

**CAUSES OF VARIATION IN DAMAGE BY FOLIVORES: THE ROLES OF
ECOSYSTEM PRODUCTIVITY AND HABITAT COMPLEXITY**

A Thesis by

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M. Sc., Tribhuvan University, 2003

Submitted to the Department of Biological Sciences
and the faculty of the Graduate School of
Wichita State University
in the partial fulfillment of
the requirements for the degree of
Master of Science

May 2009

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The following faculty members have examined the final copy of this thesis for form and content, and recommend that it be accepted in partial fulfillment of the requirement for the degree of Master of Science with a major in Biology.

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DEDICATION

To my parents, Purna Man and Purna Devi, and my sister, Smriti for their love and support.

ACKNOWLEDGMENTS

I would first like to thank my thesis advisor Dr. Leland Russell for his guidance. Without his supervision and encouragement, this research could not have been completed. I would like to thank National Science Foundation Grant for funding the research project. My thanks also go to Dr. Mary Liz Jameson, Dr. Svata Louda, Dr. Arthur Youngman, and Dr. Donald Distler, for their advice. I am grateful to Jim Mason from Great Plains Nature Center for providing sites at Pawnee Prairie.

I also thank my colleagues, especially Machale Spencer for their help during field work and thesis writing. Special thanks go to Halley Terry and Fabrice Ngansop for finishing field work in 2008.

I am also thankful to my committee members for the valuable suggestions.

I thank my parents for their love, and blessings throughout my life. And my special thanks go to my lovely sister and brother-in-law, who have been a key for my every success.

ABSTRACT

Understanding the causes of variation in herbivore damage among individual plants is important because it may lead to strategies for increasing damage to invasive weeds, thereby, reducing their population growth. My research focuses on variation in insect folivore damage to tall thistle (*Cirsium altissimum*) rosettes under differing levels of ecosystem productivity and habitat complexity. I addressed four questions. First, does ecosystem productivity affect the amount of tissue loss to insect herbivory? Second, does habitat complexity, in terms of litter and local species richness, affect tissue loss to insect herbivory? Third, is there an interaction effect between ecosystem productivity and habitat complexity on plant tissue loss to insect herbivores? Fourth, do ecosystem productivity and habitat complexity affect the fresh biomass and abundance of insect orders? Two sites with four 40 m X 40 m plots each were chosen for ecosystem productivity manipulations and individual plants within these large plots were used for habitat complexity manipulations. Nitrogen was added to experimentally increase ecosystem productivity. Plant litter and neighbor plant species richness were manipulated for habitat complexity.

I found no significant effects of ecosystem productivity and habitat complexity on folivore damage, measured as the proportion of leaves damaged over >50% of their area per tall thistle rosette. Only seasonal variation was observed for folivore damage to tall thistle rosettes with more damage in August and September in 2007 and 2008, respectively. No significant effects of ecosystem productivity and habitat complexity were observed on rosette growth in 2008, but in 2007 a marginally significant effect of litter was observed on rosette growth and there was a significant effect of litter upon survival. No significant interaction effect of ecosystem productivity and habitat complexity was seen on herbivore damage to tall thistle rosettes. Only a

few significant effects of ecosystem productivity were observed on biomass and abundance of insect orders, including Orthoptera, Hymenoptera, Heteroptera, Coleoptera. There were weak interaction effects of ecosystem productivity and litter upon insect biomass for the orders, Orthoptera, Heteroptera, Coleoptera and strong effects upon Hymenoptera. Two novel contributions of my research are large-scale manipulations of ecosystem productivity and examining effects of litter manipulation on plants at post-seedling life stages.

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INTRODUCTION

Herbivory is an interspecific interaction in which plant tissues are consumed by either vertebrate or invertebrate animals. Herbivory can take many forms ranging from consumption of leaves, flowers and seeds, to sucking of phloem and xylem sap, to attack of roots and meristems. A striking feature of herbivore-plant interactions is the large spatial and temporal variation in the amount of tissue that herbivores remove from plants (e.g., Louda et al. 1987, Reader 1992, Louda and Rodman 1996, Fagan and Bishop 2000, Muth et al. 2008, Shiojiri and Karban 2008). Within a plant population, there can be large variation in insect damage, such as between core regions and edges of the population. Fagan and Bishop (2000) found more damage to the legume *Lupinus lepidus* var. *lobbii* by leaf- and stem-feeding lepidopterans at the edge than in the core region of plant populations in early successional habitats on Mt. St. Helens. Over twice as much leaf damage was observed at edges as compared to in patch cores at sites where natural herbivory patterns were not manipulated experimentally (Fagan and Bishop 2000). Similarly, Rand (2002) found herbivore damage by beetles in the genus *Erynephala* to *Atriplex patula* var. *hastata* to be twice as great in the mid marsh zone than in the high marsh zone in a New England tidal salt marsh.

Herbivory can affect many different parameters of plant performance, including survival (Guretzky and Louda 1997), reproduction (Louda and Rodman 1996), seed production (Louda and Potvin 1995), growth rate, and plant fitness (Rauscher and Feeny 1980). For example, plant growth, reproductive effort and stem density of the native crucifer (*Cardamine cordifolia*) were all negatively affected after folivory by specialist insects like *Pieris napi macdunnoughi*, and *Aphalara* sp. (Louda and Rodman 1996). Guretzky and Louda (1997) also found greater root crown diameter, total number of leaves per plant and length of the two longest leaves for the

native thistle, *Cirsium altissimum*, on rosettes that had been protected from folivory by an insecticide application. Reproductive traits, like flower number and seed production, often are positively correlated with plant size (Meyer and Root 1993). Therefore, where herbivory reduces individual plant size it may affect seed production and thus can decrease population growth and the density of the population.

Ecosystem productivity may influence the amount of damage that herbivores inflict on plants either by affecting the size of herbivore populations or by altering plant tissue quality. According to Oksanen et al. (1981), insect damage will be highest at sites with intermediate ecosystem productivity. Very low productivity systems will have no herbivore damage because there is not enough energy filtering up through the food web to support large herbivore populations. At intermediate productivities, herbivore damage will be extensive because herbivore populations will be relatively large, but not enough energy will filter up to support large carnivore populations. At high ecosystem productivities, there will be little herbivore damage because carnivore populations are large.

Gradients in abiotic resource availabilities and environmental conditions that underlie differences in ecosystem productivity can affect the physiological status of plants. Plant physiological status, in turn, can affect the nutritional quality of plant tissues for herbivores (Joern and Mole 2005) and the concentrations of plant chemical defenses (Louda and Rodman 1996). The Plant Stress Hypothesis was proposed to include changes in plant resistance, such as chemical defenses in plant tissues, that may increase insect herbivory where environmental stresses on plants are greater (Rhoades 1983). For example, Joern and Mole (2005) showed that a grasshopper species (*Ageneotettix deorum*) feeding on Blue grama grass (*Bouteloua gracilis*) had greater impact on plant tissue quality, such as total non-structural carbohydrates, under drier

conditions. In contrast to the predictions of the Plant Stress Hypothesis, the Plant Vigor Hypothesis states that plants growing vigorously are favorable to herbivory (Price 1991). Still, controversies exist between the Plant Stress Hypothesis and Plant Vigor Hypothesis.

Habitat complexity has been considered to be an important factor influencing predator abundance and food web dynamics in invertebrate communities (Langellotto and Denno 2006). Two important potential consequences of variation in habitat complexity that ecologists have studied are variation in invertebrate community composition and variation in herbivore damage to plants. Complex habitats provide niches for insects that feed at different trophic levels. Litter, the dead plant parts, makes the habitat more complex affecting invertebrate community composition and abiotic resources. Litter affects the light penetration, soil moisture availability and also the different insects' abundances. According to Facelli (1994), seedlings of *Ailanthus altissima* were damaged and their mortality increased with greater litter accumulation due to more herbivorous arthropod activity.

The species diversity of plants surrounding an herbivore's host plant is another component of habitat complexity that can have effects on herbivory. In natural grasslands, higher insect abundance has been found in plots with greater plant species diversity (Siemann 1998). By contrast, according to Brown and Ewel (1987), herbivory removed approximately the same amount of leaf tissue per unit ground area (71.5 to 78.5 gm²yr⁻¹) despite variation in floristic diversity, composition, or amount of leaf tissue available in different tropical agroecosystems. Species rich ecosystems had constant rates of herbivory because, although levels of damage to individual species changed with community species richness, at the scale of the entire plant community the changes in levels of herbivore damage to individual species counterbalanced one another (Brown and Ewel 1987).

The ability to manipulate the amount of damage that herbivores do to plants is of applied significance in both control of invasive species and in agriculture. For example, if experiments showed greater herbivore damage in less productive ecosystems, then fertilizer application might reduce herbivore damage. Alternately, if experiments showed greater herbivore damage where litter accumulation is greater then farmers might be able to remove litter from cropland to reduce herbivore damage. Burning can be an effective management tool for increasing seedling establishment because it removes the litter. Maret and Wilson (1995) mentioned that burning enhanced native seedling establishment in Annual Exotic Grass site and Perennial Exotic Grass site at Carson Prairie of Oregon State University. With this study, effects of habitat complexity and ecosystem productivity on herbivore damage could be understood.

The present study examines causes of variation in the amount of damage by insect folivores on established (post-seedling) tall thistle (*Cirsium altissimum*) juvenile plants (rosettes). Four hypotheses are tested in this research: 1) amount of leaf tissue loss to insect herbivores by tall thistle rosettes will increase with ecosystem productivity, 2) leaf tissue loss by tall thistle rosettes to insect herbivores increases with habitat complexity in terms of litter but decreases with species richness, 3) there will be an interaction effect between ecosystem productivity and habitat complexity such that the effect of habitat complexity on damage will be greater with higher ecosystem productivity, 4) with increasing ecosystem productivity and habitat complexity, there will be more insect abundance at all trophic levels.

LITERATURE REVIEW

Understanding spatial and temporal variation in damage done by insects to plants is very complex as levels of damage can be influenced by many biotic and abiotic factors. It is necessary to understand such interactions as insect herbivores can do great damage to economically important crops. Polycultures or inter-cropping is a traditional agricultural practice that manipulates ecological conditions with the goal of reducing herbivore damage to crops. In addition, understanding causes of variation in insect damage to plants could be used to create ecological conditions in agricultural fields that maximize damage to exotic weed species (Guretzky and Louda 1997) so that losses as a result of weeds competing with economically important crops could be reduced. As a result of my research study, the factors that increase or decrease folivory of tall thistle rosette plants could be understood, including causes of spatial variation in damage between plants in different habitats and temporal variation in damage to the plants through different seasons of the year.

Louda and Rodman (1996) showed different strengths of herbivore effects on *Cardamine cordifolia* plants, a native crucifer, that grew in full sun compared to plants that grew in shade as a result of changes in plant quality and physiology like glucosinolate concentration, water stressed condition, leaf nitrogen concentration and leaf thickness. Moderate water stressed plants in the sun had lower glucosinolate concentrations and greater herbivory (Louda and Rodman 1996). The type and amount of damage to plants may depend upon a variety of factors such as life form of the plant, types of insects, and other biotic and abiotic factors. Amount of herbivore damage to plants also depends on surrounding vegetation as ecosystems with higher plant species richness lost a lower proportion of leaf area to herbivory due to counterbalancing of low rates of damage on some species with high rates of damage on others (Brown and Ewel

1987). Emphasizing the role of abiotic resource availability, the climatic release hypothesis states that favorable seasons allow greater survival of herbivores and they reach epidemic levels (Price 1991). The present study is focused on variation of damage to the rosette life form of *Cirsium altissimum* (Tall Thistle) by leaf-feeding invertebrates under different levels of ecosystem productivity and habitat complexity.

Ecosystem Productivity

There are two primary mechanisms by which ecosystem productivity and the availability of soil resources are hypothesized to affect herbivore damage: (1) effects on herbivore population sizes and (2) changes in plant tissue quality. Oksanen et al. (1981) predicts that ecosystem productivity will determine the number of trophic levels in the food web. According to Oksanen et al. (1981), the number of trophic levels will determine whether or not herbivore populations are kept small by intense predation or only are limited in size by food availability. Oksanen's model originally was developed to explain variation in vertebrate herbivores' effects on plants in relation to ecosystem productivity. Fraser and Grime (1997) and Fraser (1998) were among the first to apply this model to herbivory by invertebrates. Insect abundance varies with productivity in addition to varying with different abiotic conditions, like temperature and precipitation (Ritchie 2000). Therefore, quantifying the insect community composition is another aim of my research.

Bottom-up forces, like resource availability, can operate to limit herbivore populations, as described by the resource concentration hypothesis (Root 1973) or top-down forces, like predation and parasitism, may operate, as described by the enemies hypothesis (Herrera and Pellmyr 2004). According to the resource concentration hypothesis, plant communities with

high, dense, pure (low species diversity) stands of vegetation will have greater densities of herbivores. In contrast, the enemies hypothesis states that there will be higher densities of carnivores and parasitoids in dense vegetation that limit population densities of herbivores (Herrera and Pellmyr 2004). There are many empirical and theoretical studies that evaluate the extent to which bottom-up or top-down forces influence ecosystems. According to Schoonhoven et al. (2005), both the bottom-up and top-down forces might have complementary effects in ecosystems rather than being alternatives that occur in different ecological systems.

Traditional top-down and bottom-up models, however, are not the only ideas that address how ecosystem productivity will determine herbivores' effects on plants. The 'green desert' model is not a traditional top-down or bottom-up model because it focuses upon changes in plant quality, rather than changes in herbivore population sizes, as the main factor causing variation in damage along ecosystem productivity gradients. The 'green desert' model says that there will be less herbivory as ecosystem productivity increases due to greater amounts of secondary compounds in plants (Tschardt and Hawkins 2002). In my study I hypothesize in accordance with the resource concentration hypothesis that damage by herbivores to tall thistle rosettes will increase with ecosystem productivity. The communities that are experimentally enriched with nitrogen will have more living biomass supporting more invertebrate herbivores so that more damage will occur. Husheer et al. (2006) found no changes in herbivores' effects along gradients of ecosystem productivity as herbivory and resource availability act independently of each other on the regeneration of mountain beech (*Nothofagus solandri* var. *cliffortioides*) seedlings.

Many abiotic factors like temperature, light, soil moisture, and nitrogen concentration, also have effects on both primary producers and their consumers. The plant stress hypothesis

predicts that phytophagous insects prefer stressed plants because tissues of stressed plants have greater concentrations of nitrogenous compounds (Joern and Mole 2005). The plant vigor hypothesis states that vigorously growing plants are more susceptible to herbivores (Price 1991). For example, *Cleome serrulata* at dry, stressful sites produce more methylglucosinolate, a toxic compound that deters herbivores, than at wet sites (Louda et al. 1987). Chen et al. (2008) stated that cotton plants with low nitrogen input and herbivory produce more jasmonic acid, volatiles, and terpenoid aldehydes, all toxic plant defenses against herbivores, than plants with high nitrogen input. A taxonomically diverse set of insects, including *Pieris rapa* (Lepidoptera), consumes more plant material while feeding on plant tissues that are low in nitrogen than when feeding on tissues with high nitrogen content (Slansky and Feeny 1977, Meyer 2000). Clearly, physical, environmental factors that vary with ecosystem productivity affect interactions between producers and consumers.

Habitat Complexity

Greater amounts of litter and numbers of plant species surrounding an herbivore's host plant make the local habitat more complex. To my knowledge, no previous studies have been done regarding whether effects of habitat complexity upon herbivore damage to host plants depend upon ecosystem productivity. Habitat complexity might be high in the high productivity ecosystems due to dense vegetation, greater living biomass, canopy coverage, and greater species richness in contrast to low productivity ecosystems. This might cause greater abundance of carnivores so that the herbivore density will be reduced and damage will be less. Gratton and Denno (2003) working in coastal marshes in New Jersey, found that although habitat complexity under high ecosystem productivity initially has positive effect on densities of insects early in the growing season, at later stages of the growing season it is decreased due to predation. At the later

stages, the nymphal planthopper densities were lower in fertilized than in unfertilized meadows (Gratton and Denno 2003).

Litter

Litter accumulation, as a component of habitat complexity, can have both positive and negative effects on plants. Further, these effects can be either indirect or direct. The indirect effects of litter accumulation operate by affecting herbivores' and decomposers' activities. Invertebrate damage to cotyledons of *Ailanthus altissima* seedlings and seedling mortality increased with greater litter accumulation due to more activity of herbivorous arthropods (Facelli 1994). On the contrary, Riechert and Bishop (1990) found that litter addition increased spider densities, which preyed upon herbivores, so less herbivore damage occurred on the plants with greater litter accumulation. Increasing the litter, the microclimate may be more favorable to the predators and litter also may reduce the extent to which predators prey upon each other (Gratton and Denno 2003).

In addition to these indirect effects of litter on juvenile plant performance, litter might have direct positive effects by altering availability of physical resources. For example, greater litter accumulation might increase soil moisture availability by reducing evaporation. Alternately, litter could have direct negative effects including reducing light penetration or forming a mechanical barrier that prevents seeds from contacting soil (Facelli and Pickett 1991). Weltzin et al. (2005) found that litter has little effect on plant composition but a large effect on physical resources. He found that litter removal increased light availability, soil temperature and phosphorus content of aboveground biomass in a fen plant community in northern Minnesota, USA. According to Foster and Gross (1998), litter greatly reduced the species richness in the

grassland community by inhibiting the establishment of forb seedlings. With litter addition, changes in light availability bring changes in species and functional group composition of a California annual grassland (Amatengelo et al. 2008). Most of the studies of habitat complexity in the form of litter have been conducted to examine the effect of litter at the seedling stage. Therefore, my study is novel because it addresses the indirect and direct effects of litter upon tall thistle rosettes that are at post-seedling stages.

Species Richness

Neighbor plant species richness is the number of plant species that surround a focal plant. In diverse habitats, the density of the Mexican bean beetle (*Epilachna varivestis*) increased more on beans in monocultures than on beans intercropped with tall corn (Coll and Bottrell 1994). Long et al. (2003) showed that greater local plant species richness was positively related to densities of a specialist herbivore, the chrysomelid beetle, *Trirhabda virgata*, on its host plant, meadow goldenrod (*Solidago altissima*). Reductions in plant richness in ecosystems can strongly affect species interactions and insect communities, such as increasing susceptibility to invasion, fungal diseases, and also changes in the insect community's richness and structure (Knops et al. 1999). The diversity and composition of the plants have both direct and indirect effects on their herbivores; direct effects by determining available resources and indirect effects due to interactions between herbivores and their parasites and predators. Indirect effects of neighbor plant species composition are exemplified by the ecological concepts of "associational resistance" and "associational susceptibility." "Associational resistance" means that herbivory is reduced on a host plant associated with a taxonomically diverse set of plant neighbors (White and Whitham 2000, Brown and Ewel 2000). "Associational susceptibility" means that herbivory is greater on a host plant associated with a taxonomically diverse set of plant neighbors (White

and Whitham 2000, Brown and Ewel 1987). The present study will focus on whether the amount of folivory inflicted on tall thistle rosettes responds to differences in plant species richness or not.

It is important to examine the effect of habitat complexity at different spatial scales on the amount of herbivory host plants suffer. According to Hamback and Beckerman (2003), herbivores responded differently to different spatial scale of species richness. Herbivores might change their foraging behavior, or habitat preference, which are short-term responses. They could also respond to differences in species richness by changes in reproduction and mortality, which are long term responses. Manipulating the experimental treatments at multiple scales, such as litter manipulation at 30cm and 60cm radius surrounding herbivores' host plants, might affect folivore damage differently or might also affect plant tissue quality differently.

In the present research, I examined folivore damage to tall thistle (*Cirsium altissimum*) rosettes in relation to experimental manipulations in ecosystem productivity and habitat complexity. My research provides a novel perspective on the study of variation in herbivore damage to host plants in several ways. Most studies have manipulated ecosystem productivity at a small spatial scale but here it has been manipulated on an unusually large spatial scale (40 m X 40 m). The interaction effects of habitat complexity and ecosystem productivity on folivore damage were examined. Litter effects were addressed at post-seedling life stages, which is different from previous studies that have been performed primarily on seedling stage.

METHODOLOGIES

Study Species

The experimental plant, *Cirsium altissimum* is in the family Asteraceae and is commonly called "tall thistle." It is a monocarpic species and can be a perennial, biennial or annual (Flora of the Great Plains 1986). It can grow in moist or dry habitats. Tall thistle can be found in both disturbed and undisturbed sites; it is found in wooded habitats more often than other thistles. It is occasionally common on roadsides, in pastures, and on moderately disturbed, non-cultivated land. Tall thistle plants that live for multiple growing seasons remain in the juvenile phase until their final year when they flower, set seed and die. Plants typically develop flower heads in late July, and they set seed in August and September. The life-form at the flowering stage is known as "bolting" and the life-form at the juvenile phase is the "rosette." The tall thistle was chosen as the focal plant because it has a similar life-history to several legally-designated noxious weeds in the midwestern U.S., bull thistle (*Cirsium vulgare*) and musk thistle (*Carduus nutans*) (Guretzky and Louda 1997).

Many insects feed on tall thistle as is evident from the field, including *Vanessa cardui* (Painted lady butterfly), *Systema hudsonius* (Flea beetle) and grasshoppers, bumble bees, honey bees, butterflies and skippers. Among this diverse set of herbivores, *Vanessa cardui*, *Systema hudsonius* and grasshoppers are the primary folivores (Guretzky and Louda 1997).

Study Sites

In 2007, two sites were chosen for the experiments; the WSU Biology Field Station near Viola KS and Pawnee Prairie Park in Wichita KS. The Biology Field Station (37.49°N, 97.64°W)

is located approximately 35 miles southwest of the WSU campus. It includes 133.54 hectares of native and restored prairie and riparian woodland along the Ninnescah River. At the field station, experimental plots at lower elevations near an unnamed creek were on Elandco silt loam soils, for which water availability is high. This soil type is slightly acidic to moderately alkaline (Soil Survey of Sedgwick County, Kansas 1979). These lower elevation plots are in restored prairie. The soil type underlying experimental plots at higher elevations near 87th Street is Renfrow silty clay loam, for which water availability is moderate. This soil type is slightly acidic to moderately alkaline (Soil Survey of Sedgwick County, Kansas 1979). These plots are in native prairie. Pawnee Prairie Park (37.49°N, 97.43°W) is located on the southwest edge of Wichita. It has an area of 252.72 hectares of native and restored prairies and riparian woodlands. Soil type of the sites at Pawnee Prairie is Elandco silt loam (Soil Survey of Sedgwick County, Kansas 1979). The plots at Pawnee Prairie were agricultural fields before the area became a park. Annual precipitation in Wichita for 2007 was 96.44 cm and 136.09 cm in 2008 (<http://www.weather.gov/climate/xmacis.php?wfo=ict>, April 10, 2009).

In 2008, research was conducted only at the WSU Biology Field Station.

Experimental Design

Effects of ecosystem productivity and habitat complexity on tall thistle rosettes were tested experimentally using a split plot design. The ecosystem productivity manipulation (nitrogen addition) was applied at a large spatial scale and, therefore, was the between-plot factor. The habitat complexity manipulation (litter or neighboring plant species richness) was applied to individual rosettes and, therefore, was the within plot factor.

At each site, four 40 m X 40 m plots were established in May 2007, two plots received nitrogen addition to increase ecosystem productivity and two plots served as controls. Each

nitrogen addition plot was paired with a control plot and there was a distance of 25 m between control and nitrogen addition plots in each pair. Hereafter, I refer to each pair of a 40 m X 40 m nitrogen addition plot and its companion 40 m X 40 m control plot as a öblockö. Within each 40 m X 40 m plot, five transects were made. Along each transect, at 5 m intervals, one focal *Cirsium altissimum* rosette plant was tagged (Fig 1). In total, 35 plants were tagged in each plot. Among the 35 plants per plot, 21 were selected for the litter manipulation treatment and 14 plants were selected for the species richness treatment. There were three treatment levels for litter manipulation and two treatment levels for the species richness treatment, with seven replications for each treatment level in each plot. In 2007, both litter and species richness treatments were imposed within a 30 cm radius of each focal (tagged) plant. The rosettes that I use in 2008 were not the same rosettes used in 2007.

Nitrogen Treatment 2007

In each 40 m X 40 m plot, a total of 26.08g/m² of nitrogen in the form of urea were added twice over the entire year, on May 15-22 and August 24-31. Studies showed significant effect of nitrogen adding 12g/m² of urea per year (Gough et al. 2000).

Nitrogen Treatment 2008

Only six 40 m X 40 m plots were used in 2008. The plots that were used in 2007 at Pawnee Prairie were fully covered with poison ivy and could not be used in 2008, so one new pair of plots was established at the Field Station. Three plots received nitrogen addition and three plots were controls in which ecosystem productivity was not manipulated. In 2008, 2 plots were near the river, and 4 plots were near the roadside. The two plots near the river and two plots near

the roadside were those that had been used in the year 2007. In each nitrogen addition plot, total 26.08 g/m² of nitrogen were added twice over the entire year, in 2008, they were added on May 3rd-10th, June 18th (in the new plot at field station) and September 7th (Second round in all the plots at field station).

Litter Treatment 2007

I define "litter" as dead plant materials that were lying horizontally. For the litter treatment, there were three levels viz., litter removal, litter addition and control. Levels of the litter treatment were randomly assigned to 21 focal plants in 3 neighboring transects in each 40 m X 40 m plot. Seven plants received each level of the litter treatment in each plot. Litter addition and litter removal was performed within a 30 cm radius around focal plants. A 30 cm radius was used because clipping living neighboring plants with 30 cm significantly increased in number of leaves and root crown diameter of tall thistle rosettes in earlier research at the Field Station (O'Brien and Russell unpublished data). Litter removed from within 30 cm of each focal plant was weighed in the lab. This collected litter from all plants per plot was then mixed and divided into seven equal parts, which were put around the seven focal rosette plants receiving litter addition. Therefore, the amount of litter added to "litter addition" tall thistle rosettes was equal to the average amount of litter in a circle of 30 cm radius in each plot. The litter addition treatment approximated a doubling of the amount of litter within 30 cm of the focal tall thistle rosette. Litter manipulations were done three times: in May, August, and October.

Litter Treatment 2008

In 2008, the litter manipulation treatment was expanded to 5 levels that were randomly assigned to all 35 plants in each 40 m X 40 m plot with 7 plants receiving each treatment level. The five treatment levels were: control, litter removal within 30 cm surrounding the focal plant, litter addition within 30 cm, litter removal within 60 cm and litter addition within 60 cm. The procedure for mixing litter from litter removal focal plants and applying that litter to litter addition focal plants was the same as in 2007. Litter from 30 cm removal and 60 cm removal treatment levels within a plot was not mixed together. Litter manipulations were done three times: in July, September, and October.

Species Richness Reduction Treatment

The species richness reduction treatment was conducted only in 2007. For the species richness reduction treatment, there were two levels viz., ambient neighbor plant species richness (control) and reduced neighbor plant species richness. Within each 40 m X 40 m plot, 14 focal tall thistle rosettes were used in the species richness treatment with 7 plants receiving each treatment level. I paired species richness reduction rosettes with control rosettes. To reduce plant species richness within 30 cm of focal rosettes, all individuals of the rarest two species within a 30 cm radius of the focal plant were removed. For the controls, the same numbers of plant stems were removed as in the reduced species richness treatment level but here individuals of the most abundant species were removed. The mean number of plant species within 30 cm of rosettes in the ambient species richness treatment level was 3.21 ± 0.14 and the mean number of plant species for the reduced species richness was 1.46 ± 0.12 . Equal numbers of plants / stems were removed from both levels of the species richness reduction treatment to avoid confounding

reduction in neighbor species richness with reduction in neighbor plant / stem density. Species richness manipulations were done three times in 2007: in May, August, and October.

Herbivore damage and Rosette Performance Measurements

Five traits were measured for each focal tall thistle rosette - (1) root crown diameter, (2) rosette diameter, the widest diameter in the natural state, (3) total number of green leaves, (4) total number of leaves damaged, and (5) number of green leaves damaged over 50% of their surface area. The root crown of the rosette is the point from where the leaves arise. I noted whether the focal plant was dead or alive at each census. In 2007, these data were collected May-26 to June-6, July-31 to August-5 and October-12 to 15. In 2008, data were collected in July-15 to 22, September-14 to 20 and October-16 to 19.

Insect Sampling 2007

To evaluate whether differences in damage to tall thistle rosettes between experimental treatments were due to effects of the treatments on insect herbivore densities, I sampled insects within experimental plots using four different techniques 1) sweep-netting, 2) beating bolting tall thistles, 3) pitfall traps, and 4) sticky pads (12.9 X 7.6 cm² of Olson Products, Ohio, USA). All of the four sampling techniques provide information on the effects of ecosystem productivity on the insect community, but only the pitfall traps and the sticky pads sample insects at a small enough spatial scale to evaluate effects of the litter and species richness manipulations on the insect community. For sweep-netting, I sampled along three 40 m transects in each nitrogen addition or control plot. The transects were evenly spaced across the plot. I beat four bolting tall thistles per 40 m X 40 m plot. Insects that fell from the plants were collected on a drop sheet.

For choosing bolting plants for beating in each plot, the plot was divided into four quadrants and from the center of the plot I chose the nearest plant in each quadrant. Pitfall traps were set up within a 30 cm radius of 10 focal tall thistle rosettes per plot; 6 for the litter treatment and 4 for the species richness treatment. Sticky pads were set up within a 30 cm radius of 10 focal tall thistle rosettes per plot, as for the pitfall traps. Focal plants for pitfall traps and sticky pads were selected randomly. Insect trapping were done in July-21 to August-31 between 9am and 2pm.

After sweep netting and beating, the insects that I collected were put inside a jar containing filter papers moistened with ethyl acetate. Once the insects died, they were stored in the freezer. To set up the pitfall traps, a cup was half filled with water and a few drops of liquid soap were added to reduce the surface tension. The pitfall traps and sticky pads were left in place for 3 days. All the insects collected by the different methods, except for insects collected on sticky pads, were weighed fresh in the lab and categorized into different orders. For sticky pads, total density of insects was counted because attempting to remove the insects from the sticky pads would have broken the insect body parts.

Insect Sampling 2008

During 2008, the same insect sampling techniques were used as in 2007 (1) 3 sweep-netting transects per 40 m X 40 m plot, (2) beating four bolting plants per plot, (3) 15 pitfall traps per plot were set up in different levels of the litter treatment; 3 per each litter treatment level, and (4) 15 sticky pads per plot were set up as in the pitfall traps. The pitfall traps and sticky pads were left in place for a week. For the preservation of the insects, they were stored in the freezer and later their biomass was weighed for insects collected using each technique except sticky

pads. Insect trapping were done in August-23 to September-7. In 2008, insect trapping was done in late August, after the beginning of the fall semester, so sticky pads and pitfall traps were collected only after a week not, as in 2007, after 3 days.

Measurement of Ecosystem Productivity 2007 and 2008

To quantify ecosystem productivity in 2007 and 2008, I measured living plant biomass in the 40 m X 40 m nitrogen addition and control plots. For harvesting living plant biomass, 6 quadrants were placed per plot (3 transects / plot and 2 sampling points / transect). In each plot, these quadrants were located at 15 m intervals along the 3 parallel transects. Harvested plant material was dried at 80°C for 24 hrs and weighed.

Abiotic Resources Measurement

I measured light penetration and soil moisture availability to the experimental tall thistle rosettes. Photosynthetically active radiation (PAR) was measured at the highest point of each focal tall thistle rosette and above the surrounding vegetation's canopy using an AccuPAR model LP-80 ceptometer (Decagon Devices, Inc.). Photosynthetically active radiation was measured within a circle of 30 cm radius around the focal rosette to correspond in scale to the litter and species richness manipulations in 2007. Light was measured between 10:00 AM and 2:00 PM on September 7-21, 2007. Light measurement was taken three times in 2008: July-22 to 23 between 8:30 and 11am, September-20 to 28 between 10am and 2pm and October- 12 to 19 between 10am and 2pm. Light penetration was calculated by dividing PAR at the rosette surface by PAR above the surrounding vegetation canopy.

I measured volumetric soil moisture content at points 15 cm north and south of each focal plant, using a TDR 100/200 Soil Moisture Meter (Spectrum Technologies, Inc). Soil moisture was measured at 12 cm depth. As for the light measurement, soil moisture content was also measured only once in 2007: September (7-19) 2007, but three times in 2008: July (17-22), September (20-28), and October (12-16).

Statistical Analysis

All statistical analyses were performed using SAS version 9.1.

Efficacy of Ecosystem Productivity Treatment

Paired one-tailed t-tests were used to compare living vegetation biomass between nitrogen addition and nitrogen control plots. Within each block, nitrogen addition and control plots were paired.

Treatment Effects on Light and Soil Moisture Availability to Tall Thistle Rosettes

To examine effects of ecosystem productivity (nitrogen), habitat complexity (litter and species richness) and the interaction of ecosystem productivity and habitat complexity on (1) light penetration and (2) soil moisture availability, split-plot ANOVA (Analysis of Variance) was used in 2007 and repeated measures split-plot ANOVA was used in 2008. In 2007, the physical resources, light penetration and soil moisture availability, were measured once and in 2008 they were measured three times. Light penetration to rosettes and soil moisture by volume (%) were arcsine (square root) transformed, as were all dependent variables that were proportions in our statistical analyses.

In all split-plot ANOVAs, to explore interaction effects of ecosystem productivity and habitat complexity I used one-way ANOVA to determine in which level of the ecosystem productivity treatment there was a significant effect of habitat complexity. In all repeated measures split-plot ANOVAs, when there were significant interaction effects of time and either ecosystem productivity or habitat complexity I used one-way ANOVA to examine the effect of ecosystem productivity or habitat complexity at each time interval. When the time * nitrogen * litter interaction effect was significant, I used one-way ANOVA to determine in which season and level of the ecosystem productivity treatment there were significant effects of litter.

Effects on Herbivore Damage to Tall Thistle Rosettes

Repeated measures split-plot ANOVA was done to examine the effects of ecosystem productivity (nitrogen), habitat complexity (litter and species richness) and the interaction of ecosystem productivity and habitat complexity on herbivore damage. For each tall thistle rosette, I quantified folivore damage in two ways, 1) as the proportion of leaves that had folivore damage and 2) as the proportion of leaves that had folivore damage over >50% of their surface area.

Effects on Tall Thistle Rosette Growth

Split-plot ANOVA was used to evaluate treatment effects on tall thistle rosette growth. I analyzed proportional change in number of leaves per plant, proportional change in rosette diameter, and proportional change in root crown diameter over the growing season. For example, to calculate a rosette's proportional change in root crown diameter I divided the difference

between root crown diameter in October minus root crown diameter in May by root crown diameter in May.

Effects of Ecosystem Productivity and Habitat Complexity on Survival of Tall Thistle

Rosettes

Contingency table analyses (Chi-square tests) were used to evaluate the effect of ecosystem productivity and habitat complexity on survival rate of tall thistle rosettes. If litter was found to significantly affect survival then I used 2 X 2 contingency tables to identify pairs of levels of the litter treatment that differed in their effects on survival.

Analysis of Insect Communities

Sweep netting and beating were performed at a large spatial scale and, therefore, are useful only to evaluate differences between ambient nitrogen and nitrogen addition plots, not to evaluate effects of local habitat complexity manipulations. Paired two-tailed t-tests were used to analyze the effect of ecosystem productivity on the biomass of each arthropod order collected in sweep netting and collected by beating. Pitfall traps and sticky pads were established at the spatial scale of individual tall thistle rosettes to evaluate the effect of the habitat complexity manipulations on the insect community. Split-plot ANOVAs were done to determine the effects of habitat complexity under different levels of ecosystem productivity on total biomass of each insect order in pitfall traps and, analyzed separately, total abundance of each insect order on sticky pads.

RESULTS

Effects of Nitrogen Addition on Standing Crop Biomass

Nitrogen significantly affected living plant standing crop biomass in 2007 ($t_3 = 3.09$, $p < 0.05$). Standing crop plant biomass was increased by 17.3% in nitrogen addition plots compared to ambient nitrogen plots in 2007 (Fig 2). No significant difference was observed in standing crop plant biomass in 2008 ($t_2 = 1.53$, $0.25 > p > 0.10$). Standing crop plant biomass was only 6.7% greater in nitrogen addition plots than in ambient nitrogen plots (Fig 3).

Effects of Ecosystem Productivity and Habitat Complexity in Light Penetration

In the 2007, none of the experimental manipulations (nitrogen, litter or species richness) significantly affected light penetration to tall thistle rosettes. There was a significant effect of time on light penetration in 2008 ($F_{2,388} = 109.10$, $p < 0.0001$) (Fig 4, 5). More light penetration was observed in September than in July and October. There was marginal significance of the interaction of time, nitrogen and litter in 2008 ($F_{8,388} = 1.69$, $p = 0.10$). There was a marginally significant effect of litter in control (ambient nitrogen) plots in September in 2008 ($F_{4,100} = 2.16$, $p = 0.07$) (Fig 4).

Effects of Ecosystem Productivity and Habitat Complexity in Soil Moisture Availability

There was no significant effect of nitrogen addition, neighbor species richness or litter on soil moisture availability in 2007. Significant effects of time ($F_{2,394} = 301.59$, $p < 0.0001$) and the interaction of nitrogen and time ($F_{2,394} = 12.89$, $p < 0.0001$) were observed for soil moisture availability in 2008 with greater availability in October in ambient nitrogen plots (Fig 6, 7).

There was a significant effect of litter on soil moisture availability in nitrogen addition plots in October in 2008 ($F_{4,99} = 3.68$, $p = 0.0078$) (Fig 7). Litter removal from 60cm radius had the lowest soil moisture by volume.

Effects of Ecosystem Productivity and Habitat Complexity on Folivore Damage

There was a marginally significant effect of time on the proportion of leaves per rosette damaged over >50% of their surface area in 2007 in both the species richness ($F_{2,110} = 18.61$, $p < 0.0001$) (Fig 8, 9) and the litter manipulation experiments with greater damage in August ($F_{2,128} = 32.02$, $p < 0.0001$) (Fig 10, 11). In 2007, there was no significant effect of nitrogen, litter or the interaction of time, nitrogen and litter on the proportion damaged >50% of the leaf area. In 2008, there was significant effect of time on the proportion damaged >50% of the leaf area with greater damage in September ($F_{2,244} = 32.85$, $p < 0.0001$) (Fig 12, 13). In 2008, there was a marginally significant effect of time**nitrogen***litter* on proportion on leaves damaged ($F_{8,244} = 1.72$, $p = 0.09$). There was marginal significance for the effect of litter on proportion of leaves damaged in October ($F_{4,129} = 2.02$, $p = 0.09$) (Fig 14, 15).

Effects of Ecosystem Productivity and Habitat Complexity on Tall Thistle Rosette Growth

In 2007, species richness did not significantly affect in proportional change in root crown diameter. In 2007, there was a marginally significant effect of litter on proportional change in root crown diameter ($F_{2,67} = 2.77$, $p = 0.06$) (Fig 16) and no interaction effect of *nitrogen***litter*. In both nitrogen addition and control plots, rosettes with added litter had the lowest proportional change in root crown diameter. In 2008, nitrogen, litter and their interaction did not affect significantly the proportional change in root crown diameter. There was a marginally significant

effect of nitrogen on proportional change in total number of leaves ($F_{1,128} = 17.01$, $p=0.054$) (Fig 17). The change in total number of leaves was greater in nitrogen addition plots for all levels of the litter treatment.

Effects of ecosystem productivity and habitat complexity on tall thistle rosette survival

In 2007, there was a significant effect of litter on rosette survival ($\chi^2_2=6.64$, $p=0.03$) (Fig 18). There was a significant difference in rosette survival rates between added litter and ambient litter combinations ($\chi^2_1=6.02$, $p=0.01$) and a marginally significant difference between reduced litter and ambient litter ($\chi^2_1=3.55$, $p=0.059$). In 2008, there was significant effect of nitrogen upon survival ($\chi^2_1=6.61$, $p=0.01$) (Fig 19). There was no significant effect of litter and interaction of nitrogen*litter on tall thistle rosette survival in 2008.

Effects of Ecosystem Productivity and Habitat Complexity in Insect Community

Pitfall traps- In 2007, there was a significant effect of litter on biomass of the order Orthoptera ($F_{2,39} = 3.34$, $p=0.04$) (Fig 20, 21). Adding litter produced the greatest biomass of Orthoptera in both ambient nitrogen and nitrogen addition plots. There was a significant interaction effect of nitrogen and litter on the biomass of Hymenoptera ($F_{2,39} = 3.88$, $p=0.02$); litter affected Hymenoptera biomass in nitrogen addition plots. In 2008, there was significant nitrogen*litter interaction effect on the order Hymenoptera ($F_{4,78} = 3.05$, $p=0.02$); litter affected Hymenoptera biomass in nitrogen control plots (Fig 22, 23). There was a marginally significant nitrogen *litter interaction effect on the Coleoptera ($F_{4,78} = 2.09$, $p=0.09$); litter had a stronger effect in nitrogen addition plots. In ambient nitrogen plots, litter addition at 60cm produced the greatest biomass of

Coleoptera, but in nitrogen addition plots, litter addition at 30cm had the greatest biomass of Coleoptera.

Sticky pads-There was a significant effect of neighbor plant species richness on Orthoptera ($F_{1,25} = 4.59$, $p=0.04$); the number of individuals of Orthoptera were higher with reduced neighbor plant species richness in both ambient nitrogen and nitrogen control plots (Fig 24, 25). In 2007, there was a significant effect of litter on the Heteroptera ($F_{2,39} = 3.54$, $p=0.03$); reduced litter had greater numbers of Heteroptera than in other litter treatments (Fig 26, 27). In 2008, there were no effects of litter, nitrogen or the interaction of nitrogen and litter that approached statistical significance for any arthropod order.

Beating and sweep netting- None of the arthropod orders showed differences between nitrogen addition and control plots that approached statistical significance in either 2007 or 2008.

DISCUSSION

Effects of Ecosystem Productivity on Herbivore Damage and Plant Performance

Oksanen et al. (1981) predicted that herbivore damage would be highest in moderate productivity habitats. Lower productivity sites will not have enough energy to support large herbivore populations. Higher productivity sites will support large carnivore populations that will suppress herbivore populations, so less herbivory will occur. Contrary to Oksanen and colleagues' predictions that ecosystem productivity will influence herbivore damage, my results did not show any significant effect of ecosystem productivity on the proportion of leaves per tall thistle rosette that were damaged over >50% of their surface area in 2007 or in 2008.

Effects of ecosystem productivity on the amount of damage that herbivores inflict on host plants may result from changes in the herbivore community or changes in host plant tissue quality. In old-field grasslands at the Cedar Creek Natural History Area, Minnesota, USA, Ritchie (2000) showed that insect abundance varies with productivity in addition to varying with abiotic conditions like temperature and precipitation. In my study, however, there were few significant effects of ecosystem productivity (nitrogen addition vs. control) on the biomass and abundance of individual insect orders. Differences in availability of abiotic resources also might influence plant tissue quality and herbivore damage. According to Koppel et al. (1996), plants were less appealing to hares, rabbits, and geese in high productivity sites in Dutch salt marshes due to the plants' tougher cell walls. According to Joern and Mole (2005), grasshopper herbivory had highest impact upon carbohydrate concentration in a year with normal precipitation than dry year. More moisture might have an effect upon secondary compounds in the plant that prevent herbivory. In my study, only weak effects of ecosystem productivity were seen upon light

penetration and soil moisture availability in 2007 and 2008. Although I did not directly evaluate plant tissue quality, limited changes in abiotic resource availabilities to tall thistle rosettes may have caused only small changes in plant quality resulting in little effect on herbivore feeding and damage.

Louda and Rodman (1996) and Guretzky and Louda (1997) stated that ecosystem productivity affects plant performance. Differences in ecosystem productivity may alter competitive relationships among plants. One reason why ecosystem productivity may not have affected plant performance is because there were only weak effects on the insect community and no effect on the amount of herbivore damage to rosettes. Being an early to mid successional plant species (Guretzky and Louda 1997), tall thistle would not have strong competitive ability to utilize the available abiotic resources. Because there was little effect of the ecosystem productivity treatment on abiotic resources, even a poor competitor, like tall thistle, would be unlikely to be affected.

Constraints of my experimental design could have contributed to the absent or weak effects of ecosystem productivity on herbivore damage and performance of tall thistle rosettes. Standing crop biomass only increased by 17.3% with the addition of nitrogen in 2007 and by 6.7% in 2008. There was a significant effect on insect community composition when Ritchie (2000) altered standing crop plant biomass by >150% and that there was a significant effect on plant tissue quality when Joern and Mole (2005) increased standing crop plant biomass 50-100%. Based upon other studies, the percentage change in standing crop plant biomass between low and high ecosystem productivity plots in my research was not very much and may have provided a relatively weak test of the effect of ecosystem productivity. Also, replication of the ecosystem

productivity treatment was low; four nitrogen addition plus four control plots in 2007 and three nitrogen addition plus three control plots in 2008. The nitrogen manipulation was on a large scale, causing the number of replicates to be low. Low replication could be one reason for not seeing a significant effect of ecosystem productivity on herbivore damage. The primary advantage of large scale manipulation of nitrogen is that it allows me to examine factors like changes in arthropod population sizes that operate on larger spatial scales.

Effects of Habitat Complexity –Litter

Habitat complexity is considered as an important factor for trophic organization of terrestrial arthropod communities. Natural enemy, meaning predator and parasitoids, abundance increased with habitat complexity in other studies (Langelloto and Denno 2004). According to Gratton and Denno (2003), planthopper (an insect herbivore) density in New Jersey salt marsh was greatest in nitrogen and litter added plots at the beginning of the growing season, but by the end of the growing season planthopper densities were much less in nitrogen and litter added plots than in control plots due to rapid colonization of predators, like spiders. According to Riechart and Bishop (1990), litter addition increased spider densities and spiders preyed upon herbivorous arthropods resulting in less damage to the plants. By contrast, I found no significant effect of litter on the spider biomass and density in my research. The absence of a significant effect of litter on carnivorous arthropods (principally spiders) and very rare occurrence of other predators, like mantids, may explain why the proportion of leaves damaged >50% did not differ significantly with litter manipulation in 2007 or 2008.

In grasslands that do not burn, plant litter can accumulate to large quantities and large amounts of litter may influence plant performance. In my research, there was no significant

effect of litter on proportional growth in root crown diameter in 2008 but marginal significance was observed in 2007. Facelli (1994) stated that mortality of *Ailanthus altissima* seedlings increased with increasing litter. Foster and Gross (1998) mentioned that litter addition reduced the seedling survival of *Andropogon gerardi* and thus reduced plant diversity due to very low light penetration. In my research, the greatest rosette survival in 2007 was with the ambient (control) litter in both ambient nitrogen and nitrogen addition plots. In 2008, litter also affected tall thistle rosette survival, but the effect was stronger in nitrogen addition plots. Curiously, the strongest effect of the litter manipulation in 2008 was to reduce the rosette survival rate where litter was removed within 30cm, but only in nitrogen addition plots.

In some cases, effects of litter on plant performance may result from changes in abiotic resource levels. Facelli and Pickett (1991) found negative effects of litter on light penetration in an old-field grassland. Weltzin et al. (2005) found greater light penetration and soil temperature with litter removal in a fen plant community. I found no effect of litter on light penetration to tall thistle rosettes in 2007 and in 2008 and only the 60cm litter removal treatment level resulted in a significant decrease in soil moisture availability. Added litter caused the lowest proportional change in root crown diameter in 2007 and 2008, except in 60cm litter addition in 2008. This could be due to higher light penetration and lower soil moisture availability. To my knowledge, most studies of effects of litter accumulation on plant performance examined litter effects upon seedlings (Facelli and Pickett 1991, Foster and Gross 1998). My research appears to be the first to quantify effects of litter accumulation upon post-seedling juvenile plants.

Effects of Habitat Complexity – Species Richness

The species richness and composition of neighbor plants surrounding a host plant often has been hypothesized to influence the amount of herbivore damage to the host plant (White and Whitham 2000). Variation in herbivore damage as function of the diversity and composition of surrounding vegetation underlies the fundamental ecological concepts of “associational susceptibility” and “associational resistance”. Nevertheless, according to Brown and Ewel (1987), the herbivory was the same amount per unit ground area (71.5 to 78.5 gm⁻²yr⁻¹) despite large variation in floristic diversity, composition, or amount of leaf tissue available in the plant community of tropical agroecosystems. In the species rich community, the herbivores fed upon one species heavily and less on the other species due to which there would be counterbalance between different species richness. My results also showed no significant effect of neighbor plant species richness on the proportion of leaves damaged over 50% of their surface area on tall thistle rosettes.

One mechanism through which neighbor plant richness may affect herbivore damage to host plants is by affecting the size of predator and parasitoid populations (Root 1973). In my study, there was no significant effect of the species richness manipulation on spider abundance. I did not specifically quantify the abundance or biomass of parasitoids. The reasons for the non-significant relationship between neighbor plant species richness, arthropod community composition and herbivore damage may have been methodological. Specifically, reducing neighbor plant species richness by two species may not have been a strong enough manipulation to generate a biological response. Koricheva et al. (2000) found a difference of 12 species between species rich and control plots lead to an affect on the insect community. Methodological constraints may have limited my ability to detect an effect of neighbor plant species richness on

herbivore damage to a tall thistle rosettes as removing two plant species from the community may not have been a strong enough manipulation.

Interaction Effects of Ecosystem Productivity and Habitat Complexity on Herbivore Damage and Plant Performance

To my knowledge, only one previous study (Gratton and Denno 2003) has examined whether or not the effects of habitat complexity depend upon ecosystem productivity. Gratton and Denno (2003) found a positive effect with greater abundance of planthoppers in the complex habitat with thatch under the fertilized plots in the early season which then decreased in the late season due to an increase in predators like spiders. According to Gratton and Denno (2003), the effect of thatch addition was greater in fertilized plots than in unfertilized plots in salt marshes in New Jersey. I observed only weak interaction effects of ecosystem productivity and habitat complexity upon insect communities, mainly on the biomass and abundance of Coleoptera, Heteroptera, Orthoptera and a significant interaction effect only on Hymenoptera in 2007. No significant interaction effect of habitat complexity and ecosystem productivity was observed on herbivore damage to tall thistle rosettes.

Effects of Ecosystem Productivity and Habitat Complexity on Insect Community

Only weak effects of ecosystem productivity and habitat complexity were observed upon the over-all composition of the insect community. In spite of the weak over-all effects, a few orders seemed to consistently be more responsive to the experimental manipulations than other orders. Specifically, these responsive orders were the Orthoptera, Hymenoptera, Heteroptera, and

Coleoptera. Interestingly, these orders were also especially responsive to ecosystem productivity manipulations (Ritchie 2000) and plant species diversity manipulations (Koricheva et al. 2000) in other studies. In the above mentioned orders of arthropods, there are species that feed at different trophic levels. For the further studies, it would be useful for understanding the mechanisms that drive variation in herbivore damage, if the insects were identified and categorized according to their trophic levels, rather than according to taxonomic order.

In contrast to occasionally strong effects of ecosystem productivity and habitat complexity in the literature, I found that these factors had a weak effect in determining folivore damage to tall thistle rosettes. The novel contributions that my research made include (1) large-scale manipulations of ecosystem productivity and (2) examining litter effects at post-seedling life-stages. My recommendations for future studies are that categorizing insects according to their trophic levels rather than according to taxonomic order, and chemical analyses of the nutrient availability in leaf tissues can provide further insight into causes of spatial and temporal variation in herbivore damage to plants.

Figures

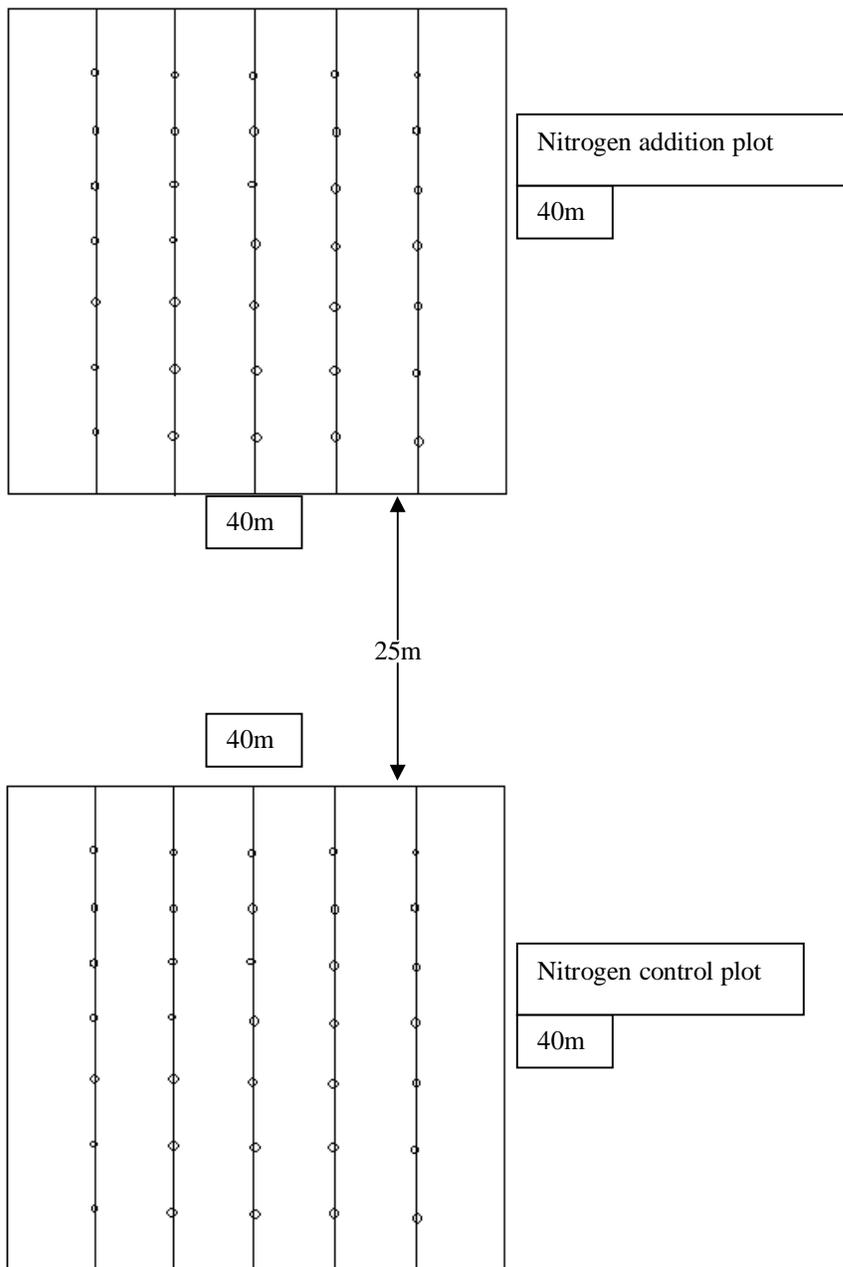


Fig 1. Representation of one block composed of a 40 m X 40 m Nitrogen addition plot paired with a 40 m X 40 m Nitrogen control plot. Circles within the 40 m X 40 m plots are locations of focal tall thistle rosettes.

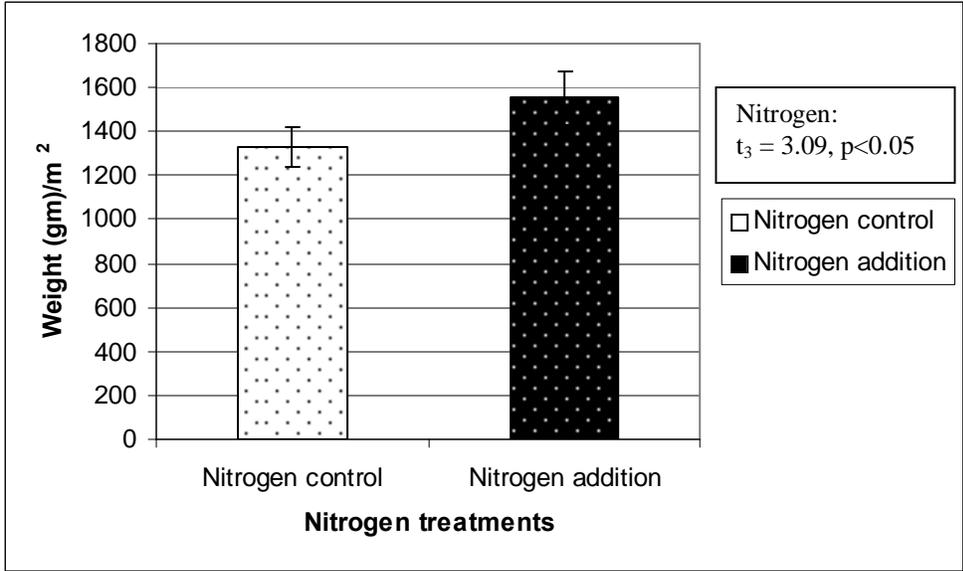


Fig 2. Standing crop plant biomass vs. nitrogen addition (2007). Means \pm standard errors are shown.

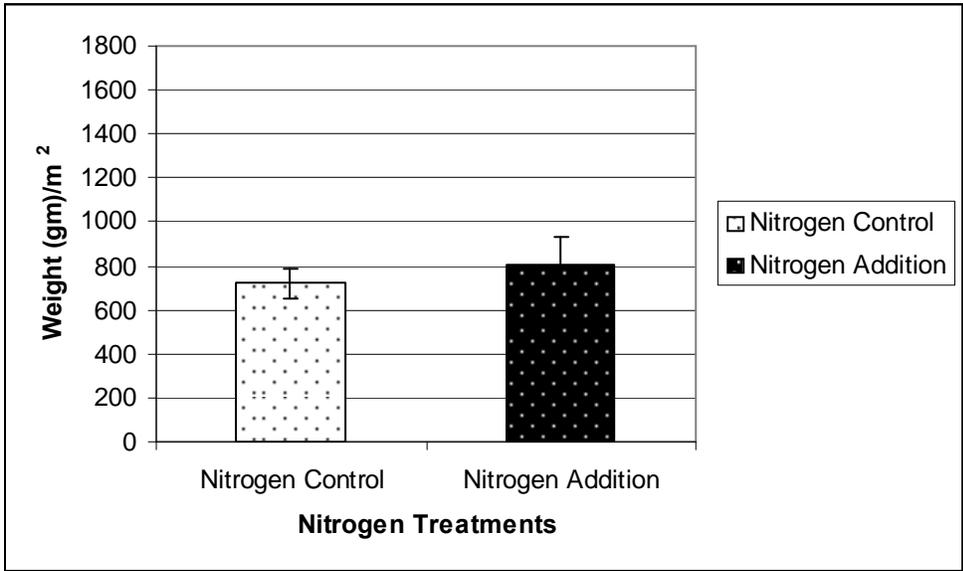


Fig 3. Standing crop plant biomass vs. nitrogen addition (2008). Means \pm standard errors are shown.

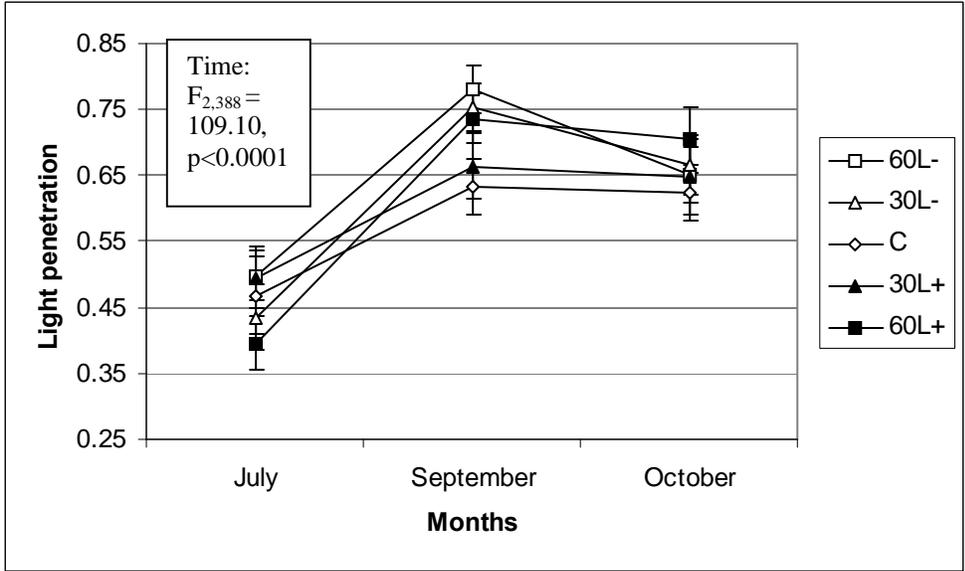


Fig4. Light penetration in nitrogen control plots (2008). Means \pm standard errors are shown.

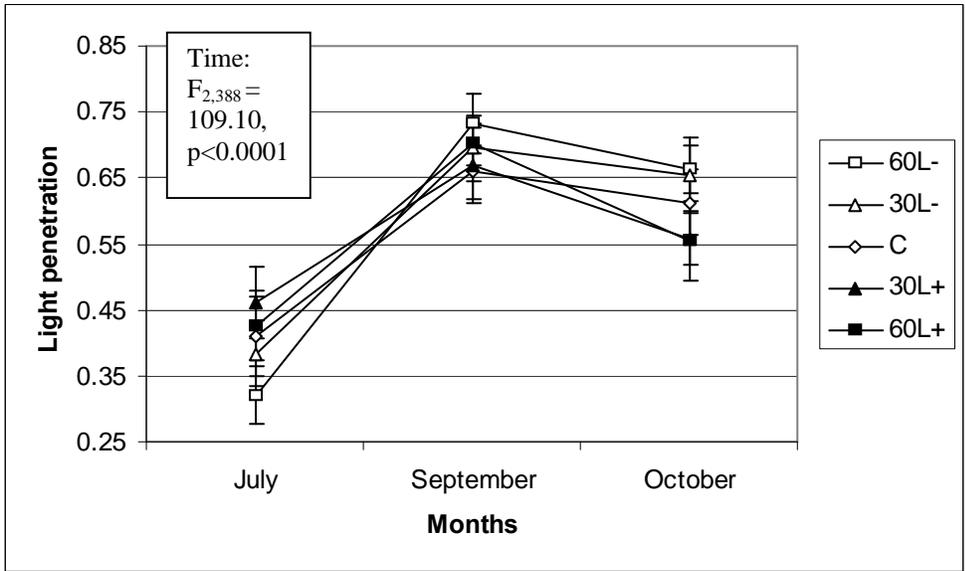


Fig5. Light penetration in nitrogen addition plots (2008). Means \pm standard errors are shown.

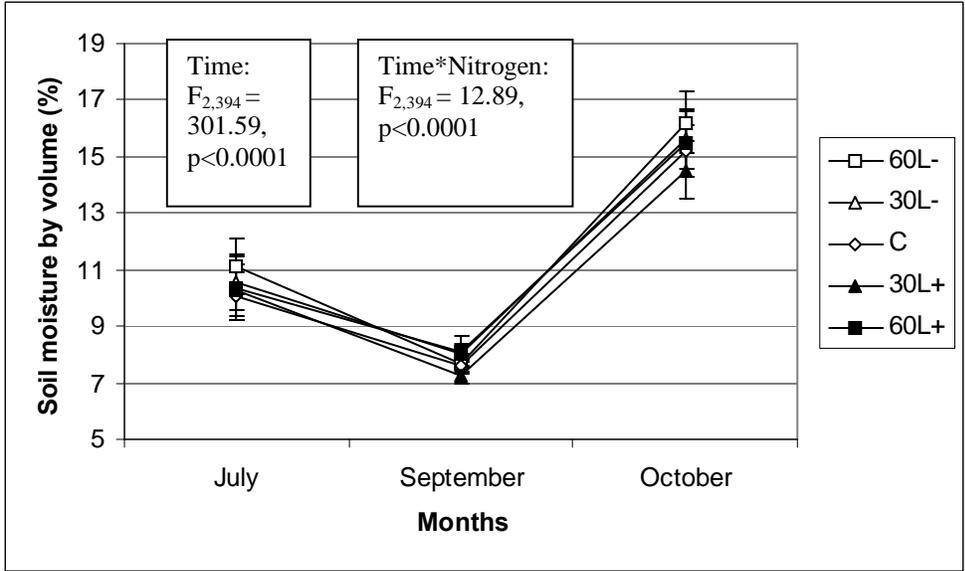


Fig6. Seasonal soil moisture variation in nitrogen control plots (2008). Means \pm standard errors are shown.

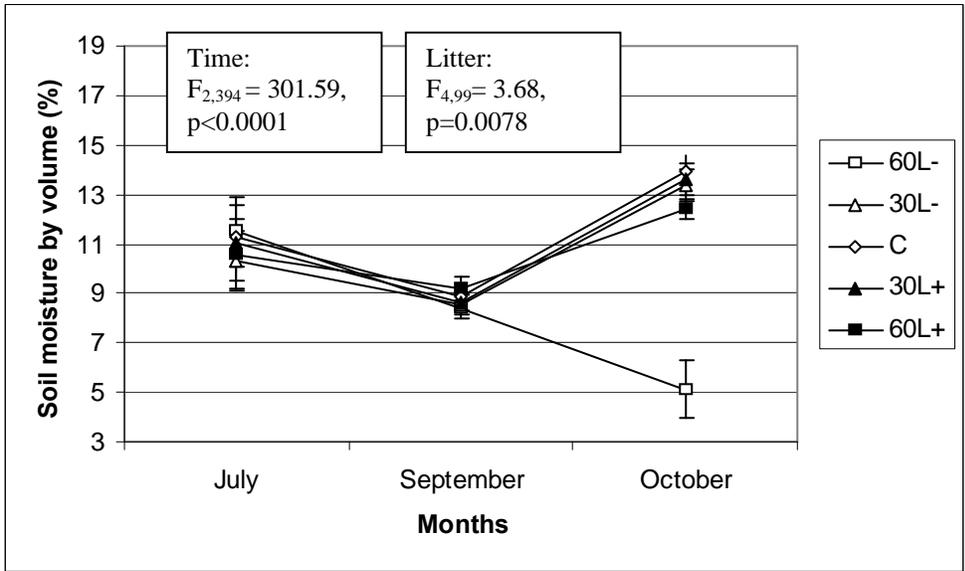


Fig7. Seasonal soil moisture variation in nitrogen addition plots (2008). Means \pm standard errors are shown.

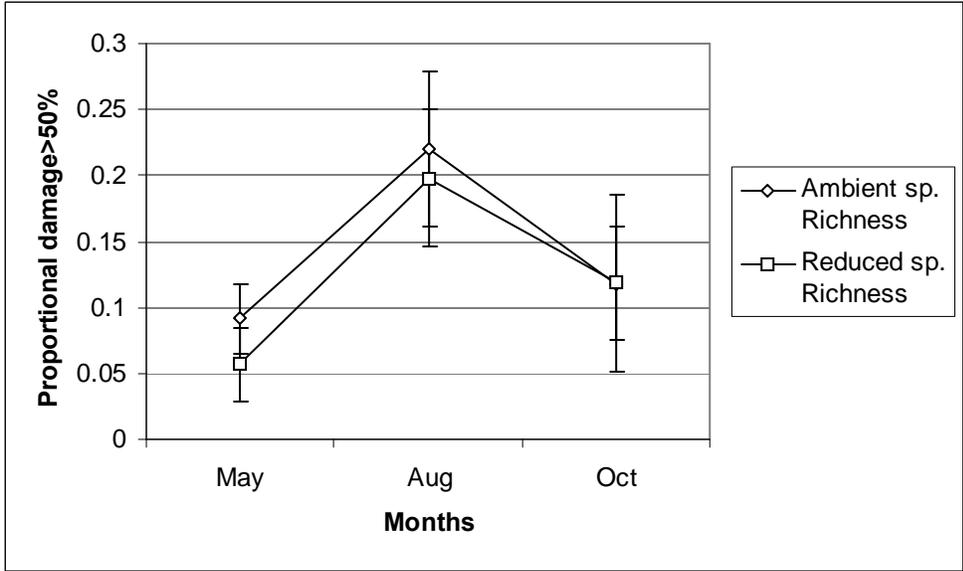


Fig 8. Seasonal variation in proportion of leaves damaged >50% of their area in relation to neighbor species richness in nitrogen control plots (2007). Means \pm standard errors are shown.

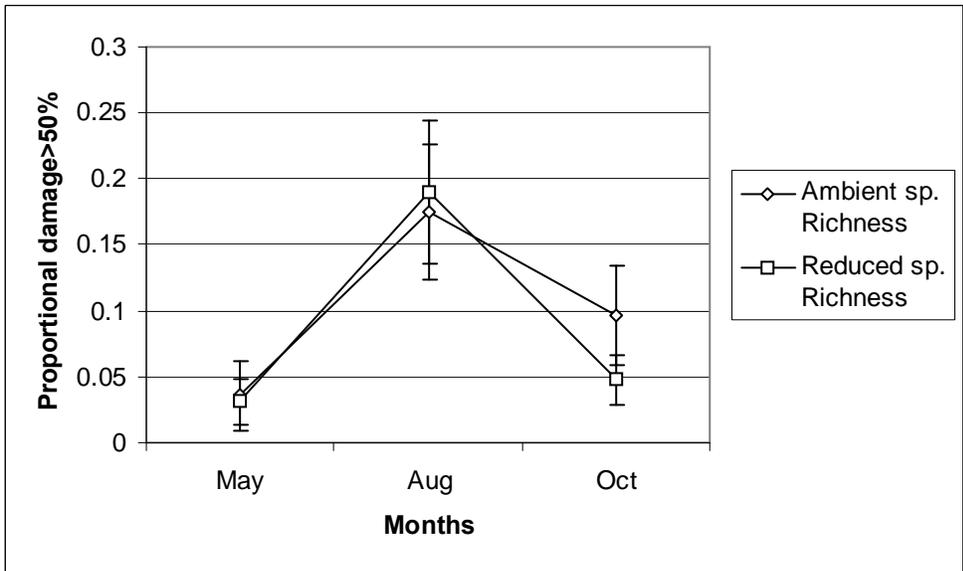


Fig 9. Seasonal variation in proportion of leaves damaged >50% of their area in relation to neighbor species richness in nitrogen addition plots (2007). Means \pm standard errors are shown.

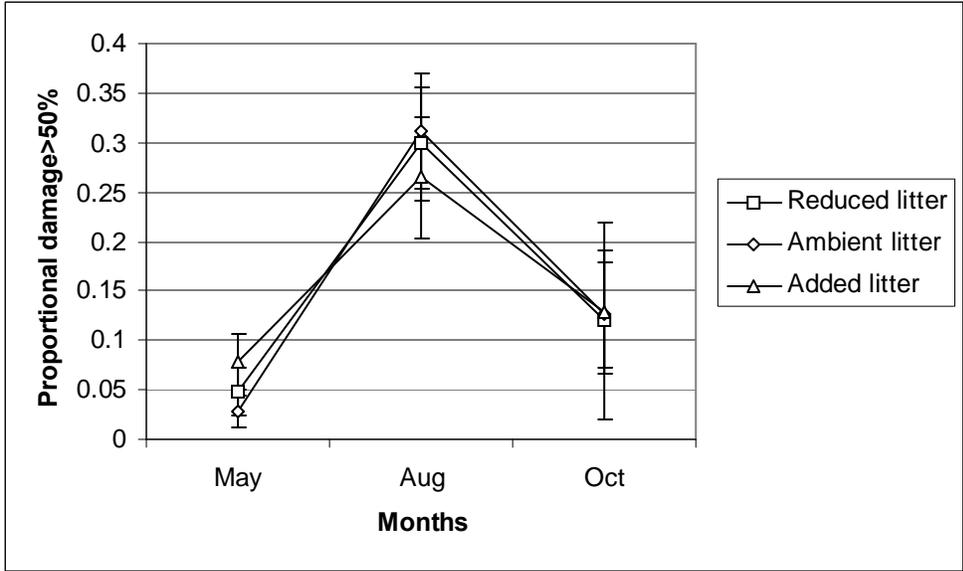


Fig 10. Seasonal variation in proportion of leaves damaged >50% of their area in relation to litter in nitrogen control plots (2007). Means \pm standard errors are shown.

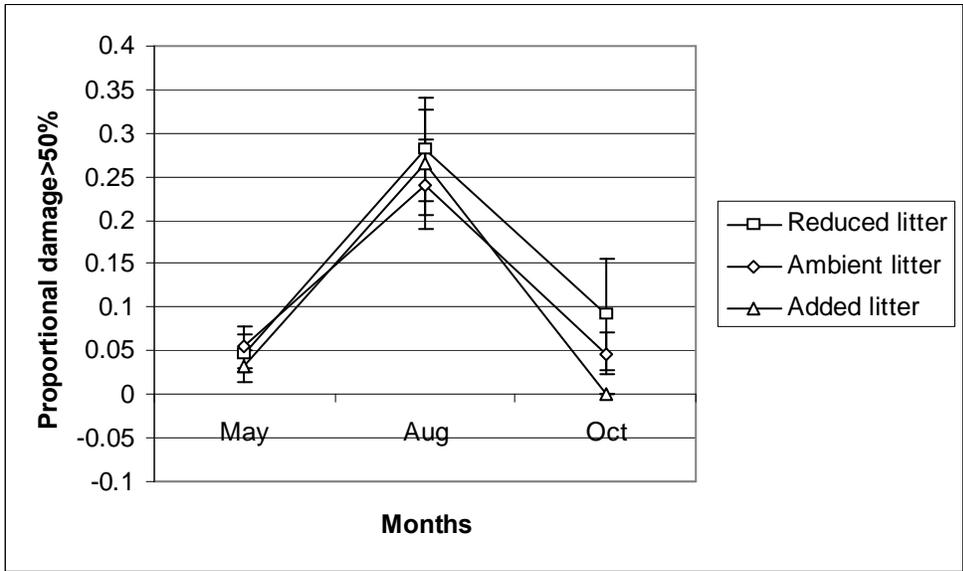


Fig 11. Seasonal variation in proportion of leaves damaged >50% of their area in relation to litter in nitrogen addition plots (2007). Means \pm standard errors are shown.

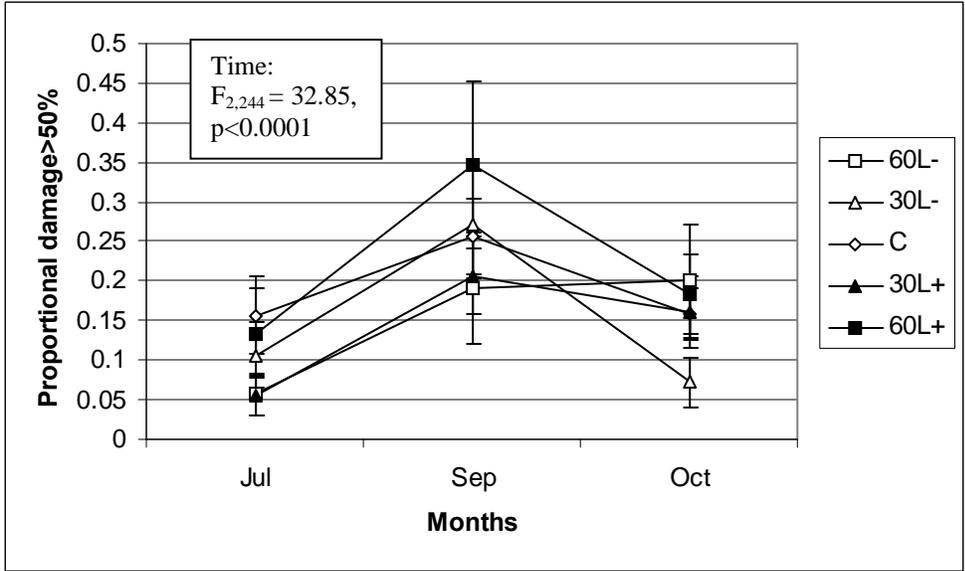


Fig 12. Seasonal variation in proportion of leaves damaged >50% of their area in relation to litter in nitrogen control plots (2008). Means \pm standard errors are shown.

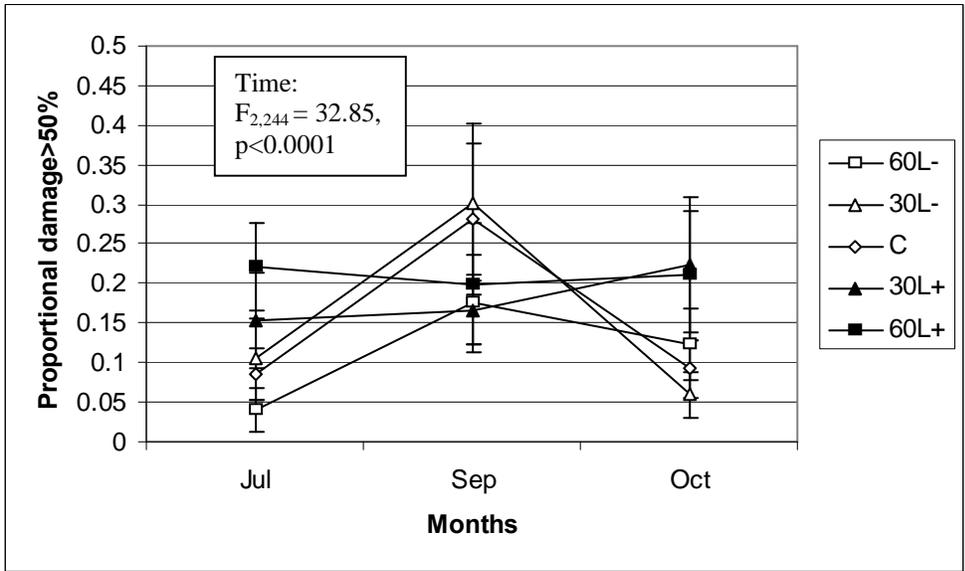


Fig 13. Seasonal variation in proportion of leaves damaged >50% of their area in relation to litter in nitrogen addition plots (2008). Means \pm standard errors are shown.

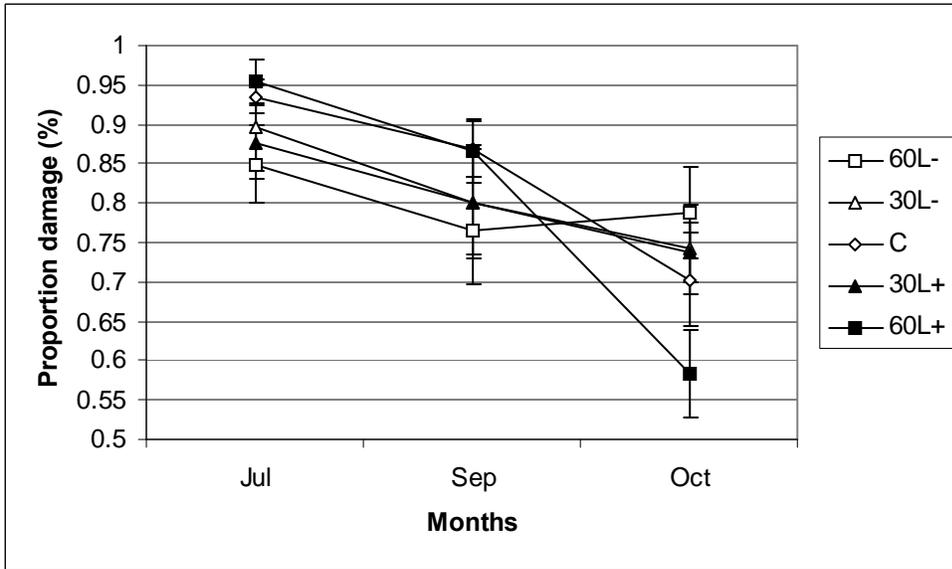


Fig 14. Seasonal variation in proportion of leaves damaged in relation to litter in nitrogen control plots (2008). Means \pm standard errors are shown.

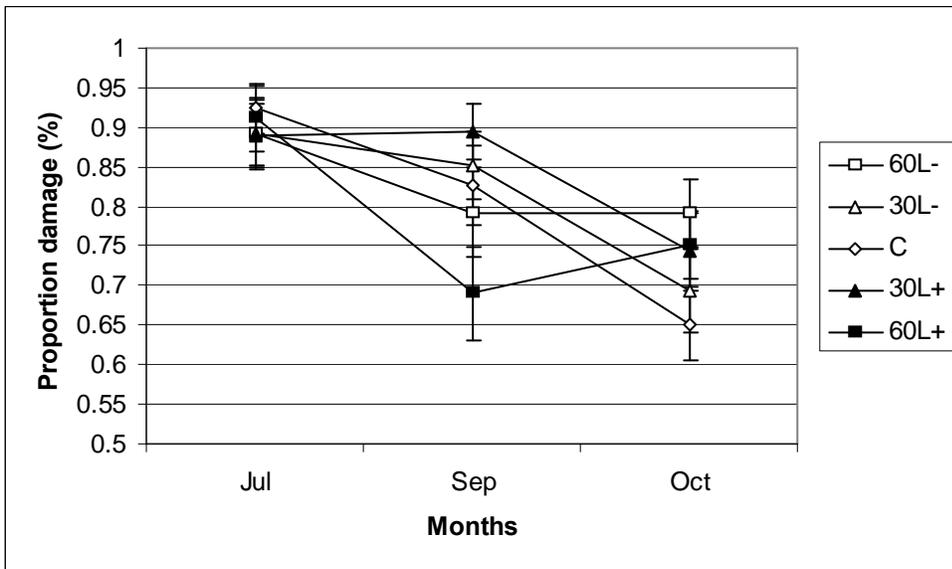


Fig 15. Seasonal variation in proportion of leaves damaged in relation to litter in nitrogen addition plots (2008). Means \pm standard errors are shown.

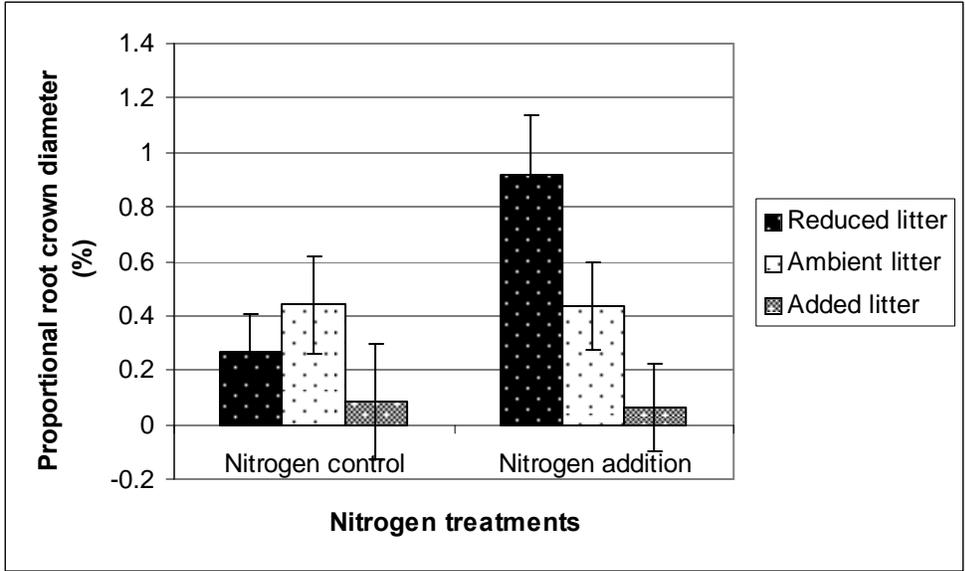


Fig 16. Proportional change in root crown diameter in nitrogen and litter treatments (2007). Means \pm standard errors are shown.

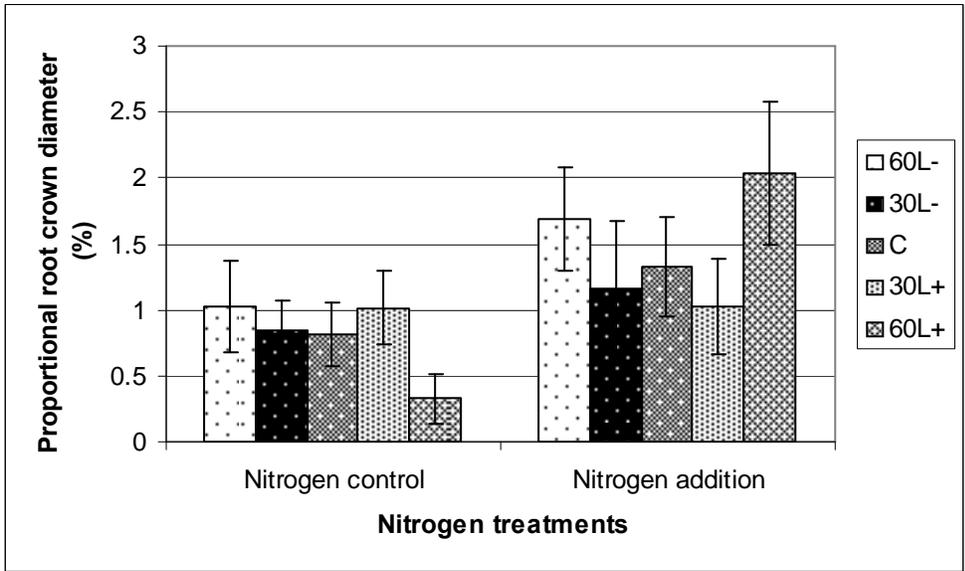


Fig 17. Proportional change in total number of leaves per rosette in nitrogen and litter treatment (2008). Means \pm standard errors are shown.

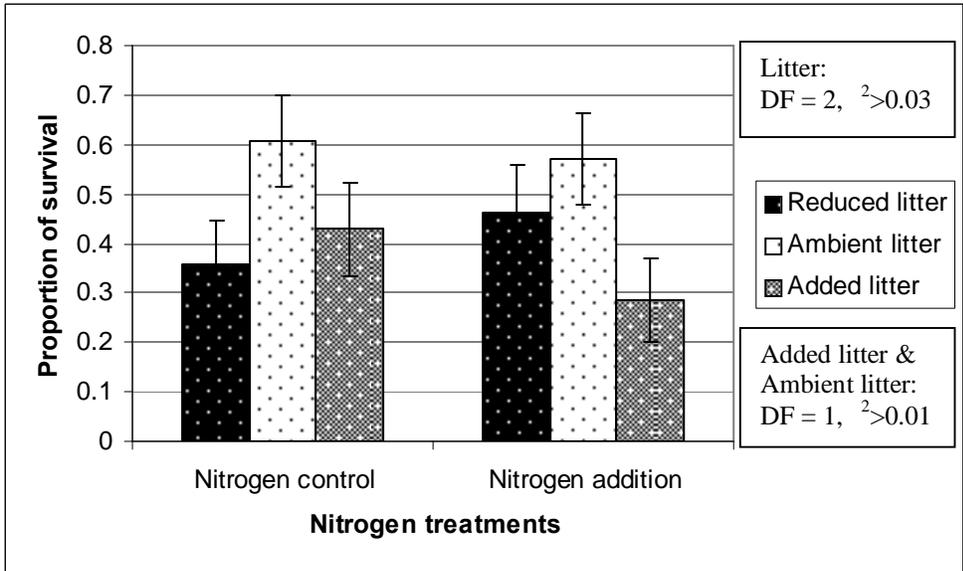


Fig 18. Tall thistle rosette survival in relation to nitrogen addition and litter (2007). Means \pm standard errors are shown.

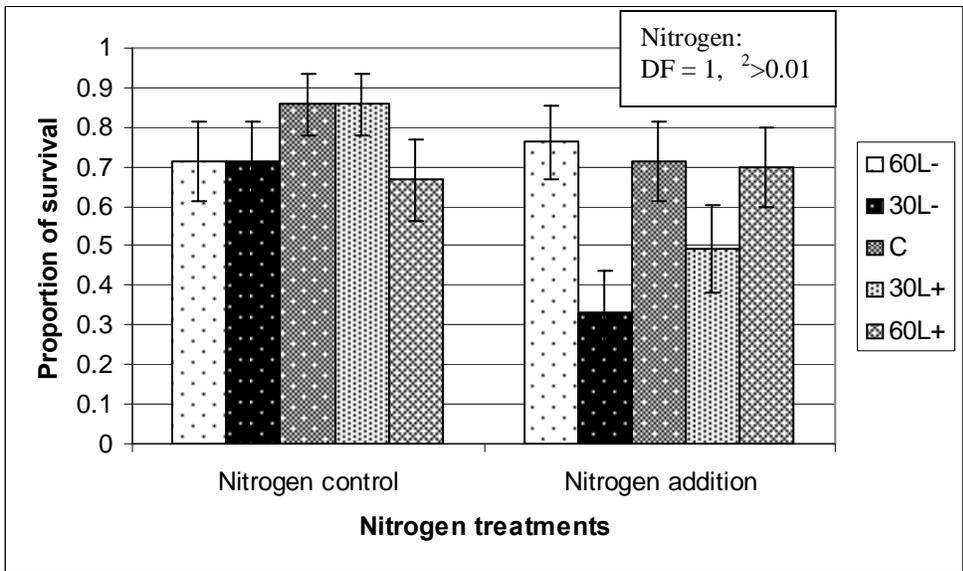


Fig 19. Tall thistle rosette survival in relation to nitrogen addition and litter (2008). Means \pm standard errors are shown.

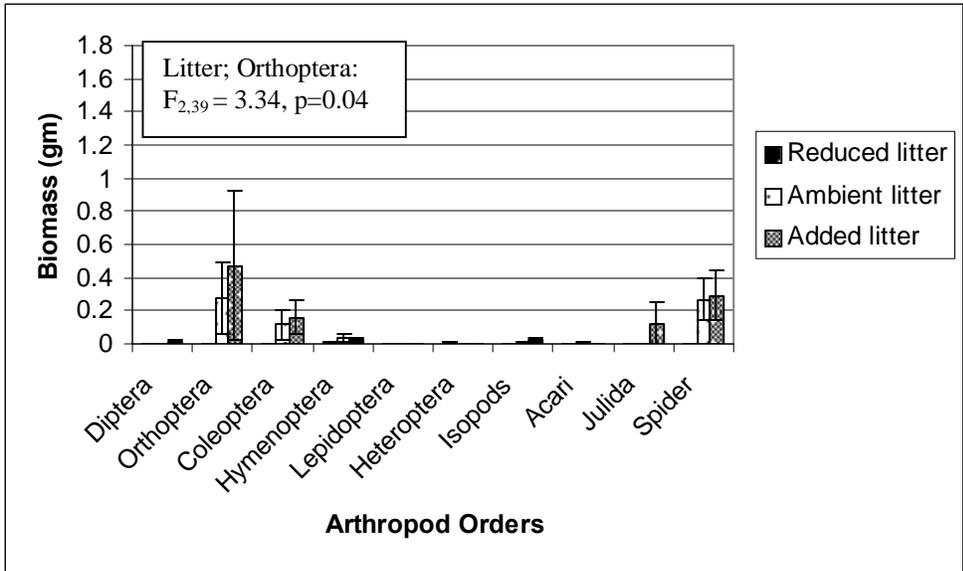


Fig 20. Insect biomass in pitfall traps in relation to litter in nitrogen control plots (2007). Means \pm standard errors are shown.

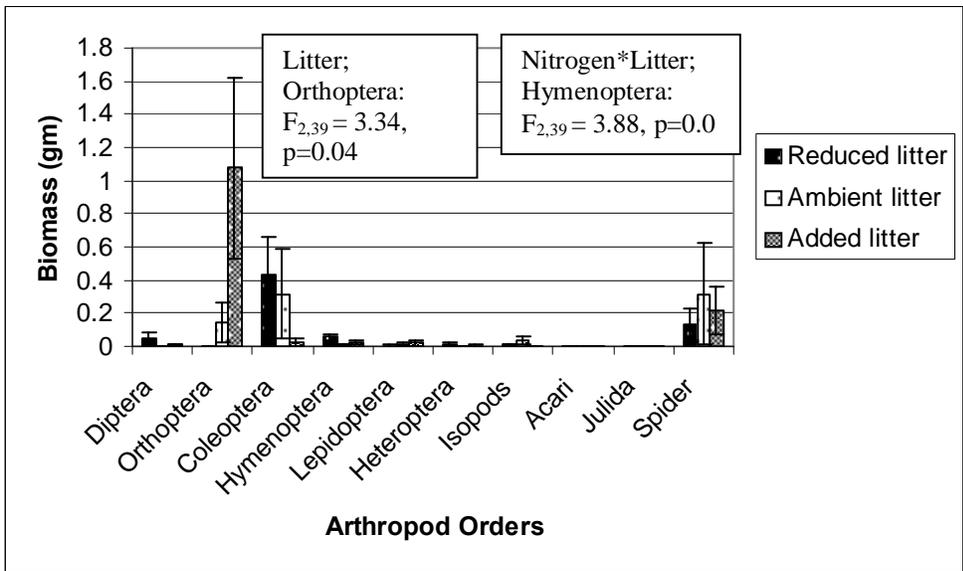


Fig 21. Insect biomass in pitfall traps in relation to litter in nitrogen addition plots (2007). Means \pm standard errors are shown.

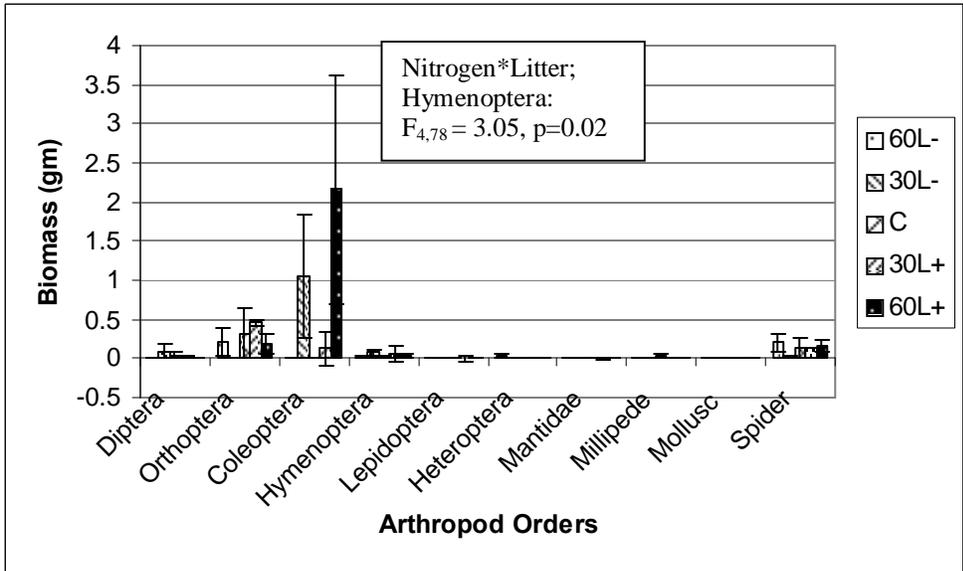


Fig 22. Insect biomass in pitfall traps in relation to litter in nitrogen control plots (2008). Means \pm standard errors are shown.

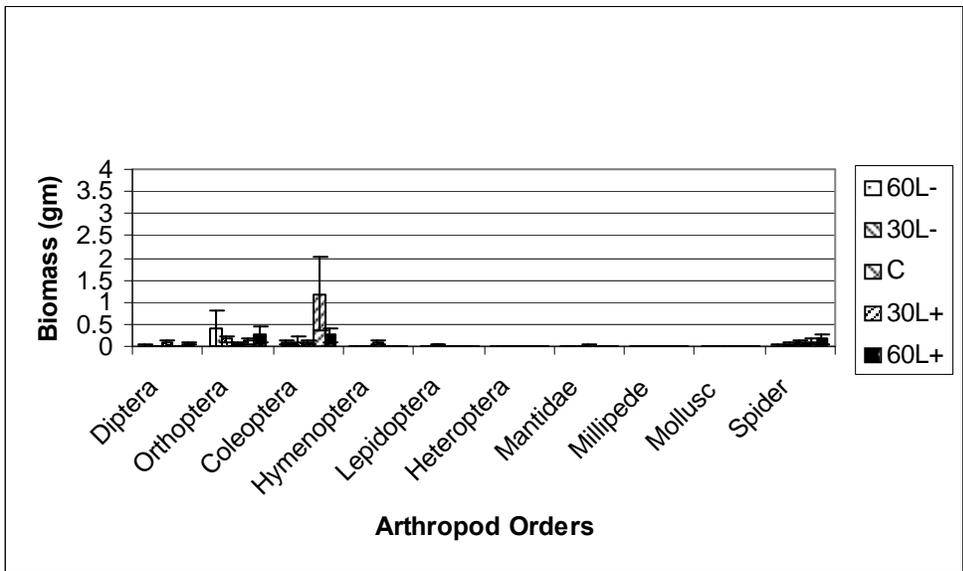


Fig 23. Insect biomass in pitfall traps in relation to litter in nitrogen addition plots (2008). Means \pm standard errors are shown.

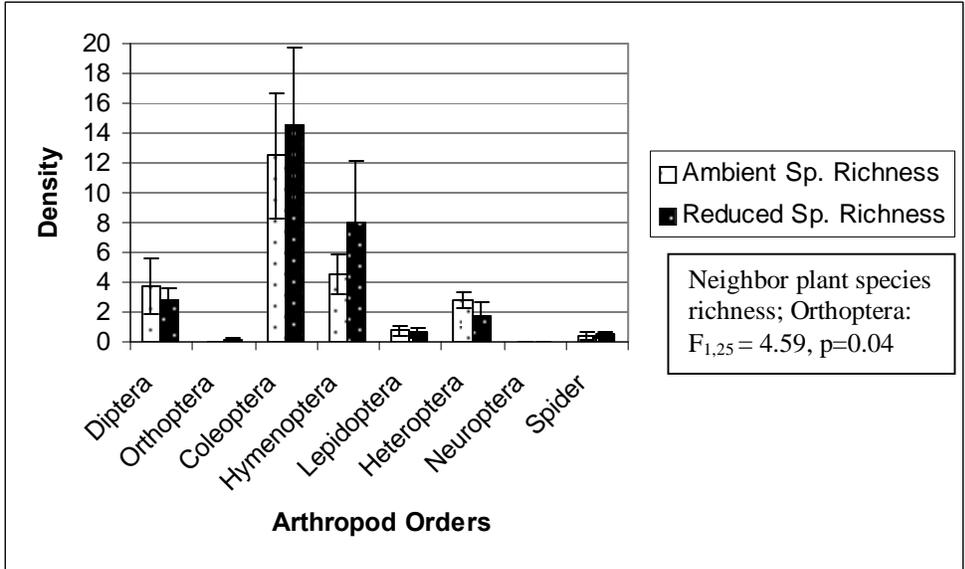


Fig 24. Insect density on sticky pads in relation to neighbor species richness in nitrogen control plots (2007). Means \pm standard errors are shown.

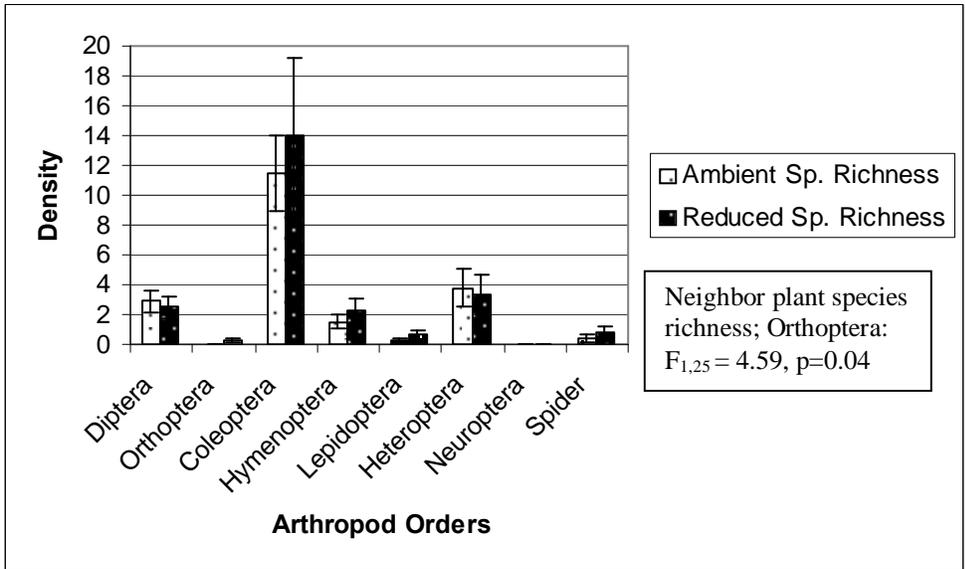


Fig 25. Insect density on sticky pads in relation to neighbor species richness in nitrogen addition plots (2007). Means \pm standard errors are shown.

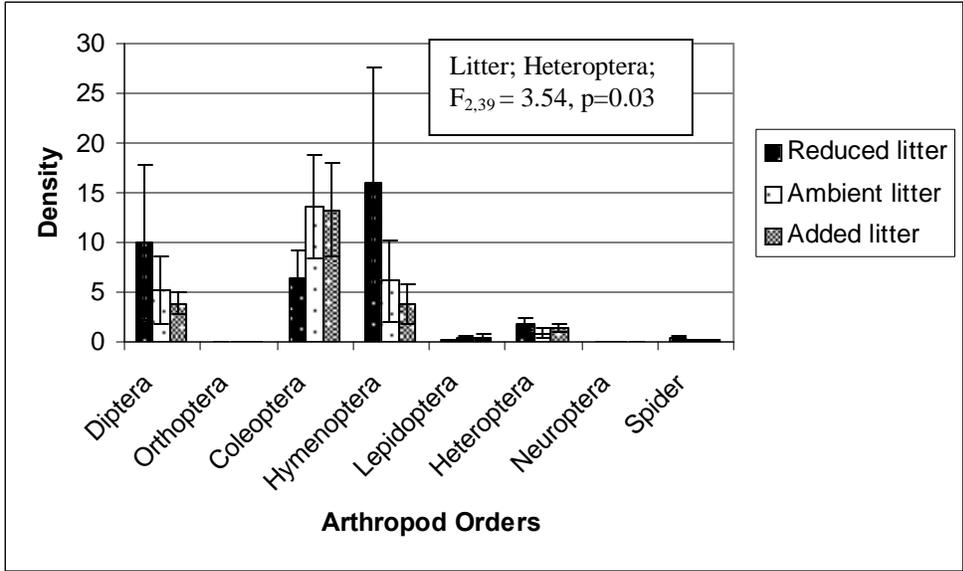


Fig 26. Insect density on sticky pads in relation to litter in nitrogen control plots (2007). Means \pm standard errors are shown.

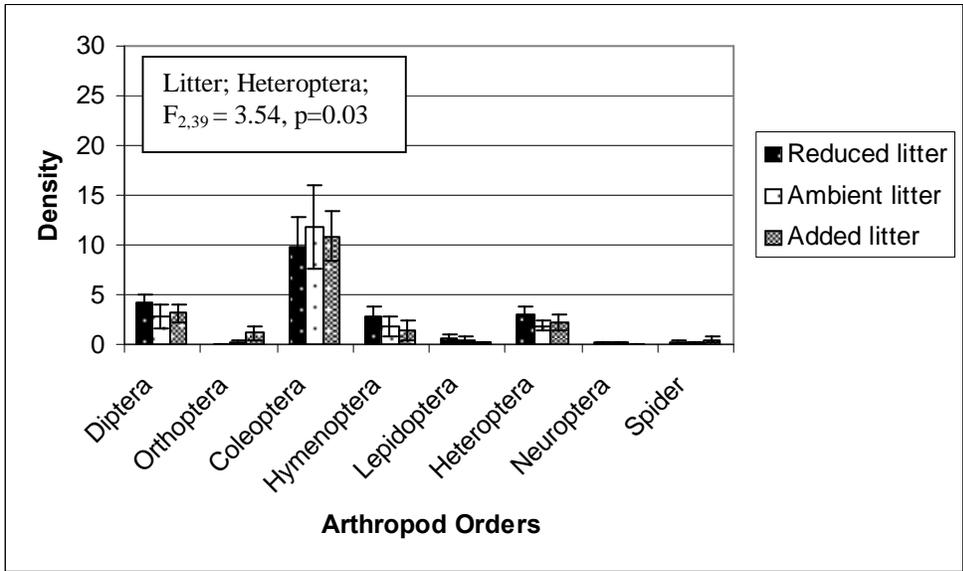


Fig 27. Insect density on sticky pads in relation to litter in nitrogen addition plots (2007). Means \pm standard errors are shown.

REFERENCES

List of References

- Amatangelo KL, JS Dukes, CB Field. 2008. Responses of a California annual grassland to litter manipulation. *Journal of Vegetation Science* **19**(5):605-612.
- Brown BJ, JJ Ewel. 1987. Herbivory in complex and simple tropical successional ecosystems. *Ecology* **68**(1):108-116.
- Chen Y, EA Schmelz, F Wäckers, JR Ruberson. 2008. Cotton Plant, *Gossypium hirsutum* L., defense in response to nitrogen fertilization. *Journal of Chemical Ecology* **34**:1553-1564.
- Coll M, DG Bottrell. 1994. Effects of nonhost plants on an insect herbivore in diverse habitats. *Ecology* **75**:723-731.
- Facelli, JM. 1994. Multiple indirect effects of plant litter affect the establishment of woody seedlings in old fields. *Ecology* **75**:1727-1735.
- Facelli JM, STA Pickett. 1991. Plant litter: Light penetration and effects on an old-field plant community. *Ecology* **72**(3):1024-1031.
- Fagan WF, JG Bishop. 2000. Trophic interactions during primary succession: Herbivores slow a plant reinvasion at Mount St. Helens. *The American Naturalist* **155**(2):238-251.
- Flora of the Great Plains. 1986. The Great Plains Flora Association. University Press of Kansas, Lawrence KS 66049.
- Foster BL, KL Gross. 1998. Species richness in a successional grassland: Effects of nitrogen enrichment and plant litter. *Ecology* **79**(8):2593-2602.
- Fraser LH, JP Grime. 1997. Primary productivity and trophic dynamics investigated in a North Derbyshire, UK, dale. *OIKOS* **80**:499-508.
- Fraser LH. 1998. Top-down vs bottom-up control influenced by productivity in a North Derbyshire, UK, dale. *OIKOS* **81**:99-108.

Gough L, CW Osenberg, KL Gross, SL Collins. 2000. Fertilization effects on species density and primary productivity in herbaceous plant communities. *OIKOS* **89**:428-439.

Gratton C, RF Denno. 2003. Seasonal shift from bottom-up to top-down impact in phytophagous insect populations. *Oecologia* **134**: 487-495.

Guretzky JA, SM Louda. 1997. Evidence for natural biological control: Insects decrease survival and growth of a native thistle. *Ecological Applications* **7**(4):1330-1340.

Hambäck P, AP Beckerman. 2003. Herbivory and plant resource competition: A mechanistic review of two interacting interactions. *Oikos* **101**:26-37.

Herrera CM, O Pellmyr. 2004. *Plant-Animal Interactions. An Evolutionary Approach*. Blackwell Publishing.

Husheer SW, AW Robertson, DA Coomes, CM Frampton. 2006. Herbivory and plant competition reduce mountain beech seedling growth and establishment in New Zealand. *Plant Ecology* **183**:245-256.

Joern A, S Mole. 2005. The plant stress hypothesis and variable responses by blue grama grass (*Bouteloua gracilis*) to water, mineral, nitrogen, and insect herbivory. *Journal of Chemical Ecology* **31**(9):2069-2090.

Knops JMH, D Tilman, NM Haddad, S Naeem, CE Mitchell, J Haarstad, ME Ritchie, KM Howe, PB Reich, E Siemann, J Groth. 1999. *Ecology Letters* **2**:286-293.

Koppel J van de, J Huisman, R van der Wal, H Olff. 1996. Patterns of Herbivory along a productivity gradient: An empirical and theoretical investigation. *Ecology* **77**(3):736-745.

Koricheva J, CPH Mulder, B Schmid, J Joshi, K Huss-Danell. 2000. Numerical responses of different trophic groups of invertebrates to manipulations of plant diversity in grasslands. *Oecologia* **125**:271-282.

Langellotto GA, RF Denno. 2006. Refuge from cannibalism in complex-structured habitats: Implications for the accumulation of invertebrate predators. *Ecological Entomology* **31**:575-581.

Long ZT, CL Mohler, WP Carson. 2003. Extending the resource concentration hypothesis to plant communities: Effects of litter and herbivores. *Ecology* **84**(3):652-665.

Louda, SM, MA Farris, MJ Blua. 1987. Variation in methylglucosinolate and insect damage to *Cleome serrulata* (Capparaceae) along a natural soil moisture gradient. *Journal of Chemical Ecology* **13**:569-581.

Louda SM, MA Potvin. 1995. Effect of inflorescence-feeding insects in the demography and lifetime fitness of a native plant. *Ecology* **76**:229-245.

Louda SM, JE Rodman. 1996. Insect herbivory as a major factor in the shade distribution of a native crucifer (*Cardamine cordifolia* A. Gray, Bittercress). *The Journal of Ecology* **84**(2):229-237.

Maret MP, MV Wilson. 2005. Fire and litter effects on seedling establishment in Western Oregon Upland Prairies. *Restoration Ecology* **13**(3):562-568.

Meyer GA, RB Root. 1993. Effects of herbivorous insects and soil fertility on reproduction of goldenrod. *Ecology* **74**(4):1117-1128.

Meyer GA. 2000. Interactive effects of soil fertility and herbivory on *Brassica nigra*. *OIKOS* **88**:433-441.

Muth NZ, EC Kluger, JH Levy, MJ Edwards, RA Niesenbaum. 2008. Increased per capita herbivory in the shade: Necessity, feedback, or luxury consumption? *Ecoscience* **15**(2):182-188.

Oksanen L, SD Fretwell, J Arruda, P Niemela. 1981. Exploitation ecosystems in gradients of primary productivity. *The American Naturalist* **118**(2):240-261.

Penner HL, WA Wehmueller. 1979. Soil survey of Sedgwick County, Kansas. United States of Department of Agriculture Soil Conservation Service in cooperation with Kansas Agricultural Experiment Station.

Price PW. 1991. The plant vigor hypothesis and herbivore attack. *OIKOS* **62**:244-251.

Rand TA. 2002. Variation in insect herbivory across a salt marsh tidal gradient influences plant survival and distribution. *Oecologia* **132**:549-558.

Raushser MD, PP Feeny. 1980. Herbivory, plant density, and plant reproductive success: the effect of *Batus philenor* on *Aristolochia reticulata*. *Ecology* **61**:905-917.

Reader RJ. 1992. Herbivory, competition, plant mortality and reproduction on a topographic gradient in an abandoned pasture. *OIKOS* **65**:414-418.

Rhoades DF. 1983. Herbivore population dynamics and plant chemistry. In: Denno RF and McClure MS (eds.). *Variable plants and herbivores in natural and managed systems*. Academic, New York.

Riechert SE, L Bishop. 1990. Prey control by an assemblage generalists predators: spiders in garden test systems. *Ecology* **71**:1441-1450.

Ritchie ME. 2000. Nitrogen limitation and trophic vs. abiotic influences on insect herbivores in a temperate grassland. *Ecology* **81**(6):1601-1612.

Root R. 1973. Organization of a plant-arthropod association in simple and diverse habitats: the fauna of collards (*Brassica oleracea*). *Ecological Monographs* **43**:95-124.

Schoonhoven LM, JJA van Loon, M Dicke. 2005. *Insect Plant Biology*. Oxford University Press Inc., New York.

Shiojiri K, R Karban. 2008. Seasonality of herbivory and communication between individuals of sagebrush. *Arthropod-Plant Interactions* **2**:87-92.

Siemann E. 1998. Experimental tests of effects of plant productivity and diversity on grassland arthropod diversity. *Ecology* **79**(6):2057-2070.

Slansky F Jr, P Feeny. 1977. Stabilization of the rate of nitrogen accumulation by larvae of the cabbage butterfly on wild and cultivated food plants. *Ecological Monographs* **47**:209-228.

Tscharntke T, BA Hawkins. 2002. *Multitrophic Level Interactions*. Cambridge University Press.

Weltzin JF, JK Keller, SD Bridgham, J Pastor, PB Allen, J Chen. 2005. Litter controls plant community composition in a northern fen. *OIKOS* **110**: 537-546.

White JA, TG Whitham. 2000. Associational susceptibility of cottonwood to a box elder herbivore. *Ecology* **81**(7):1795-1803.