NITROGEN LIMITATION AND TROPHIC VS. ABIOTIC INFLUENCES ON INSECT HERBIVORES IN A TEMPERATE GRASSLAND

MARK E. RITCHIE

Ecology Center and Department of Fisheries and Wildlife, Utah State University, Logan, Utah 84322-5210 USA

Abstract. Plant resources, predators, and abiotic conditions represent three major factors that potentially influence insect herbivore abundance in terrestrial ecosystems. In nitrogen (N)-limited environments the potential for bottom-up (plant resource) control is strong because plant quality may limit herbivore abundance. However, extremes in abiotic conditions, such as temperature and moisture, can mask such effects. I tested these hypotheses in an 8-yr field experiment that measured responses of plants and grasshoppers (Orthoptera) to N addition and exclusion of bird predators in an N-limited old-field prairie in east-central Minnesota. Plant biomass increased by 150–400%, and plant tissue N increased by 78% in response to N addition of 17 g·m^{-2}·yr^{-1}. Total grasshopper density responded positively to N addition following warm years. However, multiple regressions suggested that grasshopper densities were related much more strongly to thermal conditions than to soil N. Bird exclusion yielded weak effects that varied over time and may have been influenced by compensatory responses of other grasshopper predators to bird exclosures. Grasshopper feeding guilds differed in the relationship between their in vivo dry-matter digestibility (DMD) and plant tissue N, and this physiological difference explained their drastically different responses to N addition. Plant quality (in vivo DMD) increased with plant tissue N for mixed-feeding grasshoppers, and accordingly, their density was positively correlated with soil N. Plant quality did not change with plant tissue N for grass feeders, and their densities were negatively correlated with soil N. Both guilds responded positively to warmer thermal conditions, but mixed-feeder densities were negatively related to previous year's precipitation, and grass-feeder densities were not affected by precipitation. These results support the hypothesis that bottom-up influences of insect herbivores can be important in N-limited systems but do not support the hypothesis that more productive environments necessarily support greater top-down influences. Thermal conditions may interact with or eliminate bottom-up effects. Furthermore, different guilds within the herbivore trophic level may be influenced differently by N addition, predators, and abiotic conditions. These results suggest that exploring the mechanisms of interaction between abiotic and trophic influences within components of food webs is likely to yield many new insights into the regulation of herbivore communities.

Key words: abiotic factors; community regulation; food limitation; grasshoppers; grasslands; insects; nitrogen; predation; temperature.

INTRODUCTION

The history of ecology has been dominated by discussion of whether communities are ''regulated'' by resource supply, predators, or abiotic conditions (Andrewartha and Birch 1954, Hairston et al. 1960, Paine 1966, Menge and Sutherland 1976, 1987, Fretwell 1977, Hunter and Price 1992, Hairston and Hairston 1993). In particular, the factors regulating herbivore abundance have been hotly contested, and evidence for each factor has come from different sites and for different organisms. In terrestrial ecosystems, the debate has been focused along taxonomic lines. Vertebrates are thought to be limited by resource availability and plant production (Lack 1966, White 1984, 1993, Belovsky 1986), while invertebrates are thought to be limited primarily by predation, abiotic conditions, and/

or physical disturbance (Andrewartha and Birch 1954, Lawton and Strong 1981, Kingsolver 1989, Hairston and Hairston 1993). Terrestrial insect herbivores are central in this debate because their growth is often limited by water, nitrogen, and/or secondary chemical content of plants (Mattson 1980, Scriber and Slansky 1981, Strong et al. 1984, White 1984, Bernays 1998). They can also be limited by predators, parasites, and pathogens (Lawton and Strong 1981, Cornell and Hawkins 1995, Hawkins et al. 1997), and by abiotic conditions, particularly temperature and moisture (Andrewartha and Birch 1954, Kingsolver 1989, Joern and Gaines 1990, Ritchie 1996, Hunter and Price 1998).

A general hypothesis in ecology, which may apply to insect herbivores, suggests that the factors regulating herbivore populations depend on environmental productivity (Rosenzweig 1971, Fretwell 1977, Oksanen et al. 1981, Oksanen 1990, Hunter and Price 1992, Power 1992). Insects in strongly resource-limited en-

vironments may experience strong plant resource, or "bottom-up," effects because primary production is insufficient to sustain rapid insect population growth and high predator densities. Conversely, resource-rich environments may show stronger predator, or "top-down," effects because greater plant quality and/or productivity promotes rapidly growing herbivore populations that can sustain large predator populations.

Nitrogen (N) is probably the most common resource limiting plant production in terrestrial environments (Vitousek and Howarth 1991), and it may be a critical plant resource underpinning productivity gradients for insect herbivores (Mattson 1980, White 1984, Ritchie and Tilman 1993, Ritchie and Olff 1999). More specifically, insect herbivores may be limited most strongly by predators and parasites in environments with fertile soils and plants with N-rich tissue, but may respond to N additions most strongly in environments with infertile soils and N-poor plants (Stiling and Rossi 1997, Fraser and Grime 1998). An alternative hypothesis is that low herbivore abundance in unproductive environments may cause herbivores to be more strongly limited by predators. A given predation rate is distributed over fewer individuals, thus yielding a higher per capita mortality rate and proportionately stronger predator effects (Berryman 1987, Belovsky and Joern 1995).

These hypotheses may be too simple, however, because abiotic conditions may confound or swamp such trophic effects by reducing herbivores to densities at which neither plant food nor predators are limiting (Kingsolver 1989, Dunson and Travis 1991, Hunter et al. 1997, Hunter and Price 1998). Food web characteristics may also be important. For example, species diversity in "reticulated" food webs may dilute trophic effects both bottom-up and top-down (Strong 1992, Polis and Strong 1996). Moreover, trophic and abiotic factors may interact; greater plant resources and accompanying primary production may directly influence abiotic conditions, such as temperature (Hunter and Price 1992, Fraser 1998), or abiotic conditions may influence the efficacy of predators or diseases (Chase 1996). For example, greater plant biomass, and its associated complex architecture, may provide herbivores refuges from predators or alter ground temperatures by blocking solar radiation. Finally, abiotic conditions may influence plant quality and thus indirectly affect herbivores through a bottom-up pathway. Plant secondary chemicals may become more effective at higher temperatures (Stamp and Yang 1996, Stamp et al. 1997) and plant tissue may be of higher quality when plants are water stressed during low precipitation years (Lewis 1984, Bernays and Lewis 1986).

Another issue is that all herbivores and plants are not equal. General theories derived from simple mathematical models (Rosenzweig 1971, Oksanen et al. 1981) typically assume that herbivore and plant species act as a single trophic unit. In reality, different herbivore species consume different plant species, which themselves differ in abundance and quality to herbivores. Trophic levels can often be subdivided into component guilds or functional groups; insect herbivore communities may feature specialists on different plant types or generalists that feed on many types. The plant species eaten by each herbivore guild may be limited to different degrees by plant resources, and herbivore guilds may be differentially vulnerable to predators or have different predators. Consequently, plant resources, predators, and abiotic conditions may differ in their influence on particular herbivore guilds.

Exploring the relative importance of trophic and abiotic influences, and their potential interactions, on herbivore abundance in a diverse herbivore community remains a challenge to ecologists. Such studies require comprehensive field experiments that simultaneously manipulate predation and nitrogen availability (Hunter and Price 1992) coupled with detailed monitoring of individual species' responses to treatments. To assess the effects of abiotic conditions such as temperature and precipitation, one approach is to monitor an experiment through annually varying weather conditions and use correlations to assess the relative impacts of different factors. Because correlations do not always imply causality, direct manipulations of abiotic conditions would be preferable. However, such manipulations are difficult to perform at spatial scales relevant to even insect herbivore communities. Thus, a long-term (>5yr) field experiment subject to varying weather is a reasonable compromise with potentially powerful insights.

With such a design in mind, I tested whether plant resource availability and/or predators controlled the abundance of grasshoppers (Orthoptera: Acrididae, Tettigoniidae), a dominant order of insect herbivores, over 8 yr of annual variation in temperature and precipitation. I performed the study in a temperate grassland that is strongly N-limited: an old-field prairie at Cedar Creek Natural History Area (CCNHA), Minnesota, USA where N is known to be the major resource limiting primary productivity (Tilman 1987). In a factorial experiment, I monitored available soil-N concentrations, plant biomass, and the total density of grasshoppers (Orthoptera) in response to N addition and exclusion of bird predators. I also monitored plant and grasshopper species composition within this experiment. Annual temperature and precipitation changes were measured at the CCNHA weather station, 1.5 km from the experiment. Grasshoppers are the dominant invertebrate herbivores in this field (Huntly and Inouye 1988, Ritchie and Tilman 1992, 1993), comprising 75–85% of total herbivore live standing crop. The effects of resource availability may therefore be particularly important because grasshopper growth, development, and reproduction may be limited by the low tissue N concentration of the dominant prairie-plant species present (Heidorn and Joern 1987, Schmitz

1993, Belovsky and Slade 1995). Predation may be important because Passerine birds nest in these old fields at densities (3–9 individuals/ha) that have been shown to limit grasshopper abundance elsewhere (Joern 1986, 1992, Belovsky et al. 1990, Fowler et al. 1991, Bock et al. 1992, Belovsky and Slade 1993). Finally, abiotic conditions also may be important for grasshoppers, because years with below-average temperature and/or above-average precipitation can inhibit their productivity. Cool, wet conditions are often associated with retarded development (Scharff 1954, Dempster 1963, Gage and Mukerji 1977, Rodel 1977), increased density-independent mortality (Belovsky and Slade 1995), and/or reduced activity time (Chase 1996). Consequently, this study site is useful for testing for the relative importance of predation, food, and weather as factors regulating herbivore abundance.

METHODS

The study was conducted from 1989 to 1996 on an old-field prairie at Cedar Creek Natural History Area (CCNHA), Minnesota, USA ~40 km north of Minneapolis. This old field (Field B of Tilman 1987) is dominated by native prairie plants, including the grasses *Andropogon gerardi, Schizachyrium scoparium, Poa pratensis, Cyperus* sp., and forbs *Solidago rigida, S. nemoralis, Liatris aspera,* and *Lespedeza capitata.*

The major herbivores in these old fields are grasshoppers (Orthoptera: Acrididae, Tettigoniidae) and planthoppers (Homoptera, Cicadellidae). Thirty grasshopper species have been found in this field, with eight species accounting for 90% of the abundance. These grasshoppers can be divided into two guilds of similar diet preferences and associated feeding adaptations that have been established from wide-ranging field surveys (Mulkern et al. 1969, Joern 1984): large (>0.4 g) ''mixed feeders'' that, at CCNHA, eat a mixture of forbs and grasses, *Melanoplus femur-rubrum* and *M. bivittatus* (Ritchie and Tilman 1992, 1993), and small (<0.35 g) grass feeders *Ageneotettix deorum, Conocephalus saltans, C. strictus, M. keeleri-luridus*, and *Phoetaliotes nebrascensis.*

The major bird predators on grasshoppers are Eastern Kingbirds (*Tyrannus tyrannus*), Vesper Sparrows (*Pooecetes gramineus*), Grasshopper Sparrows (*Ammodrammus savannarum*), and American Kestrels (*Falco sparverius*). These four species combined occurred at densities of 3–9 individuals/ha during the course of the study. Other grasshopper predators include northern prairie skinks, *Eumeces septentrionalis* (10–15 individuals/ha), and various spiders (Arachnida) (0.08–0.3 individuals/m²).

To examine animal responses to N addition, this old field was divided into ten 20 × 50 m ''macroplots'' arranged in two parallel rows of five, with each randomly assigned one of three N addition rates. Three received high N addition (17 g·m⁻²·yr⁻¹ of ammonium nitrate), three received intermediate fertilization (8 g·m⁻²·yr⁻¹ of ammonium nitrate), and four were left unfertilized as controls. N was added at half the yearly rate twice per year in mid-May and late June. As reported in Tilman (1987), the high N addition treatment in these macroplots led to a doubling of plant biomass and the virtually complete dominance of the grasses *Agropyron repens* and *Poa pratensis* by the beginning of the experiment in 1989.

In May 1989, we established a pair of 9 × 9 m plots at the 10 × 20 m end of each of three of the high N addition macroplots (Fertilized) and three of the controls (Unfertilized), yielding a total of 12 experimental plots in the field. For each pair of plots, one received a bird exclosure and the other was left as a control. Bird exclosures were constructed almost identically to those of Joern (1986, 1992) and Belovsky and Slade (1993) and consisted of a canopy of 2.5-cm mesh Toron netting (J. A. Cissel, Lakewood, New Jersey, USA) erected on a wire frame 0.8 m above the ground. The sides of the canopy were anchored to the ground with wire stakes. Netting was erected in early June and then removed at the end of August each year. Because bird netting also excluded white-tailed deer (*Odocoileus virginianus*), 2 m high temporary fences were erected around control plots each year to standardize potential deer exclusion effects.

I measured N availability and plant responses to fertilizer and bird exclosure treatments. I measured soil ammonium and nitrate concentrations and plant biomass inside each of the 12 experimental plots only 7 of the 8 yr (1990–1996). Available soil N was determined in August each year from 0.01 mol/L KCl extractions of ammonium and nitrate in soil combined from four 2 × 20 cm cores per plot. Ammonium and nitrate concentrations (in milligrams per kilogram of dry soil) were determined with an AlpKem autoanalyzer (O. I. Analytical, Wilsonville, Oregon, USA) in the CCNHA soil chemistry laboratory (Ritchie and Tilman 1993). Peak plant biomass was measured in each year of the study by clipping three strips (3 × 0.1 m) of all aboveground plant material in each plot during 15–28 August. Plant material was sorted to live vs. litter, with live material sorted to species, and was weighed after drying at 45°C for 7 d.

Plant quality to herbivores was measured from the 1990–1993 samples in two ways. Dried, live plant material from each plot was ground in a Wiley mill through a 40-mesh (0.8-mm) screen. A portion of ground material was analyzed for N content in a Carlo-Erba (Strumentazione, Italy) autoanalyzer. A separate portion was analyzed for in vitro digestibility in 0.1 mol/LHCl and 2 g/L pepsin in a water bath kept at 38°C (Belovsky and Slade 1995). This assay is often correlated with soluble carbohydrate content and digestible energy content (Belovsky and Slade 1995).

I also compared these indirect measures of plant quality with in vivo digestibility of seven species from unfertilized and fertilized plots. In unfertilized plots, I

used three forb (*Solidago rigida, Lespedeza capitata, Liatris aspera,* and *Achillea millefolium*) and four graminoid species (*Agropyron repens, Poa pratensis, Schizachyrium scoparium*, and *Cyperus* sp.). I also tested the two dominant grass species from fertilized plots (*A. repens* and *P. pratensis*). These plant species accounted for >95% of plant biomass in their respective treatments. I tested adults of five different grasshopper species, including both mixed-feeding (*M. femur-rubrum* and *M. bivittatus*) and grass-feeding grasshoppers (*Phoetaliotes nebrascensis, M. keeleri-luridus, Conocephalus saltans*). Individual grasshoppers used in the trials were caught from another part of Field B with sweep nets. Grasshoppers were kept in the laboratory in 1-L canning jars with window-screen lids without food at 29°C for 24 h to clear their digestive tracts. Feeding trials consisted of presenting whole clipped plants of a single species, inserted into florists' rubber-tipped vials to avoid desiccation, to individual grasshoppers for 4 h (1000–1400) in clean jars. I tested 10 replicate individuals of each grasshopper species on each plant species. I measured digestibility as the proportion of eaten plant biomass not deposited as frass by 0800 the following morning. Although the grasshopper species tested differ markedly in their field diet preferences (Joern 1984), all species ate parts of all plant species presented.

Temperature and precipitation during the growing season are often critical abiotic conditions associated with fluctuations in grasshopper populations (Scharff 1954, Dempster 1963, Gage and Mukerji 1977, Rodel 1977, Capinera and Horton 1989). Growing degree-days is a common metric used in assessing temperature conditions for insect development (Rodel 1977) and reflects the number of days suitable for grasshopper development and the daytime temperatures encountered during those days. In this study, I calculated growing degree-days as the yearly sum of daily maximum temperatures for days with maximum temperatures >22°C, the temperature above which grasshopper development occurs (Chappell 1982, Chappell and Whitman 1990). Growing season precipitation represents precipitation during the typical period in which grasshoppers must hatch, develop into adults, mate, and lay eggs (15 May–15 September) and reflects humidity and soil moisture conditions that can affect egg and nymphal development or fungal infection rates. Using different temperature thresholds (i.e., 20° or 24°C) did not alter how different years ranked in growing degree-days. All weather data was collected from the CCNHA weather station, located <2 km from Field B. Individual grasshoppers can modify their immediate thermal amd moisture conditions by choice of microhabitats within vegetation, but weather variables encompass the range in abiotic conditions that might account for grasshopper abundance.
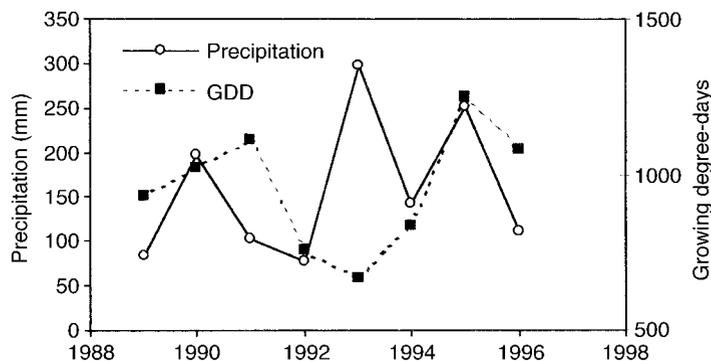
I assessed responses of grasshoppers to treatments by measuring their density and live biomass in each plot each year between 15 and 31 August. Grasshoppers were sampled only on sunny days, with maximum air temperature >25°C. In each 9 × 9 m plot, a single person swept the entire plot vigorously with a muslin net for three to four consecutive 20-min sampling periods, separated by 10-min rests to allow remaining grasshoppers time to climb back up on vegetation. Density was estimated with a catch-effort technique (Belovsky and Slade 1995), where the number of grasshoppers caught during the current sample (*y*) is regressed against grasshoppers caught in previous samples (*x*). Density was estimated from the *x*-intercept of this regression. Current number caught always declined linearly with number previously caught ($R^2 > 0.84$). All grasshoppers caught were immediately frozen at −20°C, and later thawed, sorted to species, and weighed wet. Grasshopper live biomass was calculated as the average mass per individual multiplied by estimated density.

Grasshoppers were free to move among experimental plots, so it is important to know whether treatment effects reflected community, rather than individual functional, responses to experimental treatments. Although I did not directly measure movements of individual grasshoppers, I tested the spatial scale over which grasshopper communities changed between fertilized and unfertilized plots. On three separate days in August 1990, I made 25 sweeps along each of seven transects, separated by 3 m, from 9 m inside each fertilized plot to 9 m outside each plot into an adjacent unfertilized area. Bagged grasshoppers were frozen at −20°C and later identified to species. If grasshoppers responded to experimental plots in a fine-grained manner, i.e., individuals visited more than one treatment as part of daily or weekly movements, then community shifts across treatments should be gradual. Alternatively, if grasshoppers show strong fidelity to plots, community shifts should be sharp and occur over just a few meters.

Because birds are not the only predators of grasshoppers, I measured densities of spiders captured in grasshopper sweeps from 1991 to 1996 and abundance of skinks from 1994 to 1996 inside and outside bird exclosures. Spider densities were estimated by using the same catch-effort method as for grasshoppers. Skinks were trapped nightly in each plot from 15 June to 1 September in four 20 cm diameter pitfall traps, each placed 1.5 m inside the plot edge near a corner. I avoided placing traps in the middle of plots to minimize vegetation trampling from frequent checking of traps. Pitfall traps were made of plastic, sealed-bottom flower pots buried flush with the ground surface. I covered pots with 35 × 35 × 0.8 cm thick plywood squares to provide shelter for captured skinks and other animals. Skink abundance was estimated as the number caught per 100 trap-nights. In addition, I dissected at least 30 individual grasshoppers from each plot each year (a total of 360 each year) during 1990–1993 to

FIG. 1. Varying weather conditions for a Minnesota old-field prairie during 1989–1996. The figure plots precipitation (○) during 15 May–15 September each year and annual growing degree-days (GDD, ■), the sum of daily maximum temperatures for all days in which maximum temperature exceeded 22°C.

detect the incidence of nematode parasites or dipteran parasitoids.

I assessed responses of several response variables to N addition and bird exclusion, including soil available N (ammonium + nitrate), plant biomass, grasshopper density, spider density, number of skinks per 100 trapnights, and proportion of grasshoppers with nematode or dipteran parasites. These effects were analyzed using a repeated measures ANOVA with nested blocks, with fertilizer addition as one main effect, macroplots as blocks, and bird exclosure treatments nested within macroplots. All factors, including year, were analyzed as fixed effects because all possible levels of each factor were tested. I also compared the effects of N addition and bird exclusion on grasshopper community composition, measured as the relative abundance of the eight most common species. These response variables were potentially highly correlated, and multivariate ANOVA was not possible because of the nested design. Therefore, I corrected for inflation of Type I error using Bonferroni adjustments (Zar 1999): $\alpha = 0.05/(7)^{1/2} = 0.019$ for the seven major response variables and $\alpha = 0.05/(8)^{1/2} = 0.017$ for the relative abundances of grasshopper species. Individual contrasts were tested after ANOVA with Fisher's least significant difference test. Following ANOVA, I used multiple regression to evaluate the relative importance of available soil N, weather variables, and/or the presence of bird predators in explaining plant biomass and grasshopper density. Plant biomass, soil available N, and grasshopper density were log transformed in all analyses to correct successfully for non-normal distributions. Relative abundances of grasshopper species were arcsine transformed. All statistical tests were performed with Number Cruncher Statistical System (J. Hintze, Kaysville, Utah).

RESULTS

Nitrogen addition and predator exclusion experiments were performed under highly varying abiotic conditions (Fig. 1). Growing season precipitation varied threefold, with a 50-yr record rainfall occurring in 1993 and years with 30% below-average rainfall in 1989 and 1992. Growing degree-days also varied

among years during the study, with 50-yr record heat during 1995, and temperatures 25% below normal during 1992 and 1993. Average daily maximum temperatures were strongly correlated with growing degree-days ($R^2 = 0.88$, $N = 8$, $P < 0.001$) and maximum monthly precipitation during the growing season was highly correlated with total growing season precipitation ($R^2 = 0.83$, $N = 8$, $P = 0.003$).

Nitrogen addition increased available soil solution ammonium and nitrate, by an order of magnitude ($F = 32.17$, df = 1, 46, $P = 0.005$), from an average over 1990–1996 of 0.33 ± 0.05 mg/kg (mean ± 1 SE) in unfertilized plots to 3.60 ± 0.85 mg/kg in fertilized plots. This increase in N availability highly significantly increased plant biomass and plant quality to grasshoppers. As documented by Tilman (1987), N addition increased total plant biomass by an average of 260% (Fig. 2A). However, plant biomass also varied significantly with year, and the interaction between N addition and year was significant (Table 1A). This interaction reflected greater annual variation in plant biomass in fertilized plots (Fig. 2A).

Nitrogen addition increased the quality of plants for some grasshopper species. Biomass from fertilized plots dominated by *Agropyron repens* and *Poa pratensis* had significantly higher mean tissue-N content than the mixture of *Schizachyrium scoparium, P. pratensis, Cyperus* sp., and various forb species from unfertilized plots ($F = 5.1$, df = 1, 22, $P = 0.02$, Fig. 2B). Plant tissue-N content was highly correlated with both in vitro dry-matter digestibility (DMD) (Fig. 3A) and in vivo DMD for mixed-feeding grasshopper species (Fig. 3B). However, in vivo DMD of grass-feeding grasshopper species was not correlated with increasing plant-N content (Fig. 3A). Furthermore, long-term N addition virtually eliminated plants with high secondary chemical contents. An average of 6% of biomass in unfertilized plots included plant species with known high levels of secondary compounds, such as alkaloids (*Liatris aspera*) and terpenes (*Achillea millefolium*), or physical defenses such as dense hairs (*Hieracium longipilum*). Very few (<0.2% of total biomass) such plants were found in fertilized plots.

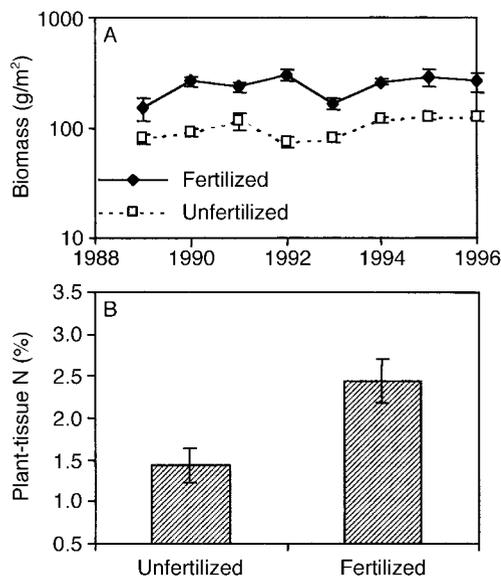Grasshopper densities exhibited an order of magni-

FIG. 2. Effects of nitrogen addition on (A) plant biomass (note log scale) during 1989–1996 and (B) percentage of nitrogen in plant tissue during 1990–1993 (years pooled). Nitrogen addition had significant effects on plant biomass in all years ($P < 0.001$) and on percentage of plant-tissue nitrogen ($P < 0.0001$).

tude in variation among years (Table 1B, Fig. 4A, B). They responded to N addition, sometimes by up to 300%, but only in certain years (Fig. 4A), as indicated by a significant interaction between N addition and year but no significant main effect of N addition (Table 1B). Mixed-feeding grasshoppers accounted for most of this response, as densities of the four most common grass-

feeding grasshoppers in unfertilized plots were 90% lower in fertilized plots in years when N addition effects were significant (Fig. 5).

Grasshopper densities beneath bird exclosures were lower, on average, than in control plots. Bird exclusion also interacted almost significantly with year (Table 1B), which reflected the fact that grasshopper densities were lower beneath bird exclosures in some years (1990, 1991) and higher in others (1996) (Fig. 3B). Spiders were significantly more abundant beneath bird exclosures (Table 2), ($F = 3.71$, df = 1, 34, $P = 0.03$), but skinks were not ($F = 0.76$, df = 1, 16, $P = 0.32$). Both spiders and skinks were significantly less abundant in fertilized plots ($F = 16.32$, df = 1, 34, $P = 0.004$; $F = 15.85$, df = 1, 16, $P = 0.016$, respectively) and the interaction between year and N addition was significant for both ($F = 12.32$, df = 5, 34, $P < 0.0001$; $F = 5.21$, df = 2,16, $P = 0.018$, respectively). Nematode and dipteran parasites were found in only 2.8% of the 1800 grasshoppers dissected from 1989 to 1993, and were not found significantly more frequently beneath bird exclosures ($F < 0.90$, df = 1, 27, $P > 0.45$) or in fertilized plots ($F < 1.12$, df = 1, 27, $P > 0.22$).

The relative abundance of different grasshopper feeding guilds shifted significantly with N addition and year. The relative abundance of the four most dominant grass feeders (*Ageneotettix deorum, Phoetaliotes nebrascensis, Melanoplus keeleri-luridus*, and *Conocophalus saltans*) declined significantly with N addition, while the relative abundance of the two mixed feeders (*M. femur-rubrum* and *M. bivittatus*) and *C. strictus* increased with N addition (Fig. 5). These shifts occurred within 3 m of the edge of fertilized plots. Be-

TABLE 1. Repeated-measures ANOVA results for evaluating year, fertilizer, and bird exclusion effects on (A) log(plant biomass) and (B) log(grasshopper density).

Source	df	ss	F	P
(A) Log(plant biomass)				
Fertilizer	1	3.18	65.01	0.0012†
Macroplot	4	0.196	3.08	0.10
Error (year)	6	0.095	···	···
Year	7	0.708	8.73	<0.0001†
Year × fertilizer	7	0.266	3.28	0.005†
Predator	1	0.0059	0.52	0.47
Fertilizer × predator	1	0.048	4.19	0.04
Year × predator	7	0.054	0.67	0.69
Error	61	3.727	···	···
Total	···	8.28	···	···
(B) Log(grasshopper density)				
Fertilizer	1	0.495	3.19	0.15
Macroplot	4	0.621	2.94	0.11
Error (year)	6	0.316	···	···
Year	7	8.916	54.47	<0.0001†
Year × fertilizer	7	1.408	8.6	<0.0001†
Predator	1	0.235	10.0	0.002†
Fertilizer × predator	1	0.025	1.08	0.30
Year × predator	7	0.377	2.31	0.037
Error	61	1.42	···	···
Total	95	13.81	···	···

† Significant effect, $\alpha = 0.016$ following a Bonferroni adjustment for multiple ANOVAs on available soil N, plant biomass, and grasshopper density, which are potentially correlated response variables.
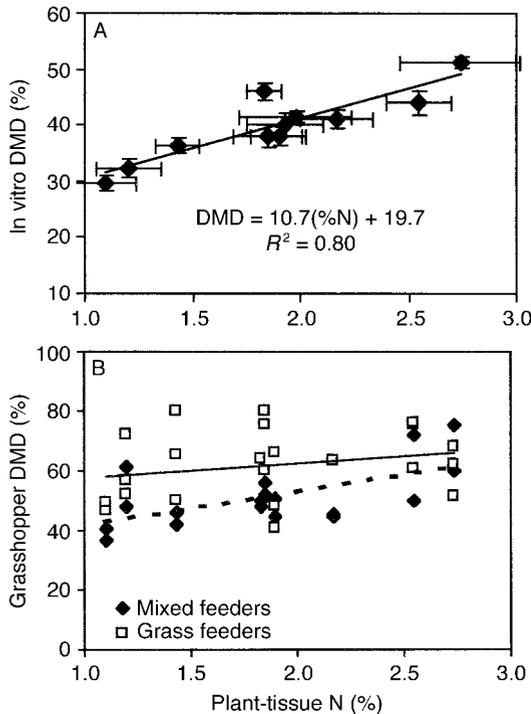
FIG. 3. Higher percentage of nitrogen in plant tissue translates into higher plant quality to grasshoppers. Relationships between mean (± 1 SE) whole plant percentage of N and (A) plant in vitro dry-matter digestibility (DMD) in 0.1 mol/L HCl and 2 g/L pepsin for nine plant species from unfertilized plots and two plant species from fertilized plots. (B) Relationships for these same plant species between percentage of N and mean in vivo DMD of three grass-feeding grasshopper species ($\square$, *Phoetaliotes nebrascensis, Conocephalus saltans*, and *Melanoplus keeleri-luridus*) and two species feeding on a mixture of grasses and forbs (dicots) ($\blacklozenge$, *M. femur-rubrum* and *M. bivittatus*). Each point in (B) represents a different grasshopper × plant species combination. The relationship for in vivo DMD vs. plant-tissue N for grass feeders was not significant ($R^2 = 0.03$, $P = 0.36$) but was significant for mixed feeders (DMD $= 29.1 + 13.6[\%N]$, $R^2 = 0.34$, $P = 0.002$).

tween 1989 and 1996, the relative abundance of most grasshopper species did not change significantly, but in unfertilized plots, the mixed feeder *M. femur-rubrum* increased while the grass feeders *M. keeleri-luridus* and *A. deorum* decreased significantly ($P < 0.001$). The relative abundance of *M. femur-rubrum* increased especially beneath bird exclosures, as revealed by a significant interaction between bird removal and year ($F = 3.32$, df $= 1$, 61, $P = 0.012$). Although relatively rare in this field, *M. bivittatus* was, over all years, relatively more abundant beneath bird exclosures (3.3% $\pm 0.21\%$, mean ± 1 SE) than in control plots (2.2% $\pm 0.34\%$) ($F = 5.36$, df $= 1$, 61, $P = 0.003$).

I used multiple regression to evaluate the relative importance of predators (presence/absence of birds), plant resources (available soil N), and abiotic conditions (growing degree-days, growing season precipitation) in explaining variation in grasshopper abun-
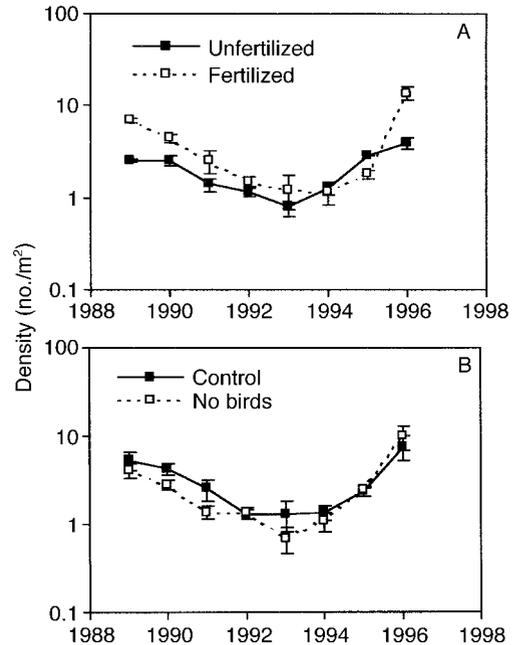

FIG. 4. Effects of (A) nitrogen addition and (B) bird predator exclusion on grasshopper densities (± 1 SE; note log scale) in a Minnesota old-field prairie. Nitrogen addition increased grasshopper density significantly during 1989–1991 and in 1996 ($P < 0.01$). Bird exclusion significantly reduced grasshopper density in 1990 and 1991 ($P < 0.05$).

dance. This analysis also helped explain the "year effects" observed in ANOVAs. First, I examined associations between these four independent variables and two dependent variables: log(plant biomass) and log(total grasshopper density) (Table 3). Log(plant biomass) was highly significantly related to available soil
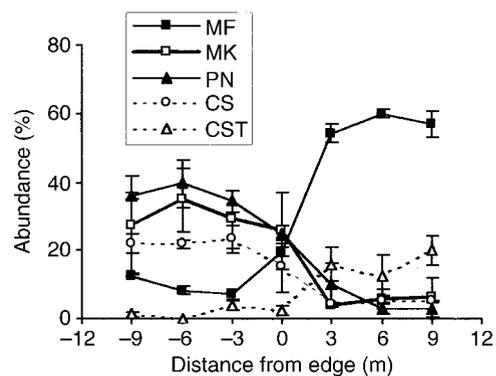

FIG. 5. Relative abundance (mean ± 1 SE) in 1990 of five grasshopper species in a Minnesota old-field prairie, sampled at different distances along three replicate transects running from unfertilized to fertilized prairie. Negative distances indicate samples in unfertilized plots, zero is the edge of the fertilized plot, and positive distances indicate samples inside the fertilized plot. The grasshopper species are *Melanoplus femur-rubrum* (MF), *Melanoplus keeleri-luridus* (MK), *Phoetaliotes nebrascensis* (PN), *Conocephalus saltans* (CS), and *Conocephalus strictus* (CST).

TABLE 2. Abundance of predators other than birds (mean ±1 SE) inside and outside bird exclosures in a Minnesota old-field prairie.

Taxa	Birds	No birds
Spiders (no./m²)	0.13 ± 0.023	0.21 ± 0.031*
Skinks (no./100 trap-nights)	3.85 ± 0.51	3.30 ± 0.36
Nematodes (% of individuals)	4.2 ± 1.2	2.8 ± 2.0
Dipterans (% of individuals)	1.8 ± 0.7	0.5 ± 0.5

* Significant difference between predator treatments (AN-OVA, $P < 0.05$). Data are pooled over both fertilizer treatments and for all years sampled.

N and growing degree-days. Log(total grasshopper density) was significantly related only to growing degree-days in the previous year. Bird exclusion and precipitation combined explained <0.1% of the variation in plant biomass (Table 3) and <3% of the variation in grasshopper density. Overall, soil N was the most important variable explaining plant biomass (31.7% of the variation) but growing degree-days was the only variable explaining grasshopper density. Other plant productivity variables, including grass biomass, forb biomass, and total plant biomass, did not significantly explain log(grasshopper density) when included simultaneously in a multiple regression with log(soil N) and previous year's growing degree-days.

The reason for the lack of partial correlation between total grasshopper density and soil N was revealed in separate multiple regressions for mixed-feeding and grass-feeding grasshoppers (species' densities pooled; Table 4). For mixed feeders, log(density) was positively related to log(soil N) and to previous year's growing degree-days, but negatively related to previous year's precipitation. For grass feeders, log(density) was also positively related to previous year's growing degree-days, but was negatively related to log(soil N) and not significantly related to precipitation.

DISCUSSION

The results suggest that thermal conditions, an abiotic factor, and nitrogen availability, a bottom-up factor, interact to influence insect herbivore abundance in this old-field prairie. Under warm thermal conditions, increased N availability can yield strong bottom-up effects on herbivores, as expected for grasshoppers in this N-limited environment. Under cool conditions, this bottom-up effect largely disappeared. Bird predators had weak and positive effects on total grasshopper density, so top-down effects were not strong. However, compensatory responses to bird exclusion by alternative predators, e.g., spiders, may have overridden direct effects of birds. Bottom-up, top-down, and abiotic conditions differed in their importance for different grasshopper feeding guilds. These results support a more complex view of trophic vs. abiotic influences on insect herbivores (Hunter and Price 1992, Cappucino and Price 1995), in which abiotic factors may interact with trophic factors, and different factors may affect guilds within an herbivore trophic level.

Thermal conditions in the previous year were strongly associated with grasshopper abundance in this old-field prairie. Densities declined by 75% in unfertilized plots and by 90% in fertilized plots following the cool years of 1992–1994. Densities increased by a factor of almost 10 following the extremely warm year in 1995. Both grass- and mixed-feeding species responded similarly to thermal conditions. Population declines in response to cool years and population increases in response to warm years have been observed elsewhere for grasshoppers (Edwards 1960, Capinera and Horton 1989, Joern and Gaines 1990, Kemp and Dennis 1993) and many other insects (Andrewartha and Birch 1954, Strong 1983, Strong et al. 1984, Kingsolver 1989). These declines could reflect a number of consequences of warmer thermal conditions on grasshopper development and vulnerability to parasitic and fungal infec-

TABLE 3. Results of simultaneous multiple regression of (A) log(plant biomass) and (B) log(grasshopper density) vs. log(N) (as available soil ammonium and nitrate), growing degree-days (GDD), and growing season precipitation.

Variable†	Coefficient ±1 SE	t	P	Percentage of variance explained
(A) Plant biomass				
Intercept	2.09 ± 0.10	20.1	<0.0001	...
Bird exclosure	−0.028 ± 0.039	−0.72	0.47	<0.1
Log($NH_4 + NO_3$)	0.27 ± 0.034	7.8	<0.0001	38.7
GDD	$8.5 \times 10^{-5} \pm 3.0 \times 10^{-5}$	2.98	0.006	11.3
Precipitation	$8.8 \times 10^{-5} \pm 1.3 \times 10^{-4}$	0.68	0.50	<0.1
	Total $R^2 = 0.50$			
(B) Grasshopper density				
Intercept	−2.5 ± 1.5	−1.66	0.10	...
Bird exclosure	−0.091 ± 0.057	−1.61	0.11	2.4
Log($NH_4 + NO_3$)	−0.0022 ± 0.049	0.04	0.96	<0.1
GDD_{t-1}	$4.3 \times 10^{-4} \pm 4.3 \times 10^{-5}$	9.89	<0.0001	58.5
$Precip_{t-1}$	$-9.3 \times 10^{-5} \pm 2.0 \times 10^{-4}$	−0.46	0.67	<0.1
	Total $R^2 = 0.61$			

† GDD_{t-1} = growing degree days in the previous year; $Precip_{t-1}$ = precipitation in the previous year's growing season.

TABLE 4. Results of simultaneous multiple regressions of (A) log(density) for mixed-feeding grasshopper species and (B) log(density) for grass-feeding grasshopper species vs. log(N) (as available soil ammonium and nitrate), growing degree days in the previous year (GDD_{t-1}), and previous year's growing season precipitation ($Precip_{t-1}$).

Variable	Coefficient ± 1 SE	t	P	Percentage of variance explained
(A) Mixed-feeding grasshoppers				
Intercept	-0.27 ± 0.33	-0.82	0.41	
Bird exclosure	-0.08 ± 0.11	-0.77	0.44	<0.1
$Log(NH_4 + NO_3)$	0.62 ± 0.09	6.27	<0.0001*	29.9
GDD_{t-1}	$8.37 \times 10^{-4} \pm 8.4 \times 10^{-5}$	4.36	<0.0001*	17.6
$Precip_{t-1}$	$-1.1 \times 10^{-3} \pm 14.2 \times 10^{-4}$	-2.81	0.006*	8.3
				(Total $R^2 = 0.56$)
(B) Grass-feeding grasshoppers				
Intercept	-1.5 ± 0.24	-6.13	<0.0001	
Bird exclosure	-0.038 ± 0.086	0.44	0.66	<0.1
$Log(NH_4 + NO_3)$	-0.61 ± 0.075	-8.13	<0.0001*	28.8
GDD_{t-1}	$5.7 \times 10^{-4} \pm 6.6 \times 10^{-5}$	8.59	<0.0001*	30.5
$Precip_{t-1}$	$2.3 \times 10^{-4} \pm 3.06 \times 10^{-4}$	0.76	0.45	<0.1
				(Total $R^2 = 0.60$)

 * Significant at $P < 0.05$.

tion (Scharff 1954, Dempster 1963, Gage and Mukerji 1977, Rodel 1977). In addition, warmer temperatures may increase food and nutrient intake by increasing activity time (Chase 1996) and digestive passage rates (Harrison and Fewell 1995). Thus, through several mechanisms, grasshopper recruitment, and thus abundance, may be influenced by thermal conditions.

Precipitation appeared less important than thermal conditions, as it was not related to total grasshopper density (Table 3B). This was due in part to differences among feeding guilds, as mixed-feeder densities were negatively related to previous year's precipitation, while grass-feeder densities were not. Moist conditions may render nymphs and eggs more vulnerable to fungal infection (Joern and Gaines 1990). If so, this vulnerability was experienced more strongly by large mixed-feeding species.

Despite the importance of thermal conditions, bottom-up influences on grasshoppers were important in this study. First, N addition greatly increased the quantity (Fig. 2) of plant material available to grasshoppers. Second, prior to 1989, N addition had shifted the plant community to a high biomass of species with high tissue N and low secondary chemical content, e.g., the grasses *Agropyron repens* and *Poa pratensis* (Tilman 1987). Finally, following sufficiently warm years, grasshopper density responded overwhelmingly to N addition (Fig. 4). Mixed-feeding grasshopper species (*Melanoplus femur-rubrum* and *M. bivittatus*) accounted for most of this response, as the resulting increase in plant N content from 1.4% to 2.5% (Fig. 2) increased plant quality (in vivo DMD) for them by 30% (Fig. 3B). Presumably because of the high biomass of high quality plant material, mixed-feeding species increased dramatically in response to added N in both absolute densities and relative abundance (Fig. 5, Table 4A). These results were unlikely to reflect ''functional'' responses of individual grasshoppers to patches of fer-

tilized and unfertilized prairie, because grasshopper community composition changed dramatically within 3 m of the edge of fertilized plots (Fig. 5).

Such bottom-up influences were not experienced by all grasshopper species. Plant quality (in vivo DMD) to grass-feeding grasshoppers was not related to plant tissue N (Fig. 3B). Not surprisingly, these grasshopper species responded negatively to N addition (Fig. 5, Table 4B). Instead, their abundance appeared to be associated almost entirely with thermal conditions (Table 4B). Therefore, N addition positively affected only the feeding guild that was limited most strongly by plant N content.

Evidence for bird predator effects on grasshoppers was equivocal. Removal of birds yielded lower, rather than higher, grasshopper densities (Table 3, Fig. 4), but a higher relative abundance of *M. femur-rubrum* and *M. bivittatus,* the primary mixed-feeding species. One hypothesis to explain this pattern is that spiders, which are also eaten by birds, responded positively to bird removals, thereby inducing compensatory predation on grasshoppers. Spiders can prey only on nymphs or smaller (<0.2 g) grasshopper species (Belovsky et al. 1990, Belovsky and Slade 1993, Chase 1996, Schmitz et al. 1997), so spiders may impact smaller, grass-feeding grasshopper species more heavily than larger species. Larger grasshoppers may also be more vulnerable to bird predators (Belovsky et al. 1990, Belovsky and Slade 1993), and thus relatively more abundant beneath bird exclosures. An alternative hypothesis is that large species are superior competitors and selective predation by birds on large species mediates asymmetric competition on smaller species. Such an indirect effect could yield higher total densities outside bird exclosures (Belovsky and Slade 1993, 1995). These two hypotheses cannot be satisfactorily distinguished with the current data but suggest interesting further avenues to explore.

Regardless of these potential indirect effects, bird predators did not impose strong top-down effects on total grasshopper densities (Tables 3, 4), as observed in some previous studies (Fowler et al. 1991, Bock et al. 1992). Instead, birds may modify herbivore species composition and the abundance and impacts of other predators, and these effects may vary among years (Joern 1992, Belovsky and Joern 1995, Belovsky and Slade 1995). The total "net" effect of all predator groups (birds, spiders, skinks) on grasshoppers in this field cannot be measured with the current experimental design. However, spiders are eaten by birds and, in this experiment, increased in abundance beneath bird exclosures (Table 2). Therefore, spider effects on grasshoppers may compensate rather than add to the effects of birds. If so, the results support the "reticulated food web" hypothesis (Strong 1992, Polis and Strong 1996) that a diversity of predators and herbivores and omnivory in terrestrial food webs will have compensatory interactions that prevent strong top-down effects.

There is increasing evidence to suggest that plant resources, predators, and abiotic conditions interact to regulate herbivore communities. Several recent studies demonstrate stronger predator effects in more productive environments (Stiling and Rossi 1997, Fraser 1998, Fraser and Grime 1998). I did not observe such effects here, as the interaction between N addition and bird exclosures was not significant for grasshoppers or plants (Table 1). Thus, the results do not support the general hypothesis that predator effects should be stronger in more productive environments (Rosenzweig 1971, Fretwell 1977, Oksanen et al. 1981, Oksanen 1990, Hunter and Price 1992). However, plant resource limitation and thermal conditions interacted strongly in this study (Table 3). This interaction reflected greater responses by grasshoppers to N addition following warm years and greater declines in density within fertilized plots following cool years (Fig. 4). Such responses could be caused by a variety of mechanisms, including temperature-mediated shifts in plant quality (Schramm 1972), or greater effects of plants with high secondary chemical content on grasshoppers in unfertilized plots (Stamp and Yang 1996, Stamp et al. 1997). Another source of interaction might be effects of shading by the higher biomass of fertilized plants on soil temperatures and egg development, as fertilized plots at CCNHA with canopies opened by pocket gopher (*Geomys bursarius*) soil disturbances contained twice the density of grasshoppers (Huntly and Inouye 1988). These and other possible mechanisms need more exploration.

Recent reviews promote the idea that no single factor appears to control insect herbivore abundances (Cornell and Hawkins 1995, Hawkins et al. 1997). Different factors may become important in different years (Belovsky and Joern 1995) or may interact. This study suggests that different factors may also influence herbivore guilds. In this old-field prairie, N appeared to limit the abundance of large, mixed-feeding grasshoppers more strongly than did bird predators or abiotic conditions (Table 5A). Thus, bottom-up influences were stronger for this guild. However, thermal conditions had a stronger influence than soil N on smaller, grass-feeding grasshoppers (Table 5B). These contrasting results suggest that herbivores within a single terrestrial food web may be composed of guilds regulated by different factors, e.g., some by predation, some by plant resources, and some by abiotic conditions.

This study reveals that bottom-up influences on insect herbivore abundance may be more important than top-down effects in strongly N-limited environments such as this old-field prairie. However, abiotic factors, such as annual thermal conditions in this study, can indeed mask trophic influences, whether bottom-up or top-down. Moreover, the results suggest that abiotic and trophic influences are not merely additive. Abiotic conditions can interact with bottom-up influences, and several recent studies suggest that abiotic conditions can enhance or inhibit predator impacts on herbivores (e.g., Chase 1996, Stiling and Rossi 1997, Fraser 1998). Furthermore, bottom-up and top-down factors may differ in their importance for guilds within an herbivore trophic level, as I found for mixed-feeding vs. grass-feeding grasshoppers. Clearly, the regulation of herbivore communities involves many more complex interactions than much current theory suggests (see Leibold 1989, Schmitz 1993, Belovsky and Joern 1995), and many new questions have emerged from recent experimental results. Future experiments that explore mechanisms of interaction among abiotic conditions, plant resources, and predators should provide important insights.

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