the local abundances of grasshoppers can include microclimate variables (temperature, humidity, light intensity, etc.), availability of food/nutrients, structural qualities, oviposition sites, suitable hiding places, or the presence of predators (Joern 1982). In addition, insect herbivores, such as grasshoppers, are often nitrogen limited (Heidorn and Joern 1987). If some plant patches are of a higher quality than others, local grasshopper densities may increase as individuals move into the patch and remain (Heidorn and Joern 1987).

Predators, when offered a choice between two or more prey types, will often show a preference for one of them (Cock 1978). This results in one or more prey type being eaten than would be expected given just the relative numbers of the prey. Thus, in the predator-prey population model involving grasshoppers and different plant types, it is important to be able to calculate the herbivore's response towards the different vegetation treatments, because these differences in grasshopper behavior can lead to differences in herbivory levels between patches and have an effect on vegetation biomass. Differences in plant biomass that result in differences of grasshopper abundance can be caused by habitat change and environmental heterogeneity, such as varying levels of nutrients in the soil.

The goal for my model was to better understand the community level interactions of nutrients, plant biomass, and grasshopper abundance. My model showed that feeding behavioral response between two vegetation treatments effects these interactions when there is an enrichment of nitrogen. By modeling the effects of grasshopper response to nitrogen enriched plots, I will be able to better predict what level of nutrients can do to the overall vegetation biomass in nitrogen enriched and control plots. I hypothesize that with positive response to either plant quality or quantity, there will be a threshold level of nitrogen addition in which the nitrogen enriched plots have the same value of plant biomass as the control plots. If the grasshopper abundance increases in fertilized patches past this threshold value, due to grasshopper response to higher quality or quantity plant resources, then there will be a decline in plant biomass in the fertilized plots compared to the unfertilized plots.

MATERIALS AND METHODS

Study System and Data Collection

The area we used for our study is a part of the ongoing Nutrient Network research, and we set up our site following specific protocol as described on the NutNet website (Nutrient Network 2008). A total of 60, 5m x 5m plots were measured and marked the summer prior to the study. The plots were organized into 6 blocks with 10 plots in each. Within each plot we ran a factorial experiment with four treatments: nutrient additions of nitrogen, phosphorus, and potassium and control. Each plot was also randomly subdivided into 4 subplots of 2.5 m x 2.5 m. These subdivisions were used to designate what area of the plot was to be used for measurements for current and future years. We took various measurements within each plot in order to understand how distribution of grasshopper abundance over a small area correlated to the parameters such as plant cover, plant biomass, and microclimatic factors.

Grasshopper counts were conducted weekly in each plot during the months of June and July in 2008 (7 weeks total). Based on the recommendations of Gardiner et al. (2005) and Gardiner and Hill (2006) we chose to collect grasshoppers through a method combining sweep netting and box quadrat trapping. We constructed a box quadrat that was 1.5 m x 1.5 m x 1 m high, making it easy to sweep net within the enclosure formed by the quadrat. In order to avoid sweep netting over an area that was being used for other plant based measurements, a designated subplot area in each plot was chosen for the grasshopper counts.

Model Description

In order to understand how nutrient addition affects grasshopper feeding occurrence and abundance, which in turn may affect plant biomass, models are needed to show these community level interactions. Schmitz (1993, 1994, 1997) developed a set of equations to describe a similar community in an old field in Ontario, Canada. His community contained three components: nitrogen (which was limiting in the community), plants, and grasshopper herbivores.

To modify Schmitz's model to fit our goals and evaluate my prediction, I first separated the nitrogen and plant biomass equations into control (denoted with a subscript *C*, 30 plots total) and nitrogen addition (denoted with a subscript *N*, 30 plots total). Fig. 5 shows the community interactions we modeled. We did not separate the grasshopper equation into control and nitrogen addition because grasshoppers are free to move into control or nitrogen addition plots to feed. Instead, I fix the grasshopper equation with a parabola to describe the grasshopper population curve that we saw in our grasshopper counts. I also converted grasshopper population to biomass by assuming each grasshopper weighed .002 kg (Pfadt 1994). I then added a feeding preference ratio denoted $w_i(t)$, in the below equation to fVH to represent the difference in time spent feeding in nitrogen addition plots relative to control plots. The following equation represents my modifications to Schmitz's model and Table 1 summarizes the descriptions of the parameters:

$$\frac{dN_C}{dt} = S_C - \mu N_C V_C \qquad 2(a)$$

$$\frac{dN_N}{dt} = S_N - \mu N_N V_N \qquad 2(b)$$

$$\frac{dV_C}{dt} = V_C\left(a\mu N_C - fw_C(t)H\right) \qquad 2(c)$$

$$\frac{dV_N}{dt} = V_N\left(a\mu N_N - fw_N(t)H\right) \qquad 2(d)$$

$$H(t) = -.12(t - 3.5)^2 \qquad 2(e)$$

The ratio, $w_i(t)$, in Equations 2(c) and 2(d) represents the preference of grasshoppers to spend time feeding in differing vegetation plots. I used two different types of feeding preference ratios, one based on grasshopper response to plots with nitrogen addition and the second one based on grasshopper response to plots with vegetation biomass. To make a feeding preference ratio of grasshoppers to plots with higher plant tissue quality, I used average occurrence field data; $w_C = 0.44$ and $w_N = 0.56$, which is the average ratio of grasshoppers we observed in nitrogen enriched plots and control plots for my feeding preference to plant quality. For the feeding preference ratio to plots with more plant biomass, I used a ratio of $w_C = V_C(t)/(V_C(t) + V_N(t))$ for the vegetation in the control plots and the ratio $w_N = V_N(t)/(V_C(t) + V_N(t))$ for the vegetation in the nitrogen addition plots.

I calculated the least square of error to find the best fit of the theoretical model to the experimental data. A program in R was written to find the best value of f that would minimize the error of the feeding preference. The same range of parameter f, from 0.5 and 0.15 kg plant biomass per week, was used for my simulation of the per capita loss ratio of vegetation biomass to grasshopper herbivory (Schmitz 1997). Denoted by E, the error between the predicted and measured values is given as follows:

$$E^2 = \sum_{t_i = datatime}\left(\frac{w_C(t_i)V_C(t_i)}{w_N(t_i)V_N(t_i)} - \frac{\overline{H}_C(t_i)}{\overline{H}_N(t_i)}\right)^2 \qquad 3(a)$$

Here, $\overline{H}_i$ is our field data of grasshopper in converted to kilograms and $w_C(t)V_C(t)$ / $w_N(t)V_N(t) = fw_C(t)V_C(t) / fw_N(t)V_N(t)$. After finding the least square of error for each model I also calculated the relative error.

$$rel.E = E \Bigg/ \sqrt{\sum_{t_i = datatime} \left(\frac{\overline{H}_C(t_i)}{\overline{H}_N(t_i)} \right)^2} \qquad 3(b)$$

As first order approximations, the model assumes the following: (i) life history traits are similar for all the plants and similar for all species for the period of summer our data was collected, (ii) plants are the only organisms uptaking nitrogen from the soil (Equation 2(a) and 2(b)), (iii) vegetation biomass production has exponential growth in the absence of grasshoppers and is only nitrogen limited (Equation 2(c) and 2(d)), (iv) Holling Type I functional form for herbivory consumption and grasshoppers are the only herbivore in the system (Equation 2(c) and 2(d)), (v) the grasshopper biomass is best fitted to a quadratic polynomial (Equation 2(e)), (vi) grasshopper abundance distribution gradient represents a feeding preference (see previous paragraph and Equation 3(a)).

Model Parameters

I searched the published literature for estimates of the parameters affecting the rates of nitrogen use, biomass production, and herbivory rates. These parameters were calculated for 30 plots for control, 30 plots for the nitrogen addition, and for the area in which we counted grasshoppers. For the supply rate of nitrogen, S_i, I estimated the bulk density of soil in the plots to be 1800 kg/m^3 (Jean Knops, *personal correspondence*) and calculated the average soil percent nitrogen in our plots to be 1.134%. I used a soil depth of 10 cm to calculate the nitrogen per area to be 0.204 kg N/m^2. With a nitrogen turnover rate of 4% per year, a growing season of six months, and a plot size of 2.25 m^2 (Jean Knops, *personal correspondence*), I calculated the S_C to be approximately 0.02 kg N per week for the 30 plots that had ambient levels of nitrogen. We fertilized the plots with 10 g per m^2 and calculated that at this nitrogen addition level S_N is 0.05 kg N per week for the 30 plots which were enriched. Next I calculated μ, the per capita uptake rate of nitrogen by the plants, using the average uptake 0.0025 kg of N per 6 months per m^2 (Riser and Parton 1982). I found μ to be approximately 0.02 kg of N per week. In prior studies the assimilation rate was calculated to be 1.0, and I used this value for my model (Schmitz 1993).

RESULTS

Feeding Preference --- Plant Quality

Grasshopper abundance is statistically higher in plots with nitrogen enrichment than control plots (Fig. 6). Plant biomass in nitrogen fertilized plots was not statistically significant more than the control plots (P = 0.669).

With no grasshoppers in the system, the model predicts that at increasing values of S_N (0.05, 0.5, 1.0 kg N per week) plant biomass in the nitrogen enriched plots will be increasingly greater than in the control plots (Fig. 7a-c). With grasshopper numbers determined by the fixed parabola added to the system, the model predicts different results. At the level of $S_N = 0.05$, the control vegetation biomass would be greater than the fertilized vegetation biomass at the end of the eight weeks (Fig. 8a). At a higher level of fertilization with $S_N = 0.5$, the model predicts that both control and fertilized plots will have approximately the same amount of plant biomass (Fig. 8b). At even higher levels of nitrogen fertilization ($S_N = 1.0$), the model predicts at this high level of nitrogen enrichment the fertilized plots would exceed the control plots in plant biomass by approximately 1.73 kg (Fig. 8c). As nitrogen fertilization increases, the vegetation biomass in the nutrient fertilized plots increases; however, the control plots have the same final plant biomass.

Feeding Preference --- Plant Quantity

Grasshopper abundance is strongly correlated with plant biomass (Fig. 9). Using the variable preference ratio for plots with greater vegetation biomass the model predicts that at $S_N = 0.05$, the plant biomass is the approximately the same as the control biomass (Figure 6a). When $S_N = 0.5$ the difference between the final plant biomass in nitrogen addition and control plots is 1.32 kg. At the highest level of enrichment with $S_N = 1.0$, the difference between the final plant biomasses is 2.80 kg. As the nitrogen addition level increases, the final plant biomass increases for both nitrogen addition and control plots. The average preference ratio based on grasshopper abundance for nitrogen enriched plots is $w_N = 0.57$ and for control plots is $w_C = 1 - w_N = 0.43$. I incorporated these constant w_i values into Equations 2(c) and 2(d).

DISCUSION

Modeling the effects of grasshopper responses to vegetation offers the ability to predict how various levels of nutrients affect the overall vegetation biomass in nitrogen enriched and control plots. Our results show that grasshopper abundance correlated to both plant quantity and plant quality. The distribution of abundance that we found is the result of grasshoppers moving into and remaining in the higher quality and more structurally complex higher biomass plots (Heidorn and Joern 1987).

When increasing the amount of S_N in my model, we assume that higher levels of nitrogen in the soil have no toxicity effects on the plants. Also when we fixed the grasshopper biomass growth to a simple parabola we assume that the grasshopper population is parabolic and what creates that parabolic shape doesn't matter to our results. To add more realism to our model we could add a carrying capacity to our plant growth equation. Without a carrying capacity my plant biomass grows exponentially over time as is shown in Fig. 7. We could also increase realism by incorporating a level of nutrient addition in which toxicity causes a decline in plant biomass, causing the system to crash as one would expect to happen in a real system.

Feeding Preference --- Plant Quality

Our empirical results show that there were no significant changes in plant biomass this summer in plots with nutrient additions; however, we saw that there were significantly more grasshoppers in the nitrogen enriched plots. We hypothesize that this increase in grasshoppers is due to an increase in plant quality in the nutrient addition plots. Based on this hypothesis, we were able to find an average abundance ratio of grasshoppers in nitrogen enriched plots to control plots which we made the feeding preference. These constant preference ratios fit our empirical data closely and gave us exceptionally low relative error values.

Our model predicted that the threshold value of nitrogen addition for plant biomass to increase in nitrogen enriched plots relative to control plots was approximate .5 kg N per week. At the nitrogen addition level we fertilized this summer ($S_N = 0.05$) our model predicted that the control plots vegetation would be greater than the nitrogen enriched plots, yet in our field data plant biomass was 1.3 kg higher in nitrogen enriched plots. This difference, between the theoretical data and empirical data, could be the result of the assumptions we used in our model and could be corrected for by incorporating more realism into our model.

Feeding Preference --- Plant Quantity

The preference ratio for plant biomass never resulted in nitrogen enriched plots having lower biomass than control plots, but at low levels of nitrogen addition the model predicted that both types of vegetation would have the same biomass at the end of eight weeks. This preference fit the experimental data strongly and had low relative errors. As nutrient addition levels increased past the threshold, the difference between the biomass in the control and nitrogen enriched plots increased.

Conclusion

There are several patterns that can be derived from the comparison of the two types of feeding preference ratios. The constant feeding preference to plant quality makes the model predict that at increasing levels of nitrogen addition only vegetation in the nitrogen enriched plots increase, but the control plots remains the same. The variable feeding preference to plant biomass predicts that at increasing levels of nitrogen both the nitrogen addition plots and the control plots increase in total plant biomass. This difference in the prediction of the control plots plant biomass is the main difference we saw between the two different models.

Our modeling results suggest that there is a threshold of nutrient addition increasing vegetation biomass. This has strong implications for future studies looking at the effects of nutrient addition. Researchers need to take into consideration that feeding preferences can be created by nutrient additions which could possibly change the outcomes of their experiments.

Further work with the model could incorporate Holling Type II response, instead of using the best fit to preference experiment data. To make the model more realistic future work could build another equation to represent the grasshopper biomass, instead of a parabola fit to observed biomass change in the 2008 data. Another possibility is to model the quality preference not as a constant preference, but instead in a mechanistic way, through a functional form.

FIGURES AND GRAPHS

Date	6/6/2008	6/27/2008	7/25/2008		7/3/2009	7/26/2009
R2	0.001	0.309	0.271		0.238	0.330
Plant Biomass	P=0.900	P=0.000	P=0.000		P= 0.094	P= 0.000
Plant Species Richness	P=0.868	P=0.011	P=0.126		P= 0.265	P= 0.114
Plant Quality	P=0.891	P=0.562	P=0.346		P= 0.003	P= 0.055

Table 1. Summarized results of multiple linear regressions of grasshopper abundance 2008 and 2009. (p> 0.05 significant). Results of plant quality are for carbon: nitrogen ratio, plant quality of phosphorus was not significant for any counts.

Parameter	Description	Values
S_C	Supply rate of nitrogen for control plot	0.02 kg / week
S_N	Supply rate of nitrogen for nitrogen addition plot	0.05, 0.5, 1.0 kg / week
μ	Per capita uptake rate of nitrogen by the plants (fraction of N taken up per kg of plant per week)	0.009375 / kg · week
a	Conversion of nitrogen into plant biomass (fraction of plant biomass produced per kg N taken up)	1.0 / kg
f	Per capita loss rate of plant biomass due to herbivory (fraction of plant biomass lost per week per herbivore)	0.05---0.15 / kg · week
w_C	Per capita preference of grasshoppers to vegetation in control plot	• For plant quality preference: 0.44 • For plant quantity preference: $V_C(t) / (V_C(t) + V_N(t))$
w_N	Per capita preference of grasshoppers to vegetation in nitrogen addition plot	• For plant quality preference: 0.56 • For plant quantity preference: $V_N(t) / (V_C(t) + V_N(t))$

Table 2. Summary of parameters for the community model.

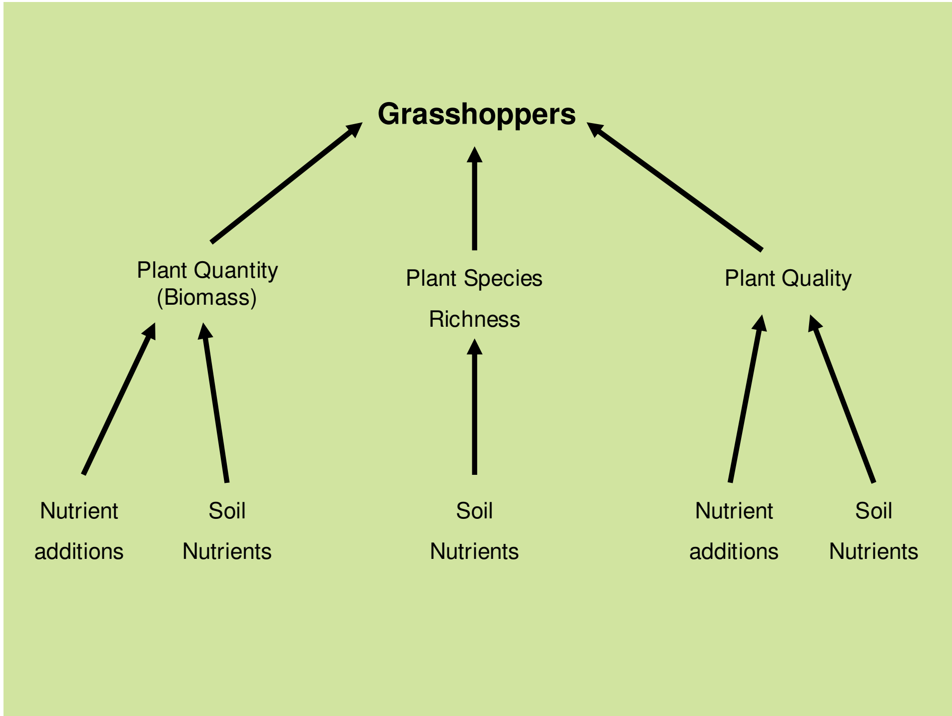


Figure 1. Our hypothesized relationship between grasshopper abundance and parameters that affect grasshopper habitat selection. All arrows indicate positive relationships. Nutrient additions and soil nutrients indirectly increase grasshopper abundance through the proposed pathways. We hypothesize that the increased soil nutrient levels will lead to higher plant productivity and increased plant quality and that this will lead to increases in grasshopper abundance. In addition, greater plant species diversity, may also lead to increased grasshopper abundance. Since it was the first year of nutrient addition, nutrient additions would have no effect on plant species diversity.

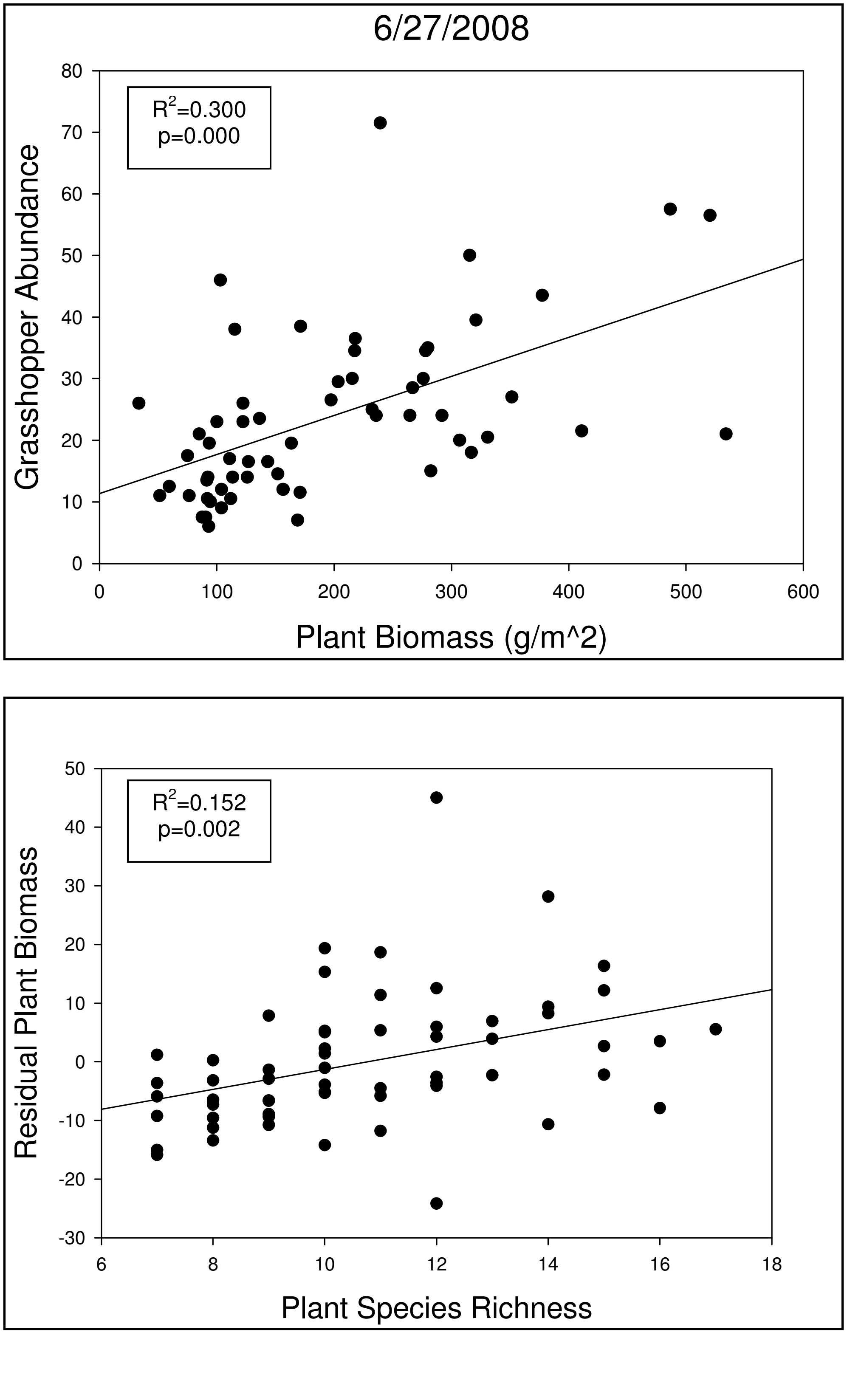
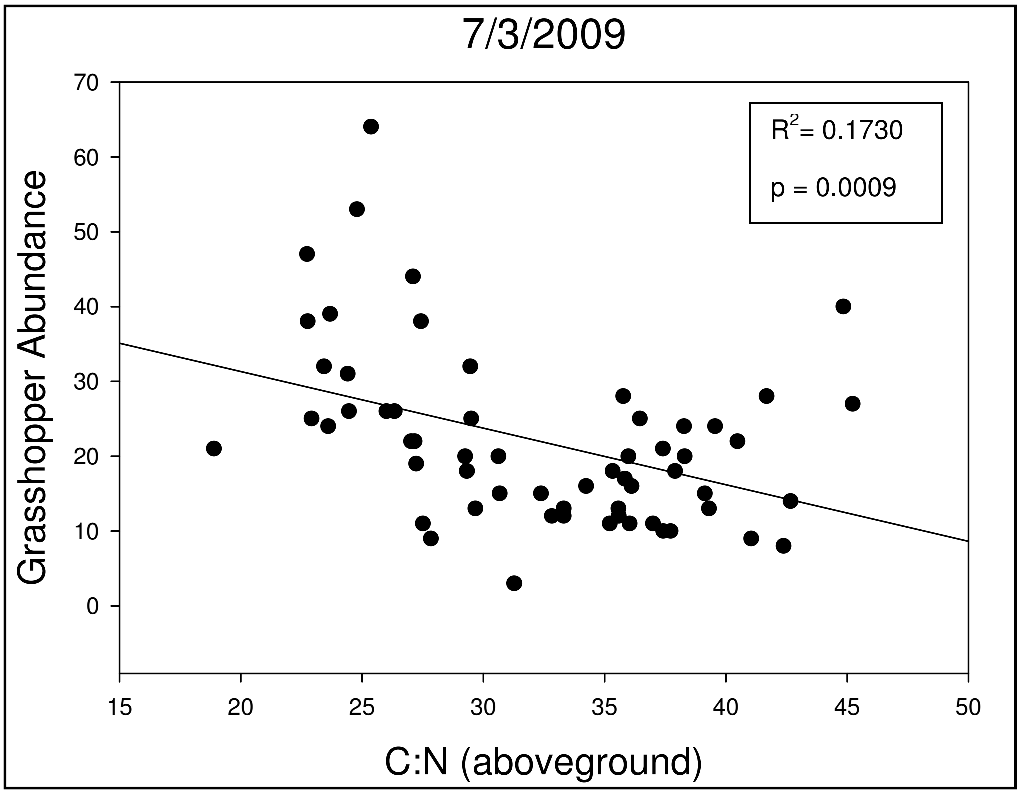


Fig. 2. Linear regression of grasshopper abundance on 6/27/2008 and plant biomass (top). Linear regression of residuals of plant biomass on 6/27/2008 versus plant species richness, the number of plant species (bottom).



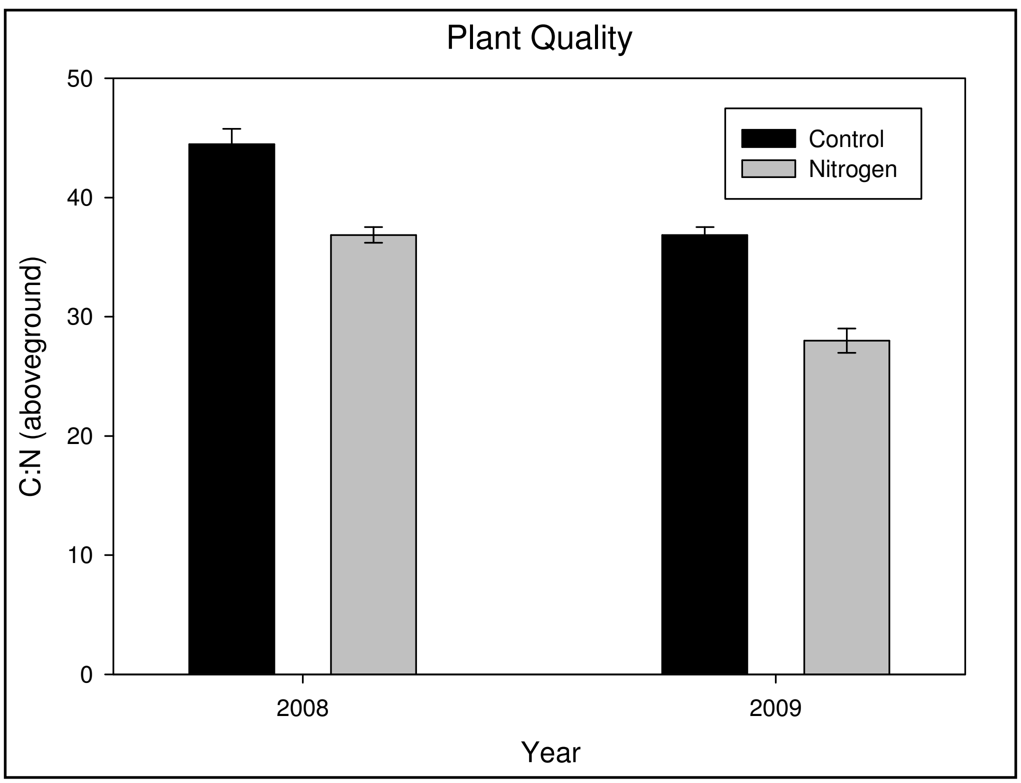
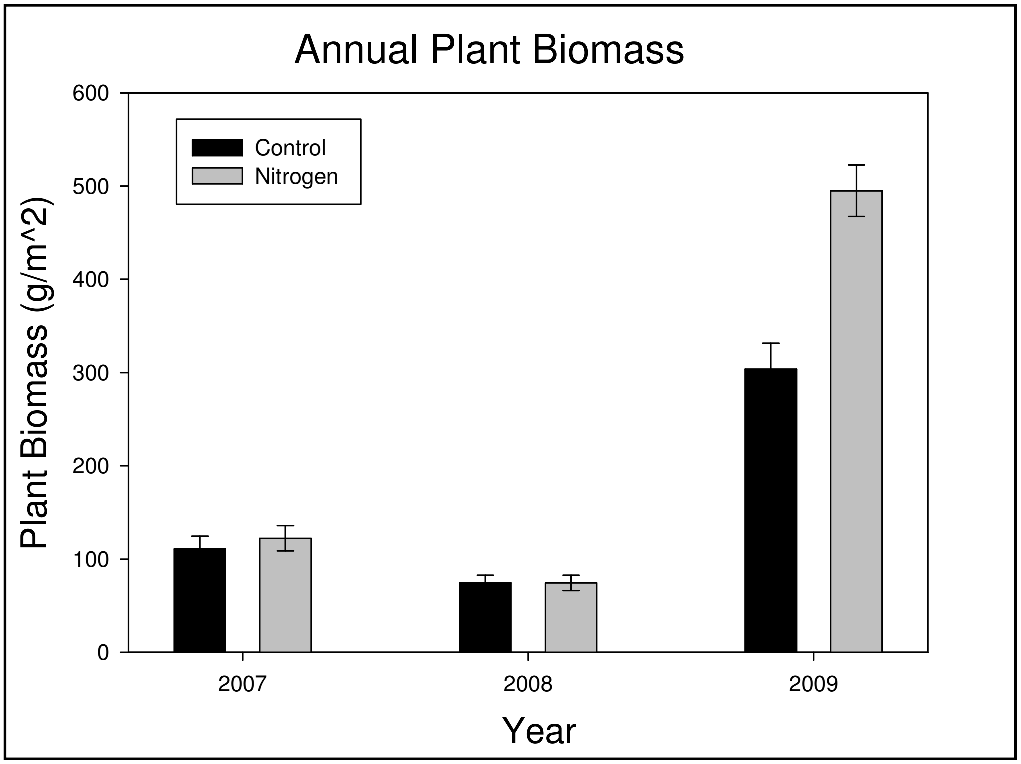


Fig. 3. Linear regression of grasshopper abundance on 7/3/2009 and C:N, the plant quality aboveground (top). C:N (grams C: grams N) for control and nitrogen enriched plants for 2008 and 2009.



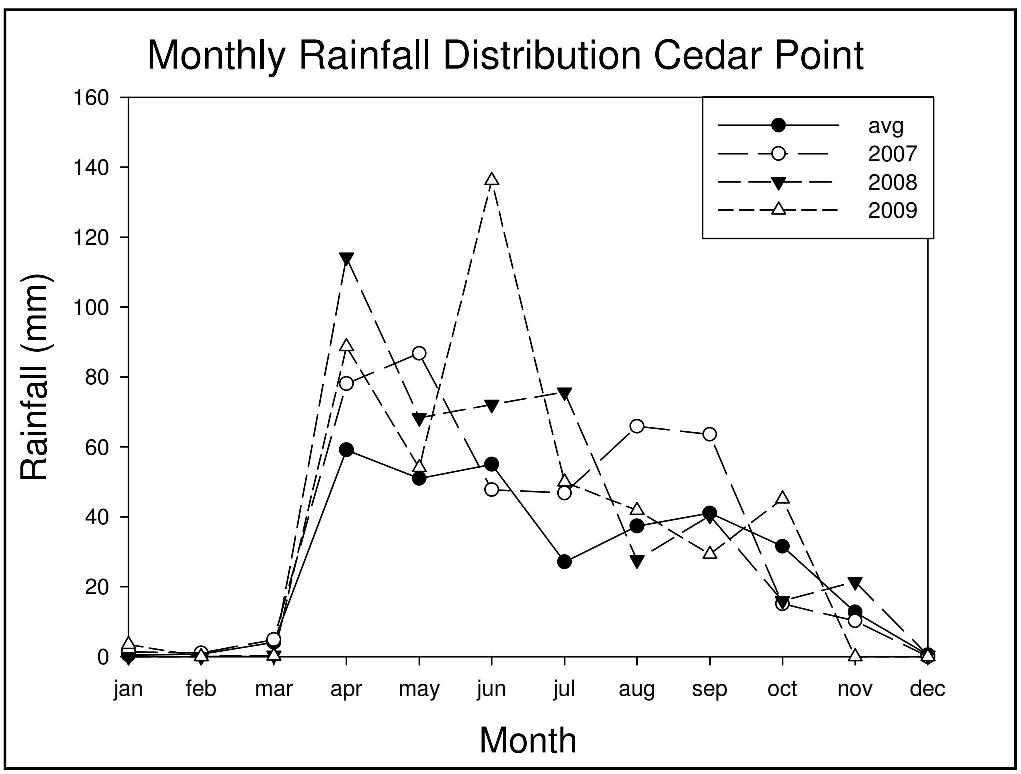


Fig. 4. Annual plant biomass in the nitrogen and control plots for 2007, 2008, and 2009 (top). Monthly rainfall distribution for the study area for 2007, 2008, and 2009 (bottom).

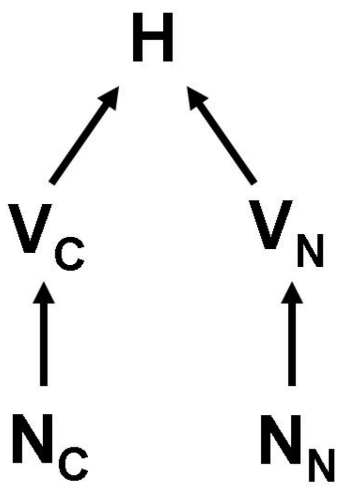


Fig. 5. Interactions of the components of the model, illustrating how grasshoppers (*H*) are able to have preference between two vegetation categories: vegetation with no nitrogen addition (V_C) and vegetation with nitrogen addition (V_N).

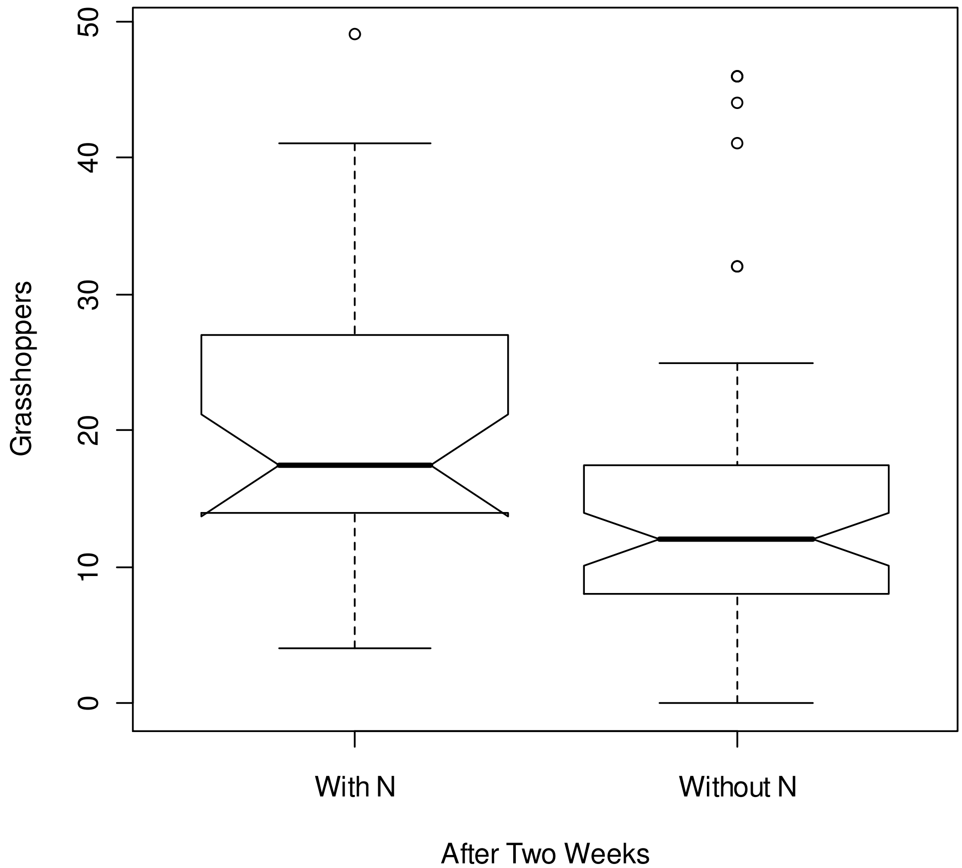


Fig. 6. The relationship between grasshopper abundance to nitrogen fertilization treatment. Nitrogen fertilized plots had significantly higher grasshopper abundance two weeks after we added nutrients (Wilcox test, p= 0.0063).

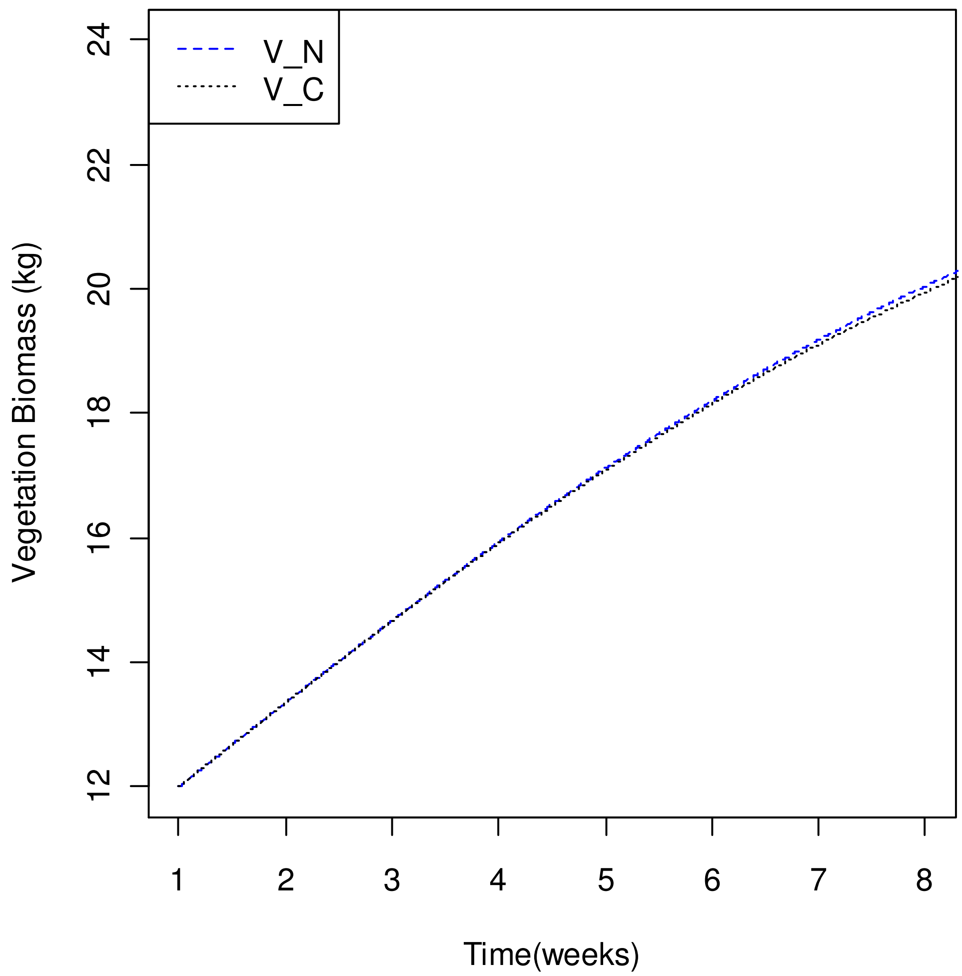

V_N
V_C
Vegetation Biomass (kg)
12
14
16
18
20
22
24
1
2
3
4
5
6
7
8
Time(weeks)

Fig. 7a.

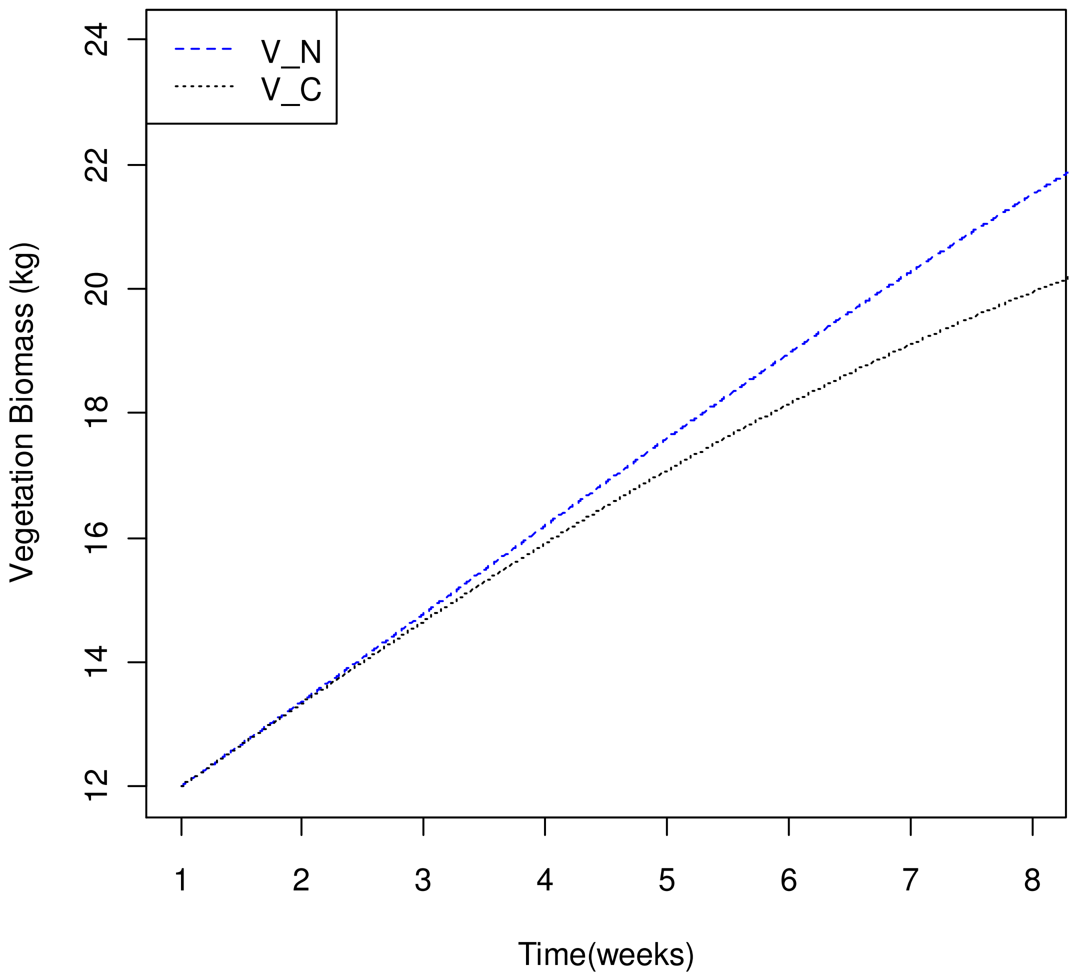

V_N
V_C
Vegetation Biomass (kg)
12
14
16
18
20
22
24
1
2
3
4
5
6
7
8
Time(weeks)

Fig. 7b.

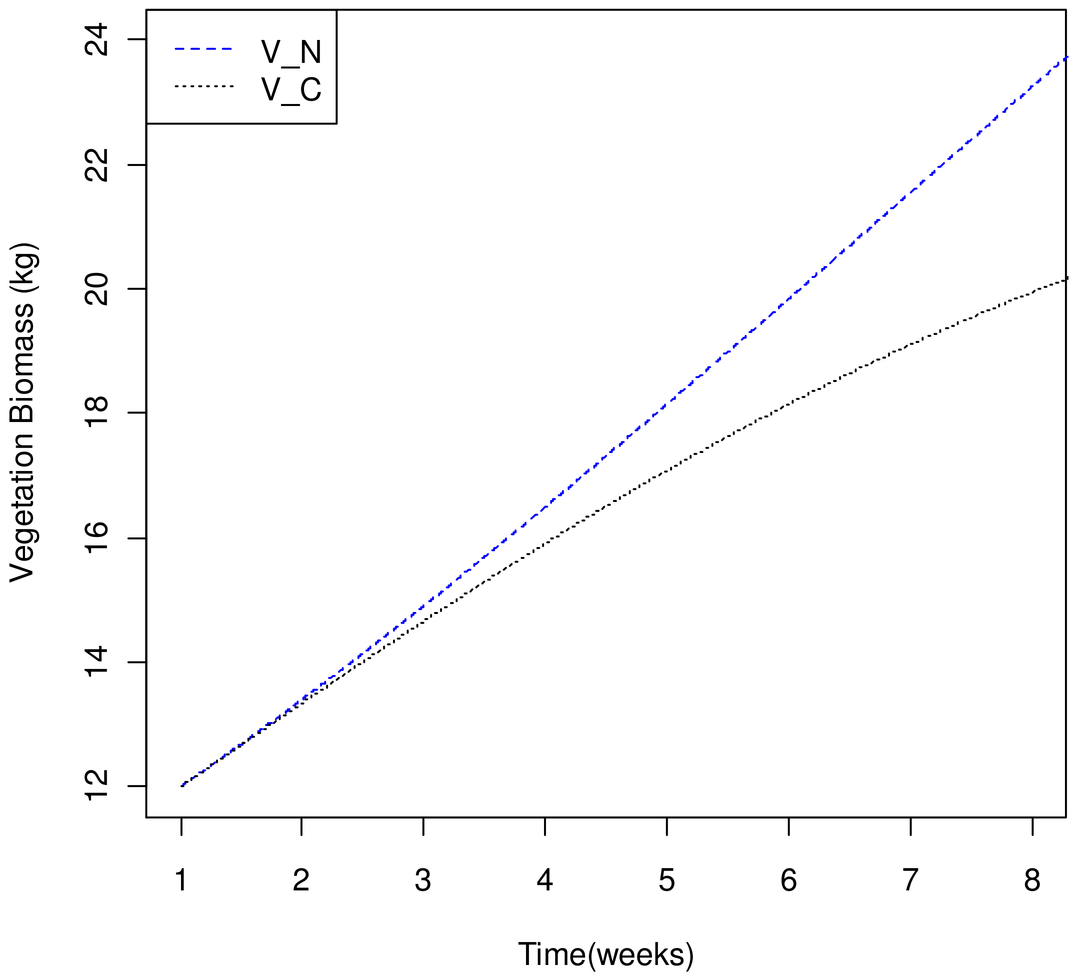


Fig. 7c.

Fig. 7a-c. Projected growth of plant biomass (kg) without grasshopper feeding as nitrogen enrichment increases in panels from 7a to 7c (S_N =0.05, 0.5, 1.0 kg N/week).

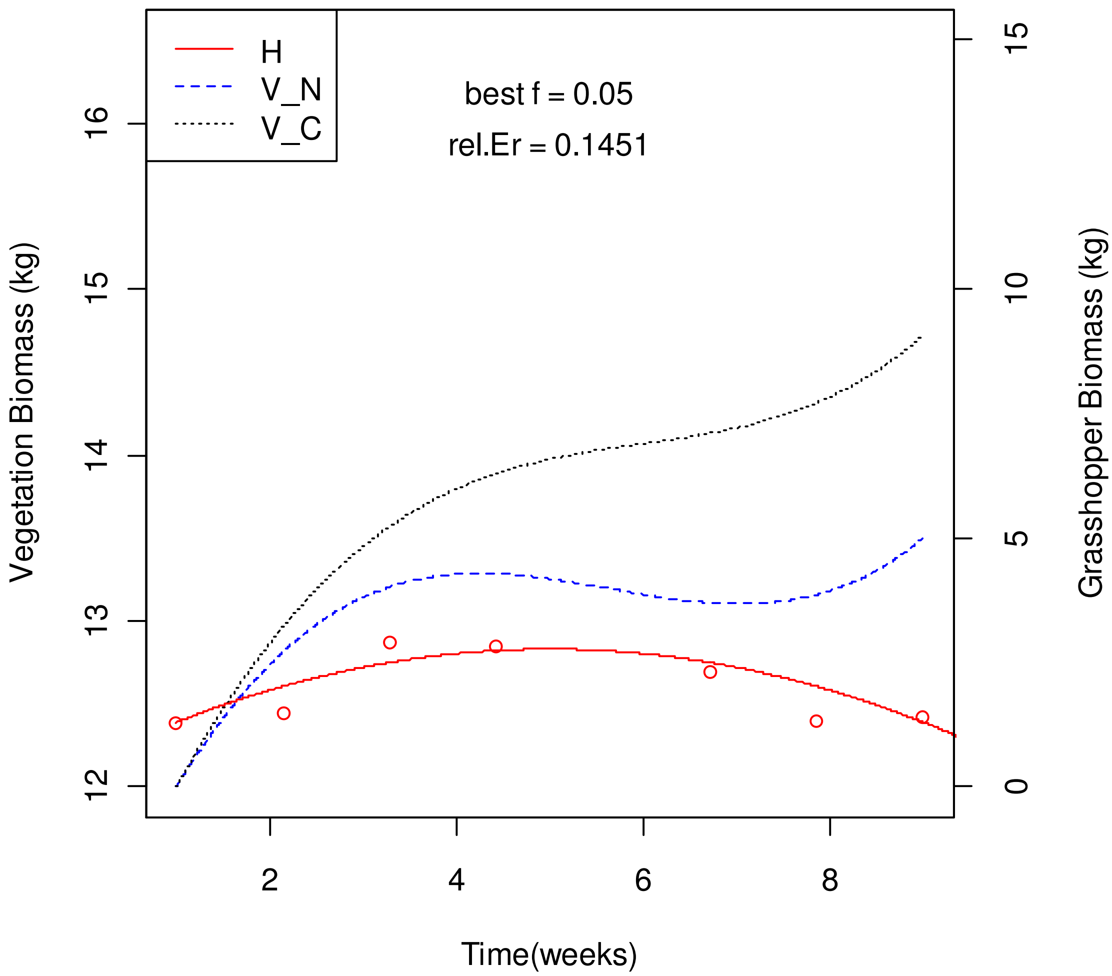

H
V_N
V_C
best f = 0.05
rel.Er = 0.1451
Vegetation Biomass (kg)
12
13
14
15
16
Grasshopper Biomass (kg)
0
5
10
15
2
4
6
8
Time(weeks)

Fig. 8a.

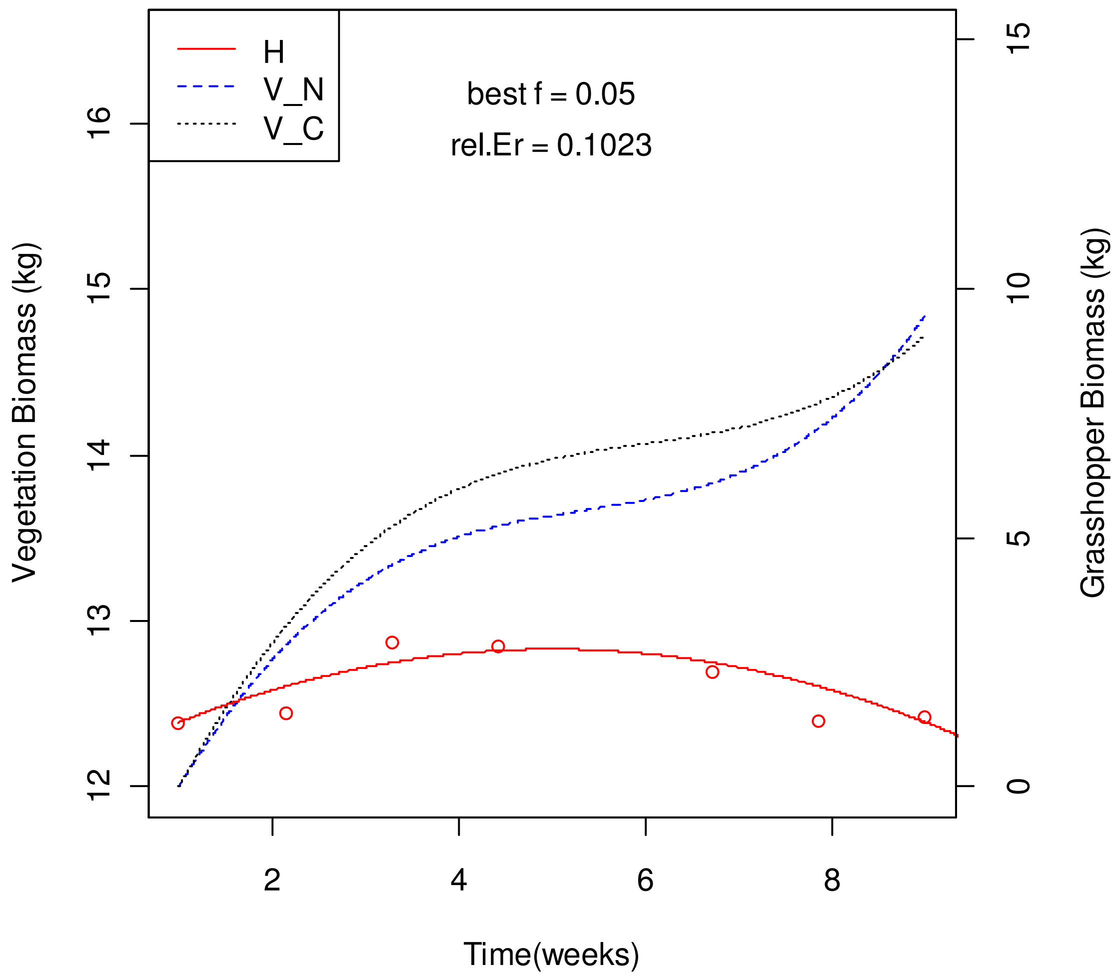

H
V_N
V_C
best f = 0.05
rel.Er = 0.1023
Vegetation Biomass (kg)
Grasshopper Biomass (kg)
Time(weeks)
12
13
14
15
16
0
5
10
15
2
4
6
8

Fig. 8b.

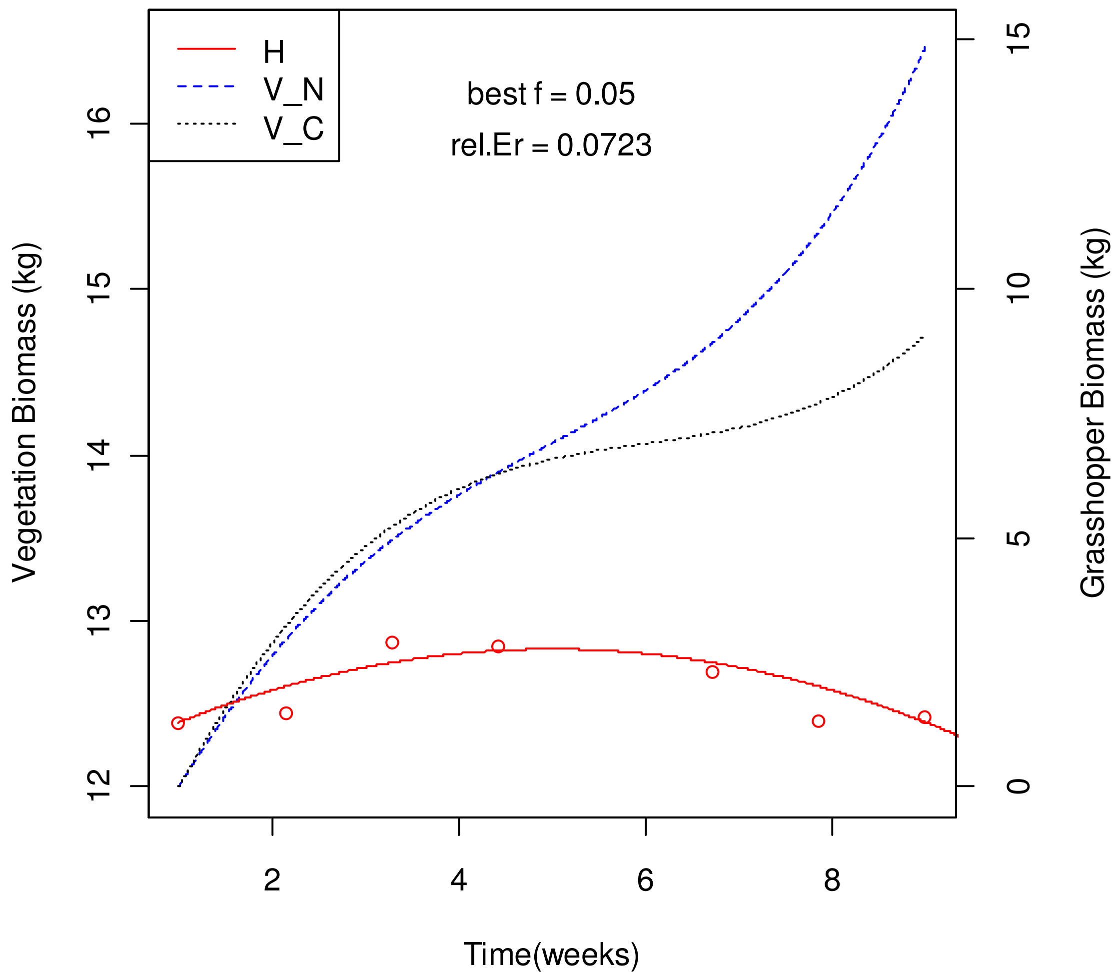


Fig. 8c.

Fig. 8a-c. Predicted effect of grasshopper feeding response to plant quality with nitrogen enrichment increasing in the figures from 8a to 8c (S_N = 0.05, 0.5, 1.0 kg N/week), on the growth of control vegetation biomass (V_C) and nitrogen addition vegetation biomass (V_N). The predicted curve for grasshopper biomass (H) and the empirical data is represented by the circles.

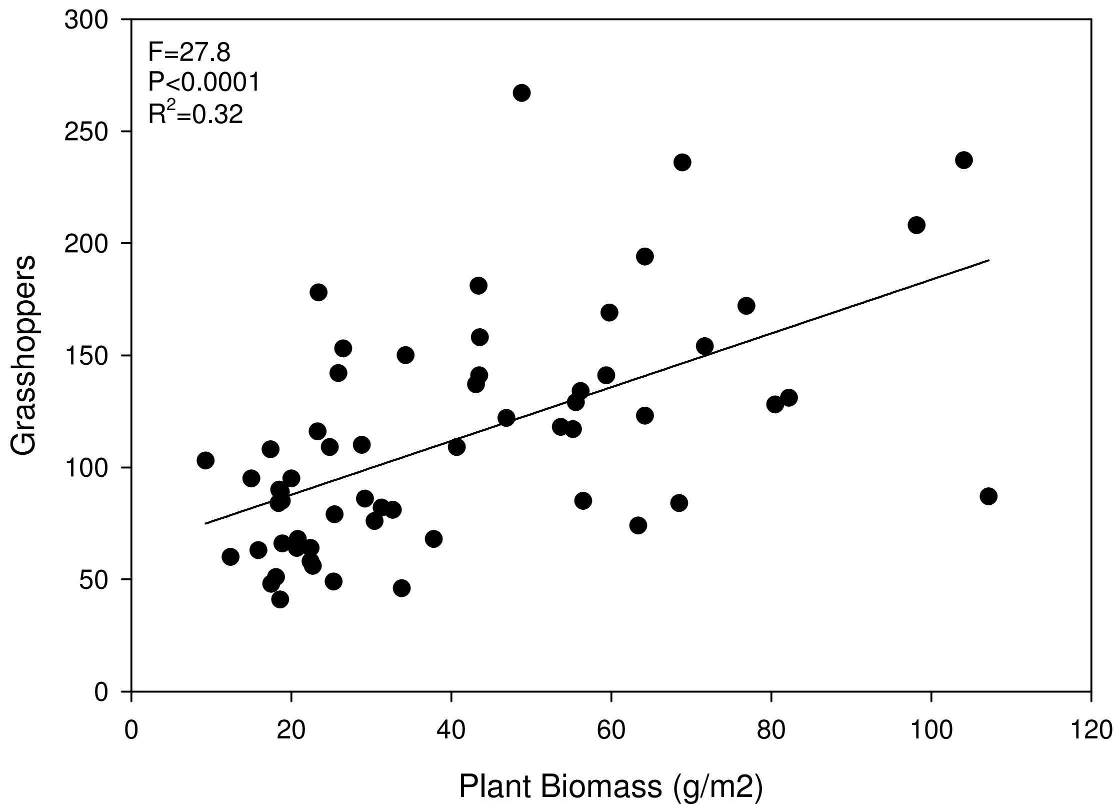


Fig. 9. The relationship of dry weight plant biomass and grasshopper abundance for all 60 plots. Grasshopper abundance is the total grasshopper count for a given plot over the season.

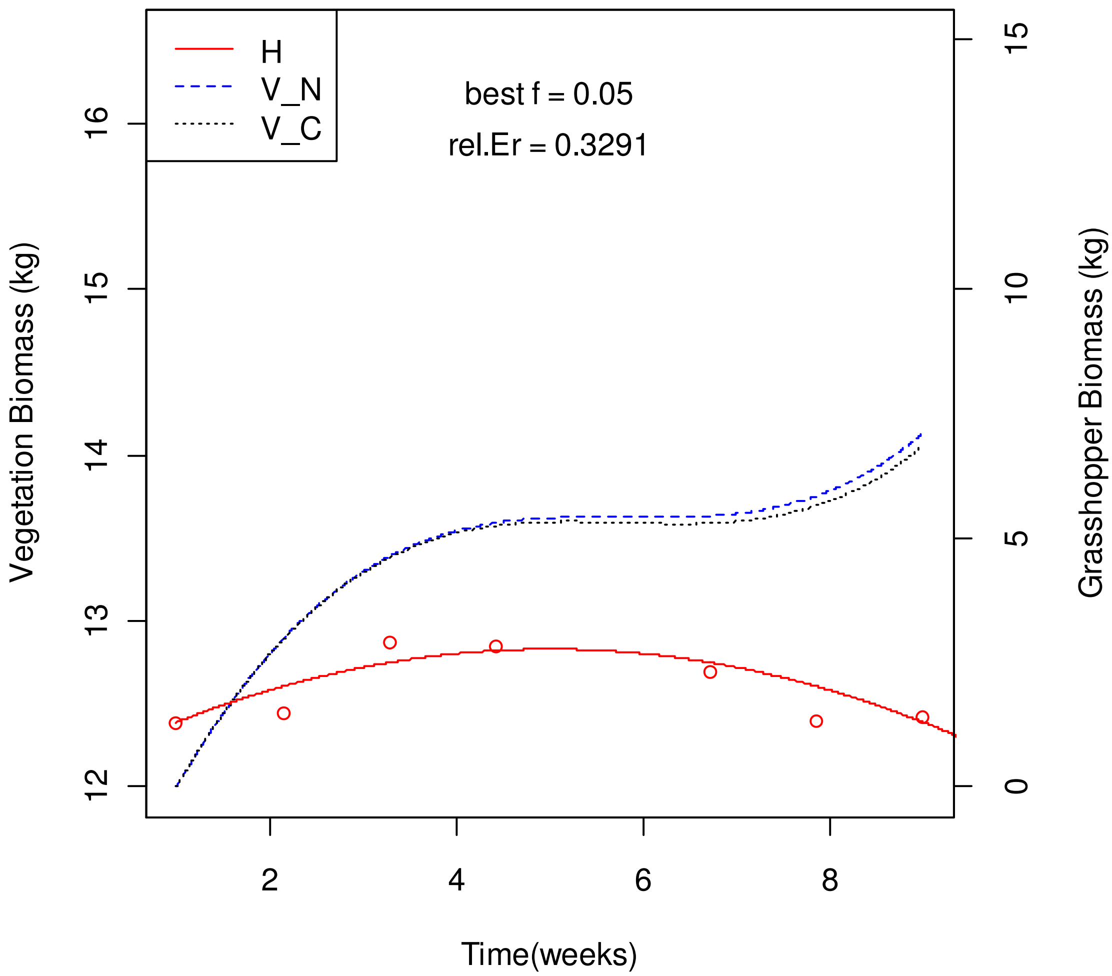

H
V_N
V_C
best f = 0.05
rel.Er = 0.3291
Vegetation Biomass (kg)
12
13
14
15
16
Grasshopper Biomass (kg)
0
5
10
15
2
4
6
8
Time(weeks)

Fig. 10a.

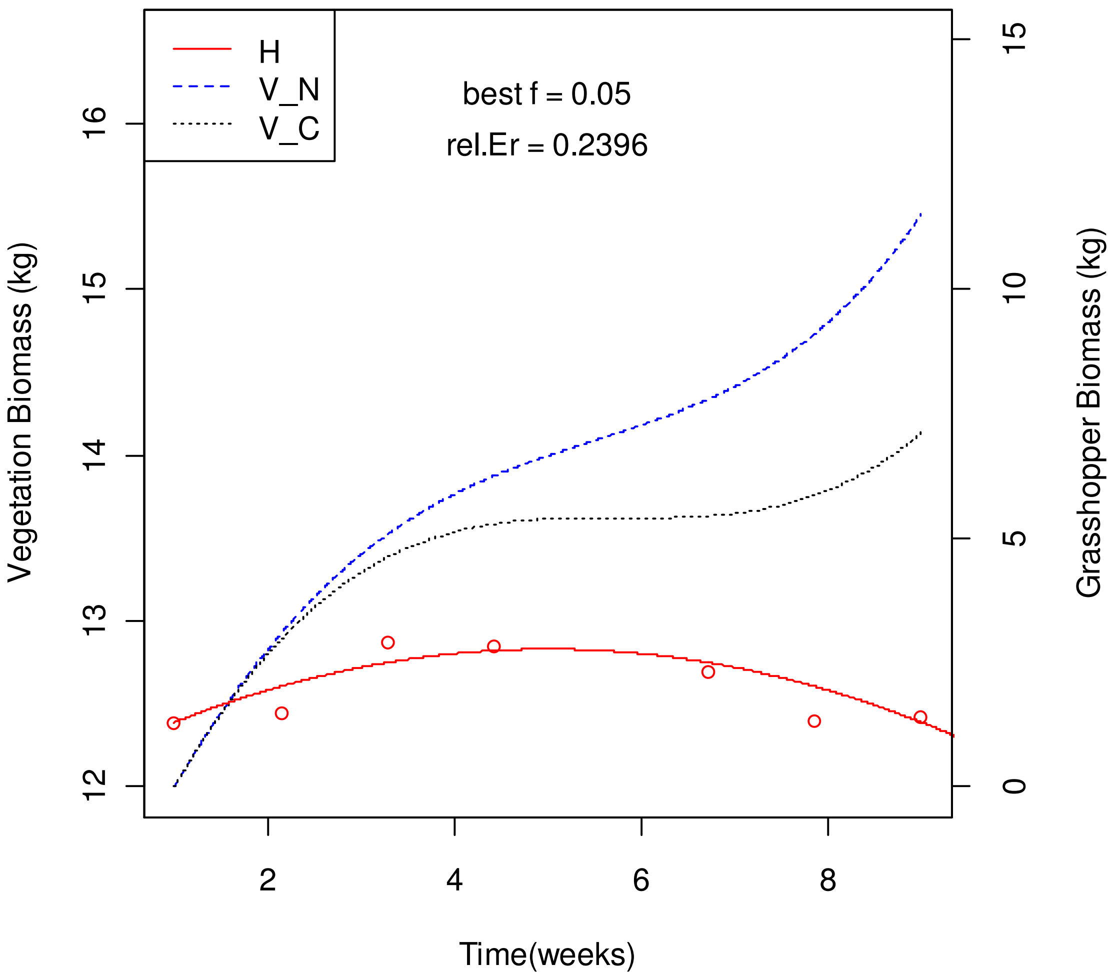

H
V_N
V_C
best f = 0.05
rel.Er = 0.2396
Vegetation Biomass (kg)
Grasshopper Biomass (kg)
Time(weeks)
12
13
14
15
16
0
5
10
15
2
4
6
8

Fig. 10b.

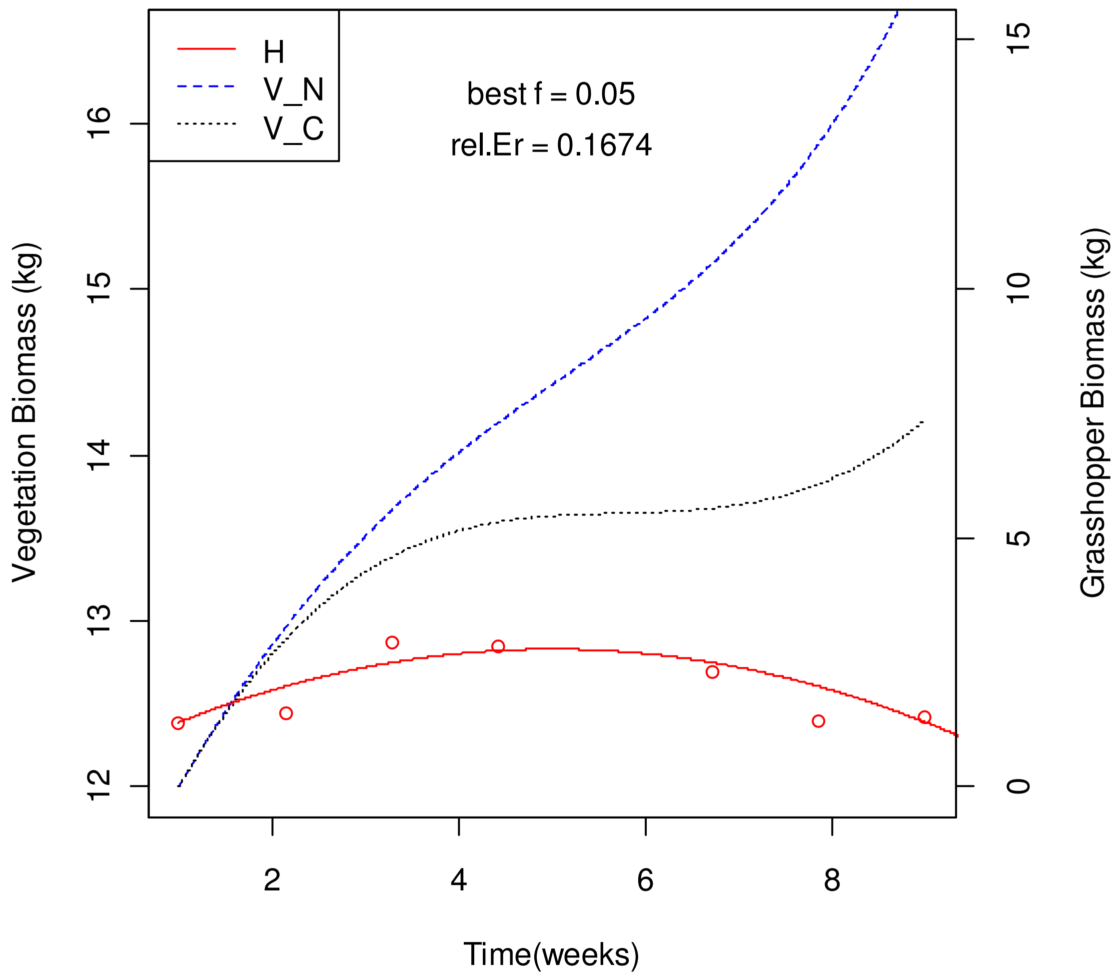


Fig. 10c.

Fig. 10a-c. Predicted effect of grasshopper feeding response to plant quantity with nitrogen enrichment increasing in the figures from 10a to 10c (S_N = 0.05, 0.5, 1.0 kg N/week), on the growth of control vegetation biomass (V_C) and nitrogen addition vegetation biomass (V_N). The predicted curve for grasshopper biomass (H) and the empirical data is represented by the circles.

LITERATURE CITED

Cock, M.J. 1978. The Journal of Animal Ecology. 47 (3): 805-816.

Gardiner, T., Hill, J., and Chesmore, D. 2005. Review of the methods frequently used to estimate the abundance of Orthoptera in grassland ecosystems. Journal of Insect Conservation. 9: 151-173.

Gardiner, T. and Hill, J. 2006. A comparison of three sampling techniques used to estimate the population density and assemblage diversity of Orthoptera. Journal of Orthoptera Research. 15(1): 45-51.

Heidorn, T.J. and Joern, A. 1987. Feeding preference and spatial distribution of grasshoppers (acrididae) in response to nitrogen fertilization of *calamovilfa longifolia*. Functional Ecology. 1(4):369-375.

Hosseini, M., Hatami, B., Saboori, A., Allahyari, H., Ashouri, A. 2005. Predation by *Allothrombium pulvinum* and *Amphitetranychus viennensis*: predation rate, prey preference, and functional response. Experimental and Applied Acarology. 37: 173-181.

Joern, A. 1982. Vegetation structure and microhabitat selection in grasshoppers (Orthoptera: Arcrididae). The Southwestern Naturalist. 27(2): 197-209.

Joern, A., Kemp, W. P., Belovsky, G. E., and O'Neill, K. 2009. Grasshoppers and vegetation communities. The Southwestern Naturalist. 63(2): 136-140.

Kemp, W. P., Harvey, S. J., and O'Neill, K. M. 1990. Patterns of vegetation and grasshopper community composition. Oecologia. 83(3): 299-308.

Nutrient Network. http://web.science.oregonstate.edu/~seabloom/nutnet/.

Pfisterer, A. B. Diemer, M. Schmid, B. 2001. Dietary shift and lowered biomass gain of a generalist herbivore in species-poor experimental plant communities. Oecologia. 135 (2): 234-241.

Pfadt, R.E. 1994. Field Guide to Common Western Grasshoppers. Assessed online : http://www.sdvc.uwyo.edu/grasshopper/meco.htm

Riser, P.J. Parton, W.J. 1994. Ecosystem analysis of the tallgrass prairie: nitrogen cycle. Ecology. 63(5): 1342-1351.

Ricklefs, R.E. Miller, G.L. 2000. Ecology 4th Edition. Freeman & Company.

Schmitz, O.J. 1993. Trophic exploitation in grassland food chains: simple models and a field experiment. Oecologia. 93(3): 327-335.

Schmitz, O.J. 1994. Resource edibility and trophic exploitation in an old-field food web. National Academy of Sciences. 91(12): 5364-5367.

Schmitz, O.J. 1997. Press perturbations and the predictability of ecological interactions in a food web. Ecology. 78(1): 55-69.