COMMUNITY ECOLOGY

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Weather variation and trophic interaction strength: sorting the signal from the noise

Abstract Weather can have important consequences for the structure and function of ecological communities by substantially altering the nature and strength of species interactions. We examined the role of intra- and inter-annual weather variability on species interactions in a seasonal old-field community consisting of spider predators, grasshopper herbivores, and grass and herb plants. We experimentally varied the number of trophic levels for 2 consecutive years and tested for inter-annual variation in trophic abundances. Grasshopper emergence varied between years to the extent that the second growing season was 20% shorter than the first one. However, the damage grasshoppers inflicted on plants was greater in the second, shorter growing season. This inter-annual variation in plant abundance could be explained using the foraging-predation risk trade-off displayed by grasshoppers combined with their survival trajectory. Decreased grasshopper survival not only reduced the damage inflicted on plants, it weakened the strength of indirect effects of spiders on grass and herb plants. The most influential abiotic factor affecting grasshopper survival was precipitation. We found a negative association between grasshopper survival and the total yearly precipitation. A finer scale analysis, however, showed that different precipitation modalities, namely, number of rainy days and average precipitation per day, had opposing effects on grasshopper survival, which were inconsistent between years. Furthermore, our results suggest that small changes in these factors should result in changes of up to several orders of magnitude in the mortality rate of grasshoppers. We thus conclude that in this system the foraging-predation risk trade-off displayed by grasshoppers combined with their survival trajectory and relevant weather variability should be incorporated in analytical theory, whose goal is to predict community dynamics.

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Introduction

The idea that ecological communities can be viewed as systems of interacting predators, herbivores, plants and soil nutrients has been an effective way of organizing thinking and empirical research in ecology. Indeed, this conceptualization has led to recent, broad insight that trophic interactions in ecological systems are controlled by an interplay between top-down (emphasizing the role of top predators) and bottom-up (emphasizing the role of competition for nutrients) biotic factors (Leibold 1989; Hunter and Price 1992; Schmitz 1994; Osenberg and Mittlebach 1996; Polis and Strong 1996; Stiling and Rossi 1997; Forkner and Hunter 2000; Oedekoven and Joern 2000; Denno et al. 2002; Moon and Stiling 2002c; Moran and Scheidler 2002; Boyer et al. 2003).

This issue of top-down and bottom-up control is strongly linked to another central theme in ecology, namely, the relative importance of biotic vs. abiotic (weather) limitation of species interactions and abundances (e.g., Andrewartha and Birch 1954; Hairston et al. 1960; Hunter and Price 1992). Random abiotic factors often mitigate deterministic biotic interactions (e.g., Andrewartha and Birch 1954; Menge and Sutherland 1987; Ritchie 1996; Hunter and Price 1998), thereby constraining ecologists' ability to develop predictive theory of trophic interactions for a broad range of ecological systems. For example, weak top-down control of trophic interactions in a system could be attributed either to a dominance of bottom-up control owing to a

biotic factor or to a random abiotic factor. Although each factor could strongly limit consumer abundance, they lead to different interpretations about the nature of trophic control of food webs. The central challenge then is in devising ways to identify and quantify the nature and strength of biotic signals and separate them from noise introduced by abiotic factors in order to predict their relative importance (Ritchie 2000).

There are two main schools of thought for how to separate signal from noise in ecological dynamics. The first, time series approach, relies on long-term data on species abundance and weather variation. This approach pieces together how historical fluctuations in abiotic conditions correlate to species abundance using advanced statistical analyses (e.g., Turchin 2003). Such analyses, however, tend to rely on inter-annual data and so often lack the detail to resolve intra-annual effects. The alternative, experimental approach, aims to pinpoint the mechanistic factors influencing trophic structure and function through detailed manipulation of putatively causal factors (e.g., Resetarits and Bernardo 2002). However, field experiments are normally local and short-term and so often do not include effects of multi-annual weather variability in analyses (but see Belovsky and Slade 1995; Ritchie 2000). This implies that much might be gained by combining experimental and correlative approaches in a complementary way (Belovsky and Slade 1995).

Adopting this combined approach is potentially useful, especially in systems, where strong intra-annual biotic factors (e.g., density-dependence, trophic interactions) control the abundance of species (Belovsky and Slade 1995; Schmitz 2000; Grimm and Uchmanski 2002) and in which abiotic conditions within a season could have a strong influence on biotic processes, such that there will be little or no carryover effects from one year to the next (Ritchie 2000; Schmitz 2000; but see Gratton and Denno 2003). Given that weather variability operates at all time scales (Ghil 2002), it stands to reason that it may influence key intra-annual processes (e.g., within-season timing of life-cycle events or strength of trophic interactions), leading to sizeable community-level effects.

We report here on a multi-annual field experiment and time-dependent statistical analyses of the strength of species interactions in a seasonal old-field community. We examine the extent to which intra-annual weather effects obscure signals from trophic interactions in two consecutive growing seasons and the mechanisms by which these effects play themselves out.

Materials and methods

Natural history

This research was completed in a meadow at the Yale-Myers Research Forest in northeastern Connecticut (Schmitz and Suttle 2001). The herbs *Solidago rugosa*, *Daucus carota*, *Aster novaean-gliae*, and *Trifolium pratense*, and the grass *Poa pratensis* dominated this meadow. We examined interactions among those plants, the grasshopper herbivore *Melanoplus femurrubrum*, and an important predator of the grasshopper (Schmitz and Suttle 2001), the sit-and-wait hunting spider *Pisaurina mira*. Previous research has consistently shown that grasshoppers preferentially exploit nutri-tionally superior grasses, and can inflict considerable damage to them when *P. mira* is absent (Beckerman et al. 1997; Schmitz et al. 1997; Schmitz and Suttle 2001; Schmitz and Sokol-Hessner 2002). The presence of *P. mira* consistently causes grasshoppers to forego feeding on grasses and to seek refuge in leafy herbs, resulting in high damage levels to herbs (Beckerman et al. 1997; Schmitz et al. 1997; Schmitz and Suttle 2001; Schmitz and Sokol-Hessner 2002). This shift in resource use by grasshoppers results in a positive indirect effect of the spider on grasses and a detrimental, negative indirect effect on herbs. Moreover, although this simplified food web does not include the entire old-field community (i.e., carnivores and herbivores), it captures most of the dynamics of this system (Schmitz 2003).

Because arthropods in this system are ectothermic, they should respond to weather variability on a very short-term basis (i.e., days to weeks) (Belovsky and Slade 1995; Pitt 1999). One major source of weather variability in our study system is the timing and duration of rainfall events. Water evaporation can effectively reduce temperatures and thus is likely to influence the thermoregulation of ectothermic organisms. Indeed, in response to cooler thermal conditions, many phytophagous insects (e.g., grasshoppers) stop feeding and take refuge in the organic debris layer underneath the plants (Uvarov 1977; Chappell and Whitman 1990; Pitt 1999). Reduced feeding associated with long or aggregated rain events may increase the mortality rate of phytophagous insects due to a heightened risk of starvation. Moreover, when feeding activity is resumed, surviving insects are expected to compensate for their poor body condition by increasing their feeding time or by foraging in highly nutritious but risky patches and thus may suffer from a high predation rate. Such reduced herbivore survival should lead to lower damage to plants.

Study design

Quantifying the strength of intra-annual biotic signals and separating them from noise introduced by environmental stochasticity requires designing a multi-annual experiment. For 2 consecutive years, we conducted an enclosure experiment in the field to test for temporal changes in the strength of direct effects of spiders on experimental populations of grasshoppers and indirect effects of spiders on grass and herb resources. A positive indirect effect of predators on plants happens, whenever predator addition to food webs results in lowered damage to plants (i.e., a net increase in plant biomass) relative to food webs containing only herbivores and plants. A negative indirect effect occurs whenever predator addition to food webs causes herbivores to inflict more damage to plants (i.e., a net decrease in plant biomass) than in food webs containing only herbivores and plants.

We conducted the experiment in standard aluminum screening enclosure cages measuring 0.25 m^2 (basal area)×1 m (height). The protocol for cage construction and placement in the field has been presented elsewhere (Schmitz 2004). The cages were arrayed in a randomized block design separated by 1.5 m and placed over natural vegetation in the field. This method of cage placement does not introduce bias in initial grass and herb composition in the cages (Schmitz 2004). We removed all animals within the cages by carefully hand-sorting through the vegetation and litter in each cage. We removed all the large insects and spiders from the cages (small spider species could not be removed). Although the size and habitat use prevented the capture of small spider species, it also precluded their ability to prey upon the grasshoppers or the treatment spiders.

The experiment consisted of two treatments and a control randomly assigned to each of 19 blocks in the first year (2000) and 15 blocks in the second year (2001). We assembled, in enclosure cages, experimental food webs composed of plants only (one-trophic-level control), plants and grasshoppers (two-trophic-level

treatment), and plants, grasshoppers, and a spider predator (three-trophic-level treatment). In early July of each year, we collected grasshoppers and *P. mira* spiders using sweep nets. We stocked each two-level and three-level treatment cage with six early instar (2nd) grasshopper nymphs, which was about 1.5 times the natural field densities at the time of stocking. At this time, we also added one spider predator to the three-level treatment cages. The spiders stocked were large enough (16–20 mm) to capture and subdue all sizes of grasshopper prey (juveniles 7–18 mm; adults 19–24 mm) (Schmitz and Suttle 2001). Note that owing to phenological variation in the emergence of grasshoppers, stocking in 2001 was delayed by 2 weeks.

We censused enclosure densities of grasshoppers and spiders over the course of the entire experiment. After initial stocking, the first three censuses were performed at 2-day intervals to ensure that grasshopper populations did not go extinct due to artifacts of initial conditions. Thereafter, enclosures were monitored every 5 days until the termination of the experiment in early September. The experiment ran for the entire life history development of the instar nymphs and terminated just before the seasonal onset of frosts that kill the arthropod community and cause the herbaceous plant community to senesce. At this time, all plants in the enclosures were clipped to the soil surface, sorted by class (grass and herb), dried at 60°C for 48 h and weighed.

Weather features

Precipitation (tipping bucket rain gauge; Omnidata), global radiation (pyranometer sensor; LiCor), and air and soil temperatures (temperature sensor; Vaisala) were measured continuously during experimentation period using an automated (Easy Logger 900 data recording system; Omnidata) meteorological station located at the Yale-Myers Research Forest.

Data analysis

We tested for indirect effects of *P. mira* on plants by comparing biomass in one-level food webs ($N_{one-level}$, plants only) with biomass in two-level webs ($N_{two-level}$, plants and grasshoppers) and three-level webs ($N_{three-level}$, plants, grasshoppers and spider) within and between years using randomized block ANOVAs for grasses and herbs individually. We used Bonferroni corrected *t*-tests to identify treatments that were significantly different. Following Schmitz et al. (2000), we calculated the strength of the direct effect of grasshoppers on plants as $\ln(N_{two-level}/N_{one-level})$. Similarly, the strength of the indirect effect of spider predators on plants was calculated as $\ln(N_{three-level}/N_{two-level})$. Note that $\ln(N_{three-level}/N_{one-level})$ is the net (direct+indirect) effect on plant biomass in three-level webs.

We tested for correlations between final plant abundances and survival of grasshoppers in the absence and presence of spiders using simple linear regressions for grasses and herbs separately. To test if these linear relationships were consistent between years, we used stepwise multiple linear regressions with year (year 2000=0 and year 2001=1), predation treatment (predator absent=0 and predator present=1), survival (proportion of surviving grasshoppers) and all possible interaction terms as independent variables.

We tested for inter-annual differences in the survival of grasshoppers with and without their spider predators in two different ways. We first used a Cox proportional hazard model (Hosmer and Lemeshow 1999) with year (year 2000=0 and year 2001=1), predation treatment (predator absent=0 and predator present=1), and the respective interaction terms as covariates. This is a commonly used survival analysis method, which allows the evaluation of effects of different predictors (i.e., covariates) on mortality rate independent of the time varying background mortality rate (Hosmer and Lemeshow 1999). To control for repeated measurements on a subject, which, in our case, were individual cages that were repeatedly censused throughout the season, we used a robust jackknife variance estimator grouped by observations per cage (Lin

and Wei 1989). Second, we compared the end-of-season enclosure densities in two-level webs (plants and grasshoppers) and three-level webs (plants, grasshoppers and spider) within and between years using a randomized block ANOVA. This was followed by Bonferroni corrected *t*-tests to identify treatments that differed.

To test for the effects of weather on grasshopper survival, we first divided each season into intervals of 10 days. Ten-day intervals are appropriate because we stocked 2nd instar nymphs, and it takes about 10 days for grasshoppers to complete each of the next three instar stages before becoming an adult (Vickery et al. 1981). This variable, however, did not meet the proportionality assumption of the Cox proportional hazard model and was thus treated as a stratification factor (a standard procedure for the Cox model; Hosmer and Lemeshow 1999). Predation treatment (predator absent=0 and predator present=1), global radiation (W/m^2), soil temperature (°C), average precipitation per day (cm), and the number of rainy days were treated as covariates in a Cox proportional hazard model allowing us to estimate a coefficient (β) for each one of them and test for its significance. Furthermore, using the exponent coefficient (e^β), we could predict the expected change in mortality risk per one unit change in the covariate. For instance, an $e^\beta=2$ for average precipitation per day (measured in centimeters) means that an increase of 1 cm in average precipitation should result in doubling the mortality risk of grasshoppers. Because of inconsistency in weather effects between years, we analyzed each year separately. Values of features of the weather that we used in our analysis correspond to measurements taken within a time window of 10 days before a mortality event occurred. Since mortality events in each cage occurred at different times during the season, substantial variability with respect to each of these abiotic factors was introduced into the analysis.

Results

We detected significant differences in the final biomass of grasses (Fig. 1a) and herbs (Fig. 1b) between the 2 years (ANOVA, $F_{1,96}$=3.96, P=0.05 and $F_{1,96}$=22.28, P<0.001, respectively). Across the 2 years, there was a significant treatment (number of trophic levels) effect on the final biomass of both grasses and herbs (ANOVA, $F_{2,96}$=11.98, P<0.001 and $F_{2,96}$=7.02, P=0.001, respectively). Additionally, the respective interaction terms (year×treatment) were significant (ANOVA, for grasses $F_{2,96}$=3.47, P=0.035 and for herbs $F_{2,96}$=3.29, P=0.042), indicating that the effect of the number of trophic levels on final plant biomass differed between the 2 years. Indeed, in 2000, we could not detect significant changes in the final plant biomass as a function of the number of trophic levels for either grasses or herbs, indicating very weak direct and indirect effects on the plants (Fig. 1a, b). Specifically, the strength of the direct effect of grasshoppers on grass and herb biomass was −0.226±0.159 and −0.053±0.161 (mean ±1 SE), respectively. The strength of the indirect effect of spiders on grass and herb biomass was −0.009±0.128 and −0.025±0.204 (mean±1 SE), respectively. In contrast, in 2001, grasshoppers in the absence of their spider predators caused a significant reduction in grass biomass, relative to the plant-only control (Fig. 1a). Similarly, there was a marginal reduction in herb biomass (Fig. 1b). Indeed, the strength of the direct effect of grasshoppers on grass and herb biomass was −1.097±0.179 and −0.385±0.181 (mean ±1 SE), respectively. The addition of predators caused a reduction in the damage inflicted to grass by grasshoppers,
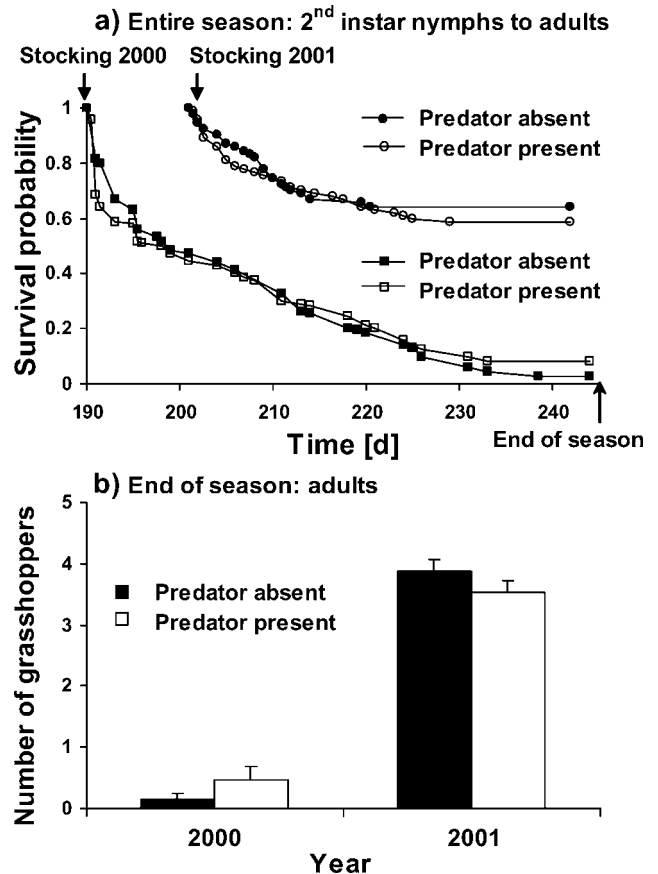
to the extent that the abundance of grass in the presence of predators was not significantly different from the plant-only control (Fig. 1a). The opposite pattern was detected for herbs. In other words, there was an increase in the damage inflicted to herbs, as shown by a significant lower abundance of herb in the three-trophic level treatment than that in the plant-only control (Fig. 1b). We estimated the strength of the indirect effect of spiders on grass and herb biomass to be 0.941 ± 0.144 and -1.799 ± 0.229 (mean±1 SE), respectively.

Using survival analysis we found that the average mortality rate of grasshoppers in 2000 was 4 times higher than in 2001 (Cox proportional hazard model, $z=-9.04$, $P<0.001$; Fig. 2a). We could not detect significant differences in grasshopper survival between the predator and no predator treatments across the 2 years (Cox proportional hazard model, $z=-0.13$, $P=0.9$; Fig. 2a). Additionally, the interaction term (year×predator treatment) was not significant (Cox proportional hazard model, $z=0.92$, $P=0.36$), indicating that this lack of numerical effect of spiders on grasshoppers was consistent between years (Fig. 2a). Similarly, final (end-of-season/experiment) number of grasshopper (Fig. 2b) varied significantly between years (ANOVA, $F_{1,64}=375.45$, $P<0.001$), but not with predator treatment (ANOVA, $F_{1,64}=0.003$, $P=0.96$). There was no significant year×predator treatment interaction (ANOVA, $F_{1,64}=3.45$, $P=0.07$).

We next used simple linear regressions to test for links between final plant abundances and survival of grasshoppers. When we examined years in aggregate, we found that final grass biomass was negatively correlated with the proportion of surviving grasshoppers in the absence ($R^2=0.348$, $F_{1,32}=17.04$, $P<0.001$), but not in the presence ($R^2<0.001$, $F_{1,32}=0.01$, $P=0.912$), of the predator (Fig. 3a).
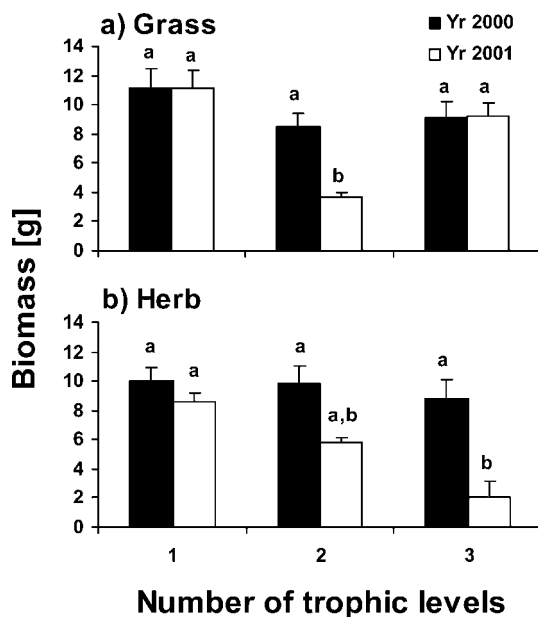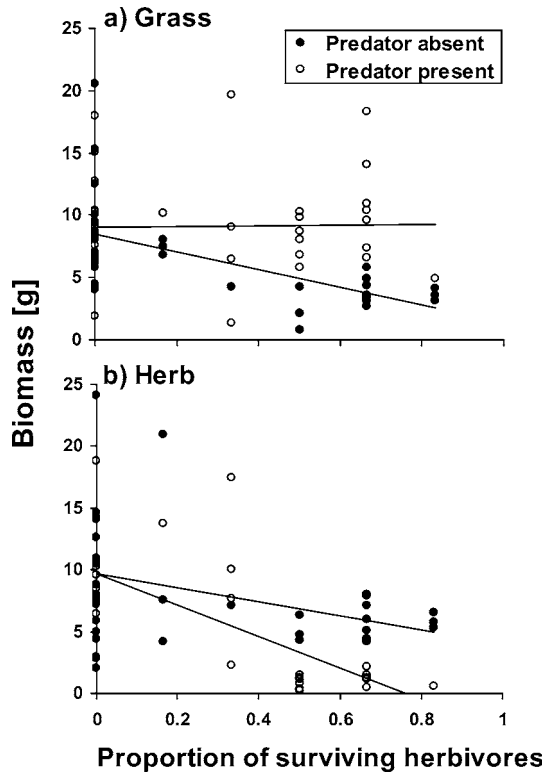

a) Entire season: 2nd instar nymphs to adults

Fig. 2 The effect of year and spider predator on **a** survival and **b** final (end-of-season) number of grasshoppers (±1 SE). Due to phenological differences in the emergence of grasshoppers between years, the season in 2001 was 20% shorter than that in 2000. *d* Day

In contrast, final herb biomass was negatively correlated with grasshopper survival during both predation treatments (predator absent $R^2=0.146$, $F_{1,32}=5.45$, $P=0.026$, and predator present $R^2=0.499$, $F_{1,32}=31.85$, $P<0.001$; Fig. 3b). However, the slope of the line for the predator-present treatment was steeper than that of the predator-absent treatment, indicating a stronger numerical effect of grasshoppers on herbs, when they were exposed to predation risk (Fig. 3b).

To test if the above relationships between grass biomass and herbivore survival were consistent between years, we used stepwise multiple linear regressions ($R^2=0.229$, $F_{2,65}=10.924$, $P<0.001$). Our analysis showed that final grass biomass was negatively correlated with the proportion of surviving grasshoppers ($t=-4.236$, $P<0.001$), and that there was a significant predation treatment×survival interaction effect ($t=3.927$, $P<0.001$). However, we could not find a significant effect of year or predation treatment on grass biomass ($P=0.435$ and $P=0.621$, respectively). Additionally, none of the two- and three-way interaction terms (except for the one mentioned above) were significant ($P\geq0.85$ in all cases), indicating that our results were consistent between the 2 years.
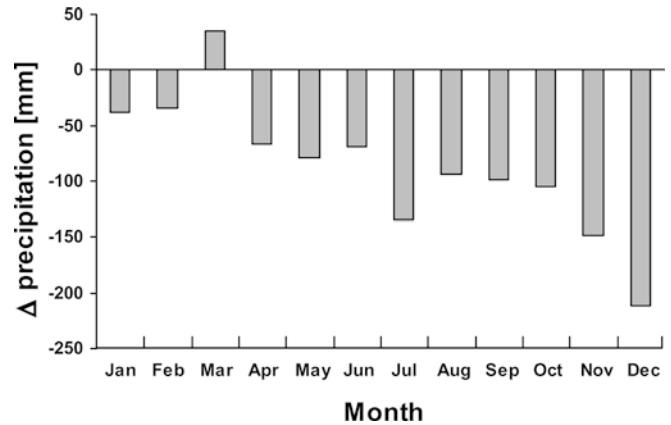
Applying a similar analysis for the final herb biomass ($R^2=0.362$, $F_{2,65}=20.026$, $P<0.001$), we detected signifi-

Fig. 1 Final (end-of-season) biomass (±1 SE) of **a** grass and **b** herb plants in food webs of varying number of trophic levels. *Different letters* indicate significant differences between columns. *Yr* Year

Fig. 3 The negative correlation between survival of grasshoppers and final biomass of **a** grass and **b** herb plants in the presence and absence of a spider predator when years were aggregated

Fig. 4 Monthly differences in the cumulative precipitation between years (Δ=year 2001–year 2000). Total precipitation in 2000 was significantly higher than that in 2001 (Wilcoxon signed test, $Z=$ −2.90, P=0.004). *Jan* January, *Feb* February, *Mar* March, *Apr* April, *Jun* June, *Jul* July, *Aug* August, *Sep* September, *Oct* October, *Nov* November, *Dec* December

cant year×survival and predation treatment×survival interaction effects ($t=$−3.195, P=0.002 and $t=$−3.272, P=0.002, respectively). However, we could not find a significant effect of year, predation treatment or survival on the herb biomass (P=0.991, P=0.839 and P=0.683, respectively). Additionally, the interaction terms, year× predation treatment and year×predation treatment×survival, were not significant (P=0.747 and P=0.866, respectively).

Of the variation in plant biomass that can be explained by the regression analyses (30–36%), the majority of it is attributed to the combined effect of the foraging-predation risk trade-off displayed by grasshoppers and their survival trajectory. When these factors were included in the analysis, we could not detect differences in plant biomass between the 2 years. We thus next searched for links between grasshopper survival and abiotic conditions.

Total precipitation in 2000 was significantly (Wilcoxon signed test, $Z=$−2.90, P=0.004) higher than that in 2001 by ~200 mm (Fig. 4). However, we could not detect significant differences in global radiation, soil temperature and air temperature between years (Table 1). Using these abiotic factors as covariates in a Cox proportional hazard model, we found that in both years the most influential factors were number of rainy days and average precipitation per day; however, effects were stronger by several orders of magnitude in 2000 than in 2001 (Table 2). Furthermore, these two factors had opposing effects on survival of grasshoppers within each year, which were also inconsistent between years. Specifically, a 1-day increase in the number of rainy days in 2000 should increase mortality risk by three orders of magnitude, while similar effect in 2001 should reduce mortality risk by 80%. Similarly, in 2000 an increase of 1 cm in average precipitation per day should reduce mortality risk by 15 orders of magnitude, while in 2001 the same effect should result in an increase of up to 74% in mortality rate of grasshoppers. The effects of global radiation and soil temperature on grasshopper survival were also not consistent between years. Specifically, global radiation had a negative effect on grasshopper survival in 2000, but a positive effect in 2001. Additionally, soil temperature had a negative effect on grasshopper survival in 2000;

Table 1 Summary statistics of the daily global radiation, soil temperature, and air temperature as measured at the Yale-Myers Research Station during the years 2000-2001

[a]There were no significant differences between years with respect to all three abiotic factors (Wilcoxon signed test applied to daily measurements)

	Global radiation (W/m²)[a]		Soil temperature (°C)[a]		Air temperature (°C)[a]	
	2000	2001	2000	2001	2000	2001
Mean	64.63	65.52	10.34	10.17	9.33	9.05
Median	59.99	60.99	11.81	12.86	11.19	10.39
Minimum	0.91	2.50	−1.08	−0.30	−15.99	−9.97
Maximum	133.02	132.36	23.28	23.04	23.45	26.98
Coefficient of variation	0.57	0.58	0.83	0.92	1.08	1.17
Wilcoxon signed test	$Z=$−0.22, P=0.83		$Z=$0.57, P=0.57		$Z=$−0.36, P=0.72	

Table 2 The effects of predation treatment and weather features[a] on grasshopper survival. *NS* Not significant, *LRT* likelihood ratio test

Year	Predation		Global radiation (W/m²)		Soil temperature (°C)		Average precipitation per day (cm)		Number of rainy days		Model statistics
	e^β	Statistics	e^β	Statistics	e^β	Statistics	e^β	Statistics	e^β	Statistics	
2000	–	NS	1.05	$z=2.79, P=0.005$	–	NS	1.04×10^{-15}	$z=-6.31, P<0.001$	2.92×10^{3}	$z=6.31, P<0.001$	LRT=124, $df=7$, $P<0.001$
2001	–	NS	0.89	$z=-5.52, P<0.001$	–	NS	1.74	$z=3.40, P<0.001$	0.21	$z=-8.40, P<0.001$	LRT=61, $df=5$, $P<0.001$

[a] Treating these factors as covariates in a Cox proportional hazard model enabled us to estimate a coefficient (β) for each factor and to test for its significance. In addition, using the exponent coefficient (e^β) we could predict the expected change in average mortality risk of grasshoppers per one unit change in each of these covariates. For instance, an increase of 1 cm in average precipitation per day in 2000 should reduce mortality risk of grasshoppers by factor of 1.04×10^{-15}

however, we could not detect any effect of this same variable in 2001 (Table 2).

Discussion

We undertook this study to examine temporal variation in the strength of food web interactions in a typical New England meadow community. Using experimentally assembled food webs, we varied the number of trophic levels and tested for inter-annual variation in trophic abundances. We then investigated possible links between trophic abundances and weather variability to identify the relevant scales and processes required to predict community dynamics.

Grasshopper emergence varied between years to the extent that the season in 2001 was 20% shorter than that in 2000. The development and maturation of grasshopper eggs depend on a certain exposure to moisture level and the acquisition of a sufficient number of heating degree-days integrated over the entire year (Isley 1938; Stauffer and Whitman 1997; Fisher et al. 1999; Beckerman 2002). Thus, when integrated over such a long period, even small changes in any of these limiting factors could translate into significant changes in grasshopper emergence. Indeed, although inter-annual weather variability seemed relatively low, we could still detect considerable phenological differences in grasshopper emergence.

Grasshoppers inflicted greater damage to plants during the shorter season than during the longer one. In 2000, we could not detect any effect of the number of trophic levels on either grass or herb biomass. However, in 2001 grasshoppers inflicted significant damage to plants, which varied as a function of the presence of spider predators. Specifically, *P. mira* spiders had no net direct effect on grasshopper density, but their presence brought about an increase in grass biomass and a decrease in herb biomass. This outcome is consistent with expectations of the indirect effects of predators on plants that are mediated entirely by changes in grasshopper foraging behavior to decrease predation risk (Schmitz 1998). In the absence of predators, grasshoppers appear to preferentially exploit nutritionally superior grasses. The presence of *P. mira* caused grasshoppers to forego feeding on grasses and to seek refuge in leafy herbs, resulting in high damage levels to herbs.

Abiotic factors could influence this old-field community in many different ways, resulting in a relatively complex study system, which might be difficult to resolve. Indeed, at first glance, it seems that many patterns and processes in this old-field community were affected by weather variability. However, when we examined the results more carefully, we found that, of the variation in plant biomass that can be explained by our statistical analyses (30–36%), the majority of it is attributed to the combined effect the foraging-predation risk trade-off displayed by grasshoppers and their survival trajectory. Decreased grasshopper survival not only reduces the damage inflicted to plants, it weakens the strength of indirect effects of *P. mira* spiders

on grass and herb plants. Indeed, when the survival of grasshoppers in 2000 was ≤10%, no net effect of number of trophic levels on plant biomass could be detected. Clearly, in this system, both the foraging-predation risk trade-off displayed by grasshoppers and their survival should be incorporated in models aiming to predict plant dynamics.

Studies on grasslands have rigorously investigated the role top-down vs. bottom-up control processes play in structuring the community (Schmitz 1994; Belovsky and Slade 1995; Chase 1996; Moran et al. 1996; Ritchie 2000; Moran and Scheidler 2002). Recent studies on terrestrial systems, however, have demonstrated that bottom-up and top-down processes often interact to influence community dynamics, suggesting that these two control types should not be viewed separately (Osenberg and Mittlebach 1996; Stiling and Rossi 1997; Forkner and Hunter 2000; Oedekoven and Joern 2000; Denno et al. 2002; Moon and Stiling 2002a, b, c Moran and Scheidler 2002; Boyer et al. 2003). Previous research on this old-field community, along with the current study, illustrate that plant abundances are strongly regulated by top-down control (Beckerman et al. 1997; Schmitz et al. 1997). Increased precipitation is likely to have a positive effect on plant growth, however, and since there was more rain in 2000 than in 2001, one should ask how these two different control processes interacted to influence plant abundances. We suggest that because most of the differences in plant abundances between the 2 years could be explained using the foraging-predation risk trade-off displayed by grasshoppers in combination with their survival, the net effects of these bottom-up factors on plant biomass were marginal.

Abiotic factors such as weather influence populations directly through physiology and/or indirectly through ecosystem processes (Stenseth et al. 2002). We found that weather variability had direct effects on grasshopper survival that resulted in indirect effects on plant abundances. However, the most influential factor was precipitation. Water evaporation can effectively reduce temperatures and thus is likely to influence the thermoregulation of ectothermic organisms such as grasshoppers. In response to cooler thermal conditions, grasshoppers stop feeding and take refuge in the organic debris layer underneath the plants (Uvarov 1977; Chappell and Whitman 1990; Pitt 1999). Thus, long or aggregated rain events may increase the mortality rate of grasshoppers due to a heightened risk of starvation. Indeed, when we examined years in aggregate we found a negative association between grasshopper survival and total precipitation. However, rain could also enhance plant growth and, thus, might result in a positive effect on grasshopper survival. Using number of rainy days and average precipitation per day as covariates in a Cox proportional hazard model, we found evidence for both positive and negative effects of these factors on grasshopper survival, which also were inconsistent between years. This suggests that the complex of weather variables have different interactions with grasshopper physiology in different years. Furthermore, our analysis shows that small changes in number of rainy days or average precipitation per day should result in changes of up to several orders of magnitude in mortality rate of grasshoppers. We interpret this to mean that grasshopper survival is highly sensitive to changes in the distribution and duration of rainy events.

There are two main schools of thought for how to conduct empirical community research, namely, the experimental and correlative approaches. In spite of individual strengths, when used independently neither approach is sufficient for gaining an overall understanding of community dynamics. There is a large body of evidence in the ecological literature illustrating that, by adopting the experimental approach, ecologists investigating terrestrial systems are able to pinpoint the key biotic factors [e.g., plant characteristics and quality (Joern and Behmer 1997; Denno et al. 2000, 2002; Oedekoven and Joern 2000; Gratton and Denno 2003), herbivore feeding mode (Moon and Stiling 2002b), interactions among herbivores (Moon and Stiling 2002c), herbivore behavioral response to predator (Beckerman et al. 1997; Schmitz et al. 1997; Schmitz 2003), predator behavior/feeding mode (Moran and Hurd 1998; Baldridge and Moran 2001; Schmitz and Suttle 2001), intra-guild predation (Finke and Denno 2002, 2003; Sokol-Hessner and Schmitz 2002)] influencing community structure and function. Clearly, the experimental research approach can effectively reduce the added complexity of environmental stochasticity, when developing models, whose aim is to predict community dynamics. Instead of introducing stochasticity for each possible direct and indirect interaction (i.e., coefficient) in a community model, one should focus only on the few interactions that are related to these important modalities. However, when such key modalities are highly sensitive to variability in abiotic factors the above mechanistic understanding would be insufficient to predict community dynamics. In such a case, it would be better first to adopt the more correlative approach of time series analysis to quantify the effect of abiotic factors on these key processes and then to explicitly incorporate only the relevant factors in the community model. This implies that experimental and correlative approaches should be complementary (Belovsky and Slade 1995).

In conclusion, by adopting an experimental approach, we were able to pinpoint two important intra-annual patterns that can strongly influence the dynamics of this old-field community, namely, the foraging-predation risk trade-off displayed by grasshoppers and their survival trajectory. Moreover, we found that the latter, herbivore survival, is negatively correlated with cumulative precipitation, but is highly sensitive to small changes in the distribution and duration of rainy events. We thus, suggest that the next logical steps in investigating this old-field system should be: (1) adopting the more correlative approach of time series analysis in order to arrive at generalizations about the effects of weather variability on herbivore survival, and (2) explicitly incorporating the above two intra-annual patterns and relevant abiotic factors in analytical theory, whose goal is to predict

community dynamics. By using this approach, we effectively reduce complexity and thus are likely to obtain a tractable understanding of community dynamics.

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