

## Does shrub invasion indirectly limit grass establishment via seedling herbivory? A test at grassland-shrubland ecotones

Bestelmeyer, Brandon T.<sup>1</sup>; Khalil, N.I.<sup>1,2</sup> & Peters, Debra P.C.<sup>1</sup>

<sup>1</sup>USDA-ARS Jornada Experimental Range and Jornada Basin LTER, Las Cruces, NM 88003, USA; <sup>2</sup>Current address: Department of Biology, Case Western Reserve University, Cleveland, OH 44106, USA; USDA-ARS Jornada Experimental Range, MSC 3JER Box 30003, New Mexico State University, Las Cruces, NM 88003-0003, USA; Tel. +1 5056465139; Fax +1 5056465889; E-mail bbestelm@nmsu.edu

### Abstract

**Question:** Does shrub invasion at ecotones indirectly limit grass establishment by increasing mammalian seedling herbivory?

**Location:** Chihuahuan Desert, New Mexico, USA.

**Methods:** We tested the hypothesis that herbivore-related mortality of seedlings of the dominant perennial grass *Bouteloua eriopoda* would be highest in shrub-dominated portions of grassland-shrubland ecotones. We tested the hypothesis in two Chihuahuan Desert sites featuring similar shrub encroachment patterns but different shrub species, grass cover, and different abundances of small mammals. Within each site we transplanted *B. eriopoda* seedlings to grass-dominated, middle, and shrub-dominated positions of replicate ecotones during the time of year (mid-summer) when they would naturally appear and monitored seedling fates. We estimated population size/activity of putative small mammal herbivores.

**Results:** Seedlings were killed by mammals in greater numbers in shrubland than in grassland or middle ecotone positions at the site with large herbivore numbers. At the site with low herbivore numbers, most seedlings were killed in middle ecotone positions. The abundance patterns of herbivores did not parallel patterns of seedling herbivory across the ecotones or between sites.

**Conclusions:** Seedling herbivory is an important process and is related to vegetation composition, but the mechanisms underlying the relationship are not clear. We speculate that variation in small mammal foraging behavior may contribute to seedling herbivory patterns. Restoration strategies in the Chihuahuan Desert need to account for the abundance and/or behavior of native herbivores.

**Keywords:** Alternative state; *Bouteloua eriopoda*, Chihuahuan Desert; Desertification; *Dipodomys*; Foraging behavior; *Lepus californicus*; Restoration; Small mammal.

**Nomenclature:** Allred (1997).

### Introduction

The transformation of Chihuahuan desert grasslands to shrublands over the last century is among the most dramatic and unequivocal examples of an ecosystem transition to an alternative state (Buffington & Herbel 1965). Similar transitions have occurred in other parts of the world (e.g. Scholes & Archer 1997). Schlesinger et al. (1990) proposed a model of regional grassland to shrubland conversions in which grass loss due to grazing and drought initiates a positive feedback system that leads to increasing soil resource heterogeneity favoring shrubs. Shrub invasion, however, may have a significant indirect effect on grasses by favoring the abundances of native grass herbivores.

*Bouteloua eriopoda* (Black grama) is among the most important grass species in the northern Chihuahuan Desert and formerly dominated over 36 million ha of the southwestern United States (Wright & Streetman 1958). This grass has undergone large declines due to periods of heavy livestock grazing, drought, and encroachment by the shrubs *Prosopis glandulosa* and *Larrea tridentata* (Fredrickson et al. 1998; Gibbens et al. 2005). There have been numerous failed attempts to restore *B. eriopoda* (Herrick et al. 2006), and the micro-environmental conditions favoring *B. eriopoda* establishment occur infrequently (Neilson 1986; Peters 2000). In addition to abiotic factors, the activities of native animals may also limit grass recruitment (Brown & Heske 1990; Curtin et al. 2000). Herbivory on seedlings and adults can result in significant biomass loss, mortality, and diminished recruitment (Norris 1950; Kerley et al. 1997; Havstad et al. 1999). Herbivorous animals, especially kangaroo rats (*Dipodomys* spp.), woodrats (*Neotoma* spp.), and lagomorphs are both locally abundant and widespread in the Chihuahuan Desert (Holechek et al. 1993; Whitford 1997). The belief that rodents and lagomorphs hastened the demise of grasses in the Chihuahuan Desert led to eradication programs in the early 20th century (Herrick et al. 2006).

Shrub encroachment may indirectly amplify herbivory on grasses by promoting rodent and lagomorph abundance (Reynolds 1950; Holechek et al. 1993; Whitford 1993). Rodent abundance in degraded, mesquite-dominated states can be twice that in undegraded *B. eripoda*-dominated states (Wood 1969). Rodent abundance patterns led to the hypothesis that increases in shrub cover increase herbivore pressure on grass seedlings and remaining grasses (Campbell 1929). Here, we tested the effects of varying degrees of shrub encroachment on *B. eripoda* seedling herbivory by examining herbivory in different positions along dynamic grassland to shrubland ecotones (Peters et al. 2006a, b). Our objectives were: 1. To test the prediction that the number of seedlings killed by herbivores would increase from the grass-dominated to shrub-dominated positions of ecotones (seedling herbivory hypothesis). 2. To test the seedling herbivory hypothesis at two Chihuahuan Desert sites that differ in the dominant encroaching shrub species, the overall abundance of grass, and overall abundances of rodents and lagomorphs. We predicted that seedling herbivory would be less intense at the site with fewer rodents and lagomorphs. 3. To test a key assumption underlying the seedling herbivory hypothesis: that the abundances of herbivorous rodents and lagomorphs are highest in shrub-dominated areas.

## Methods

### Study areas

Studies were conducted at two sites located in the northern Chihuahuan Desert. The sites were chosen to reflect two different but well-understood cases of shrub invasion involving distinct contexts and different overall levels of rodent abundance. The first site is the Jornada Basin Long-Term Ecological Research site (LTER) and includes both the USDA Agricultural Research Service Jornada Experimental Range and New Mexico State University Chihuahuan Desert Rangeland Research Center near Las Cruces, Doña Ana County, New Mexico, USA. Long-term (80 year) mean annual precipitation (MAP) is  $245 \pm 87$  mm and mean monthly temperature (MMT) ranges from 3.8 to 26.1 °C (<http://jornada-www.nmsu.edu>). Ecotones at Jornada include the dominant grasses, *B. eripoda*, *Sporobolus* spp., and *Aristida* spp., and the dominant shrub *Prosopis glandulosa*. Soils at ecotones were classified as coarse-loamy Calciargids and the site has been grazed by cattle at moderate levels since the late 1960s. The second site is the Sevilleta LTER site located in the Sevilleta National Wildlife Refuge in Socorro County, New Mexico, USA. Long-term MAP is  $232 \pm 79$  mm and MMT ranges from 2.6 to 24.6 °C

(<http://sev.lternet.edu>). Dominant grasses were *B. eripoda* and *Pleuraphis jamesii*. The dominant shrub was *Larrea tridentata*. Soils ranged from loamy-skeletal to fine-loamy Typic Haplocalcids and Sevilleta has been ungrazed by livestock since 1973.

### Ecotone design

Three blocks were selected at each site that featured clear ecotones between grass-dominated and shrub-dominated areas. Blocks were from 5–10 km apart at each site. Within each block, we located three positions oriented perpendicular to the ecotone. The positions were defined as grass-dominated, middle, and shrub-dominated along which grass cover decreased and/or shrub cover increased. Positions were 100 × 300 m areas and were visually selected to feature different proportions of grass and shrub cover within an ecotone. Adjacent positions within a block were from 50 to 300 m apart depending on the rate of vegetation change across space. Vegetation cover was subsequently quantified within positions using 5, 100-m long line-point intercept transects (10-cm intervals) spaced 20 m apart and centered within each position.

### Seedling herbivory experiment

*B. eripoda* seedlings were grown in a greenhouse prior to transplanting in the field in order to minimize germination failures and seed losses due to wind and animal disturbances. *B. eripoda* seeds were collected at the Sevilleta NWR in August 2001. In June–July 2002, caryopses were placed a few mm deep in a 50:50 mixture of commercial topsoil and native soil within 2.5 cm × 2.5 cm × 6.4 cm plug flats and watered in greenhouse conditions until the seedlings were 3–6 weeks old. The variance in age occurred because many plugs were reseeded due to initial germination and establishment failures (ca. 64 % of plugs). The experiment was initiated in July (Jornada) and August (Sevilleta) of 2002 after the start of the rainy season when *B. eripoda* seedlings are expected to become established in the field (Peters 2000). Within each of the three positions of each block, seedlings were placed in groups of 10–15 seedlings/tray at 12 (Jornada) or 10 (Sevilleta) points within each grid (2190 total seedlings). Fewer points were used at Sevilleta due to the limited seedling numbers available. Points were systematically located on a single transect (a diagonal across the grid) within each grid and each point was separated by ca. 30 m. At each point, trays were buried with field soil to be flush with the soil surface. Trays were placed 50 cm from a *B. eripoda* plant to control for local microclimate. Distance to the nearest shrub was measured as a covariate.

After tray placement, seedling status was recorded every 1–3 days for 3 weeks during which time they were watered with ca. 1 ml/seedling/visit to ensure initial establishment and survival despite inadequate rainfall. Seedlings that survived the 3 week period were visited at approximately 2 (pre-winter) and 9 months (post-winter) after initial placement. An additional observation at 6 months was possible at Sevilleta. Livestock were not present in any of the blocks at either site during the experiment.

At each visit, seedlings were classified into one of five categories: (1) alive and undamaged, (2) alive but damaged by herbivores either through folivory or digging at the roots, (3) dead or entirely absent due to herbivory, (4) dead (but present) due to desiccation or unknown stress, and (5) resprouted after apparent death from herbivory.

### *Herbivore abundance*

We estimated differences in the abundance of potential mammalian herbivores among positions within blocks (rodents and lagomorphs). Of the rodents, we considered only species of *Dipodomys* and *Neotoma* to be potential herbivores because of their large size, herbivorous habits, and their identification as keystone taxa in the Chihuahuan Desert (Brown & Heske 1990; Kerley et al., 1997). Other small, common taxa (*Chaetodipus*, *Perognathus*, and *Onychomys*) were not considered. We trapped rodents using live traps (model XLK, H.B. Sherman Inc., Tallahassee, FL, USA). During September–October 2002 we placed one trap at each of 96 stations within each position. Stations were arrayed as a 6 × 16 grid with 20 m spacing between stations. Traps were baited with rolled oats and commercial bird seed and were operated for three nights. We used the minimum number of animals known to be alive in comparisons among positions.

Lagomorphs, particularly *Lepus californicus* (black-tailed jackrabbit), are known to include *B. eriopoda* as dominant component of their diets (Fatehi et al. 1988). Activity of *L. californicus* and *Sylvilagus audubonii* (desert cottontail) was estimated using densities of fecal pellets. Fecal pellets have been used as a relative measure of habitat use in the Chihuahuan Desert (Marín et al. 2003 and see Westoby & Wagner 1973). A direct census of rabbits was deemed impractical because the detection of rabbits in shrublands is difficult. In April 2003, we counted all pellets occurring within 25 cm × 25 cm quadrats at each of the 96 rodent trapping stations. Because the pellets decompose slowly, pellet densities reflect the cumulative use of habitat over the duration of the experiment and beyond.

### *Data analysis*

Differences in plant cover and herbivore abundance metrics were compared using mixed effects linear models (MIXED procedure; Anon. 1999). Cover data were arcsine-square root transformed prior to analysis.

To analyse seedling mortality, we used repeated measures mixed effects linear models (MIXED procedure; Anon. 1999). We considered two responses: (1) the number of seedlings killed by herbivores and (2) the number of surviving seedlings (after losses due both to herbivory and other factors, and including damaged seedlings). Block was used as the random variable, site and position were fixed effects, and time of observation was the repeated effect where the subject was the seedling tray nested within position. We included the initial number of seedlings in a tray as a covariate because of slight differences in seedling number (the average was ca. 11 seedlings/tray; range, 10–14). Additionally, we examined the effects of the size of the nearest *B. eriopoda* plant and the distance to the nearest shrub in the models.

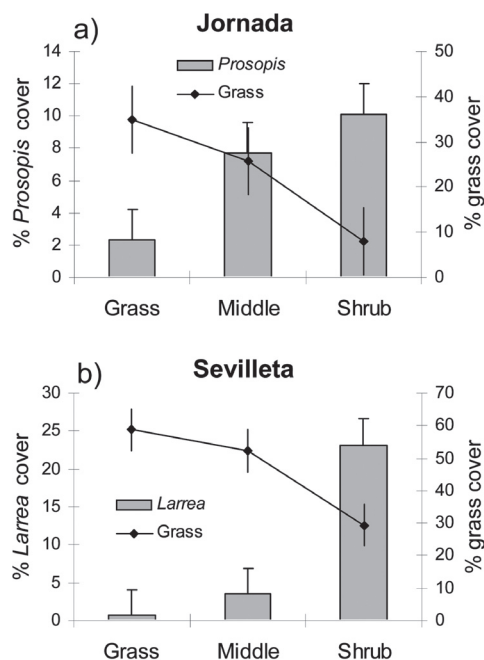
We considered three temporal covariance structures for each model including compound symmetry, first-order autoregressive, and power (Anon. 1999). We used the minimum Akaike's Information Criterion to determine the best-fitting covariance structure. In all cases, compound symmetry provided the best fit and was used in the final models. Finally, we used the mixed effects models without repeated measures to assess the effect of position on the number of seedlings that survived at ca. 2 months and 9 months after tray placement.

## **Results**

### *Ecotone structure*

Measurements confirm that the ecotones examined at both Jornada and Sevilleta featured significant variation in grass and shrub cover, but the nature of the variation differed between the sites (Fig. 1). At Jornada, perennial grass cover was similar between the grass and middle positions and was lower at the shrub position. Conversely, shrub cover was similar at the middle and shrub positions and was lowest at the grass position.

At Sevilleta, grass and shrub cover were both similar between the grass and middle positions and differed from the shrub end. Bare ground, however, was higher in the middle than the grass position (Mean ± SE = 14.6 ± 1.1 and 10.6 ± 1.1%, respectively). The abruptness of the Sevilleta ecotones made it difficult to position grids firmly in a distinct 'middle' zone.



**Fig. 1.** Canopy cover of (a) *Prosopis* shrubs and perennial grasses in each ecotone position at Jornada and (b) *Larrea* shrubs and perennial grasses at Sevilleta. Values are least-squares mean estimates  $\pm$  1 SE from mixed linear models.

#### Objective 1: Differences in seedling herbivory and seedling survival across the ecotones

Ecotone position had a significant effect on the number of seedlings killed over time by herbivores at both sites (Table 1). At Jornada, herbivore-related deaths were highest in the shrub position and the grass and middle positions were similar (Fig. 2a). At Sevilleta, the middle position exhibited the highest herbivore-related deaths and the

grass and shrub positions were similar (Fig. 2b). Neither *B. eriopoda* plant size nor distance from the nearest shrub affected herbivory at Jornada but both of these variables were significant at Sevilleta where herbivory was higher closer to shrubs and adjacent to larger *B. eriopoda* plants. Death rates were positive, decelerating curves and most seedlings were killed by herbivores by the end of the experiment (67–75% at Jornada, 52–78% at Sevilleta). Position-by-time interactions were never significant.

The number of seedlings surviving also differed among positions at Jornada, but not at Sevilleta (Table 1). At Jornada, survival rates were lowest in the shrub position and did not differ between the grass and middle positions (Fig. 2b). Survival was also positively related to shrub distance at Jornada. Survival at Sevilleta was positively related to shrub distance and negatively related to *B. eriopoda* patch size. In both sites, seedlings declined rapidly in the first few weeks and a few seedlings usually persisted in each position until the end of the study.

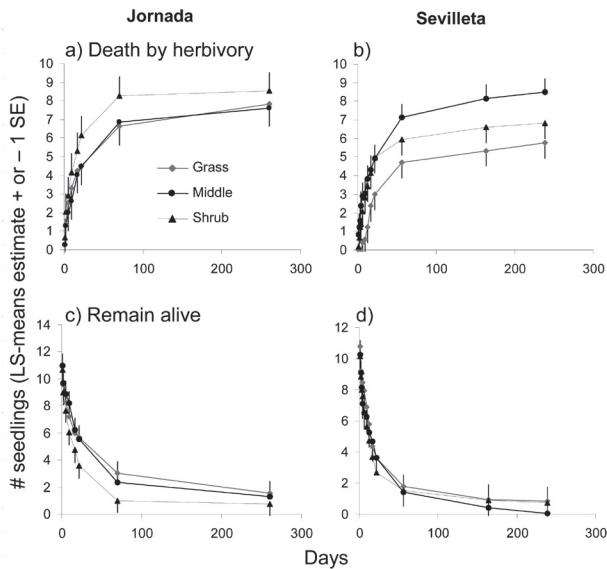
At Jornada, the number of seedlings surviving to 70 days differed among positions ( $F = 6.5$ ;  $df = 2, 100$ ;  $P = 0.002$ ; Fig. 3a), but survival to 260 days did not differ among positions ( $F = 1.84$ ;  $df = 2, 100$ ;  $P = 0.16$ ; Fig. 3b). At Sevilleta, seedling survival did not differ among positions at either 56 days ( $F = 0.03$ ;  $df = 2, 82$ ;  $P = 0.97$ ; Fig. 3c) or 239 days ( $F = 0.01$ ;  $df = 2, 82$ ;  $P = 0.99$ ; Fig. 3d).

#### Objective 2: Differences in seedling herbivory and survival between sites

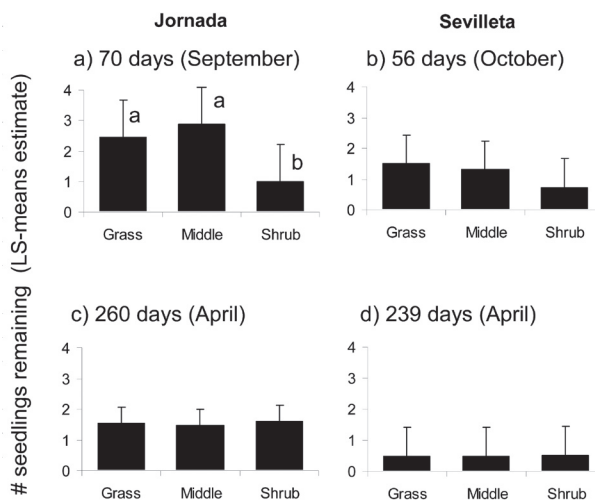
Neither seedling herbivory ( $F = 0.65$ ;  $df = 1, 4.44$ ;  $P = 0.46$ ) nor the number of seedlings surviving ( $F = 0.08$ ;  $df = 1, 4.29$ ;  $P = 0.79$ ) differed overall between the Jornada and the Sevilleta sites. There was, however, a significant site-by-location interaction for both herbivory ( $F = 7.22$ ;  $df = 2, 634$ ;  $P = 0.0008$ ) and survival ( $F = 4.13$ ;  $df = 2, 605$ ;  $P = 0.017$ ).

**Table 1.** Results of repeated measures mixed models where the response variable is either the number of seedlings killed by herbivores or the number of seedlings surviving (after the cumulative effects of seedling mortality by herbivory and abiotic factors). ‘Position’ is the tray placement on the ecotone (grass, middle, or shrub), ‘Time’ is time after seedling tray placement, ‘Patch size’ is the size of the nearest *Bouteloua eriopoda* patch, and ‘Shrub distance’ is the distance to the nearest shrub. Test statistics are based on Type III sums of squares (Anon. 1999).

Model	Term	Jornada			Sevilleta		
		df	F	P	df	F	P
Death by herbivory	Position	2,49.4	3.05	0.05	2,40.8	8.48	< 0.001
	Time	7,737	138	< 0.001	11,960	155	< 0.001
	Position $\times$ time	14,463	0.56	0.90	22,615	1.33	0.14
	Patch size	1,278	0.92	0.33	1,607	17.14	< 0.001
	Shrub distance	1,569	0.15	0.70	1,451	24.51	< 0.001
Surviving	Position	2,50.4	4.11	0.02	2,29.2	1.38	0.27
	Time	7,757	240	< 0.001	11,950	282	< 0.001
	Position $\times$ time	14,484	1.35	0.17	22,621	1.06	0.38
	Patch size	1,281	0.68	0.41	1,190	33.4	< 0.001
	Shrub distance	1,588	4.00	0.04	1,159	27.0	< 0.001



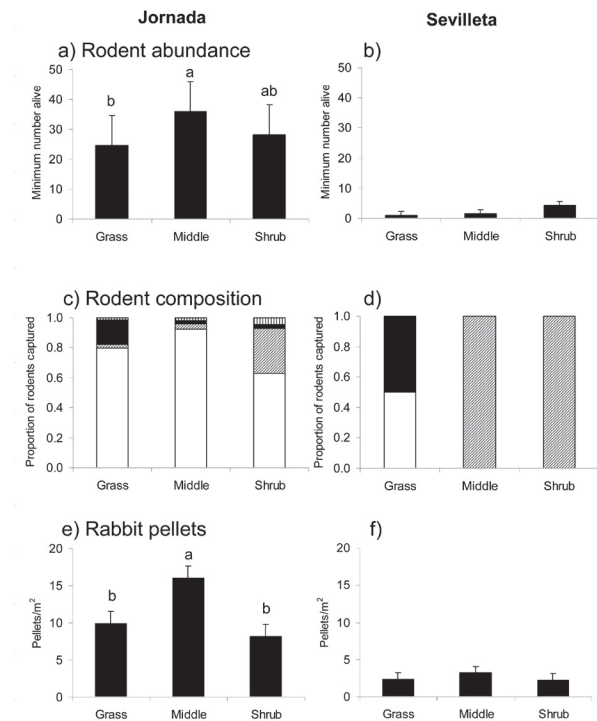
**Fig. 2.** Least-squares means estimates from repeated measures mixed linear models of the number of seedlings killed by herbivores in each ecotone position over time at (a) Jornada and (b) Sevilleita and the number of seedlings remaining alive over time (accounting for both herbivory and other causes of death) at (c) Jornada and (d) Sevilleita. Only half of the standard error bars are shown to improve clarity.



**Fig. 3.** Least-squares means estimates from mixed linear models of the number of seedlings remaining alive in each ecotone position in a pre-winter census (a) 70 days after initiation of the experiment at Jornada and (b) 56 days at Sevilleita and a post-winter census (c) 260 days at Jornada and (d) 239 days at Sevilleita. Bars with different letters are significantly different within sites at  $P < 0.05$ .

### Objective 3: Differences in mammal abundance between sites and among positions

Overall abundances of herbivorous rodents ( $F = 7.94$ ;  $df = 1, 4$ ;  $P = 0.05$ ) and rabbit pellet densities ( $F = 43.8$ ;  $df = 1, 4$ ;  $P = 0.003$ ) were much higher at Jornada than Sevilleita (Fig. 4a, b and e, f). Total herbivorous rodent abundance exhibited marginally (i.e.,  $P < 0.10$  but  $> 0.05$ ) significant differences among positions at Jornada ( $F = 4.82$ ;  $df = 2, 4$ ;  $P = 0.09$ ). The dominant herbivorous rodent at Jornada was *Dipodomys ordii*, followed by *D. merriami* and *D. spectabilis*. *Neotoma* spp. (*albigula* and *micropus*) were rare (Fig. 4, c, d). There were no significant differences in the abundance of any individual species among positions at Jornada. No differences in total herbivorous rodents were observed among positions at Sevilleita ( $F = 3.5$ ;  $df = 2, 4$ ;  $P = 0.13$ ). *D. merriami* was dominant followed by *D. spectabilis* and *D. ordii*. *Neotoma* was absent. *D. merriami* was significantly more abundant in shrub positions than in



**Fig. 4.** For each ecotone position, the abundance of herbivorous rodents, rodent composition, the density of lagomorph pellets recorded on grids at Jornada (a, c, e) and Sevilleita (b, d, f) respectively. For graphs c and d, the open bar is *Dipodomys ordii*, the slash pattern is *D. merriami*, the solid black is *D. spectabilis*, and the vertical stripe pattern is *Neotoma albigula*. Values are least-squares mean estimates  $\pm 1$  SE or proportions derived from least-squares means estimates from mixed linear models. Bars with different letters are significantly different within sites at  $P < 0.05$ .



middle or grass positions at Sevilleta ( $F = 9.80$ ;  $df = 2, 4$ ;  $P = 0.03$ ). Lagomorph pellet densities showed clear differences at Jornada ( $F = 6.74$ ;  $df = 2, 4$ ;  $P = 0.03$ ) and the middle position had the highest densities. Again, no differences were observed at Sevilleta ( $F = 0.82$ ;  $df = 2, 4$ ;  $P = 0.50$ ).

## Discussion

### *Differences in herbivory across ecotones*

Herbivore impacts on seedlings were significant and clearly varied across ecotones at both sites, but the pattern of variation differed between sites. The Jornada pattern was consistent with the hypothesis that rodent herbivores have a greater effect in shrublands than in grasslands (Campbell 1929; Whitford 1993; Kerley et al. 1997). In concert with other factors, herbivory contributed to differences in pre-winter seedling survival across grassland-shrubland ecotones. Even though differences in seedling survival did not persist over the winter in this experiment, we speculate that the ecotone-dependent differences could translate into variation in adult grass populations under climatic conditions that are generally favorable to *B. eriopoda* recruitment (Neilson 1986; Peters 2000). These differences in survival would be especially important in extensive areas where *B. eriopoda* plants have been extirpated and where vegetative recolonization by stolons (Wright & Van Dyne 1976) is not possible.

One assumption underlying the seedling herbivory hypothesis is that the abundance of potential herbivores should increase with shrub cover (Wood 1969; Whitford 1993). This assumption was not supported at Jornada. Grassland and shrubland ecotone positions did not differ from each another in either rodent numbers or lagomorph pellet densities, but the middle positions had higher values than grassland. Because nearly all herbivory events were associated with clean, straight or diagonal cuts on remaining stems and with digging and whole plant removal, we suspect that small mammals were the most important herbivores (Kerley et al. 1997). Thus, the increased herbivory observed in shrublands may be due to differences in small mammal foraging behavior (Manson et al. 1998). It is possible that seedlings were more apparent and easily located by mammals in shrubland microsites due to the sparse vegetation (e.g., Ostfeld & Canham 1993) or that seedlings were more preferred in shrublands because other resources were less available.

In contrast to Jornada, Sevilleta exhibited increased herbivory in the middle ecotone positions. Like Jornada, most herbivory events indicated mammalian herbiv-

ores. Because neither total rodent numbers nor rabbit pellet density varied across the ecotones at this site, we cannot attribute the herbivory patterns to differences in mammal abundance. Although *D. merriami* abundance did differ, this rodent was most abundant in shrub rather than middle positions. Additionally, there was little consistent difference in vegetation structure between the grassland and middle positions of the ecotones. We speculate that the relatively high herbivory in the middle positions of the Sevilleta ecotones may also be due to variation in small mammal foraging behavior. Herbivory was positively related to the size of adjacent *B. eriopoda* plants and proximity of shrubs, suggesting an effect of local habitat structure in reducing predation risk (e.g. Thompson 1982). Furthermore, *Lepus californicus* often prefers shrub cover for diurnal resting, but nocturnal foraging can occur in adjacent grasslands. The jackrabbits may forage more heavily in areas adjacent to high shrub cover than in areas farther from cover (Johnson & Anderson 1984; McAdoo et al. 1987). The lack of significant differences in pellet densities, however, casts doubt on this explanation.

Although pre-winter seedling survival differed among ecotone positions at Jornada, there were no differences at Sevilleta. Thus, variation in seedling survival caused by herbivory was overwhelmed by other sources of seedling mortality at Sevilleta. Our results suggest that the influence of variation in seedling herbivory across ecotones might be less important for *B. eriopoda* recruitment at Sevilleta than at Jornada.

### *Differences in herbivory between the sites*

Despite large differences between Jornada and Sevilleta in our metrics of herbivore abundance, herbivore-caused mortality was similar. There are several possible explanations for the similarity. First, the soil disturbances and odors associated with the experimental treatments may have increased overall rates of seedling discovery and herbivory by mammals (Ostfeld & Canham 1993). The experiment should not have biased the within-ecotone comparisons, however. Second, it is possible that only a few individual herbivores are required to inflict large seedling losses. Thus, variation in herbivore abundance over the range of values observed in this study may not drive variation in seedling herbivory. Third, it is possible that other, unmeasured herbivores were driving the patterns. We do not feel that this is likely because (1) seedling deaths indicated mammalian, rather than insect, herbivores and (2) exclusively diurnal mammals that we did not measure (e.g. *Spermophilus spilosoma*) were not observed to be common during this study.

### Implications for *B. eriopoda* recovery and restoration

Our study is the first to confirm experimentally that seedling herbivory is a potential mechanism by which native herbivores could cause spatial variation in the recruitment of *B. eriopoda* (e.g. Nickel et al. 2003). This result suggests two strategies to facilitate *B. eriopoda* recovery under suitable climate conditions. First, shrub removal prior to restoration attempts may not only alleviate resource competition on *B. eriopoda*, as is commonly emphasized (e.g. Van Auken 2000), but also alter habitat conditions favorable to herbivory. Even if resource competition from shrubs is not important in some situations, shrub removal may still be a necessary manipulation. Second, seedling recruitment may be more successful when populations of herbivorous mammals are very low (i.e., lower than recorded in this study), such as when kangaroo rat populations crash due to heavy rainfalls and the loss of stored foods (Brown & Ernest 2002). Through this mechanism, it is possible that extreme climatic events may have both direct (providing water resources; Peters 2000; Reynolds et al. 2004) and indirect (reducing seedling predators) positive effects on *B. eriopoda* recruitment. Maintenance of predator populations that are routinely killed by land managers in the Chihuahuan Desert, such as coyotes (*Canis latrans*) might also limit small mammal populations and indirectly improve grass establishment (Henke & Bryant 1999).

### Conclusions

Despite an increasing appreciation of the existence of alternative stable states in ecosystems (Bestelmeyer et al. 2004; Suding et al. 2004) we often know little about the mechanisms underlying them. Mechanistic experiments that are arrayed across ecotones between states, such as we have performed, can be a useful means of identifying factors that are able to constrain recovery and restoration. With this approach, we showed that:

- Seedling herbivory is an important force in Chihuahuan Desert grasslands;
- There is significant variation in seedling herbivory among vegetation states, but;
- Herbivore numbers in a habitat type do not reflect herbivory rates.

These results must be considered in light of the fact that black grama grass recovery events are generally rare in the Chihuahuan Desert, so it is difficult to evaluate the consequences of factor interactions or temporal variations in factor importance in a short-term study. Experiments such as ours would need to be replicated in key years over several decades to evaluate the long-term, broad-scale impact of seedling herbivory. Short-term experimental

studies can, however, draw attention to the kinds of constraints that may appear over the long-term as monitoring studies and restoration actions are designed.

**Acknowledgements.** This work was supported by a grant from the National Science Foundation (NSF; DEB 0004526), the NSF-supported Jornada Basin LTER project (DEB 0080412), and appropriated funds to the USDA-ARS Jornada Experimental Range. Tamara Hochstrasser, Janos Garadnai, Jennifer Johnson, Sarah Meadmore, Star Gallagher, and Amy Slaughter assisted with field work. Kris Havstad, John Ludwig, Mike Austin, and an anonymous reviewer provided valuable comments on the manuscript.

### References

- Anon. 1999. *SAS/STAT Software, Changes and Enhancements through Release 6.12*. SAS Institute, Inc. Cary, NC, US.
- Allred, K.W. 1997. *A field guide to the flora of the Jornada plain*. 2nd ed. New Mexico Agricultural Experiment Station Bulletin 739, Las Cruces, NM, US.
- Bestelmeyer, B.T., Herrick, J.E., Brown, J.R., Trujillo, D.A., & Havstad, K.M. 2004. Land management in the American Southwest: a state-and-transition approach to ecosystem complexity. *Environ. Manage.* 34: 38-51.
- Brown, J.H. & Ernest, S.K.M. 2002. Rain and rodents: complex dynamics of desert consumers. *BioScience* 52: 979-987.
- Brown, J.H. & Heske, E.J. 1990. Control of a desert-grassland transition by a keystone rodent guild. *Science* 250: 1705-1707.
- Buffington, L.C. & Herbel, C.H. 1965. Vegetational changes on a semidesert grassland range from 1858 to 1963. *Ecol. Monogr.* 35: 139-164.
- Campbell, R.S. 1929. Vegetative succession in the *Prosopis* sand dunes of southern New Mexico. *Ecology* 10: 392-398.
- Curtin, C.G., Kelt, D.A., Frey, T.C. & Brown, J.H. 2000. On the role of small mammals in mediating climatically driven vegetation change. *Ecol. Letters* 3: 309-317.
- Fatehi, M., Pieper, R.D. & Beck, R.F. 1988 Seasonal food habits of black-tailed jackrabbits (*Lepus californicus*) in southern New Mexico. *Southw. Nat.* 33: 367-369.
- Fredrickson, E., Havstad, K.M. & Estell, R. 1998. Perspectives on desertification: south-western United States. *J. Arid Environ.* 39: 191-207.
- Gibbens, R.P., McNeely, R.P., Havstad, K.M., Beck, R.F. & Nolen, B. 2005. Vegetation change in the Jornada Basin from 1858 to 1998. *J. Arid Environ.* 61: 651-668.
- Havstad, K.M., Gibbens, R.P., Knorr, C.A. & Murray, L.W. 1999. Long-term influences of shrub removal and lagomorph exclusion on Chihuahuan Desert vegetation dynamics. *J. Arid Environ.* 42: 155-166.
- Henke, S.E. & Bryant, F.C. 1999. Effects of coyote removal on the faunal community in western Texas. *J. Wildlife Manage.* 63: 1066-1081.
- Herrick, J.E., Havstad, K.M. & Rango, A. 2006. Remediation research at the Jornada: Past and future. In: Havstad, K.M.,

- Schlesinger, W.H. & Huenneke, L.F. (eds.) *Structure and function of a Chihuahuan Desert ecosystem: the Jornada Basin LTER*, pp. 278-304. Oxford University Press, UK.
- Holechek, D.A., Valdez, J., Tembo, A., Saiwana, L., Fusco, M. & Cardenas, M. 1993. Jackrabbit densities on fair and good condition Chihuahuan desert range. *J. Range Manage.* 46: 524-528.
- Johnson, R.D. & Anderson, J.E. 1984. Diets of black-tailed jackrabbits in relation to population density and vegetation. *J. Range Manage.* 37: 79-83.
- Kerley, G.I.H., Whitford, W.G. & Kay, F.R. 1997. Mechanisms for the keystone status of kangaroo rats: graminivory rather than granivory? *Oecologia* 111: 422-428.
- Manson, R.H., Ostfeld, R.S. & Canham, C.D. 1998. The effects of tree seed and seedling density on predation rates by rodents in old fields. *Ecoscience* 5: 183-190.
- Marín, A.I., Hernández, L. & Laundré, J.W. 2003. Predation risk and food quantity in the selection of habitat by black-tailed jackrabbit (*Lepus californicus*): an optimal foraging approach. *J. Arid Environ.* 55: 101-110.
- McAdoo, J.K., Longland, W.S., Cluff, G.J. & Klebenow, D.A. 1987. Use of new rangeland seedings by black-tailed jackrabbits. *J. Range Manage.* 40: 520-524.
- Neilson, R.P. 1986. High-resolution climatic analysis and southwest biogeography. *Science* 232: 27-34.
- Nickel A.M., Danielson B.J. & Moloney K.A. 2003. Wooded habitat edges as refugia from microtine herbivory in tall-grass prairies. *Oikos* 100: 525-533.
- Norris J.J. 1950. Effects of rodents, rabbits, and cattle on two vegetation types in semidesert range land. *New Mexico State Univ. Agricult. Exp. Station Bull.* 353: 1-23.
- Ostfeld, R.S. & Canham, C.D. 1993. Effects meadow vole population density on tree seedling survival in old fields. *Ecology* 74: 1792-1801.
- Peters, D.P.C. 2000. Climatic variation and simulated patterns in seedling establishment of two dominant grasses at a semi-arid-arid grassland ecotone. *J. Veg. Sci.* 11: 493-504.
- Peters D.P.C., Gosz, J.R., Pockman, W.T., Small, E.E., Parmenter, R.R., Collins, S.L. & Muldavin, E. 2006a. Integrating patch and boundary dynamics to understand and predict biotic transitions at multiple scales. *Landscape Ecol.* 21: 19-33.
- Peters, D.P.C., Bestelmeyer, B.T., Fredrickson, E.L., Herrick, J.E., Monger, C.M. & Havstad, K.M. 2006b. Disentangling complex landscapes: new insights to forecasting arid and semiarid system dynamics. *BioScience* 56: 491-501.
- Reynolds, H.G. 1950. Relation of Merriam kangaroo rats to range vegetation in southern Arizona. *Ecology* 31: 457-463.
- Reynolds, J.F., Kemp, P.R., Ogle, K. & Fernandez, R.J. 2004. Modifying the 'pulse-reserve' paradigm for deserts of North America: precipitation pulses, soil water, and plant responses. *Oecologia* 141: 194-210.
- Schlesinger, W.H., Reynolds, J.F., Cunningham, G.L., Huenneke, L.F., Jarrell, W.M., Virginia, R.A. & Whitford, W.G. 1990. Biological feedbacks in global desertification. *Science* 247: 1043-1048.
- Scholes, R.J. & Archer, S.A. 1997. Tree-grass interactions in savannas. *Annu. Rev. Ecol. Syst.* 28: 517-544.
- Suding, K.N., Gross, K.L. & Houseman, G. 2004. Alternative states and positive feedbacks in restoration ecology. *Trends Ecol. Evol.* 19: 46-53.
- Thompson, S.D. 1982. Microhabitat utilization and foraging behavior of bipedal and quadrupedal heteromyid rodents. *Ecology* 63: 1303-1321.
- Van Auken, O.W. 2000. Shrub invasions of North American semiarid grasslands. *Annu. Rev. Ecol. Syst.* 31: 197-215.
- Westoby, M. & Wagner, F.W. 1973. Use of a crested wheatgrass seeding by black-tailed jackrabbits. *J. Range Manage.* 26: 349-352.
- Whitford, W.G. 1993. Animal feedbacks in desertification: an overview. *Revista Chilena de Historia Natural* 6: 243-251.
- Whitford, W.G. 1997. Desertification and animal biodiversity in the desert grasslands of North America. *J. Arid Environ.* 37: 709-720.
- Wood, J.E. 1969. Rodent populations and their impact on desert rangelands. *New Mexico State Univ. Agricult. Exp. Station Bull.* 555: 1-17.
- Wright, N. & Streetman, L.J. 1958. Past performance and future potential of black grama for southwestern ranges. *J. Range Manage.* 11: 207-214.
- Wright, R.G. & Van Dyne, G.M. 1976. Environmental factors influencing semidesert grassland perennial grass demography. *Southw. Nat.* 21: 259-274.

Received 27 April 2006;

Accepted 6 December 2006;

Co-ordinating Editor: M. Austin.