

BOTTOM-UP REGULATION OF PLANT COMMUNITY STRUCTURE IN AN ARIDLAND ECOSYSTEM

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Abstract. We conducted a long-term rodent enclosure experiment in native grass- and shrub-dominated vegetation to evaluate the importance of top-down and bottom-up controls on plant community structure in a low-productivity aridland ecosystem. Using multiple regressions and analysis of covariance, we assessed how bottom-up precipitation pulses cascade through vegetation to affect rodent populations, how rodent populations affect plant community structure, and how rodents alter rates of plant community change over time. Our findings showed that bottom-up pulses cascade through the system, increasing the abundances of plants and rodents, and that rodents exerted no control on plant community structure and rate of change in grass-dominated vegetation, and only limited control in shrub-dominated vegetation. These results were discussed in the context of top-down effects on plant communities across broad gradients of primary productivity. We conclude that bottom-up regulation maintains this ecosystem in a state of low primary productivity that constrains the abundance of consumers such that they exert limited influence on plant community structure and dynamics.

Key words: Chihuahuan desert; grassland; long-term study; precipitation; shrubland; small mammals.

INTRODUCTION

A pervasive challenge in community ecology is to understand the relative roles of bottom-up (e.g., resource) and top-down (e.g., consumer) regulatory forces on species composition, abundance, dynamics, and interactions (Oksanen et al. 1981, Power 1992, Polis 1999, Oksanen and Oksanen 2000, Ernest and Brown 2001). With regard to controls in herbaceous plant communities, net primary production is positively correlated with precipitation across a moisture gradient from desert to savanna (Webb et al. 1983, Huxman et al. 2004), and the strength of top-down forces in plant community composition of grasslands increases with net primary production (Chase et al. 2000). This suggests that net primary production is a strong regulator of trophic interactions but that the relative importance of top-down control on plant community structure and dynamics will be weakest in arid ecosystems where net primary production is chronically low (Leibold 1996, Leibold et al. 1997, Chase et al. 2000).

Water is widely acknowledged to be the key limiting resource in aridland ecosystems where the amount and timing of precipitation events strongly affect net primary productivity (Moen et al. 1993, Whitford 2002). Thus, the threshold-delay pulse-reserve model for aridland ecosystems (Ogle and Reynolds 2004, Reynolds et al. 2004) suggests strong bottom-up control of plant community composition and structure which, in turn,

controls consumer abundance and dynamics (Schwinning et al. 2004). On the other hand, numerous experimental studies have demonstrated strong consumer control on the composition, production and diversity of aridland plant communities (Brown and Heske 1990, Curtin et al. 1999, Gutiérrez and Meserve 2000). The mechanisms driving these changes involve consumption of green tissue, seed predation, shifts in species interactions, and alteration of responses to bottom-up inputs (Inouye et al. 1980, Kerley et al. 1997). These seemingly contradictory patterns result from nonlinear dynamics between rainfall, net primary production and consumers (Brown et al. 2001), which impart high temporal variation in the strength of bottom-up and top-down controls on trophic interactions in aridland ecosystems (Meserve et al. 2003, Kelt et al. 2004).

Reconciling these competing hypotheses regarding the primacy of top-down and bottom-up controls in aridland ecosystems requires long-term experimental manipulation of consumer and producer communities (Brown et al. 2001, Meserve et al. 2003). Here, we present results from a small mammal exclusion experiment designed to evaluate the relative role of bottom-up and top-down controls on plant community structure in low-productivity grass- and shrub-dominated Chihuahuan Desert ecosystems characterized by persistent resource limitation in response to highly variable seasonal and annual precipitation (Whitford 2002). Specifically, we assess how bottom-up pulses cascade through vegetation to affect rodent populations and how rodent populations affect plant community structure and dynamics. We also evaluate changes in plant functional groups comprised of species prone to rodent consumption (e.g.,

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winter annuals, forbs, grasses [Kerley et al. 1997]) to understand shifts in dominance or community composition between plots with and without rodents. Finally, we measure the effects of small mammals on the rates of plant community change over time.

METHODS

Study site

This study was conducted in the Sevilleta National Wildlife Refuge (SNWR), a 100 000-ha wildlife refuge located along the Rio Grande in Central New Mexico, USA. Mean annual temperature is 13.2°C, with a low of 1.6°C in January and a high of 25.1°C in July. Average annual precipitation is 255 mm, approximately 60% of which occurs during the monsoon season from July through September and the remainder primarily from winter frontal systems. The relative contribution of summer monsoon and winter rains varies considerably from one year to the next.

The SNWR occurs at the transition between Great Plains grassland and Chihuahuan Desert grassland and shrubland biomes. Although the area was previously grazed by domestic cattle, cattle were removed from the site in 1973. Vegetation is dominated primarily by two C₄ perennial grasses, *Bouteloua gracilis* and *B. eriopoda*, and a long-lived C₃ shrub, *Larrea tridentata* (Kröel-Dulay et al. 2004). Annual and perennial forbs occur throughout the site but abundances vary seasonally and annually depending on precipitation. Common rodents include *Perognathus flavus* (silky pocket mouse) and *Dipodomys ordii* (Ord's kangaroo rat) in the grassland, and *Dipodomys merriami* (Merriam's kangaroo rat) and *P. flavus* in the creosote shrubland. These species forage mainly on forb seeds, and to a lesser extent on leaves and insects (Ernest et al. 2000). Overall, rodent densities are higher in shrubland compared to grassland (Ernest et al. 2000, Friggens 2003).

Study design and field methods

We established replicate small mammal exclosures and open controls in grassland and shrubland areas dominated by *B. eriopoda* and *L. tridentata*, respectively. Pretreatment data were collected in 1995 and the fenced exclosures were constructed in 1996. In each vegetation type, a 192 × 192 m area was divided into four 96 × 96 m blocks. Each block contained two paired, adjacent 36 × 36 m experimental plots, one open control, and one closed to rodent access. Open control plots had their corners delimited by fence posts. Plots closed to rodent access were fenced with hardware cloth and poultry wire. Fences were buried 70 cm deep in the soil to prevent rodents from entering the exclosures through subterranean tunnels. The top 40 cm of the fences were covered with flashing to prevent rodents from climbing over them. Additional efforts to maintain treatment plots without rodents involved seasonal (spring and fall) rodent trapping inside the exclosures, and destruction of tunnels connecting burrows located outside the treat-

ment plots. During the years of the study, rodent trapping within treatment plots removed between 0 and 0.5 rodents per plot per season, equivalent to 0–3.8 rodents/ha in comparison to external densities ranging from 4 to 24 rodents/ha.

In each plot, vegetation was measured in 36 permanently located 1-m² quadrats arrayed in an evenly spaced (5.8 m) 6 × 6 grid. The cover of all plant species in each quadrat was visually estimated each year using a 1-m² quadrat frame divided into 10 × 10 cm units to facilitate cover estimates. Cover of annual species was assessed during May when annuals peak in abundance and biomass whereas perennial cover was estimated in September at the end of the summer growing season.

At each site, densities of rodent communities were recorded in three permanent mark-recapture trapping webs near our experimental treatments. Each web covers a 3.14-ha area and contains 12 rows of 12 stakes radiating out from a central point (Parmenter et al. 2003). Rodents were trapped with Sherman live traps twice a year for three consecutive nights. From 1989 to 1993 rodents were trapped once in May/June and again in July/August; since 1994 the second trapping period occurred in September/October.

Precipitation data were obtained from automated meteorological stations located within 2000 and 700 m of the grassland and shrubland exclosures, respectively. Winter–spring precipitation was obtained by summing total precipitation from October (the previous year) to May. Summer precipitation was obtained by summing precipitation from June to September each year.

Data analyses

For statistical analyses, treatment and control plots were used as sampling units, whereas the 36 quadrats within a plot were used as subsamples. Annual values (from 1995 to 2004) of cover and species richness were determined for each quadrat, and then averaged among quadrats in a plot. Annual values of cover and species richness were also calculated for shrub, grass, forb, and annual plant functional types. Some dependent variables (i.e., cover and species richness of annual functional types and grasses, community heterogeneity, and rodent densities) were transformed logarithmically to achieve homogeneity of variance and normal distribution. Hence statistical analyses were carried out on 16 plots per year, yielding a total of 160 non-independent plot samples over 10 years.

To determine if rodents increased small-scale compositional variability, we calculated plant community heterogeneity at the plot scale for each year as the mean dissimilarity in species composition and cover among each of the 36 quadrats in each treatment or control plot (Collins 1992). We used Euclidean distance (ED) as our measure of heterogeneity. With this index, as the degree of difference in composition among sample units increases heterogeneity, as measured by ED, increases. We used ED rather than percent similarity (PS) because

ED is less confounded by differences in species richness among samples.

We used time-lag analysis to determine the effects of rodents on the rate of community change over time (Collins 2000). To do so, we calculated Euclidean distance (ED) on average species cover values ($N = 36$) in each treatment and control plot over all time lags from 1995 to 2004. We plotted ED values at each time lag to produce a measure of the relative rate of community change over time. For each time series, the slope of the linear regression of the square root of the time lag vs. ED was used as our measure of rate of community change (Collins et al. 2000). One-way ANOVA was used to determine if community heterogeneity differed between treatment and control plots.

We used repeated-measures ANOVA to determine if measures of plant community structure (i.e., cover, species richness, heterogeneity) differed between treatment and control plots in grassland and shrubland areas. We used analysis of covariance (ANCOVA) to evaluate the relationship between total and seasonal precipitation and measures of plant community structure in treatment and control plots.

Rodent densities were calculated by dividing the total number of unique individuals captured in a trapping session by the trapping area of the web (4.91 ha; Friggens 2003). We used multiple regression analyses to evaluate the effects of seasonal precipitation on rodent density. Winter–spring and summer precipitation measures of the current and of the previous year were used as independent variables to predict mean annual rodent density.

RESULTS

We found no significant differences in the cover, species richness and heterogeneity of grass or shrub vegetation between rodent access and rodent removal treatments (Figs. 1 and 2, Appendix A). The same was true when time effects were considered in the repeated-measures analyses (Appendices B and C). Pillai's trace statistics indicated no evidence for nonlinear vegetation change through time in either treatment or control plots. Despite a marginally nonsignificant interaction term between vegetation type and treatment (Appendix A), there were no significant differences in cover of summer annuals between control and treatment plots in grass (repeated-measures MANOVA, $F_{1,6} = 3.06$, $P = 0.131$) or shrub vegetation (repeated-measures MANOVA, $F_{1,6} = 1.14$, $P = 0.324$). In addition, the rates of plant community change over time did not differ between treatment and control plots in grass (one-way ANOVA, $F_{1,7} = 0.02$, $P = 0.877$; control = 0.34 ± 1.41 [mean \pm SE], treatment = 0.90 ± 2.55) or shrub vegetation (one-way ANOVA, $F_{1,7} = 0.616$, $P = 0.462$; control = -2.61 ± 1.28 , treatment = -1.51 ± 1.17).

Cover and diversity of plant functional groups were positively related to seasonal precipitation, although the strength of these relationships varied (Appendix E).

Overall, cover and species richness in shrub vegetation were positively related to winter rainfall, whereas cover, species richness and community heterogeneity in grassland plots were positively related to summer rainfall (Appendix E). We found only one case in which vegetation in treatment and control plots responded differently to precipitation. In shrublands, control plots had higher community heterogeneity (6866 ± 492) in response to winter rainfall than rodent removal plots (5399 ± 492 ; Appendix E). Overall, we found no significant precipitation \times treatment interactions (Appendix E).

Consumer density was significantly positively related to total annual precipitation in a given year and the previous year in shrublands, but not in grasslands (Appendix F). Consumer density was significantly positively related to previous year's summer precipitation in shrublands, and nearly so in grasslands (Fig. 3, Appendix F). Rodent density was significantly higher in shrub- compared to grass-dominated vegetation (11.7 ± 5.0 vs. 8.4 ± 1.2 rodents/ha respectively, one-way ANOVA on logarithmic transformed data, $F_{1,30} = 4.92$, $P = 0.034$).

In summary, our results show that rodents have thus far exerted little control on plant community structure in desert grassland, and only limited control on shrub vegetation in this aridland ecosystem. Over a nine-year period in grass-dominated vegetation, rodent removal did not promote directional changes in plant community structure over time, did not modify the cover and species richness of plant functional groups nor of the whole plant community, and had little effect on the responses of plant community structure and functional groups to seasonal precipitation. In shrub vegetation, rodent removal decreased community heterogeneity in response to rainfall, but did not alter cover and species richness of the plant community as a whole, nor of plant functional types, and did not alter the rate of community change over time.

DISCUSSION

The general lack of significant treatment effects on cover and species richness of plant functional types shows that rodents exert minimal top-down control on these aridland plant communities. Unlike studies in comparable ecosystems (Brown and Heske 1990, Curtin et al. 1999, Meserve et al. 2003), rodent removal did not significantly increase the cover or species richness of winter annuals at our site (Inouye et al. 1980, Guo et al. 1995) nor did it promote higher grass cover as has been found repeatedly in North and South American arid and semiarid vegetation (Brown and Heske 1990, Kerley et al. 1997). Additionally, in contrast to other studies, the lack of change in cover of functional types observed in our study suggests that competitive interactions among plant functional types were not affected by rodent removal. Unlike other studies (e.g., Davidson et al. 1985, Guo and Brown 1996, Kerley et al. 1997), we found no

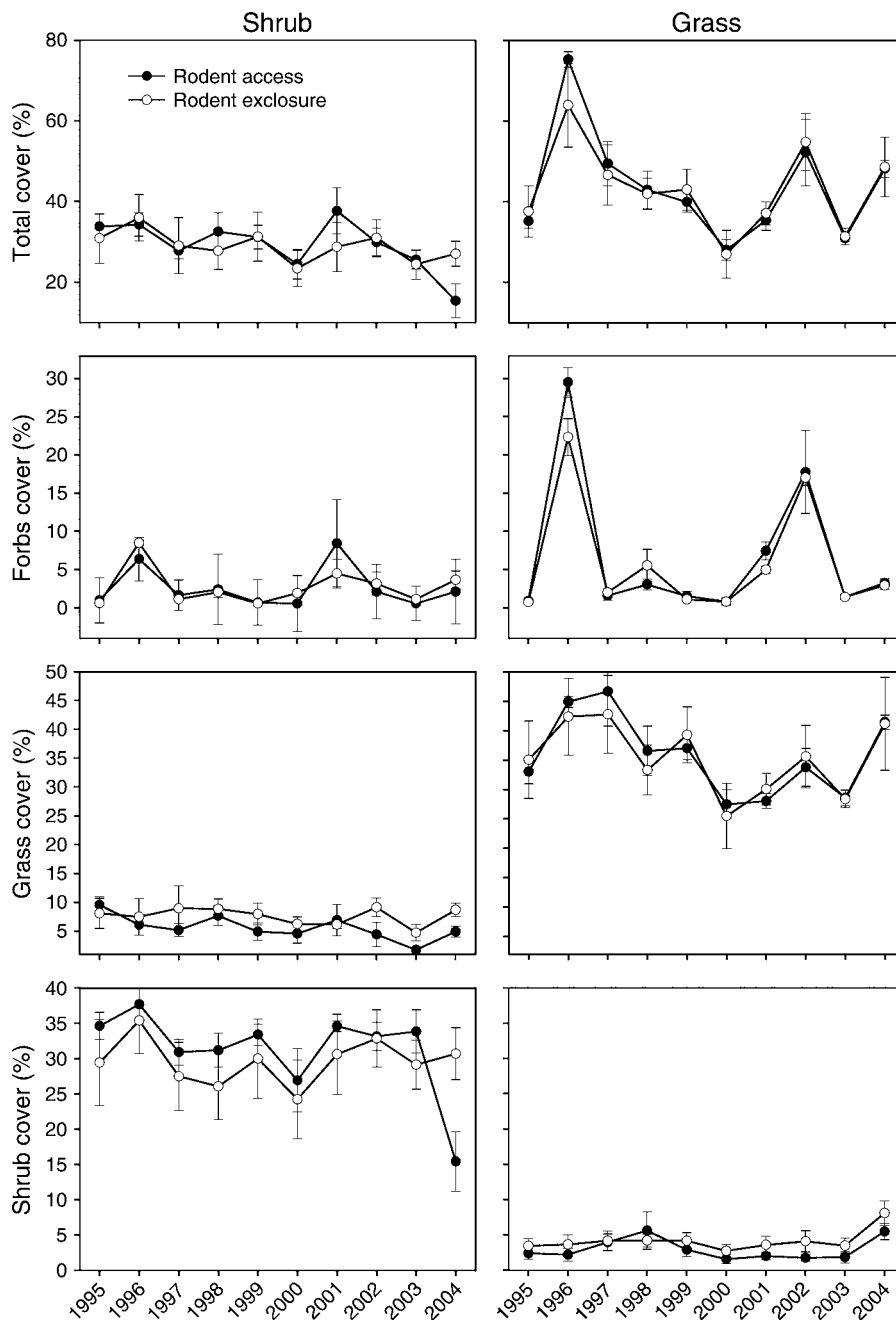


FIG. 1. Cover of functional groups in grass- and shrub-dominated vegetation in rodent removal (exclusion) and control (access) plots from 1995 to 2004. Means (\pm SE) were calculated using four measurement points.

evidence that rodent removal decreased the abundance of summer annuals or increased the abundance of competitively superior winter annuals. Thus, we found no evidence that rodents affected the interaction of different functional types in our system.

After nine years of experimental manipulations, we found weak evidence for top-down control by rodents on plant community structure in shrub-dominated vegetation where rodent removal reduced the response

of vegetation to seasonal precipitation (Appendix E). Plots with rodents were more heterogeneous than plots without rodents in years with high summer rainfall. This vegetation response is likely related to foraging behavior of the common small mammals at this site, and to a lesser extent, to changes in cover of a few plant species in response to seed predation or herbivory. The dominant rodent in these shrublands, *D. merriami*, stores seeds in shallow soil depressions (scatterhoards), which increases

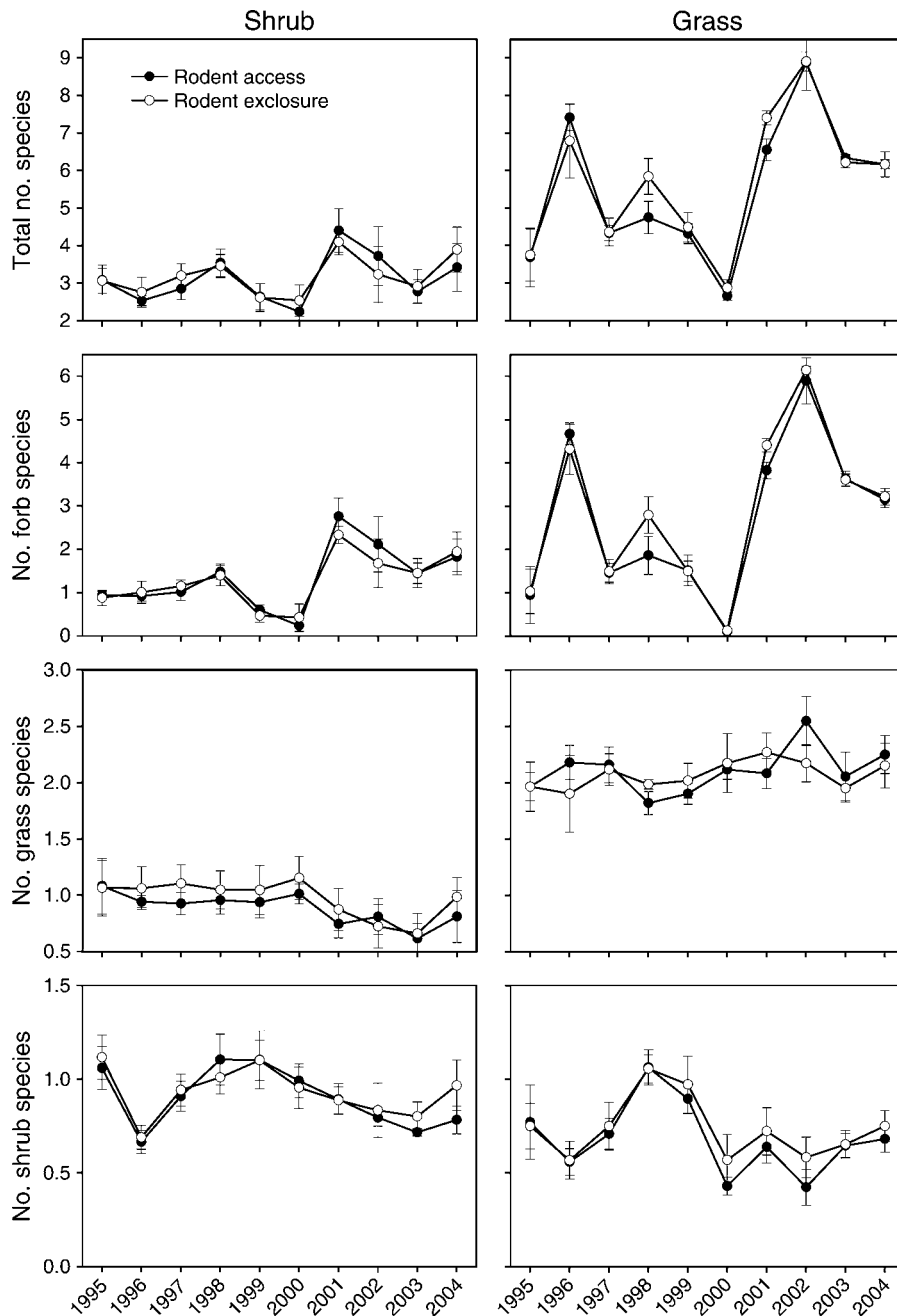


FIG. 2. Species richness of functional groups of grass- and shrub-dominated vegetation in rodent removal and control plots from 1995 to 2004. Means (\pm SE) were calculated using four measurement points.

the spatial heterogeneity of the soil seed bank (Price and Joyner 1997). At our study site, seed germination under greenhouse conditions from soil samples from plots with rodents was higher than from soils taken from plots without rodents (Koontz 2005). Because we only detected rodent effects in conjunction with high seasonal rainfall, community heterogeneity in areas with rodents likely increased due to the germination of seeds in scatterhoards rather than higher total germination and

establishment rates, because we found no significant difference in cover and species richness between treatment and control plots (Appendices A, B, and E). In contrast, we found no effect of precipitation on heterogeneity between treatment and control plots in grassland (Appendix E), because the dominant grassland rodents, *D. ordii* and *P. flavus*, store seeds in burrows (larderhoards) below the soil surface reducing their ability to germinate in response to rainfall events

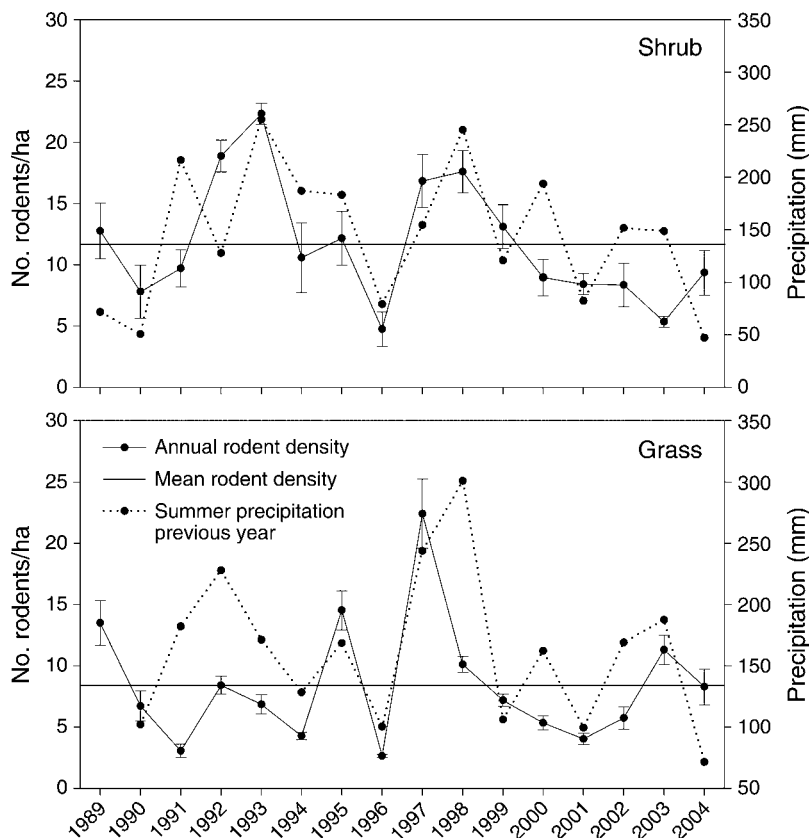


FIG. 3. Rodent density and summer precipitation (mm) of the previous year in grass- and shrub-dominated vegetation, 1989–2004. Means (\pm SE) were calculated using six measurement points.

and their contribution to aboveground community structure.

Our results document strong bottom-up regulation of plant community structure and rodent populations in this low-productivity desert ecosystem, a relatively rare phenomenon. Indeed, there is considerable evidence that rodents exert strong top-down control on cover and diversity of prairie, grassland, tundra, and forest plant communities in North America (Batzli and Pitelka 1970, Howe and Brown 2001, Manson et al. 2001; but see Gibson et al. 1990); in taigas (Moen et al. 1993), in African grasslands (Goheen et al. 2004), and in arid mixed vegetation in South America (Meserve et al. 2003). In contrast, our study demonstrated that bottom-up inputs cascade up through the system such that producers respond rapidly to precipitation (Figs. 1 and 2, Appendix C), whereas rodents increase the following year in response to plant production in the previous year (Fig. 3, Appendix F). Moreover, our findings indicate that the timing of top-down control was dictated by bottom-up inputs, and that those were more dependent on past than on current densities of consumers, since rodent densities were relatively low during seasons of high precipitation (Fig. 3, Appendix F). Our results support the idea that control by bottom-up and top-down forces in aridland ecosystems shifts through time

(Ostfeld and Keesing 2000, Meserve et al. 2003) but in our case bottom-up forces set the stage for only short periods of relatively weak top-down control.

The delayed increase in rodent abundance in response to previous season precipitation again reflects bottom-up control on rodent density mediated by the plant community. In contrast, we found limited evidence for top-down control by rodents on plant community structure once rodent populations increased in response to higher plant production. Soil nitrogen and carbon pools, and nitrogen mineralization rates, are low at our study site compared to many other ecosystems (Zak et al. 1994, Stursova et al. 2006). In addition, N availability, which also drives net primary production, changes in response to the amount and timing of precipitation events (Kieft et al. 1998, White et al. 2004). Thus, we infer that the predominance of bottom-up control results from strong resource limitation in our system.

Conceivably, this plant community could be regulated by consumer groups other than small mammals. For example, invertebrates and birds have been shown to affect vegetation structure in aridland plant communities (Davidson et al. 1985, Kerley et al. 1997) and grazing by large ungulates dramatically alters plant species composition and abundance, and net primary

production (Gosz and Gosz 1996, Ryerson and Parmenter 2001). At our study area, winter and breeding bird abundances are low whereas ants are relatively common, yet because we found few differences in vegetation structure inside and outside the exclosures we suspect that ants and birds are not strong regulators in this ecosystem.

At SNWR bottom-up regulatory forces set this desert ecosystem in a state of low primary productivity that constrains the growth of consumer populations to a point where they have limited influence on plant community structure. Extensive evidence (Milchunas and Lauenroth 1993, Yates et al. 2002, Chase 2003) supports the conclusion that precipitation and primary productivity define to a large extent the biomass of herbivores and the effects of herbivores on biomass and species composition across global scales. In this context, low-productivity ecosystems sustain low herbivore biomass, which results in subtle, at best, effects on aridland plant community structure and dynamics. In the context of larger scale patterns (Chase et al. 2000), our system lies at the low end of the precipitation (255 mm/yr) and net primary productivity ($184 \text{ kg}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$) gradients which results in a particularly low rodent (consumer) density of 10 ± 0.9 individuals/ha compared to other arid or semiarid ecosystems where rodents have a greater influence on plant community structure (e.g., 20 individuals/ha in Arizona (Ernest et al. 2001), >50 individuals/ha in Central Chile (Yunger et al. 2002)). Therefore, at our site, rodents are not abundant enough to cause major alterations to plant community composition. These findings conform at least partly to the general patterns reported by Chase et al. (2000), where herbivory in ecosystems with low primary production does not alter species composition, but reduces plant biomass. The lack of treatment effects on plant cover suggests no changes in biomass due to rodent herbivory; however, declines in biomass caused by browsing may not be detected as reductions in plant cover. Therefore our results regarding the effects of herbivores on biomass responses are equivocal.

It is hypothesized that the regulation of plant communities depends on the number of trophic levels of the system, on plant defense resources, and on the level of primary productivity that sustains variable densities of consumers that are interactively controllers or controlled by plants (Hulme 1996, Leibold et al. 1997, Oksanen and Oksanen 2000). In addition, local environmental factors, such as disturbance, size and frequency of rainfall events, and spatial variation in resources may confound the community response to seasonal precipitation and net primary production. Characterizing the interactions between producers, consumers and precipitation is an important first step toward understanding the temporal dynamics of bottom-up and top-down regulatory forces in ecosystems. In our arid Chihuahuan Desert system, rodents exerted no top-down control on plant community dynamics, species richness, composi-

tion and cover in desert grassland and exerted only minor, transient effects in shrub-dominated vegetation. Hence, we conclude that bottom-up forces strongly regulate vegetation structure and dynamics in this ecosystem. We suspect that the lack of top-down control results from chronically low rates of net primary production, which constrains densities of rodents and other consumers and sets the stage for strong bottom-up regulation. Whether or not subtle but persistent effects of consumers will eventually lead to changes in community composition in this system remains to be determined.

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APPENDIX A

Repeated-measures analysis of cover and species richness of functional types in grass- and shrub-dominated vegetation in areas with and without rodents (*Ecological Archives* E087-167-A1).

APPENDIX B

Repeated-measures ANOVA of cover and species richness of grass- and shrub dominated vegetation testing for effects of time (T), vegetation type (V), treatment (Tr), and their interactions (*Ecological Archives* E087-167-A2).

APPENDIX C

A figure showing mean (\pm SE) of cover and species richness of annual forbs in rodent removal and control plots in grass- and shrub-dominated vegetation (*Ecological Archives* E087-167-A3).

APPENDIX D

Means (\pm SE) of cover, species richness, and heterogeneity of the grass and shrub vegetation in control and treatment plots. The two columns on the right summarize values for control and treatment plots across both vegetation types (*Ecological Archives* E087-167-A4).

APPENDIX E

Analysis of covariance (ANCOVA) of cover and species richness of grass- and shrub-dominated vegetation in control and treatment plots in response to seasonal rainfall (*Ecological Archives* E087-167-A5).

APPENDIX F

Multiple regressions of rodent densities in grass- and shrub-dominated vegetation against annual and seasonal precipitation from current and previous years between 1989 and 2004 (*Ecological Archives* E087-167-A6).