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Refuge effects of a cactus in grazed short-grass steppe

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Abstract

Question: Which factors influence the effectiveness of biotic refuges for harbouring grazing-sensitive species in pastures with a long history of grazing by large herbivores? Previous research showed that spiny clumps of the cactus *Opuntia polyacantha* provided refuges from cattle grazing for plants and for inflorescence production on short-grass steppe. In this paper, seven factors that may have a potential positive influence on the refuge effects of cactus at a landscape scale were assessed.

Location: Short-grass steppe of the Great Plains of North America.

Methods: The study was conducted in eight long-term grazed pastures and their respective ungrazed controls that were established 60 years ago.

Results: Heavy grazing intensities were necessary for some positive effects of cactus to manifest, and some refuge effects changed to negative effects under lower grazing pressure. Refuge effects increased with plant community productivity due to greater abundances of grazing-sensitive species, and greater grazing intensities in the more productive areas. Cover of cactus cladodes (spine-covered pads) inside clumps appeared to be the main limiting factor for refuge effects, probably by limiting available space for grazing-sensitive species in the clumps. Other factors such as size and density of cactus clumps, and the presence of large refuges in the proximity of clumps had minor influence on the effectiveness of cactus refuges.

Conclusions: The effects of biotic refuges largely varied with ecological conditions and structural characteristics of the refuge. Refuge effects were mainly influenced by grazing intensity, plant community productivity, and structural characteristics of the biotic refuges. A conceptual model of factors influencing refuge effects at a local landscape scale in plant communities grazed by large herbivores is presented.

Key words: Biotic refuge; Cactus clump structure; Cattle grazing; Grazing intensity; *Opuntia polyacantha*; Plant diversity; Plant-herbivore interaction; Positive interaction; Productivity.

Introduction

Positive interactions among plants may occur when neighbours favourably modify physical and/or biotic conditions (Bertness & Callaway 1994). Generally, these positive interactions occur in the presence of disturbance or stress (e.g. Pugnaire et al. 2004), and when the benefactor species achieves a certain spatial complexity (e.g. size, density) above which positive effects are significant (Coull & Wells 1983). This is because a potential positive interaction among neighbour plants may only manifest if its strength exceeds the negative effects of competition among those neighbours (Brooker & Callaghan 1998). Therefore, the magnitude of a given positive association may vary with level of disturbance and over gradients of biotic and abiotic conditions.

Several conceptual models predict that positive interactions become stronger as disturbance intensity increases, because neighbours can provide a buffer from extreme disturbance and stress (Huston 1994; Bertness & Callaway 1994; Brooker & Callaghan 1998; Bertness 1998). This prediction is mainly supported by field experiments on physical disturbance and stress, while the role of increasing herbivore pressure in promoting positive interactions within the community has been given less attention (Callaway & Walker 1997). An important positive interaction between plants can occur when one plant provides a refuge from grazing to other plants in the community (Callaway et al. 2000). A biotic refuge acts through physical impedance of herbivore foraging, but may also provide an associational avoidance that acts through behavioural impedance during foraging decisions at the community level (Milchunas & Noy-Meir 2002).

The protective role of a biotic refuge may change as a function of plant community productivity. The Milchunas et al. (1988) model predicts a greater role of herbivores in altering plant communities under conditions of greater productivity, implying that biotic refuges would be relatively more important in productive

communities. Adaptations to more productive conditions (tall growth forms with relatively greater investment in above-ground rather than below-ground production) enhance grass competitiveness for light, but make the species more vulnerable to grazing by large herbivores. These grazing-sensitive tall species may better survive in biotic refuges. The Bertness & Callaway (1994) conceptual model predicts greater consumer pressure in plant communities with greater productivity and, therefore, greater biotic refuge effects in more productive locations. Milchunas & Noy-Meir (2002) reviewed studies of geologic refuges from grazing and found greater positive effects in productive communities than in relatively drier, less productive communities. However, biotic refuges differ from geologic refuges because the refuge may also compete with the species it harbours, and competition may vary with productivity.

Effectiveness of biotic refuges may also depend upon their spatial distribution, temporal persistence, and degree of protection from grazing. Callaway & Walker (1997) suggest the hypothesis that biotic refuge importance increases with density, size, or age. Callaway et al. (2000) found that the refuge effects of the spiny *Cirsium obvalatum* on palatable plants of meadows increased with size and age. McAuliffe (1984) reported that refuge effects of the spiny cactus *Opuntia fulgida* on two small barrel-cacti increased with the accumulation of spine-covered stem joints beneath the canopy, which increases the degree of protection.

The existence of a source of seeds of grazing-sensitive species near biotic refuges may increase its effectiveness as a refuge. Thus, the distance to other refuges and the abundance of grazing-sensitive species in these other refuges may increase probabilities of successful dispersal. While these are basic hypotheses of island biogeography and metapopulation biology (see Hanski & Gilpin 1997), we are unaware of any studies addressing interactions between biotic and other refuge types.

Here we analyse some of the conditions that may potentially increase the role of cactus clumps as biotic refuges in a grassland community of the short-grass steppe of Colorado, USA. *Opuntia polyacantha* is a common slow-growing, long-lived cactus in this grassland (Milchunas et al. 1989). Its spiny, prostrate, branched cladodes (pads) commonly form short dense clumps about 15 cm tall. Range managers have attempted to reduce cactus density through mechanical removal, herbicides, and burning (Mueller & Forwood 1994), because visual observations indicate cattle do not graze in cactus clumps. However, *O. polyacantha* is not completely undesirable because we previously showed that it provides a micro-environment and refuge that favours abundance and inflorescence production of grazing-sensitive desirable plants (Rebollo et al. 2002).

The importance of seven factors that may have a potential positive effect on the refuge effects of the cactus was assessed. The specific objectives of the present research were the following. 1. To analyse the positive effects of cactus clumps over a range of environments, and in particular to test the hypotheses that positive effects increase with (a) grazing intensity and with (b) plant community productivity. 2. To analyse the characteristics of cactus clumps that contribute to its effectiveness as a biotic refuge, and to test the hypothesis that positive effects increase with (c) abundance of cactus at the site level, (d) size of the individual clumps, and (e) density of cladodes, indicator of density of thorns and degree of protection of the cactus clumps (thorniness) within individual clumps. 3. To assess the potential interaction between cactus clumps and other plant refuges, and to test the hypothesis that positive effects of the cactus increase with (f) proximity to other larger refuges (wire-fenced exclosures) and with (g) abundance of grazing-sensitive species in these larger refuges.

Methods

Study area

The study was conducted at the Central Plains Experimental Range (CPER) in the northern portion of the short-grass steppe, Colorado, USA (40°49' N, 104°46' W) at a mean elevation of 1660 m. Mean annual precipitation is 321 mm and mean monthly air temperature ranges from -5 °C in January to 22 °C in July. The topography is flat, with gently rolling slopes between uplands and lowlands. Coarse soils predominate, with a sand content ranging from 52 to 74% (Yonker et al. 1988).

Two main subtypes of short-grass communities are distinguished: (1) shrublands, with conspicuous presence of the shrub *Atriplex canescens*, more abundant on relatively coarser-textured lowland soils; (2) grasslands without tall shrubs, more abundant on relatively finer-textured soils. In general, both of community types have a similar non-shrub species composition and are dominated by perennial short grasses, mainly *Bouteloua gracilis* and *Buchloe dactyloides* (Milchunas et al. 1989). Shrublands are more productive than grasslands, primarily due to locations on relatively coarser soils and the contribution of the shrub component (Liang et al. 1989). These authors found a total above-ground net primary production of 148 g.m⁻².a⁻¹ for shrublands on sandy-loam soils and of 90 g.m⁻².a⁻¹ for grasslands on sandy-clay loam soils. Without shrubs included, the production for shrublands was 137 g.m⁻².a⁻¹. Using some of the same pastures as those in this study, Milchunas et al. (1994) observed that differences in production between

sandy-soil shrublands and finer textured level uplands were greater than differences among long-term lightly, moderately, and heavily grazed treatments.

Opuntia polyacantha is the second most dominant species in terms of basal cover (Milchunas et al. 1989). Mean diameter of *Opuntia* clumps is ca. 60 cm, with an annual increase of ca. 7.5 cm (Turner & Costello 1942, who estimated that clumps varying from 61 to 93 cm in diameter require 10 - 15 years to develop.

Long-term moderate grazing treatments (each ca. 130 ha) and wire-fenced grazing exclosures (60 m × 60 m) were established at the CPER in 1939. From 1939 to 1963, stocking rates in these grazing treatments averaged 1.1 ha per yearling heifer per month over a six-month period during the growing season, representing 40% removal of the above-ground production. Since 1964, the treatments were managed so that ca. 54 g.m⁻² of herbage remained at the end of the grazing season in autumn. Mean annual removal remained 40% (36 g.m⁻² removed over 90 g.m⁻² mean production) even though management changed from taking 40% to leaving a constant residual. Cattle are the most abundant large herbivore, representing 85% of above-ground herbivory (Lauenroth & Milchunas 1991). Although a set grazing intensity was established in each large pasture, there are local differences in grazing intensity due to the unevenness in the spatial distribution of cattle grazing. Some locations in lightly stocked pastures can be grazed as heavily as similar topographic locations in heavily stocked pastures (Varnamkhandi et al. 1995).

Experimental design

Eight replicate long-term moderately grazed pastures and their respective ungrazed fenced exclosures were studied (Rebollo et al. 2002). Four pastures were located in shrublands and four in grasslands. At each pasture, we sampled the grazed areas contiguous to the fenced exclosures to allow comparisons of treatments with similar within-site soil and topographic units (i.e. across-fence comparisons of adjacent areas). This also allowed us to analyse the potential interactions between relatively small-size, short-term biotic refuges of cactus clumps (mean size 0.74 m², mean age 15 a; clump density of 2000/ha) and relatively large-sized, long-term fenced exclosure refuges (3500-4000 m² and 60 a old), by comparing the refuge effects of cactus in grazed areas located adjacent and distant from these large refuges. Eight 40 m-long parallel linear transects were located at each pasture, four under grazed and four under ungrazed conditions. The transects were located in the grazed area in the windward side according to the predominant wind direction (SW) during seed fall (autumn/early winter) to maximize potential seed dispersal from the fenced exclosure.

Measurements

We estimated, and describe below, (1) effects of cactus clumps on vegetation; (2) influence of the following factors on those cactus effects: site-level abundance of cactus clumps; (3) size of individual cactus clumps; (4) cover of cladodes in the individual cactus clumps; (5) relative cattle grazing intensity.

1. Each transect was divided into ten sampling points, 4 m apart, ordered in the grazed treatment from closest to furthest from the ungrazed fenced exclosure. At each sampling point, a 40 cm × 40 cm quadrat was located in the nearest cactus clump, and an additional adjacent quadrat was placed outside the clump. Only clumps > 50 cm × 50 cm were sampled in order to avoid those too small to act as potential refuges, and to ensure they were over 8 a old. Percentage aerial cover (visually estimated percentage of quadrat area beneath the canopy) and number of inflorescences of each plant species were recorded in mid-late summer. A total of 1280 quadrats were sampled in the sites, 640 quadrats were inside and 640 quadrats outside cactus clumps.

2. An estimate of the abundance of cactus clumps at each site was obtained from the distance from each cactus clump to the respective sampling point in the transect, assuming a random pattern of clumps. Clump density per ha was calculated (Barbour et al. 1987) as:

$$10\,000 / (2 \times \text{mean distance in m}^2).$$

3. The size of each cactus clump was estimated by measuring the length of the main and its perpendicular axes (D and d , respectively). Clump area was estimated by adjusting the clump shape to an ellipse:

$$\text{area} = p \times (D/2 \times d/2).$$

4. In the quadrats inside cactus clumps, cladode cover was visually estimated as an indicator of the density of thorns because cladodes do not differ substantially in thorniness. Cladode cover was the percentage of quadrat area occupied by live and dead cladodes. Dead cladodes were included because they keep their spines.

5. Relative cattle grazing intensity at each site was estimated along the transects in the grazing treatment by counting cattle faecal pats in a 2 m-strip on both sides of the transect (160 m² per transect × 4 transects × 1 treatment × 8 sites = 5120 m²). Senft (1983) found that except for fence lines and watering areas with relatively high faecal deposition rates, the amount of nitrogen removed from an area by consumption was directly related to the amount of nitrogen returned through faecal deposition.

Variables for statistical analyses

The response variables were the ten vegetation parameters on which cactus was found to have refuge effects from cattle grazing in a previous study in the short-grass steppe (Rebollo et al. 2002). They include species diversity (H'), and aerial cover and inflorescence

productions of several functional groups (see Tables 3 and 4). Inflorescence production data were analysed as inflorescence production per unit of cover. For each vegetation parameter, we considered the difference between inside and outside cactus clumps in the grazed treatment to be an indicator of the intensity of the refuge effects of cactus because there were no positive effects of cactus inside the enclosure. These cactus effects were calculated by averaging over all inside-cactus-clumps within a site and subtracting the average of the outside-cactus-clumps value within that site. For the factors 'size of the biotic refuges', 'density of thorns in the biotic refuge' and 'proximity to the large refuge' averaging was within a variable level within a site. We considered one explanatory variable for each of the seven factors potentially influencing the refuge effects (Table 1 and see specific objectives in the Introduction section) except for the abundance of grazing-sensitive species inside the large refuge. For this factor, the indicator used as explanatory variable changed depending on the vegetation parameter analysed. We categorized cactus clumps into three size-classes (< 0.5 m², 0.5-1 m² and > 1 m²) and three cover-classes of cladodes (less than 30%, 30-40%, and greater than 40%). The effects of size and cladode cover were tested by comparing the cactus effects of the two extreme classes.

Data analysis

Statistical analyses among the explanatory variables were performed in order to determine multicollinearity. The relationship between pairs of explanatory variables were analysed through correlation, χ^2 , and student's *t* test depending on whether the explanatory variables were categorical or continuous. Interdependence was found only between one categorical and five continuous variables (see Results section).

Student *t*-tests were performed to assess the positive influence of categorical explanatory variables on the effects of cactus. We attempted to separate the interdependence of categorical explanatory variables from continuous explanatory variables using analysis of covariance (ANCOVA) with the continuous explanatory variables as covariates. If the covariate decreases or eliminates the effect of the categorical explanatory variable, it implies that this factor may have acted through the covariate (Cox 1958, p. 65). Simple linear regressions were performed to test the positive relationship between the continuous explanatory variables and the effects of cactus. In order to test the positive effects of the seven factors on the protective effect of the cactus (directional hypotheses), 1-tailed instead of 2-tailed tests were used.

Results

Grazing intensity, cladode cover inside cactus clumps, species diversity inside the large refuges, and abundance of forbs and species that decrease with grazing inside the large refuges were significantly higher on the more productive shrublands compared with grasslands (Table 2). No other relationships among explanatory variables were significant.

Refuge effects on the vegetation parameters were estimated as the difference in the parameter value between inside and outside cactus clumps in the grazed treatment, because there were no positive effects of cactus inside the enclosure. Eight of the ten vegetation parameters (Table 2) showed greater refuge effects of cactus in shrublands, although only three parameters [cover of perennials, species that decrease with grazing (decreasers), and species diversity (*H'*)] were significantly different (Table 3). These results indicate greater positive effects of cactus on the more productive sites and, in some cases, the effects of cactus were only positive on these sites. Species were not gained or lost, but the increase in *H'* was due to evenness (data not shown). The significant effect of plant productivity on species diversity (*H'*) was removed after adjusting for grazing intensity, cladode cover inside cactus clumps, or species diversity in adjacent large refuges. The significant effect of plant productivity on cover of species that decrease with grazing was removed after adjusting for cladode cover inside cactus clumps. This suggests that some differences in the cactus effects might be mediated through effects of plant productivity on these three covariables.

None of the ten vegetation parameters showed significantly greater refuge effects of cactus in clumps with greater cover of cladodes (Table 3). In contrast, the mean values of some vegetation parameters suggested greater refuge effects in clumps with less cover

Table 1. Factors potentially having a positive influence on the refuge effects of cactus, explanatory variables indicating those factors, and type of explanatory variable: cat = categorical; cont = continuous

| Factor | Explanatory indicator | cat/cont |
|--|--|----------|
| Plant community productivity | Shrublands (more productive) and grasslands (less productive) | cat |
| Size of the biotic refuge | Two different size-classes (< 0.5 m ²) and (> 1 m ²) | cat |
| Density of thorns in biotic refuge | Two different cover-classes of cladode cover (< 30% and > 40%) | cat |
| Proximity to the large refuge | Two 20 m-long subtransects, adjacent to and distant from large enclosures | cat |
| Grazing intensity | No. of cattle faecal pats/ha/site | cont |
| Density of biotic refuges | No. of cactus clumps/ha/site | cont |
| Abundance of grazing-sensitive species inside the large refuge | Value of vegetation parameters inside ungrazed enclosure | cont |

Table 2. Significant relationships between the explanatory variables. Summary of student *t*-analyses used to test the effects of plant community productivity (relatively low productivity grasslands vs. relatively high productivity shrublands) on cattle grazing intensity, cladode cover inside cactus clumps, species diversity (*H'*) inside the large refuges, and abundance of forbs and species that decrease (↓) with grazing inside the large refuges.

| | Low Grassl. | High Shrubl. | <i>F</i> | <i>P</i> |
|---------------------------------|----------------|-----------------|----------|----------|
| Graz. int. (# of faecal pat/ha) | 647.5 | 1370 | 9.46 | 0.022 |
| Clad. cov. (%) | 36.9 | 39.9 | 4.40 | 0.081 |
| <i>H'</i> | 1.53 | 1.86 | 5.86 | 0.052 |
| Forbs (% in cover) | 3.30 | 6.77 | 6.17 | 0.048 |
| Species ↓(% in cover) | 8.85 | 20.76 | 12.53 | 0.012 |

of cladodes. None of the ten vegetation parameters had a significantly greater refuge effect in larger cactus clumps compared with smaller ones or in areas located nearer to fenced exclosures compared with further ones (data not shown).

Cattle grazing intensity had a significant positive relationship with the effect of cactus on the inflorescence production of *B. gracilis* and on the cover of perennials (Table 4). In both cases, the effects of cactus switched from negative to positive with increasing grazing intensity. The positive effects of cactus on cover of forbs, cool-season perennial forbs, and species diversity (*H'*) were positively associated with the respective value of that particular parameter within the adjacent large refuge. The abundance of cactus clumps at the sites had no significant relationships with the effects of cactus.

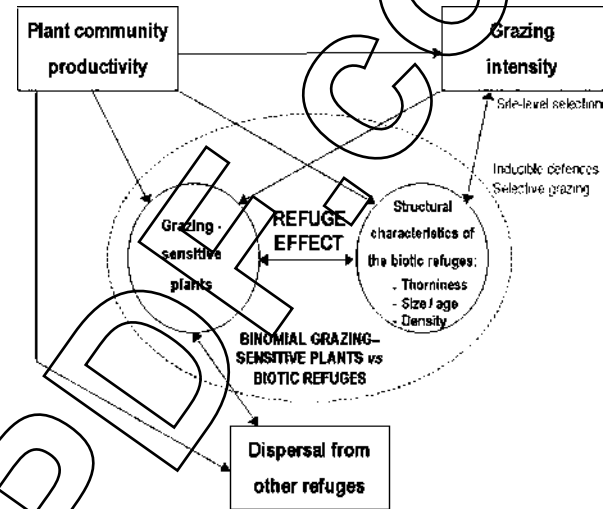


Fig. 1. Conceptual model of factors influencing effects of biotic refuges at a local landscape scale in plant communities grazed by large herbivores.

Discussion

Grazing intensity and cactus refuge effects

We assumed that refuge effects at a local landscape scale can depend on grazing intensity, productivity, dispersal from other refuges, and structural characteristics of the biotic refuge (Fig. 1). Our results support the hypothesis that positive effects of biotic refuges increase with grazing intensity. In some cases, the effect of the cactus was negative for grazing-sensitive plants in the lower part of the grazing gradient and switched to positive when the grazing pressure increased. A potential positive interaction between grazing-sensitive plants and biotic refuges may manifest only when the negative

Table 3. Summary of student *t*-analyses used to test the positive effects of plant community productivity (relatively low productivity grasslands vs. relatively high productivity shrublands) and density of thorns on the effects of cactus for ten vegetation parameters. Effects of cactus were estimated as the difference in each vegetation parameter between inside and outside cactus clumps in the grazed treatment (see Methods section). Density of thorns was estimated as the percentage of the cactus clumps occupied by cactus cladodes.

| | Plant community productivity | | | | Density of thorns | | | |
|---|-------------------------------------|--------------------------------------|-------------------|--------------|------------------------------|------------------------------|-------------------|----------|
| | Low Productivity (Grasslands) | High Productivity (Shrublands) | <i>t</i> value | <i>P</i> | < 30% of cladode cover | > 40% of cladode cover | <i>t</i> value | <i>P</i> |
| Species diversity (<i>H'</i>) | 0.0426 | 0.2252 | 2.335 | 0.029 | 0.1752 | 0.1064 | -0.596 | 0.719 |
| Covers (%) | | | | | | | | |
| Forbs | 0.4188 | 1.2750 | 0.875 | 0.205 | 0.1093 | 1.1973 | 1.052 | 0.155 |
| Small barrel-cacti | 0.0500 | 0.0000 | -0.747 | 0.760 | -0.0234 | 0.0058 | 1.356 | 0.098 |
| Perennials | -2.1250 | 3.9313 | 4.810 | 0.002 | 6.4239 | 0.6229 | -1.850 | 0.957 |
| Cool-season perennial forbs | 0.5250 | 1.7375 | 1.575 | 0.080 | 1.2639 | 1.3880 | 0.151 | 0.441 |
| Species that decrease with grazing (decreasers) | -0.4125 | 2.7188 | 2.781 | 0.016 | 1.5110 | 1.0283 | -0.383 | 0.646 |
| Inflorescence productions (# / unit cover): | | | | | | | | |
| <i>Bouteloua gracilis</i> | 0.2023 | 0.3764 | 0.856 | 0.210 | 0.6719 | 0.2430 | -1.458 | 0.916 |
| Cool-season perennial grasses | 0.0948 | 0.1351 | 0.311 | 0.380 | 0.1505 | 0.0957 | -0.446 | 0.669 |
| Cool-season perennial forbs | 0.0489 | 0.0999 | 0.604 | 0.285 | 0.1539 | 0.0121 | -1.886 | 0.960 |
| Total vegetation | 0.2592 | 0.1190 | -0.514 | 0.687 | 0.4358 | 0.1294 | -2.309 | 0.981 |

Table 4. Linear regressions used to analyse the positive relationship between grazing intensity, abundance of biotic refuges and species abundance in adjacent large refuges on the effects of cactus for the ten vegetation parameters studied. Effects of cactus were estimated as differences between inside and outside cactus clumps in the grazed treatment (see Methods section).

| | <i>n</i> | Grazing intensity (cattle faecal pats/ha) | | | Biotic refuges (clumps/ha) | | | Adjacent large refuges (% in cover) | | |
|---|----------|--|--------|----------|-------------------------------|--------|----------|--|--------|----------------------------|
| | | Intercept | Slope | <i>R</i> | Intercept | Slope | <i>R</i> | Intercept | Slope | <i>R</i> |
| Species diversity <i>H'</i> | 8 | -0.006 | 0.035 | 0.486 | 0.090 | 0.000 | 0.237 | -0.500 | 0.373 | 0.652 * |
| Cover (%): | | | | | | | | | | |
| Forbs | 8 | 0.380 | 0.116 | 0.168 | 0.874 | -0.000 | 0.015 | -1.239 | 0.414 | 0.794 ** |
| Small barrel-cacti ² | 7 | -0.019 | 0.003 | 0.547 | -0.016 | 0.004 | 0.324 | -0.003 | -0.078 | 0.523 |
| Perennials | 8 | -3.525 | 1.098 | 0.597 * | 2.909 | -0.001 | 0.419 | -4.630 | 0.221 | 0.349 |
| Cool-season perennial forbs | 8 | 0.286 | 0.209 | 0.345 | 1.286 | -0.000 | 0.098 | -0.489 | 0.564 | 0.808 ** |
| Species that decrease with grazing | 8 | -0.614 | 0.438 | 0.388 | 1.785 | -0.000 | 0.215 | -0.595 | 0.118 | 0.410 |
| Inflorescence productions (# / unit cover): | | | | | | | | | | |
| <i>Bouteloua gracilis</i> | 8 | -0.084 | 0.092 | 0.649 * | 0.213 | 0.000 | 0.204 | | | Not estimated ¹ |
| Cool-season perennial grasses | 8 | 0.169 | -0.013 | 0.154 | 0.185 | -0.000 | 0.313 | | | Not estimated ¹ |
| Cool-season perennial forbs | 8 | 0.155 | -0.020 | 0.348 | 0.124 | -0.000 | 0.529 | | | Not estimated ¹ |
| Total vegetation | 8 | 0.318 | -0.032 | 0.172 | 0.185 | 0.000 | 0.008 | | | Not estimated ¹ |

* = $P < 0.05$; ** = $P < 0.01$; ¹Not estimated because inflorescence production per unit cover was considered not to be affected by seed dispersal from large refuges; ²Based on seven sites due to one site being a statistical outlier.

effect of grazing outside the biotic refuge is greater than the negative effect of competition inside the refuge. This agrees with predictions that positive interactions among plants may become more important as disturbance or stress increase (Huston 1994; Bertness & Callaway 1994; Callaway & Walker 1997; Brooker & Callaghan 1998). Thus, refuge effects of our cactus may contribute to the low sensitivity of the short-grass steppe to heavy grazing; here we may have a mechanism of resilience to changing grazing pressures, similar to what Milchunas & Noy-Meir (2002) suggested for geologic refuges. Other types of disturbance may be buffered as well.

Plant community productivity and cactus refuge effects

Results also supported the hypothesis that positive effects of biotic refuges in grazed plant communities increase with productivity (Fig. 1). Plant adaptations to more productive conditions enhance grass competitiveness for light, but make the species more vulnerable to grazing by large herbivores (Milchunas et al. 1988). Grazing in grasslands in more productive environments changes species composition more than in less productive environments. This may explain why Callaway et al. (2000) reported large refuge effects of spiny plants in productive pastures in the Caucasus, and Rebollo et al. (2002) found relatively small refuge effects by cactus in this semi-arid short-grass steppe. This is also true locally for short-grass steppe; more productive shrublands and grasslands in swales are more sensitive to grazing than less productive sites (Milchunas et al. 1989; Cibils 1999). In our case, cactus had greater positive effects on species that decrease with grazing on the more productive shrublands. This group is comprised of productive mid-height grasses, such as *Pascopyrum smithii*, that are

taller than the dominant short grasses in this community. Our results also supported the hypothesis that some refuge effects were a consequence of an increase in grazing intensity in the more productive compared to less productive areas (Fig. 1), as suggested in the conceptual model of Bertness & Callaway (1994). Thus, our results suggest that a greater cattle grazing intensity in productive communities may explain the greater positive effects of cactus on species diversity (H') found in those communities.

Relationships between structural characteristics of cactus clumps and refuge effects of cactus

Structural characteristics of biotic refuges, such as abundance of thorns, and size and density of biotic refuges, can positively influence refuge effects. In the particular situation of *Opuntia* in short-grass steppe a decrease in the refuge effects of the cactus with the abundance of thorns (estimated from abundance of cladodes inside clumps) was found. This finding may be due to a trade-off between an increase in protection versus a decrease in space for neighbours, or that an increase in thorn density above some level does not increase protection. Some of the most highly protected cactus clumps had a cladode basal cover of greater than 50% of the area. The branched, thick, prostrate cladodes constrain the space available for the grazing-sensitive species in the cactus clumps. This spatial constraint is probably the main limiting factor for refuge effects of this cactus. Competition for water between cactus and herbaceous species is low, because of the little overlap between other species and the near-surface, extensive distribution of *Opuntia* roots (Dougherty 1986). Rebollo et al (2002) showed there would be many positive

effects of cactus if the abundance of other species was recalculated as if they proportionately occurred in the area also occupied by cactus.

The protection of biotic refuges can increase with grazing intensity (Fig. 1). Several authors have pointed out that grazing intensity may affect the degree of protection of grazing-resistant species by promoting inducible defenses such as thorniness (Cooper & Owen-Smith 1986). We did not find that cattle grazing intensity affects cladode cover in the cactus clumps, and Rebollo et al. (2002) did not find differences in cladode cover within clumps between ungrazed and grazed areas. In the case of *Opuntia polyacantha* in short-grass steppe, increases in thorniness through inducible defences do not occur, because the cactus is rarely grazed by large herbivores.

Our results did not support the hypothesis that positive effects may increase with size or age of the biotic refuges (Callaway et al. 2000), although trends in the data were in this direction. For the studies that found a significant increase in positive interactions with age and size of refuge plants, age appears to be the main factor (Pugnaire et al. 1996). In the case of cactus, larger clumps are produced either by branching of a single original plant or by the close aggregation of several individuals produced by seeds from a single fruit (Turner & Costello 1942). The absence of relationships between clump size and refuge effects may be due to clump size not necessarily being related to cactilage.

Our results do not support the hypothesis that facilitation intensity may increase with refuge density. Density of biotic refuges may affect refuge effectiveness in grazed plant communities in two ways. First, high densities of biotic refuges (grazing-resistant species) may influence site-level selection by herbivores, resulting in avoidance of entire areas even though some palatable species are present (Milchunas & Noy-Meir 2002). In the present study, we did not find differences in grazing intensity with cactus clump density, which may have influenced the presence of differences in refuge effects. Second, the effectiveness of refuges may increase because a greater density may favour dispersal and colonization of refuge-dependent species, such as predicted by island biogeography theory. Because of the high density of cactus clumps in this system, clump density may not limit refuge effects. Density of *Opuntia* clumps ranged from 370 to 4800 per ha.

Although biotic refuge density did not influence refuge effects per individual unit in this study, factors affecting the abundance of biotic refuges across a landscape can have a large influence on total refuge effects. The abundance of biotic refuges may vary across gradients of plant community productivity and grazing intensity (Fig. 1), however the intensity and direction of the response appears to be species-dependent. Turner &

Castello (1942) and Milchunas et al. (1989) found that *Opuntia* in short-grass steppe is less abundant on productive swales and depressions than on less productive uplands. By contrast, the shrub *Atriplex canescens*, which can also promote refuge effects in the short-grass steppe, are more abundant on more productive coarser-textured soils and lowlands (Cibils 1999). Grubb (1992), comparing the incidence of spines in different types of vegetation, concluded that there is a horseshoe shaped relationship with resource-availability or productivity, with maxima at the ends of the spectrum. The density of potential biotic refuges has been reported to increase, decrease, or remain almost invariant with grazing intensity (Callaway et al. 2000; Cibils 1999; Rebollo et al. 2002), and responses vary within a given productivity, evolutionary history of grazing, and grazing treatment category. Therefore, the refuge effects per individual biotic refuge generally increase with plant productivity and grazing intensity, but the density of biotic refuges shows a high variety of responses depending on the particular species involved.

The relative importance of biotic refuges in different environments

Biotic refuges can be an important mechanism to improve the stability of grazed communities at the local landscape scale, because the refuge effects increase with grazing intensity and abundance of grazing-sensitive species (Fig. 1). These effects may be more intense in areas with greater plant community productivity where the grazing intensity by large herbivores may be greater, and grazing-sensitive species are more abundant.

At a larger scale than the local landscape scale, Milchunas & Noy-Meir (2002) suggested an interaction between plant community productivity and evolutionary history of grazing on plant diversity in explaining the intensity of geologic refuge effects. These authors provided evidence that refuge effects in more productive environments may be more important in protecting diversity than refuges in less productive ones, and the effects of protection may be greater in communities with short compared to long evolutionary history of grazing. Thus, refuges may be equally important in unproductive stressful environments with short evolutionary history of grazing as they are in more productive environments with a long evolutionary history. These predictions may be directly applicable to biotic refuges, unless competitive relationships between grazing-sensitive species and biotic refuges change through gradients of plant productivity and evolutionary history of grazing, or these gradients change the structural characteristics of the biotic refuges (density, size, growth form, degree of protection, etc).

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