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Seasonal variation in top-down and bottom-up processes in a grassland arthropod community

Abstract Both top-down and bottom-up processes are common in terrestrial ecosystems, but how these opposing forces interact and vary over time is poorly understood. We tested the variation of these processes over seasonal time in a natural temperate zone grassland, a field site characterized by strong seasonal changes in abiotic and biotic conditions. Separate factorial experiments manipulating nutrients and cursorial spiders were performed in the wet and dry seasons. We also performed a water-addition experiment during the summer (dry season) to determine the degree of water limitation during this time. In the spring, nutrient addition increased plant growth and carnivore abundance, indicating a bottom-up control process. Among herbivores, sap-feeders were significantly enhanced while grazers significantly declined resulting in no net change in herbivore abundance. In the summer, water limitation was predominant increasing plants and all herbivores while nutrient (N) effects were non-significant. Top-down processes were present only in the spring season and only impacted the guild of grazing herbivores. These results show that bottom-up limitation is present throughout the season in this grassland, although the specific limiting resource changes as the season progresses. Bottom-up processes affected all trophic levels and many different guilds, while top-down effects were limited to a select group of herbivores and did not extend to the plant trophic level. Our results show that the relative strengths of top-down and bottom-up processes can shift over relatively short periods of time in habitats with a strong seasonal component.

Keywords Top-down · Bottom-up · Grassland · Trophic structure · Seasonal variation

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Introduction

The role of top-down and bottom-up processes in terrestrial systems has been a topic of great debate in the ecological literature for some time (Schmitz et al 2000; Halaj and Wise 2001). While previous arguments often focused on the existence of the two processes (Hairston et al 1960; Power 1992; Strong 1992), more recent arguments have stressed the interactions of such processes (Letourneau and Dyer 1998; Forkner and Hunter 2000; Denno et al. 2002; Moran and Scheidler 2002). Good factorial experiments simultaneously manipulating top-down and bottom-up factors have shown that these processes vary in space (Stiling and Rossi 1997; Fraser and Grime 1998; Forkner and Hunter 2000; Denno et al. 2002; Moran and Scheidler 2002). For instance, within a salt marsh habitat, natural variation in plant quality and habitat complexity altered the bottom-up processes that control the herbivorous insect, *Prokelisia*, while having little effect on top-down control (Döbel and Denno 1994; Denno et al. 2002). Conversely, in an oak forest, increases in plant quality tended to increase the strength of top-down control (Forkner and Hunter 2000). Variation in the strength of top-down and bottom-up processes may be evident within the same system but different geographic areas (Marquis and Whelan 1994; Floyd 1996; Forkner and Hunter 2000) or even within a single field site (Denno et al. 2002). One source of variation that has received less attention is variation in time (Moran and Scheidler 2002), which could be an important component of highly seasonal systems.

Grasslands have received a relatively large amount of attention with regard to top-down and bottom-up control (Bock et al. 1992; Schmitz 1994, 1998; Chase 1996, 1998; Moran et al. 1996; Beckerman et al. 1997; Schmitz et al. 1997; Moran and Hurd 1998; Ritchie 2000; Schmitz and Suttle 2001; Moran and Scheidler 2002), and these studies have demonstrated that both top-down and bottom-up processes are prevalent.

Although top-down and bottom-up factors have been demonstrated in many grasslands, it is likely that much

variation exists in the strengths of these interactions. Examining the patterns and mechanisms of this variation should be the next step in understanding trophic interactions in these ecosystems.

At our field site, a natural grassland in central Arkansas, strong seasonal variation in rainfall and temperature is likely to affect top-down and bottom-up processes. We therefore simultaneously manipulated nutrients and spiders during both the wet and dry seasons. Previous experiments in nearby field sites indicated that variation in cursorial spiders and nutrients (especially N) are important top-down and bottom-up factors (Moran and Scheidler 2002). In a separate experiment, we manipulated water abundance during the summer months, when rainfall is low at our field site. We developed three a priori hypotheses (1) water is the most important bottom-up factor during the summer months, (2) nitrogen limitation is the important bottom-up factor in the spring when rainfall tends to be high, and (3) top-down processes are stronger in the spring when abiotic conditions are favorable for plants and consumers. Although we predict that this grassland is not an equilibrium community (Fretwell 1977; Oksanen et al. 1981), spring is the time when we predict rapid growth of arthropod populations and when it is therefore likely that predator impacts will be pervasive (Moran et al. 1996).

Materials and methods

Field site

The field is a 30 ha mixed forest and grassland habitat located in Conway Co., near the town of Center Ridge in central Arkansas (35°19.24N, 92°33.24W). The experimental area is a natural prairie dominated by the native grass, little bluestem (*Schizachyrium scoparius*), which co-occurs with other grasses (mostly dropseeds, *Sporobolus* spp.) and numerous forb species, with lanceleaf coreopsis (*Coreopsis lancolata*), venus looking-glass (*Specularia perfoliata*), false garlic (*Nothoscordum bivalve*), toothwort (*Dentaria laciniata*), and sunflower (*Helianthus* spp.) being most common. There are also scattered trees, mostly post oak (*Quercus stellata*), blackjack oak (*Q. marilandica*), black hickory (*Carya texana*), and shortleaf pine (*Pinus echinata*). This combination of grassland and scattered trees creates a savanna-like habitat. The arthropod assemblage is typical for grasslands with many herbivorous Homoptera, Orthoptera, Coleoptera, and Lepidoptera, which co-occur with predatory Araneae, Hymenoptera, Coleoptera, and Mantodea. Coleoptera and Homoptera are the most common herbivores while the most common predatory arthropods are the spiders (Araneae), particularly cursorial species. The most abundant species of spiders are *Rabidosa rabida*, *R. punctulata*, *Oxyopes* spp., *Sassacus* spp., and *Sitticus* spp. Previous experiments have shown that these cursorial spiders are the most important arthropod predators in this ecosystem (Baldridge and Moran 2001, Moran and Scheidler 2002).

It is likely that this field site is affected strongly by seasonal variation in climate. Spring is characterized by mild temperatures and abundant rainfall, while summer tends to exhibit high temperatures and a scarcity of rainfall (Fig. 1). Consequently, most increases in plant biomass and growth in consumer populations occurs in the spring. Fire, the major disturbance event in this system, is also common in the late summer and autumn (Skelton et al. 2003).

To determine the seasonal changes in arthropod community structure without experimental manipulation, we sampled three
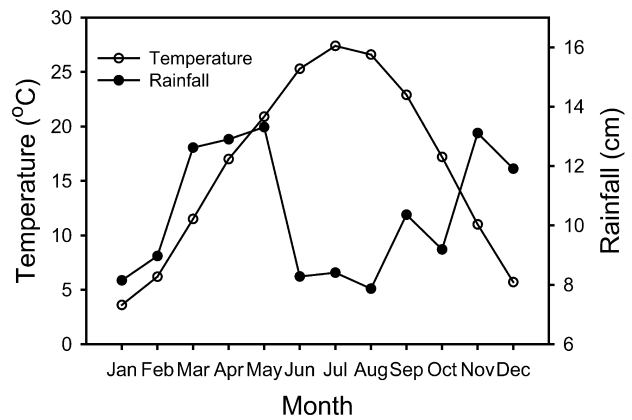
Fig. 1 Average seasonal temperature and rainfall patterns in central Arkansas. Courtesy of the National Weather Service, Little Rock, Arkansas

10 m ×0.20 m transects by D-vac once per month from March until September. Captured arthropods were sorted to order and trophic level. Trophic levels were further sorted into guilds: sap-feeders and grazers for herbivores, and specialists and generalists for carnivores.

Experimental design

We established 20 plots in a 2×2 factorial experiment in the summer of 2000, manipulating nutrients and predator density. Plots were 3 m ×3 m and bounded by 60 cm high aluminum flashing. The top of the aluminum had a 5 cm inward facing lip, which was coated with Tangletrap (Tanglefoot, Grand Rapids, Mich.), to prevent the movement of non-flying arthropods. Nutrients were enhanced by adding a nitrogen-based fertilizer (30 N, 2 P, 4 K) at a rate of 30 g/m². Hand searching and removal of cursorial spiders once per week reduced the density of these predators below normal levels. This experiment was performed for 100 days, from 23 June to 30 September, which corresponds to the dry season when temperatures are high and rainfall low (Fig. 1).

At the end of the experiment, the entire plot was sampled by D-vac for arthropods. Arthropods were sorted to order, trophic position (herbivores, carnivores, or detritivores) and counted. The herbivore trophic level was further divided into the sap-feeding and grazing guilds while carnivores were divided into specialists and generalists. Sap-feeders are mainly of the orders Homoptera and Hemiptera that have piercing-sucking mouthparts and feed on phloem fluid, while grazers are those arthropods with typical mandibulate mouthparts. Generalist carnivores are those predators that consume a wide variety of taxa (e.g. cursorial spiders) and specialists are those that feed on only one or a few taxa (e.g. parasitoids). Although some species of arthropods are omnivorous, most get the majority of their resources from one trophic level (Oksanen and Oksanen 2000). We classified detritivores as those arthropods that feed on dead organic matter or those that feed on fungi. Plants were sampled once at the end of the experiment by removing all aboveground, live biomass from a 1 m² quadrat from the center of each plot (to reduce the probability of edge effects). The plant biomass was then sorted to species, dried, and weighed.

We performed a 2×2 factorial experiment in the spring of 2001, with the same design and sampling as the experiment described above. This experiment began on 10 March and ended on 17 June, which corresponds to the time of rapid growth of plants and consumers when temperatures are relatively mild and rainfall is high.

We performed a water addition experiment in the summer of 2001. We established 12 open plots (i.e. no barriers), each 5 m ×5 m in the prairie habitat. Six randomly selected plots were given
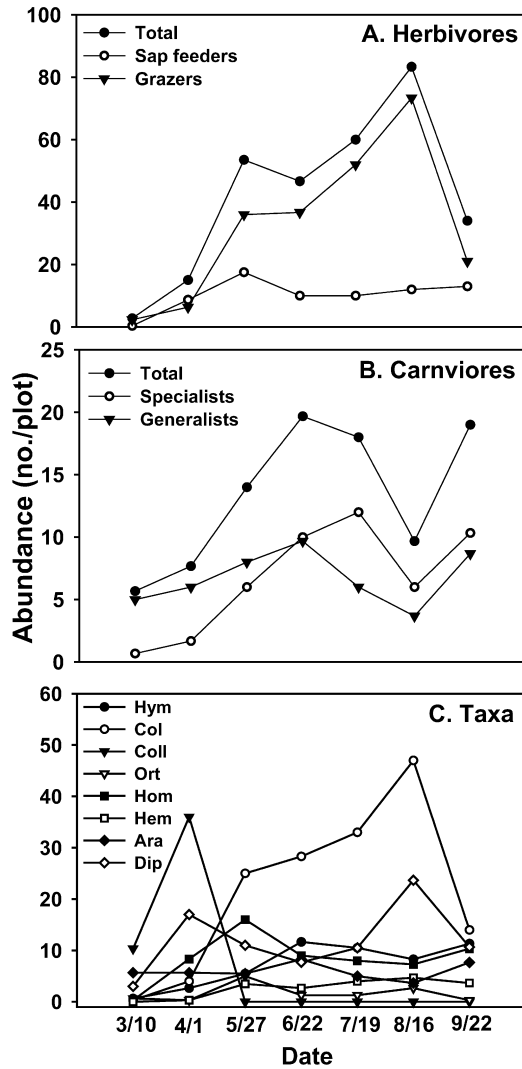
Fig. 2 Arthropod abundance trends throughout the growing season for **A** herbivores, **B** carnivores, and **C** taxonomic groups in our field site. Each data point is mean abundance calculated from transects (1 per plot) sampled across three plots, Transect = 2 m². (*Hym* Hymenoptera, *Col* Coleoptera, *Coll* Collembola, *Ort* Orthoptera, *Hom* Homoptera, *Hem* Hemiptera, *Ara* Araneae, *Dip* Diptera. Average SE: herbivores =10.46, sap feeders =3.34, grazers =7.12, carnivores =2.89, specialists =1.65, generalists =2.31, Hym =1.61, Col =4.84, Coll =3.32, Ort =0.77, Hom =2.26, Hem =1.54, Ara =1.87, Dip =4.07)

additional water at a rate of 2.54 cm per week, which is well above the average rainfall, but equal to normal rainfall in the spring (Fig. 1), and within the range of rainfall seen in wet summers. We did not perform a water addition experiment in the spring, since doing so would increase moisture availability above what is normally seen in this system. Arthropods were sampled five times during the experiment, once before treatment manipulation and four times during water addition. Sampling was accomplished by placing sticky traps on the ground in the center of each plot. Each trap was a 10 cm ×10 cm wooden board painted with Tangletrap. We also destructively sampled the entire plot by D-vac at the end of the experiment. Arthropods from the D-vac samples were sorted with the same methods utilized in the two factorial experiments. Plants were sampled from a 1 m² quadrat once before treatment manipulation began and once at the end of the experiment.
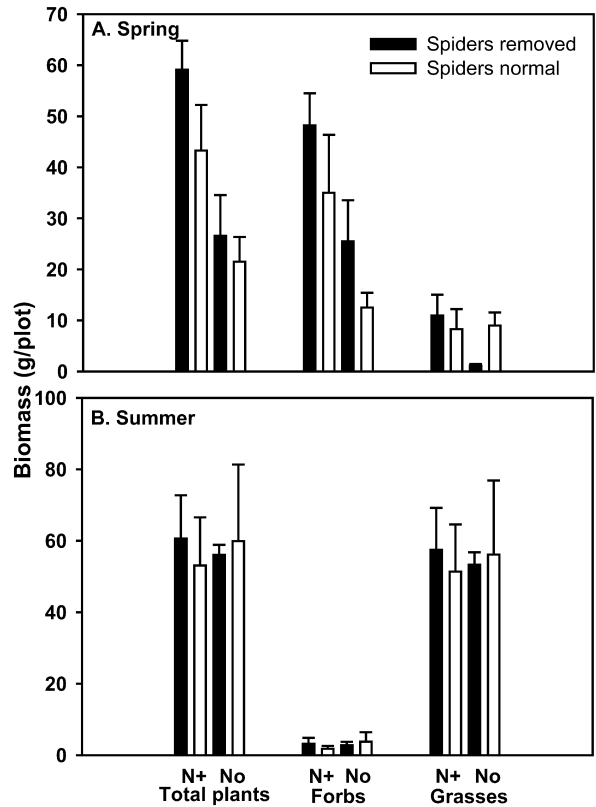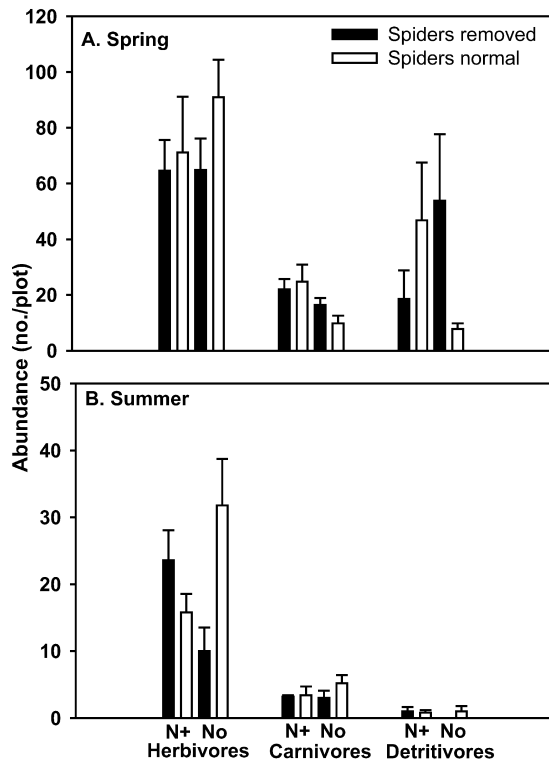

Fig. 3 Biomass ± 1SE of plant community in response to nutrient and spider manipulation during **A** the spring experiment and **B** the summer experiment. *N+*, nutrients added; *No*, nutrients normal. Sample area =1 m²)

Analysis

All data that violated the homogeneity of variances assumption were $\log_{10}$-transformed prior to analysis. Herbivore load was calculated as the amount of herbivorous arthropod biomass per 100 g of plant biomass (Root 1973). Data from the two factorial experiments were analyzed by two-way ANOVA. Data from the water experiment, where we measured each plot multiple times, were analyzed by repeated measures MANOVA (profile analysis, Von Ende 2001). All data are presented in figures as untransformed means ±1 SE of the mean.

Results

Herbivores increased during the course of the season then declined rapidly in September (Fig. 2A) in the non-experimental grassland samples. Grazing arthropods were much more common than sap-feeders and showed a large increase in their abundance during the mid-summer. Sap-feeders exhibited a minor peak in May. Carnivores generally increased during the season although there was a slight reduction in abundance during August (Fig. 2B). Generalists were more common early in the season while specialists were more common at the end of the season. Among taxonomic groups, the Coleoptera were the most abundant, especially during the mid-summer when a large number of flea beetles (subfamily
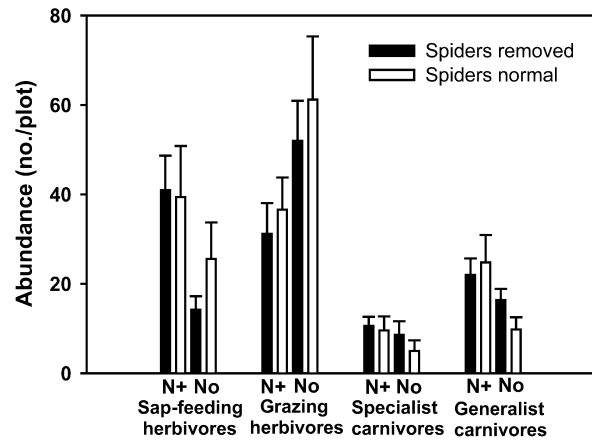
Fig. 4 Abundance ±1 SE of arthropods in response to nutrient and spider manipulation during **A** the spring experiment and **B** the summer experiment (*N+* nutrients added, *No* nutrients normal, sample area =9 m²)

Fig. 5 Abundance ±1 SE of arthropod guilds in response to experimental manipulation of nutrients and carnivore abundance in spring experiment (*N+* nutrients added, *No* nutrients normal, sample area =9 m²)

Fig. 6 Herbivore load ± 1SE in response to nutrient and spider manipulation during **A** the spring experiment and **B** the summer experiment (*N+* nutrients added, *No* nutrients normal)
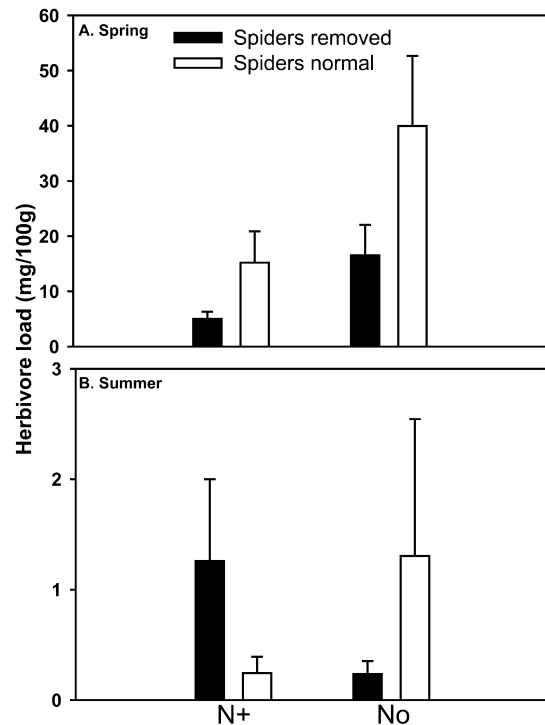
Alticinae) were present. Other numerically abundant groups included the Homoptera and Diptera. Collembola showed an early peak in the spring (Fig. 2C), but these are mostly fungivores, part of the detritivore food chain, and therefore were not of great interest in this study.

In the factorial experiments, we removed an average of 25.90±1.88 spiders per plot in the spring and 14.80±1.56 spiders per plot in the summer. The number removed declined over the course of the experiments indicating our removal was successful, and the density of spiders removed is comparable to other experiments (Moran and Scheidler 2002). The lower number of spiders removed in the summer experiment was a function of fewer spiders present during that time of year, not a reduced capture efficiency of the researchers.

Nutrient addition caused a significant increase in overall plant biomass (two-way ANOVA, $F_{1,16}=14.75$, $P=0.001$) while spider reduction effects were non-significant (Fig. 3A) in the spring experiment. Forb response was similar to the overall plant response, with a significant nutrient effect (two-way ANOVA, $F_{1,16}=8.40$, $P=0.010$) and non-significant spider effect. For grass biomass, there was a significant nutrient × spider interaction (log₁₀-transformed data, two-way ANOVA, $F_{1,16}=0.784$, $P=0.022$), as grass biomass declined in plots with normal nutrient levels and spiders removed (Fig. 3A). Nutrient addition and spider removal had no significant effect on overall plant biomass during the summer experiment, nor was there any significant effect on forbs or grasses (Fig. 3B). By late September, when the summer experiment ended, most of the biomass was composed of grass, whereas forb biomass was very low (Fig. 3B).
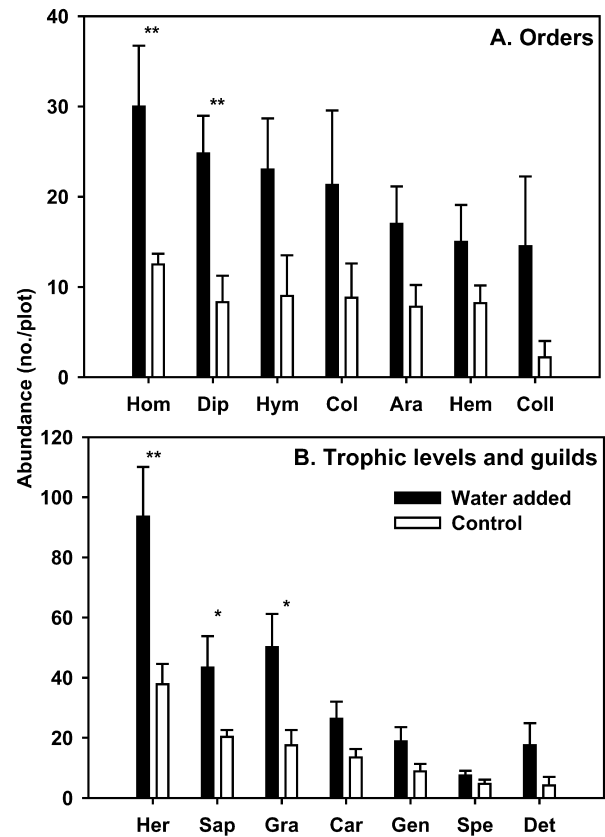
Spider and nutrient treatment effects on total herbivores were non-significant in the spring (Fig. 4A). However, carnivore abundance was enhanced in nutrient addition plots (two-way ANOVA, $F_{1,16}=6.565$, $P=0.021$)
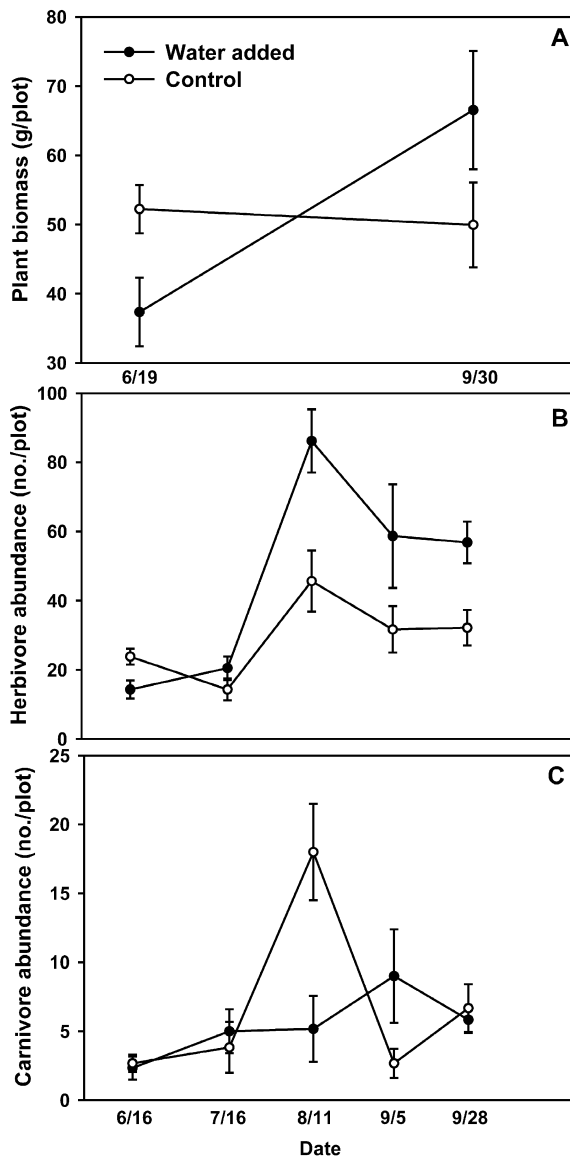
Fig. 7 Response ±1 SE for water addition experiment for **A** plant biomass, **B** herbivorous arthropod abundance, and **C** carnivorous arthropod abundance. Sample area =1 m^2 for plants and 100 cm^2 (sticky trap) for arthropods

Fig. 8 Abundance ±1 SE of arthropods in final D-vac samples from water experiment for **A** orders of arthropods and **B** trophic levels and guilds of arthropods. * $P<0.05$, ** $P<0.01$. (*Hom* Homoptera, *Dip* Diptera, *Hym* Hymenoptera, *Col* Coleoptera, *Ara* Araneae, *Hem* Hemiptera, *Coll* Collembola, *Her* total herbivores, *Sap* sap feeding herbivores, *Gra* grazing herbivores, *Car* total carnivores, *Gen* generalist carnivores, *Spe* specialist predators, *Det* detritivores, sample area =25 m^2)

regardless of spider treatment. There was also a significant nutrient × spider interaction on detritivores (log$_{10}$-transformed data, two-way ANOVA, $F_{1,16}$=5.324, P=0.035). In the summer experiment, there was a significant nutrient × spider interaction effect on herbivorous arthropods (two-way ANOVA, $F_{1,16}$=9.918, P=0.006). Herbivores tended to be more abundant under spider removal treatment in nutrient enhanced plots, while the opposite pattern was evident in normal nutrient plots (Fig. 4B). Nutrient and spider effects on carnivores and detritivores were non-significant.

A guild analysis of the spring experiment showed that, although total herbivores showed no significant treatment response, sap-feeders were significantly higher in nutrient addition plots (Two-way ANOVA, $F_{1,16}$=6.21, P=0.024) and grazers were significantly lower ($F_{1,16}$=5.44, P=0.033, Fig. 5). Among carnivores, generalists were significantly higher in nutrient addition plots (Two-way ANOVA, $F_{1,16}$=6.57, P=0.021, Fig. 5) while specialists showed no response. Spider removal had no effect on any carnivore or herbivore guild in the spring. There were no treatment effects on any order or guild of arthropods in the summer factorial experiment.

Herbivore load was significantly higher in nutrient-normal plots (two-way ANOVA, $F_{1,16}$=5.78, P=0.029) while spider removal caused a significant decrease in herbivore load ($F_{1,16}$=4.96, P=0.041, Fig. 6A) in the spring experiment. The interaction term was non-significant. There was no significant main or interaction effect on herbivore load in the summer experiment (Fig. 6B). We note that herbivore load was substantially lower and exhibited higher variance in the summer compared to spring. The high variance was apparently caused by the presence of a few large-bodied Orthoptera (grasshoppers) that reached maturity late in the summer and were present in some of the plots. Although not very abundant, a single
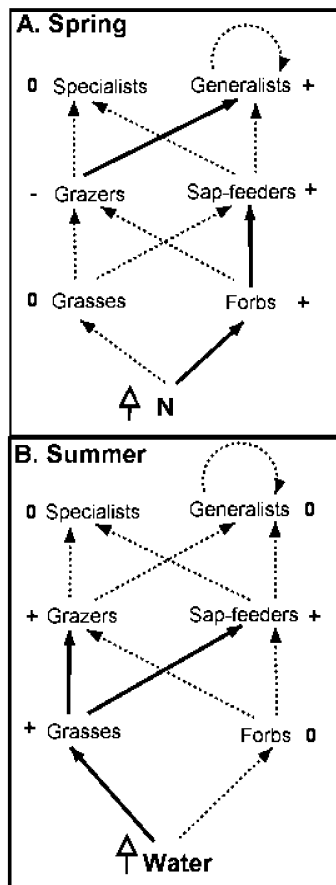
Fig. 9 Trophic diagrams of the effects of **A** nutrient enhancement in spring and **B** water enhancement in summer. *Arrows* indicate energy flow through the system. *Thick arrows* indicate a relatively strong interaction, *dotted arrows* indicate a relatively weak interaction. +, 0, − indicate response to resource enhancement

large individual contributed disproportionately to the consumer biomass measurement.

The addition of water in the summer caused an increase in plant biomass over time (significant treatment × time interaction, repeated measures MANOVA, Wilks' Lambda =0.595, $F_{1, 10}$=6.793, P=0.026, Fig. 7A). Biomass was lower in water addition plots before the experiment began, a function of random chance in the assignment of plots to treatments. However, in water addition plots biomass increased during the course of the experiment while control plots showed a slight decline, so that by the end of the experiment the water addition plots had higher biomass (Fig. 7A). Herbivore abundance on sticky traps was significantly higher in water addition plots during the course of the experiment (treatment × time interaction, repeated measures MANOVA, $F_{4,7}$=10.376, P=0.005, Fig. 7B). Water addition had no effect on carnivorous arthropod abundance (Fig. 7C). The final D-vac sample generally agreed with the sticky trap samples. Water addition caused a significant increase in Homoptera and Diptera and the trend was for higher abundance in all orders (although variance was high). No taxonomic group

showed any decline in abundance (Fig. 8A). Herbivores were over two times more abundant in water addition plots; this was caused by an increase in both sap-feeders and grazing insects (Fig. 8B). Neither total carnivore abundance nor the guilds of carnivores were affected by water addition (Fig. 8B).

Discussion

This system's natural history is important because it demonstrates seasonal changes in growth, which is crucial for interpreting the results of the experimental manipulations. Spring is characterized by a rapid increase of forbs, most of which are C3 plants, species that are adapted to spring growing conditions. Summer is characterized by a rapid growth of grasses, especially little bluestem (*Schizachyrium scoparius*), which is the dominant warm-season (C4) species. Therefore, the types of plants dominating this community show a dramatic shift as the season progresses. There is a commensurate shift in the arthropod community with sap-feeding arthropods peaking early in the season and grazers increasing until the end of the season. By mid-summer, flea beetles (grazers) are by far the most abundant herbivore. Carnivorous arthropods also show shifts in abundance with generalists common in spring and specialists common in summer.

The bottom-up effects on plants varied according to season. The addition of N-fertilizer caused a relatively strong effect in the spring but no detectable effect during the summer. However, the plant community did respond to water addition in the summer, showing a shift in the important limiting resource. Therefore, the plant community is subject to bottom-up limitation throughout the season, although the specific resource changes. The type of plant responding to resource enhancement was limited to the dominant plant type of the season, with the spring forbs responding to N and the summer grasses to water addition. Therefore, this plant community is a non-equilibrium system showing temporal shifts in plant species and limiting resources each season.

Bottom-up effects on the plant community were transmitted to higher trophic levels as well, albeit in a complex manner. The arthropod community responded strongly to nitrogen addition in the spring, but not in the summer. Instead, water availability became the major limiting resource in the summer. Embedded in these general bottom-up responses were complex interactions. In the spring, sap-feeding herbivores were almost two times more abundant in nitrogen addition plots while grazers showed a decline of similar magnitude. These opposite responses cancelled each other out so that there was no net change in herbivore abundance. Bottom-up effects also caused an increase in carnivore abundance, particularly generalist predators. Conversely, in the summer there was an overall net increase in herbivore abundance, with both sap-feeders and grazers responding positively to water addition but this effect did not extend to carnivores.

The arthropod community did not respond strongly to experimental manipulation of top-down processes. This was in contrast to a previous experiment when top-down effects of cursorial spiders were strong, especially at the end of the season (Moran and Scheidler 2002). However, that previous experiment was in an old-field site that had much richer soil and higher productivity. Although this study did not detect strong top-down control by cursorial spiders, it appeared that other predators were still able to exert substantial influences. Unmanipulated generalist predators such as hemipterans and web-building spiders, did increase significantly with nutrient addition in the spring. We suggest that the decline in grazing herbivores in nutrient addition plots was due to this increase in generalist predators. Sap-feeding herbivores were able to increase in the presence of higher generalist predator density probably because nitrogen availability is a more important factor than predation in regulating their abundance (Mattson 1980; Vince et al. 1981; Denno et al. 1986), at least in the spring season when climatic conditions are favorable. We suggest top-down processes are less important in the summer because the harsh abiotic conditions become the overwhelming limiting factor.

It was interesting that carnivorous arthropods did not increase in the summer water experiment in a similar fashion to the spring experiment, since herbivore abundance (i.e. available prey) was higher in water addition plots. Therefore, the bottom-up effect was attenuated at higher trophic levels in the water experiment. Carnivorous arthropods may respond to increased nitrogen concentrations in their prey more strongly than abundance of prey (Fagan et al 2003), which would produce the patterns we observed. This shows that an increase in nitrogen, and subsequent increase in plant and prey quality, can more easily "cascade" up the food chain than water, which probably affects only plant quantity. Thus, the specific resource may influence strongly the trophic interactions of this system.

Herbivore load was higher when cursorial spiders were present at normal density in the spring, the opposite of what was predicted. We hypothesize that this indirect effect is caused by cursorial spiders preying on other predators. Our removal of cursorial spiders (extreme generalist predators) reduced intraguild predation within the system (Rosenheim et al. 1993; Snyder and Ives 2001) allowing other generalist predators to maintain control of herbivores, especially grazing herbivores. Since there was no net change in carnivore abundance, this explanation would be valid only if other predators were more efficient at consuming herbivores. Herbivore load was also lower in nutrient addition plots. The higher density of predators in these plots probably explains this trend through their control of grazing herbivores. In the summer, herbivore load was much lower compared to spring and showed no response to treatment manipulations.

There were also several significant nutrient × spider interaction effects. For instance in the spring, grass biomass was lower in the nutrient normal and spider reduced plots. However, in the spring grasses are a minor component of the plant community while forbs, which responded strongly to the nutrient main effect, are dominant. Detritivores in the spring and herbivores in the summer also showed significant interaction effects. We were not able to detect any mechanism for these responses by examining trophic levels or individual taxonomic groups, as all of these showed non-significant treatment responses.

The results of this study show the importance of natural history in trophic level interactions. Other grassland studies that have shown strong top-down regulation throughout the season have been in systems with different dominant herbivores, such as grasshoppers (Schmitz 1998; Schmitz and Suttle 2001) or homopterans (Denno et al. 2002; Moran and Scheidler 2002). Our system was numerically dominated by beetles in the summer when top-down effects are absent. Beetles have highly sclerotinized bodies and are therefore relatively well-protected from predation. Consequently, they showed no response to manipulations of generalist predators. Other important natural history components of our system are the physical structure of the site. Compared to old-fields (Moran and Scheidler 2002), that tend to have rich soils and adequate water supply, this site is on a south-facing slope and has very thin soils and poor water retention. These characteristics combined with the weather patterns create seasonal changes in resource limitation and prevent this system from ever reaching equilibrium.

This non-equilibrium community can be represented by a change in the trophic structure during different times of the year shown in our proposed food webs (Fig. 9A, B). In the spring, increases in nitrogen levels cause an increase in forbs which "cascades" up the food chain to sap-feeding herbivores and generalist predators. It appears that this bottom-up effect modified top-down effects through the selective predation of generalist predators on grazing herbivores (Fig. 9A). In the summer, the effects are predominantly bottom-up as an increase in water causes an increase in grass growth and a subsequent increase in both herbivore guilds. However, this effect does not extend to the carnivores (Fig. 9B). These different food webs show how shifting resource limitation may alter trophic interactions.

These results show that top-down and bottom-up processes can vary temporally within a system. Bottom-up regulation appears prevalent through time, although the specific resource changes from nutrients to water as the season progresses. Top-down processes are less common and only appear in the spring season during favorable abiotic conditions. Classical theory of trophic interactions generates predictions for equilibrium communities (Fretwell 1977; Oksanen et al. 1981; Hunter and Price 1992; Forkner and Hunter 2000). However, this system shows no evidence of equilibrium. Instead, the seasonal changes in this experiment produce different trophic responses to top-down and bottom-up manipulation. Therefore, it might be useful for ecologists to view trophic structure as a temporally shifting dynamic. In our case, the shift was due to a change in the specific limiting

resource and a shift in the energy pathway through different plant types and animal guilds. The results of our study are likely to occur in systems such as grasslands that have a strong seasonal component (Uriarte and Schmitz 1998). We predict that other systems that have this characteristic (e.g. most temperate habitats) will also demonstrate strong seasonal variation in top-down and bottom-up processes. Therefore, researchers must be mindful that even when top-down and bottom-up processes are present, they may exhibit short-term shifts in strength over time, which may have profound effects on ecosystem function.

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