Effects of livestock watering sites on alien and native plants in the Mojave Desert, USA

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Abstract

Increased livestock densities near artificial watering sites create disturbance gradients called piospheres. We studied responses of alien and native annual plants and native perennial plants within 9 piospheres in the Mojave Desert of North America. Absolute and proportional cover of alien annual plants increased with proximity to watering sites, whereas cover and species richness of native annual plants decreased. Not all alien species responded the same, as the alien forb *Erodium cicutarium* and the alien grass *Schismus* spp. increased with proximity to watering sites, and the alien annual grass *Bromus madritensis* ssp. *rubens* decreased. Perennial plant cover and species richness also declined with proximity to watering sites, as did the structural diversity of perennial plant cover classes. Significant effects were focused within 200 m of the watering sites, suggesting that control efforts for alien annual plants and restoration efforts for native plants should optimally be focused within this central part of the piosphere gradient.
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1. Introduction

Artificial watering sites can have significant ecological effects in arid and semi-arid desert ecosystems where standing surface water is uncommon. One major effect is the focused grazing and activity patterns of large herbivores around artificial watering sites

(Andrew, 1988). This focused activity results in a disturbance gradient called a "piosphere" which is centered on the watering site (Lange, 1969). Piosphere gradients have been quantified in terms of large herbivore trail densities (Lange, 1969; Andrew and Lange, 1986a), activity levels (Thrash et al., 1995), and dung accumulations (Lange, 1969; Andrew and Lange, 1986a; Turner, 1998a). They can be created by both wild and domesticated animals and they occur worldwide.

The activity gradient of large herbivores within the piosphere can have many secondary effects. For example, the characteristics of soil nutrients (Tolsma et al., 1987; Perkins and Thomas, 1993; Turner, 1998a, b), soil compaction (Andrew and Lange, 1986a), microtopography (Nash et al., 2003), cryptogamic crusts (Rogers and Lange, 1971; Andrew and Lange, 1986a), and seedbanks (Navie et al., 1996) can vary with proximity to watering sites. Plant communities vary in biomass, cover, defoliation (Andrew and Lange, 1986b; Tolsma et al., 1987; Soltero et al., 1989; McClaran and Anable, 1992; Fusco et al., 1995; Fernandez-Gimenez and Allen-Diaz, 1999) species composition (Andrew and Lange, 1986b; Tolsma et al., 1987; Tueller and Platou, 1991; Perkins and Thomas, 1993; Nash et al., 1999; but see Van Rooyen et al., 1994 for exceptions), and reproductive output (Riginos and Hoffman, 2003). Generalized "ecosystem health" can also vary with grazing intensity near artificial watering sites (de Soyza et al., 1997). Although various environmental impacts associated with piospheres have been documented, much information that could help in the management of these impacts is still unknown. Information specific to the effects of piospheres created by domestic livestock is particularly important in the management of rangelands.

The potentially differing distributions of alien and native plants within piospheres are an important topic that deserves more study. Plant invasions into desert regions may be limited by low soil nutrient levels (Brooks, 1999a, 2003), and concentrated livestock use can increase availability of soil nutrients (Weir, 1971; Perkins and Thomas, 1993). Livestock also remove plant biomass (e.g. Webb and Stielstra, 1979), which may reduce the ability of native plants to compete with and impede plant invasions. Livestock also serve as dispersal vectors for plants, potentially facilitating the invasion of alien species (Sheeley et al., 2002). Although numerous studies indicate that the abundance of alien species can increase with proximity to artificial watering sites (Andrew and Lange, 1986b; Rogers and Whalley, 1989; Tueller and Platou, 1991; Fusco et al., 1995; Landsberg et al., 1997), some studies reported no relationship (Andrew and Lange, 1986b; McClaran and Anable, 1992). Other issues remain unstudied, such as the response of alien plant communities to grazing gradients within piospheres (e.g. alien richness and covariation among alien species), and the effects of landscape features on alien plant distributions within the piosphere (e.g. shrub–intershrub gradients). This information is needed to design effective early detection and control plans for alien plants near livestock watering sites.

The effect of piospheres on plant species richness is another topic that deserves more attention. In general, intermediate levels of livestock grazing are thought to maximize plant species richness (Sousa, 1984). This hypothesis applies in ecosystems with high productivity where high plant cover may otherwise preclude the coexistence of many species. However, it is unclear if high grazing levels promote plant species richness in ecosystems with low productivity such as deserts. Only two studies of plant species richness are associated with piospheres, and the authors report differing results. Landsberg et al. (1997) reported an absence of consistent trends in species richness within 8 piospheres in Australian rangelands, whereas Fernandez-Gimenez and Allen-Diaz (1999) report that

species diversity decreased at a mountain-steppe site, increased at a mid-elevation steppe site, and did not change with proximity to artificial watering sites at a desert-steppe site in Mongolia.

Structural diversity of perennial plants is another landscape variable that has not been described in the context of the piospheres. Structural diversity reflects the variation in numbers (richness) and distribution (evenness) of structural components (cover, height, and volume). High structural diversity of plants is particularly important for birds (Wiens, 1969), and anthropogenic disturbances such as grazing can affect birds (Wiens, 1973) and reptiles (Jones, 1981; Berry, 1997) through changes in vegetation structure in arid and semi-arid ecosystems. These types of data are needed to evaluate the potential effects of vegetation changes on wildlife communities near watering sites.

The objective of this study was to produce new information to better evaluate the ecological effects of piospheres in desert ecosystems. Specifically, we quantified variation in cover and species richness of alien and native annual plant species, and variation in cover, species richness, and structural diversity of perennial plants, within piospheres in the Mojave Desert of western North America. We also evaluated historical land uses that may have simultaneously affected community composition, distribution, and abundance of plants in this region. We predicted that alien annual plant cover and diversity would be higher, whereas native annual and perennial plant cover, species richness, and perennial plant structural diversity would be lower, with increasing proximity to watering sites.

2. Materials and methods

2.1. Study area

This study was conducted within the 194 km^2 Pilot Knob grazing allotment (35°20′30″N, 117°20′28″W), managed by the United States (US) Department of the Interior, Bureau of Land Management (BLM, 1980), in the west-central Mojave Desert, California, USA (Fig. 1). Elevations at the Pilot Knob grazing allotment range from 780 to 1430 m. Rainfall occurs primarily during the winter months of October–April (81% of 168 mm average annual rainfall) as estimated from the Randsburg and Goldstone weather stations located 28 km west and 52 km east of the allotment boundaries, respectively (www.ncdc.noaa.gov). Soils in the study area are derived from Quaternary alluvium of basaltic and granitic parent material.

Perennial vegetation was characterized by native shrubs typical of the Mojave Desert. *Larrea tridentata* comprised most of the perennial plant cover at 8 of the watering sites used in our study, and *Coleogyne ramossisima* dominated cover at 1 site. Sub-dominant perennial species present at all 9 watering sites included *Acamptopappus sphaerocephalus*, *Ambrosia dumosa*, *Ericameria cooperi* var. *cooperi*, *Grayia spinosa*, and *Lycium andersonii* (Appendix A). Annual vegetation was comprised mostly of winter germinating species, especially the aliens *Erodium cicutarium*, *Schismus* spp., and *Bromus madritensis* ssp. *rubens* (hereafter called *Bromus rubens*), and by the natives *Amsinckia tessellata*, *Lasthenia californica*, and *Guillenia lasiophyllum*, in addition to numerous other native species (Appendix B). Plant nomenclature throughout this paper follows Hickman (1993).

Land within and adjacent to the Pilot Knob grazing allotment has experienced various types of human activities from pre-historical to recent times. Native Americans used the area from at least 1200 B.C. to possibly as late as 1820 A.D. (National Register of Historic
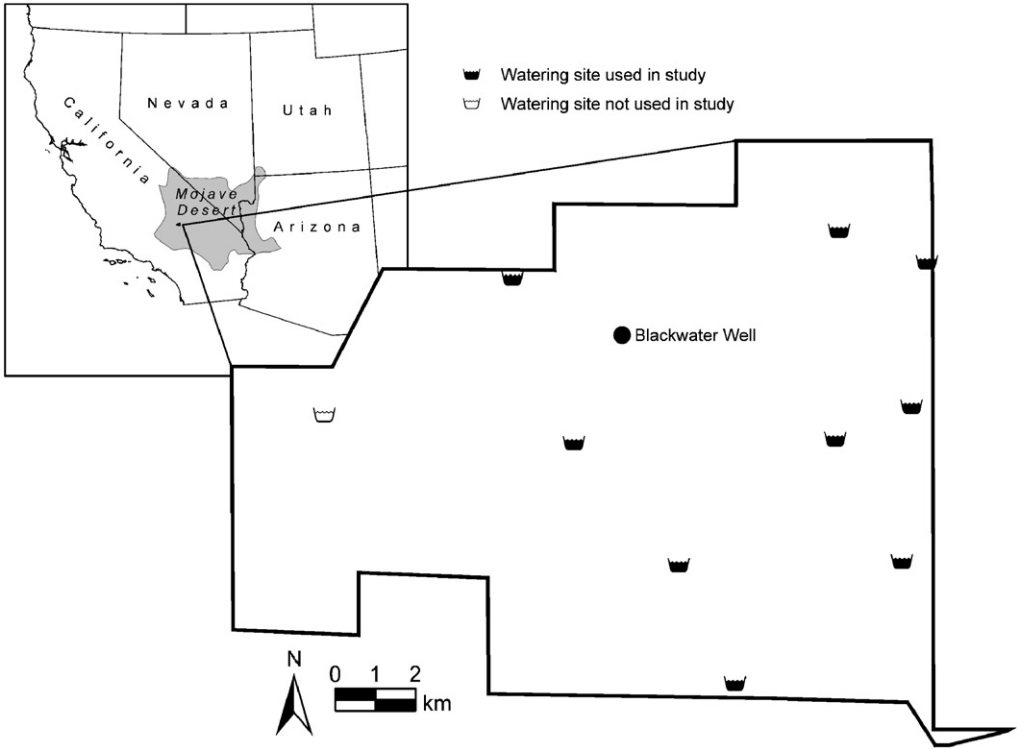
Fig. 1. Location of the Pilot Knob grazing allotment in the Mojave Desert, California.

Places, 2000; J. Reed pers. communication). Historical records indicate that livestock grazing occurred in the vicinity of Pilot Knob beginning in the 1870s (Birnie, 1876; Palmer, 1891; Spears, 1892; Starry, 1974). The first BLM records of a formal Pilot Knob allotment for livestock grazing are from the early 1940s (BLM allotment records, Ridgecrest Field Office), at which time the allotment was 396 km^2 and extended eastward ~14 km beyond the current boundaries shown in Fig. 1. Most artificial watering sites in the allotment were in place by the 1950s and early 1960s. In 1982, the allotment was reduced 51% to its current size of 194 km^2, and in 1991 a boundary fence was constructed, limiting livestock use of watering sites to those located within the 1982 allotment boundaries (Fig. 1).

Stocking rates on the Pilot Knob allotment are only known from 1973 to the present (BLM allotment records, Ridgecrest Field Office). From 1973 to 1977 ~1000 cattle grazed the 194 km^2 allotment 2–3 months each year, except for in 1975 when ~1600 sheep grazed for about 2 months. A period of non-use extended from 1978 to 1981, followed by a 2-yr period of sheep grazing (~1000 sheep grazed for about 2 months each year) and then a 12-yr period of cattle grazing (~20–150 cattle for 9–10 months each year). Grazing was discontinued in 1996 when a conservation organization purchased the grazing permit and discontinued livestock use. The only other large herbivores that grazed this allotment during the 1900s were feral burros, but their herd size was relatively small (<30 individuals).

2.2. Sampling design

Blackwater Well, the primary source of water within the current allotment boundary (Fig. 1), has been subjected to many different types of disturbances over the years. During this study, the site included numerous buildings, troughs, tanks, a corral, and a windmill. We excluded Blackwater Well from analysis and focused instead on the numerous artificial watering sites to which water was either piped or trucked at points throughout the allotment. We specifically wanted to evaluate the piosphere effects of livestock grazing with minimal confounding effects from other anthropogenic disturbances.

Each artificial watering site was comprised of a watering tank and trough surrounded by a denuded zone where perennial vegetation had been completely removed (Fig. 2). The denuded zone has been also referred to as a "sacrifice zone" (Perkins and Thomas, 1993). The specific locations of the tanks and troughs appeared to have shifted historically within each denuded zone, as indicated by remnants scattered about the sites. We therefore defined "watering site" as the total area within the denuded zone. Accordingly, the diameter of the watering sites ranged from 15 to 70 m, based on the average distances across the center of the sites to perennial shrubs on opposite sides of the sites.

At each artificial watering site we sampled along a single vector that began at the edge of the watering site, ran parallel to the elevation contour, and did not intersect other major anthropogenic disturbance features (e.g., roads). By orienting the vector parallel to the elevation contour, we minimized within-site variations in soil and vegetation

Fig. 2. An typical livestock watering site comprised of a tank, trough, and denuded zone, at the Pilot Knob grazing allotment, California.

characteristics that are often associated with localized elevation gradients. By not intersecting other major disturbance features, we minimized their potentially confounding effects and focused our analyses on piosphere effects. These conditions were met for 9 of the 10 artificial watering sites within the allotment (Fig. 1).

We measured annual and perennial plants at 0, 50, 200, and 800 m from each watering site. At each distance, vegetation was sampled along a transect centered on the vector, and extending 30 m perpendicularly from each side of the vector (60 m total length). We did not sample beyond 800 m from the watering sites to reduce the potential confounding effects of dirt roads that would have been frequently intersected at greater distances.

2.2.1. Annual plant sampling

Sampling stations for annual plants were established at five points spaced 15 m apart along each 60 m vegetation transect. At each station, the nearest beneath-canopy and interspace microhabitats were sampled. Beneath-canopy microhabitats were located on the north side of perennial plants $\geqslant 50$ cm in diameter, which were mostly woody shrubs, but in a few cases were perennial bunch grasses. Interspace microhabitats were located in open spaces >1 m from the nearest perennial plant canopy. Prior studies indicate that annual plant composition in the Mojave Desert can differ greatly between these microhabitats, typically with greatest annual plant biomass beneath perennial shrubs (Shreve, 1931; Went, 1942; Muller, 1953; Brooks, 1999a).

Annual plant cover and species richness were measured in a 10×20 cm sampling plot within each microhabitat. Cover was measured using a 10-pin point frame (2 cm pin spacing) placed at three random locations perpendicular to the long axis of the sampling plots. This resulted in 30 pins/plot. Pins were lowered perpendicular to the soil surface and the total number of contacts with live plant species were recorded until the pin reached mineral soil. Species richness was measured as the total number of annual plant species rooted within the sampling plot. There were 360 annual plant sampling plots: 9 watering sites × 4 distances × 5 stations × 2 microhabitats. Annual plants were sampled at the same locations during spring 1998 and 2000.

2.2.2. Perennial plant sampling

Perennial plant cover and height were measured using two methods: (1) larger individuals and mixed-species clumps ($\geqslant 50$ cm canopy diameter) were measured within 6 contiguous 10×10 m ($100\,\text{m}^2$) sampling plots centered along each 60 m vegetation transect; and (2) the more numerous, smaller individuals (<50 cm diameter) were measured within 3×3 m ($9\,\text{m}^2$) sampling plots centered within each $100\,\text{m}^2$ plot. Two measurements of canopy cover were recorded for each individual or mixed-species clump: the greatest horizontal diameter and the diameter $90°$ to the first. Perennial plant cover was calculated assuming a circular canopy ($A = \pi r^2$) where the radius was half the average of the two diameter measurements. Four height measurements were recorded at the highest point in the shrub canopy in each of 4 cardinal compass directions within each perennial plant canopy, and averaged to determine plant height. Species richness was measured as the total number of perennial plant species rooted within each 10×10 m ($100\,\text{m}^2$) sampling plot. There were 216 perennial plant sampling plots at each of the two spatial scales (100 and $9\,\text{m}^2$): 9 watering sites × 4 distances × 6 plots. Perennial vegetation was sampled only in spring 2000.

2.3. Data analyses

2.3.1. Annual plant analyses

Data were analysed as a split-plot-in-space-and-time design, with watering site as the random block effect, and distance from the watering site, microhabitat, and year as fixed effects. The five stations within each 60 m transect were treated as sub-samples, and the transects as replicates for each distance from the edge of the watering sites. An example of this design is found in Steel and Torrie (1980). Statistical tests were run with SAS statistical software, using the generalized linear mixed model function (PROC MIXED) with the GLIMMIX macro (Little et al., 1996). The generalized linear mixed model gave us flexibility in defining random and fixed effects, and in specifying the Poisson distribution, which was an appropriate fit for point-frame and richness count data (Steel and Torrie, 1980).

We grouped annual plant data into general categories for separate analyses. Cover was evaluated separately for all annual plants, natives, aliens, proportion of native to alien, and specific alien species. Richness was evaluated separately for all annual plants, natives, and aliens. We used the sequential Bonferroni method to minimize Type I error rates when making multiple comparisons (Sokal and Rohlf, 1995), such as when evaluating pair-wise differences between distances from the watering sites. Effects were considered significant at $p \leqslant 0.05$.

2.3.2. Perennial plant analyses

We analysed perennial plant cover, richness, and structural diversity data as a randomized complete block design, with watering site as the random block effect, distance from the watering site as the fixed effect, the six sampling plots within each 60 m transect as sub-samples, and the transects as statistical replicates. Total cover was analysed assuming a normal distribution using SAS PROC MIXED (Little et al., 1996). Cover for individual species was not normally distributed and could not readily be transformed. Consequently, we converted cover values into ranks and tested for treatment effects using the non-parametric Friedman's Test, and then made multiple comparisons between treatments using the Tukey Honestly Significant Difference method (Zar, 1999).

We calculated perennial plant species richness at 100, 300, and 600 m^2 scales within each transect. For the 100 m^2 scale we averaged the number of species in each of the 6 sampling plots, for 300 m^2 we averaged the combined species number for plots 1–3 and 4–6, and for 600 m^2 we summed the species in all 6 plots. Richness data were analysed assuming a Poisson distribution using SAS PROC MIXED with the GLIMMIX macro (Little et al., 1996).

We analysed structural diversity of plant cover by first defining 5 cover classes (<0.5, 0.5–1, 1–2, 2–4, and >4 m^2) based upon break points in the frequency distribution of individual shrub cover values. We calculated density (individuals/100 m^2) within each size class for each sampling plot, and then used these values to compute indices of diversity (H, Shannon–Wiener index), evenness (J, Pielou index), and richness (S, total number of classes present) (Ludwig and Reynolds, 1988). Diversity and evenness were analysed assuming a normal distribution using SAS PROC MIXED, while richness was analysed assuming a Poisson distribution using SAS PROC MIXED with the GLIMMIX macro (Little et al., 1996). Density could not readily be transformed into a normal distribution, so values were ranked and analysed using Friedman's Test.

3. Results

During the winter of October 1997 through April 1998, rainfall was 224 mm, or 165% of the long-term average. In contrast, winter rainfall during 1999–2000 was 59 mm, or 43% of the long-term average. Total annual plant cover and species richness were accordingly higher in 1998 (37 point hits/plot, 3 spp./0.02 m^2) than in 2000 (5 point hits/plot, 2 spp./0.02 m^2).

3.1. Alien and native annual plant cover and species richness

Total annual plant cover increased with increasing proximity to watering sites ($F_{3,24} = 21.37$, $p < 0.0001$), but this trend was only significant when overall productivity was relatively high in 1998 (distance × year interaction: $F_{3,24} = 3.39$, $p = 0.0343$). Distance effects occurred primarily between 50 and 0 m from the watering sites (Fig. 3a). In the interspace, annual plant cover averaged 13, 13, and 14 point hits/plot at 800, 200, and 50 m, then jumped to 43 point hits/plot at 0 m. This represented a 67% increase in cover from 50 to 0 m. In the beneath-canopy, annual cover averaged 49, 47, and 51 point hits/plot at 800, 200, and 50 m, then increased to 64 point hits/plot at 0 m. This increased annual cover only 22% from 50–0 m. Distance effects were significantly stronger in the interspace than the beneath-canopy microhabitat (distance × microhabitat: $F_{3,24} = 16.82$, $p < 0.0001$).

Cover of alien and native annual plants responded very differently to the watering site gradient. Alien annual cover increased ($F_{3,24} = 31.58$, $p < 0.0001$) (Fig. 3b), whereas native annual cover decreased ($F_{3,24} = 6.70$, $p = 0.0019$) (Fig. 3c), with increasing proximity to watering sites. Most effects occurred within 200 m of the edge of the watering sites (Fig. 3b, c). Effects were more dramatic in the interspace than the beneath-canopy microhabitats, although the distance × microhabitat interaction was significant for aliens ($F_{3,24} = 25.55$, $p < 0.0001$), but not for natives ($F_{3,24} = 2.14$, $p = 0.1214$). In the interspace, alien cover increased by 78% from 0 to 200 m, whereas in the beneath canopy it increased only 44% (Fig. 3b).

The proportional cover of alien annual plants relative to total annual plants also increased significantly with increasing proximity to watering sites ($F_{3,24} = 17.67$, $p < 0.0001$), and the effect did not vary significantly between years ($F_{3,24} = 2.41$, $p = 0.0915$). This was due to the simultaneous increase in alien cover and decrease in native cover approaching watering sites (Fig. 3b, c). The strongest effects on proportional cover of aliens also occurred within 200 m of the edge of the watering site in the interspace microhabitat (distance × microhabitat interaction; $F_{3,32} = 5.37$, $p = 0.0041$). Also, the proportional alien cover was relatively high even at 800 m from the watering sites, where it was 56% in the interspace and 76% in the beneath-canopy microhabitat in 1998. In 2000, the proportional alien cover at 800 m was 68% in the interspaces and 72% in the beneath-canopy. Overall, proportional alien cover did not vary significantly between years ($F_{1,8} = 0.05$, $p = 0.7808$).

Although total alien annual plant cover increased with proximity to watering sites in 1998, responses of individual alien species varied (Fig. 4). Alien cover was dominated by three of the six alien species present in our samples, comprising 96% of the total alien cover. Cover of the alien forb *E. cicutarium* ($F_{3,24} = 10.34$, $p = 0.0001$) (Fig. 4a), and the alien grass *Schismus* spp. ($F_{3,24} = 9.36$, $p = 0.0003$) (Fig. 4b) increased with proximity to
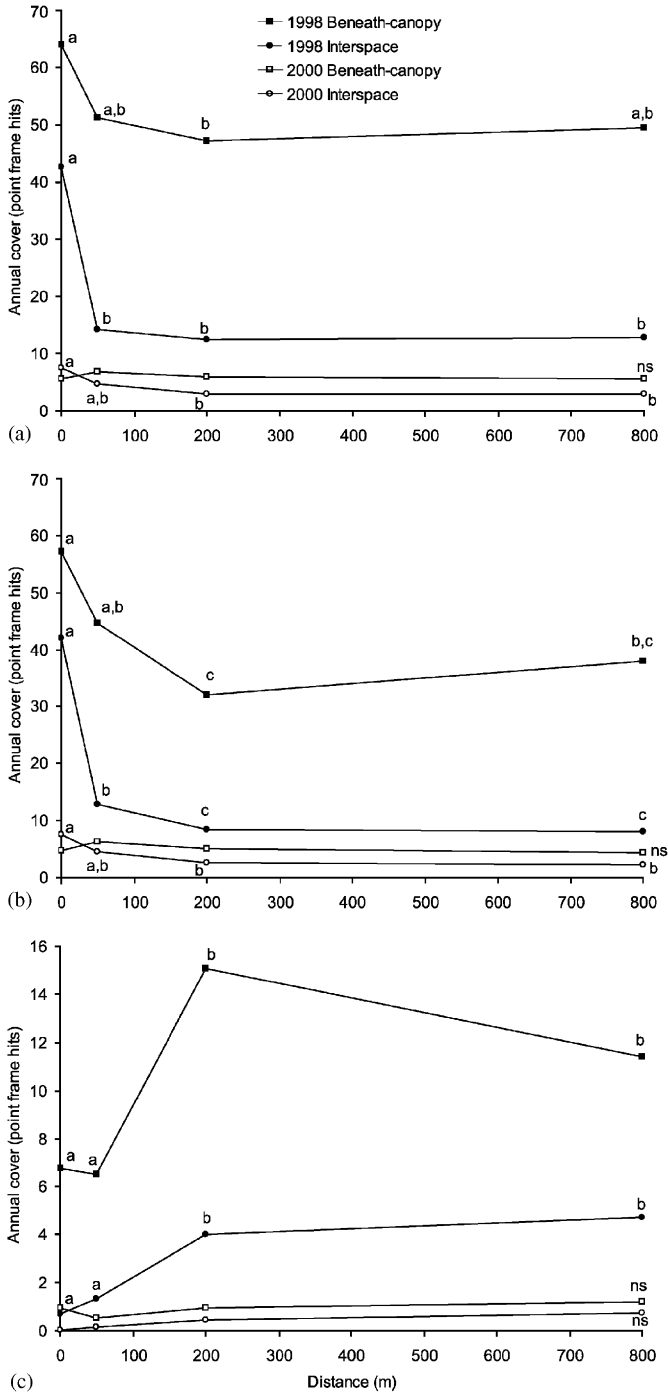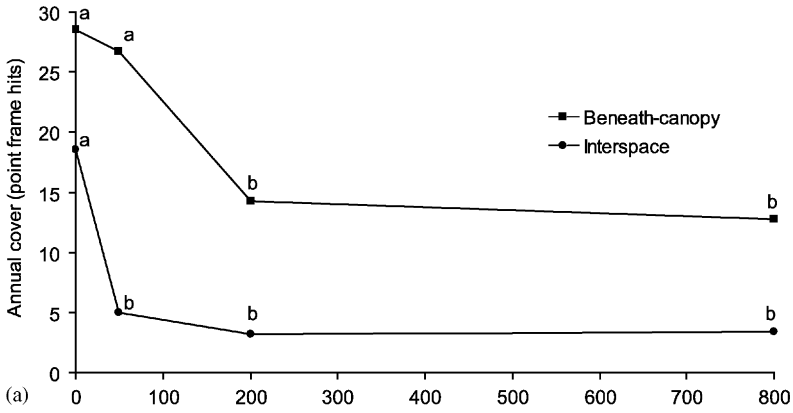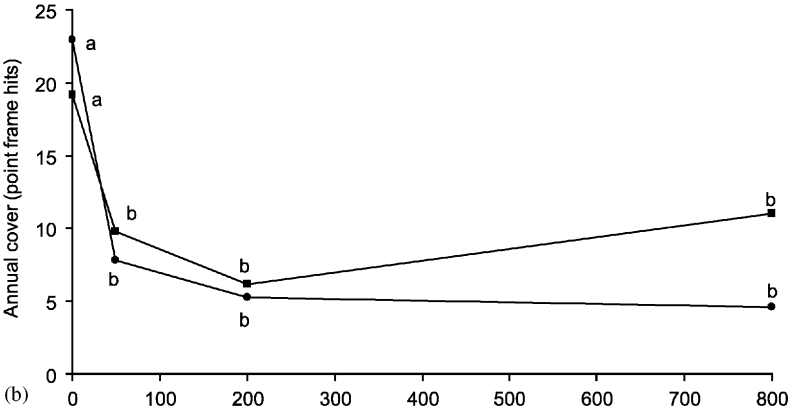
Fig. 3. Annual plant cover of all species (a), aliens (b), and natives (c) in beneath-canopy and interspace microhabitats at four distances from artificial watering sites ($n = 9$ sites) during spring 1998 and 2000 at the Pilot Knob grazing allotment, California. Differing letters indicate significant differences between distances within microhabitats within years ($p \leqslant 0.05$, ns = no significant distance effect).
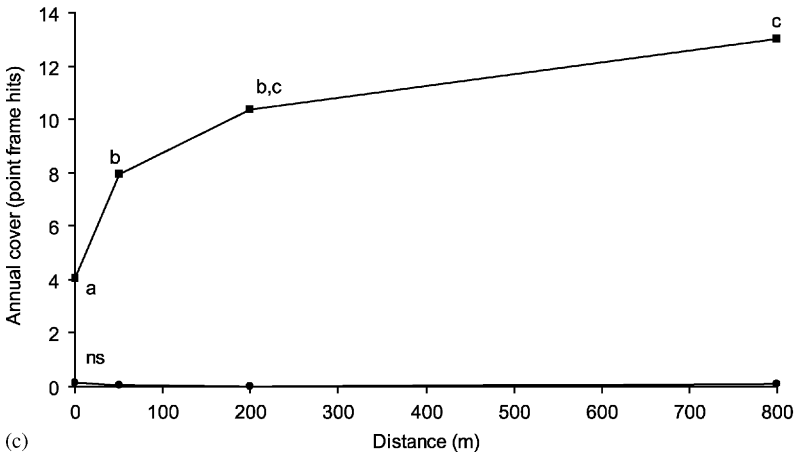
Fig. 4. Cover of individual alien species at four distances from artificial watering sites ($n = 9$ sites) during spring 1998 at the Pilot Knob grazing allotment, California. Differing letters indicate significant differences between distances within microhabitats ($p \leqslant 0.05$, ns = no significant distance effect).

Table 1

Total species richness, alien richness, and native richness ($0.02\,m^2$) within beneath-canopy and interspace microhabitats at four distances from artificial watering sites ($n = 9$ sites) during spring 1998 at the Pilot Knob grazing allotment, California

Species richness	Distance from watering site (m)			
	0	50	200	800
Beneath-canopy				
Total	4.4a	5.0a,b	5.6a,b	5.9b
Alien	2.9a	3.0a	3.0a	2.9a
Native	1.5a	2.1a,b	2.5a,b	3.1b
Interspace				
Total	2.3a	3.9b	5.4c	4.9c
Alien	2.0a	2.0a	1.9a	1.7a
Native	0.2a	1.9b	3.4c	3.2c

Differing letters indicate significant differences between distances within microhabitats for each of the three species richness analyses ($p \leqslant 0.05$).

watering sites. In contrast, cover of the alien annual grass *B. rubens* decreased with proximity to watering sites ($F_{3,24} = 4.16$, $p = 0.0167$) (Fig. 4c). Significant effects occurred within 200 m of watering sites for these alien species.

Data for most native annual plant species could not be analysed statistically due to their low abundances and high variances among sites. However, three of the 60 native species comprised 45% of the total native cover and were amenable to statistical analyses. Only one native species, *L. californica,* responded significantly to the piosphere ($F_{3,24} = 7.49$ $p = 0.0011$), generally decreasing with proximity to watering sites, especially within 200 m of the watering sites. The other two common native annuals, *Amsinckia tessellata* ($F_{3,24} = 2.53$, $p = 0.0811$) and *G. lasiophylla* ($F_{3,24} = 0.69$, $p = 0.5696$), did not vary significantly within the piosphere.

Piosphere effects on alien richness were not significant in either the beneath-canopy or interspace microhabitats (Table 1). In contrast, total annual plant species richness ($F_{3,24} = 20.33$, $p < 0.0001$) and native annual plant richness ($F_{3,24} = 21.48$, $p < 0.0001$) decreased with proximity to watering sites in 1998. This decrease was more dramatic within interspace than beneath-canopy microhabitats (distance × microhabitat: $F_{3,24} = 8.89$, $p < 0.0001$ for total richness; $F_{3,24} = 10.43$, $p < 0.0001$ for native richness). In the interspace microhabitat, total annual plant richness declined 28% from 200 to 50 m, then 41% from 50 to 0 m. This trend was due to native species richness, which declined 44% and 90% over these same two intervals. In the beneath-canopy microhabitat, total annual plant richness declined 25% from 800 to 0 m, also due to native richness, which declined 52% over this interval.

3.2. Native perennial plant cover, species richness, and structural diversity

Perennial plant cover declined with proximity to watering sites ($F_{3,24} = 30.98$, $p < 0.0001$), primarily from 50 to 0 m where it declined by 50% (Fig. 5). This trend was due primarily to significant declines in moderate to small-sized plants such as *E. cooperi* var. *cooperi* ($\chi^2 = 40.32$, $p < 0.0001$, d.f. = 3), *L. andersonii* ($\chi^2 = 26.33$, $p < 0.0001$,
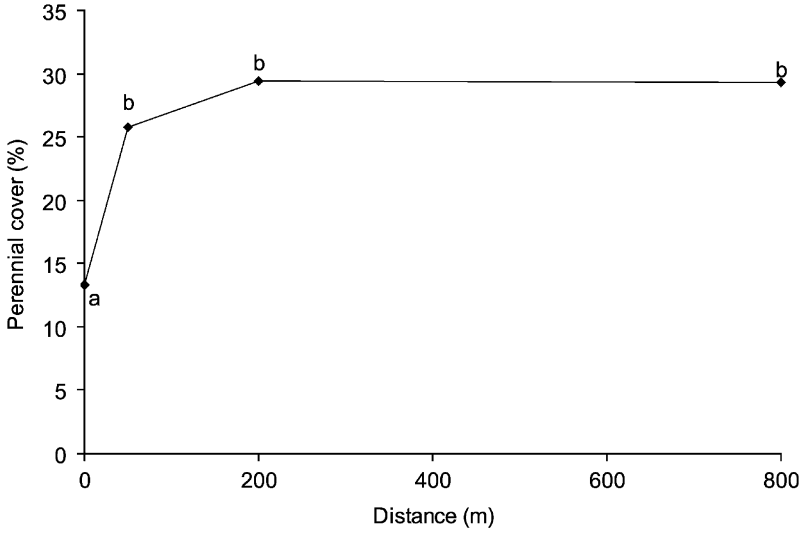
Fig. 5. Total perennial plant cover at four distances from artificial watering sites ($n = 9$ sites) during spring 1998 at the Pilot Knob grazing allotment, California. Differing letters indicate significant differences between distances within microhabitats ($p \leqslant 0.05$, ns = no significant distance effect).
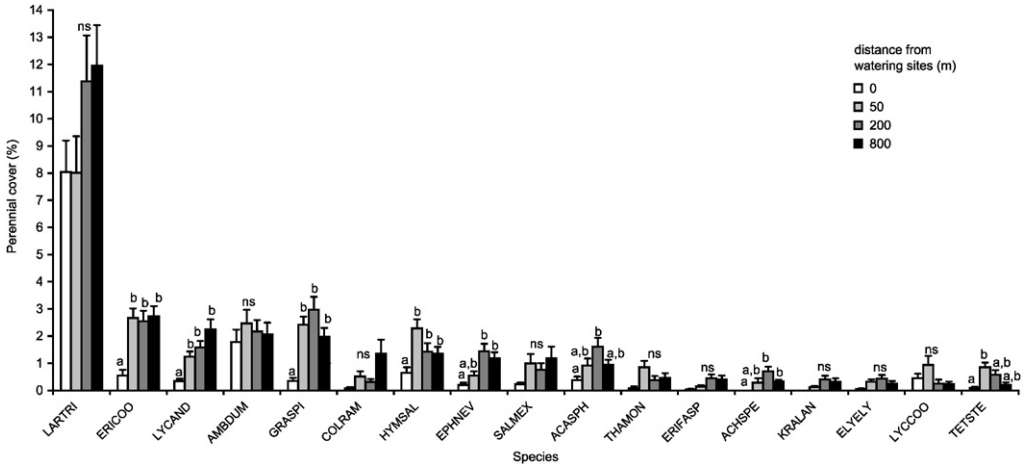

Fig. 6. Cover of individual perennial plant species at four distances from artificial watering sites ($n = 9$ sites) during spring 2000 at the Pilot Knob grazing allotment, California. Differing letters indicate significant differences between distances for each species ($p \leqslant 0.05$, ns = no significant distance effect). Species codes are listed in Appendix A.

d.f. = 3), *G. spinosa* ($\chi^2 = 39.70$, $p < 0.0001$, d.f. = 3), *Hymenoclea salsola* ($\chi^2 = 23.71$, $p < 0.0001$, d.f. = 3), *Ephedra nevadensis* ($\chi^2 = 18.55$, $p = 0.0003$, d.f. = 3), *A. sphaerocephalus* ($\chi^2 = 13.72$, $p = 0.0033$, d.f. = 3), *Achnatherum speciosa* ($\chi^2 = 16.45$, $p = 0.0009$, d.f. = 3), and *Tetradymia stenolepis* ($\chi^2 = 10.34$, $p = 0.0159$, d.f. = 3) (Fig. 6). Cover of the largest shrub, *L. tridentata*, generally declined with proximity to watering sites, but the trend was not significant ($\chi^2 = 5.64$, $p = 0.1305$, d.f. = 3).

Table 2
Total perennial species richness at three spatial scales at four distances from artificial watering sites ($n = 9$ sites) during spring 2000 at the Pilot Knob grazing allotment, California

Scale (m^2)	Distance from watering site (m)			
	0	50	200	800
100	5a	9b	9b	8b
300	7a	11b	12b	11b
600	9a	13b	13b	13b

Differing letters indicate significant differences between distances for each of the three scales ($p \leqslant 0.05$). All perennial species were native.

Table 3
Density of perennial plants by size class at four distances from artificial watering sites (100 m^2, $n = 9$ sites) during spring 2000 at the Pilot Knob grazing allotment, California

Perennial plant size classes (m^2)	Distance from watering site (m)			
	0	50	200	800
<0.5	25a	57b	84b	82b
0.5<1.0	4a	14b	12b	11b
1.0<2.0	3a	9b	9b	10b
2.0<4.0	2a	5b	5b	5b
⩾4.0	4a	5a,b	6b	7b

Differing letters indicate significant differences between distances for each of the five size classes ($p \leqslant 0.05$).

Perennial species richness also declined with proximity to watering sites at the 100 m^2 ($F_{3,24} = 11.01$, $p < 0.0001$), 300 m^2 ($F_{3,24} = 12.74$, $p < 0.0001$), and 600 m^2 ($F_{3,24} = 8.91$, $p = 0.0004$) sampling scales. These declines were focused near the watering sites, where there were four fewer species at 0 m than 50 m. The percent declines over this interval were similar for the 100 m^2 (53% decline), 300 m^2 (64%), and 600 m^2 (69%) sampling scales (Table 2).

Density of perennial plants within each of five cover size classes declined significantly with proximity to watering sites: <0.5 m^2 plant canopy cover class ($\chi^2 = 37.24$, $p < 0.0001$, d.f. = 3), 0.5–1 m^2 ($\chi^2 = 57.41$, $p < 0.0001$, d.f. = 3), 1–2 m^2 ($\chi^2 = 38.17$, $p < 0.0001$, d.f. = 3), 2–4 m^2 ($\chi^2 = 16.19$, $p = 0.0010$, d.f. = 3), and >4 m^2 ($\chi^2 = 14.54$, $p = 0.0014$, d.f. = 3). Significant effects for all size classes were focused between 0 and 50 m of the watering sites (Table 3), although the most dramatic effect was a 70% difference in plant density between 200 and 0 m within the <0.5 m^2 cover size class. These effects were reflected in statistical differences in cover class richness ($F_{3,24} = 25.00$, $p < 0.0001$) and diversity ($F_{3,24} = 8.35$, $p = 0.0006$), primarily between 0 and 50 m, but not in cover class evenness ($F_{3,24} = 0.61$, $p = 0.6132$) (Table 4). Similar results were observed for perennial plant height. However, because perennial height and cover were significantly correlated ($r^2 = 0.66$), we only reported results for perennial cover.

Table 4
Richness, evenness, and diversity (Shannon–Weiner) of cover size classes of perennial plants at four distances from artificial watering sites ($100 \, m^2$, $n = 9$ sites) during spring 2000 at the Pilot Knob grazing allotment, California

	Distance from watering site (m)			
	0	50	200	800
Cover Richness (S)	2.74a	4.19b	4.28b	4.17b
Cover Evenness (J)	0.67a	0.74a	0.69a	0.69a
Cover Diversity (H)	0.71a	1.06b	1.00b	0.98b

Differing letters indicate significant differences between distances for each of the three diversity indices ($p \leqslant 0.05$).

3.3. Observations within the denuded zone

We did not sample vegetation within the denuded zone immediately adjacent to the watering tanks, although we know by definition that there was no woody perennial plant cover in that zone. Alien annual plant cover appeared to be far higher inside compared to outside the denuded zone, and was dominated by *E. cicutarium* and *Schismus* spp. We also observed alien species within the denuded zone that were either very rare in our samples (e.g. *Descurania sophia*) or did not occur at all in our samples (e.g. *Marrubrium vulgare* and *Hordeum* spp.). Soil compaction also appeared to be higher close to the denuded zone, as indicated by the increasing difficulty in pounding metal stakes into the ground, which was especially evident as we proceeded from 200 to 0 m from the watering sites.

4. Discussion

Our results lend support to previous research indicating that artificial watering sites can have significant effects on plant communities in desert ecosystems. We demonstrated positive effects of piospheres on plant cover of aliens, and negative effects on plant cover, species richness, and structural diversity of natives. Richness of alien annual species was the only variable that did not respond significantly to the piosphere gradient. This may have been due to the lesser ability to detect a significant trend in alien than in native richness, because there were only six alien annual species sampled compared to 54 native annuals and 22 native perennials sampled (Appendices A and B).

Most of our significant effects occurred within 50–200 m from the edge of the watering sites. This pattern may be attributed to a number of factors. First, the cumulative effects of past livestock grazing may be more localized around watering sites in our study compared to other grazing studies, due to the relatively short grazing history at the watering sites. Second, the effects of other forms of disturbance may be stronger than the effects of grazing at the outer edge of our sampling gradient, thereby masking grazing effects outside of 200 m. Third, for annual plants in particular, proportional cover of aliens is relatively high across the Mojave Desert irrespective of piosphere effects (Brooks and Berry, 2006), requiring particularly intense disturbance to raise it even higher. For example, proportional biomass of alien annual plants ranged from 66% during a wet year to 91% during a dry year at 34 sites located in wildland areas in the Mojave Desert (Brooks and Berry, 2006). These values are comparable to the range of alien cover at the end of

the piosphere gradient (at 800 m) in our study, which were 56% in interspace and 76% in beneath-canopy microhabitats during the wet year, and 68% in interspace and 72% in beneath-canopy during the dry year. Fourth, some combination of these factors may explain why there were few additional piosphere effects on vegetation beyond 200 m from the edge of watering sites. This fourth option seems most likely; the vegetation patterns within piospheres result from interactions between the overall disturbance history and plant community characteristics at the Pilot Knob grazing allotment.

4.1. Responses of alien annual plants to watering sites

The positive association of alien plant cover with artificial watering sites may have been caused by reduced competition due to lower cover of natives, higher tolerance of aliens than natives to high disturbance levels, increased availability of soil nutrients and water, or any combination of these factors. Alien plant propagules also have an increased likelihood of being introduced to watering sites by vehicles or supplemental feed that is hauled to the sites (Sheeley et al., 2002). The combination of favorable site conditions and dispersal vectors focused on watering sites may allow alien species to establish in desert regions that are otherwise unsuitable for them, pre-positioning them within the landscape for subsequent spread during periods of high rainfall.

The abundances of individual alien plant species are typically, but not always, higher with increased proximity to watering sites. The aliens *B. tectorum* and *S. altissimum* were both most abundant close to watering sites in North American sagebrush steppe (Tueller and Platou, 1991). The exotic forb *S. iberica* was more prevalent in a zone <500 m from water in the Chihuahuan Desert (Fusco et al., 1995). A number of exotic grasses were generally associated with grazing gradients surrounding sheep camps in Australian rangelands (Rogers and Whalley, 1989), and *Schismus barbatus* and *Carrichtera annua* were more prevalent near water sites in Australian chenopod shrublands (Landsberg et al., 1997). In a case from southern Australia, the alien *M. vulgare* was only found near watering troughs, whereas the alien *S. barbatus* was equally abundant throughout the same piospheres (Andrew and Lange, 1986b). Although *S. barbatus* was not listed as an alien species in Andrew and Lange (1986b), we recognize it as native to the Middle East (Bor, 1968), and therefore alien to Australia. We have also observed *M. vulgare* immediately adjacent to livestock watering sites in the Mojave Desert, where it presence within the lower elevation creosotebush (*L. tridentata*) zone seems to be directly related to moisture leaking from water tanks and troughs. Absolute abundance of the exotic perennial grass *Eragrostis lehmanniana* did not vary with proximity to watering sites in the semi-arid grasslands of the Sonoran Desert in the southwestern United States (McClaran and Anable, 1992). However, its relative abundance increased as native abundance decreased close to watering sites in that same study.

We also observed differing responses to piospheres among individual alien plant species. Specifically, the distribution of one alien species, *B. rubens*, differed from that of the other three alien species by decreasing with proximity to watering sites. This alien annual grass is of particular concern for land managers in the Mojave Desert because it promotes fires where fires were historically infrequent (Brooks, 1999b; Brooks and Esque, 2002; Brooks and Minnich, 2006). However, our results should not necessarily be construed as evidence that livestock grazing is an effective tool for reducing cover of *B. rubens* and potentially reducing fire frequency. Other studies indicate that livestock grazing can promote the

dominance of *B. rubens* at landscape scales (Brooks, 1999a), which may lead to increased frequency of fire (Brooks et al., 2003). A 100 ha fire that occurred within the Pilot Knob allotment in 1980 was fueled primarily by *B. rubens* (BLM, Desert District fire records). It should also be noted that *Schismus* spp., which was positively associated with watering sites in our study, can also promote the spread of fire (Brooks, 1999b).

Although high levels of livestock grazing near the watering sites may have negatively affected *B. rubens*, it is also possible that high cover of other alien species, especially *E. cicutarium* and *Schismus* spp., may have competitively reduced *B. rubens* cover near the watering sites. Studies integrating the effects of livestock grazing with interactions among alien species, and evaluating how the resultant plant communities affect fuel conditions and fire behavior, are needed before conclusive statements can be made regarding the use of livestock grazing to manage alien plants and fire hazard in desert regions.

The variable responses that have been reported for alien plant species within piospheres may be due to the influences of environmental and land-use factors other than disturbance from livestock grazing. For example, interspecific interactions among the unique combinations of species present at each study site may produce differing responses, especially between sites with and without certain highly competitive plant species. Unique combinations of environmental conditions, land use histories, and different types of livestock may also produce differing responses among study regions. The life history characteristics of the invasive species and the recentness of their invasion may influence their spatial distributions within piospheres. Since these factors will always vary, it may be difficult to reliably predict the distributions of alien plants within piosphere gradients.

The effects of artificial watering sites on annuals, especially alien species, were more dramatic in the interspace than the beneath-canopy microhabitat. One possible reason is that cattle may spend more time grazing within interspaces than beneath large shrubs, imparting a greater grazing and trampling effects within interspaces, and resulting in a small–scale shrub-intershrub disturbance gradient within the larger piosphere gradient. Another possible explanation is that the nutrient inputs from livestock may have their greatest relative effect within interspaces. Interspace microhabitats have naturally lower levels of soil nutrients compared to beneath-canopy microhabitats (Brooks, 1999a). Thus, if absolute levels of soil nutrients are increased across the landscape, then the proportional change should be highest in interspaces.

4.2. Responses of native annual and perennial plants to watering sites

We found that cover and species richness of native annual and perennial plants were negatively associated with livestock watering sites in the Mojave Desert. Native plants in shrub-dominated plant communities of western North America evolved with relatively little influence from large native ungulates (Mack and Thompson, 1982). As a result, there were relatively weak selective pressures to evolve mechanisms to resist, or recover from, grazing by these animal species. Thus, native plants in shrubland ecosystems such as the Mojave Desert are in general poorly adapted to livestock grazing, especially intense levels focused around artificial watering sites (Painter, 1995).

The cover and diversity of native annual plants were significantly lower near watering sites, possibly due to either increased competition from alien annuals (Brooks, 2000) or decreased population levels caused by the cumulative effect of seedhead removal by livestock over many years (O'Connor and Pickett, 1992). Repeated grazing during the

spring growing season appears to have resulted in a downward spiral in seed densities and species richness of annual plants in the Sonoran Desert of North America (Waser and Price, 1981). Sheep grazing coupled with off-highway vehicle recreation also led to significantly lower soil seedbank densities in the western Mojave Desert (Brooks, 1995).

Native perennial plants also displayed consistent declines in cover with increasing proximity to watering sites. Some of these species are key livestock forage plants that typically decrease in dominance under heavy grazing (Vallentine, 2001). The decreaser species that followed this trend in our study included *G. spinosa*, *E nevadensis*, and *A. speciosa*, while the other decreasers *A. dumosa*, *K. lanata*, and *A. hymenoides* displayed similar but non-significant trends. In contrast, increaser species are those that increase in dominance under heavy grazing (Vallentine, 2001). Two of the increaser species in our study, *E. cooperi* and *H. salsola*, did not follow this pattern. They actually declined with proximity to watering sites. The fact that these increaser species decreased in cover with proximity to watering sites indicates that grazing levels were very high and the quality of the range condition was very low within 200 m from the watering sites in this study.

Perennial cover was also reported in another piosphere study from the eastern Mojave Desert (Bleeker, 1988). In that study of seven watering sites, cover of the shrubs *L. tridentata* and *C. ramossisima* did not appear to vary along the piosphere gradient, but cover of the shrubs *A. sphaerocephalus* and *A. dumosa*, and the perennial grasses *A. hymenoides* and *H.* [*Pleuraphis*] *rigida*, generally decreased with proximity to watering sites. These results suggest that piosphere effects occurred beyond 200 m, because sampling within piosphere gradient in that study began at 200 m (Bleeker, 1988). However, Bleeker did not report any inferential statistics, and relied on general descriptions of spatial patterns of plant species at each watering site. When the raw data reported in Bleeker (1988) were re-analysed, we found that only *A. dumosa* significantly varied within the piosphere ($F_{2,10} = 6.17$, $p = 0.0180$). It is possible that some of Bleeker's distance vectors may have projected up or down slopes, increasing statistical error variance as the vectors passed from one plant community type into another. Although this added variance may have obscured actual distance effects, the descriptive information reported by Bleeker (1988) was insufficient to determine if this occurred.

4.3. Responses of plant structural diversity to watering sites

Structural richness of perennial plant cover was greatly reduced within 50 m of watering sites in our study. Although density of shrubs in all five size classes that we analysed was significantly lower at 0 than 50 m from the watering sites, the major difference occurred within the smallest size class ($<0.5 \text{ m}^2$). Another study from the western Mojave Desert indicated that anthropogenic disturbances, including livestock grazing, can reduce the cover of perennial plants 50%, while not significantly affecting plant structural diversity (Brooks, 1995, 1999a, c). That previous study also reported that birds, lizards, and nocturnal rodents were less abundant and speciose in disturbed areas. These differences were attributed to reduced cover of perennial plants, biomass of annual plants, and biomass of the soil seedbank. Another study from Australia reported significant effects of heavy compared to light livestock grazing on birds and reptiles (James, 2003). Although the study did not evaluate effects on plant structural diversity, James (2003) attributed differences to loss of plant cover and the additional water available for wildlife near watering sources.

4.4. Management recommendations

Although we did not sample within the denuded zone adjacent to the watering tanks and troughs, it is obvious that perennial plant cover in those areas is completely absent and could benefit from restoration efforts. In addition, the extremely high cover of alien annual plants coupled with the general lack of native annual plants within the denuded zone, suggest that active control of aliens and restoration of natives annuals are likely needed.

Alien species that are already present at watering sites should be prioritized for control based on their potential to spread beyond the watering sites and become significant management problems. Prioritization can be done using a ranking system such as Warner et al. (2003) or Morse et al. (2004). Control plans should take into account what may happen if they successfully eliminate or reduce the dominance of the target species. For example, the reduction in biomass of one alien species may benefit one or more other aliens (e.g. Brooks, 2000), and these aliens may create even greater management problems.

When defining management goals within the Mojave Desert, a target of 50% proportional biomass of aliens should be adopted, because that is the approximate background dominance of alien species in this region (Brooks and Berry, 2006). This target is calibrated for years of above-average rainfall, so effectiveness monitoring to evaluate management actions should included assessments of proportional alien biomass during years of high-rainfall as well. Additional data are required to further refine this target to include separate values for different regions or plant community types in the Mojave Desert.

Control of alien annual plants, and restoration of native annuals, should focus primarily on the area 200 m from watering sites at the Pilot Knob grazing allotment. Special attention should be devoted to the interspace microhabitat where the negative piosphere effects were strongest. Restoration of native perennial plant cover, species richness, and structural diversity should focus primarily on the area 50 m closest to the watering sites. Small shrub species ($<0.5\,m^2$) should be primarily used to restore plant structural diversity. These management guidelines likely apply to watering sites in other livestock grazing allotments in the Mojave Desert, since grazing histories and vegetation types in the current study are similar to those found elsewhere in the region. Additional studies are needed to determine how broadly they apply to other deserts of North America, and the world.

Appendix A

Perennial species sampled and the number of watering sites on which they occurred (out of 9 total sites) at the Pilot Knob grazing allotment. All sampled species were native.

Species name	Species code	# of sites
Shrubs		
Acamptopappus sphaerocephalus	ACASPH	9
Ambrosia dumosa	AMBDUM	9
Coleogyne ramosissima	COLRAM	3
Ephedra nevadensis	EPHNEV	7
Ericameria cooperi var. *cooperi*	ERICOO	9
Eriogonum fasciculatum var. *polifolium*	ERIFASP	6
Grayia spinosa	GRASPI	9
Hymenoclea salsola	HYMSAL	8
Krascheninnikovia lanata	KRALAN	8
Larrea tridentata	LARTRI	8
Lycium andersonii	LYCAND	9
Lycium cooperi	LYCCOO	7
Salazaria mexicana	SALMEX	5
Tetradymia stenolepis	TETSTE	6
Thamnosma montana	THAMON	4
Xylorhiza tortifolia var. *tortifolia*	XYLTOR	5
Perennial Grasses		
Achnatherum hymenoides	ACHHYM	1
Achnatherum speciosum	ACHSPE	7
Elymus elymoides	ELYELY	6
Poa secunda ssp. *Secunda*	POASEC	2
Perennial Herbs		
Mirabilis bigelovii	MIRBIG	4
Cacti		
Opuntia echinocarpa	OPUECH	4

Appendix B

Annual species sampled and the number of watering sites on which they occurred (out of 9 total sites) at the Pilot Knob grazing allotment.

Species name	Sites
Alien Forbs	
Descurainia sophia	4
Erodium cicutarium	9

Alien Grasses

Bromus rubens	9
Bromus tectorum	4
Bromus trinii	6
Schismus spp.	9

Native Forbs

Amsinckia tessellata	9
Anisocoma acaulis	1
Astragalus didymocarpus	4
Camissonia campestris	3
Camissonia claviformis	1
Caulanthus cooperi	1
Centrostegia thurberi	2
Chaenactis stevioides	1
Chamaesyce albomarginata	1
Chorizanthe brevicornu	4
Chorizanthe watsonii	5
Coreopsis bigelovii	3
Cryptantha circumscissa	5
Cryptantha nevadensis	6
Cryptantha pterocarya	6
Descurainia pinnata	1
Dichelostemma capitatum	1
Eriastrum spp.	5
Eriogonum maculatum	5
Eriogonum nidularium	1
Eriogonum pusillum	4
Eriophyllum pringlei	3
Eriophyllum wallacei	1
Eschscholzia minutiflora	5
Gilia brecciarum ssp. *neglecta*	2
Gilia minor	2
Gilia spp.	6
Guillenia lasiophylla	8
Lasthenia californica	8
Layia glandulosa	1
Linanthus bigelovii	1
Linanthus dichotomous	2
Loeseliastrum matthewsii	1
Lotus humistratus	4
Lupinus odoratus	1
Malacothrix coulteri	2
Malacothrix glabrata	4
Mentzelia spp.	4
Monoptilon bellidiforme	1
Nama demissum	1

Oxytheca perfoliata	2
Pectocarya penicillata	4
Pectocarya platycarpa	2
Pectocarya setosa	2
Phacelia distans	3
Phacelia fremontii	1
Phacelia tanacetifolia	9
Pholistoma membranaceum	4
Salvia columbariae	1
Stephanomeria parryi	2
Stylocline psilocarphoides	2
Uropappus lindleyi	1
Native Grasses	
Vulpia microstachys	6
Vulpia octoflora	5

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