LIVESTOCK ACTIVITY AND CHIHUAHUAN DESERT ANNUAL-PLANT COMMUNITIES: BOUNDARY ANALYSIS OF DISTURBANCE GRADIENTS

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Abstract. The impact of domestic livestock on soil properties and perennial vegetation is greatest close to water points and generally decreases exponentially with distance from water. We hypothesized that the impact of livestock on annual-plant communities would be similar to that on perennial vegetation. We used multivariate analysis and semivariograms to locate boundaries and to determine the number and width of different annual-plant zones (referred as biotic zones) on long-term livestock disturbance gradients in the northern Chihuahuan Desert, New Mexico. We estimated abundance of annuals in 0.5-m² quadrats placed at 30-m intervals on 10 livestock disturbance gradients originating at water points. Tansy mustard, *Descurainia pinnata,* was abundant in severely disturbed areas and also in areas that are known to have high soil nitrogen content. *Amaranthus palmeri* was abundant in half of the transects in the zones nearest the water points. The relationships of annual-plant abundance and species richness with distance from water points and with perennial-plant cover were not significant ($R^2 < 0.1$). The number of boundaries and sizes of zones varied with distance from water points, with seasons, and with duration of grazing. The first biotic zone (most severely impacted by cattle) ranged from 75 to 795 m radius for winter–spring annuals and from 165 to 1065 m radius for the summer annuals. Variability in the number and size of biotic zones along grazing gradients was spatially correlated with the frequency and intensity of disturbance, with landscape position, and with patchiness of soil features. There were fewer and larger zones of summer annuals than of winter–spring annuals. Boundary analysis of livestock disturbance gradients provided a method with replication for assessing the impact of long-term livestock grazing on annual-plant communities. Livestock create nutrient-rich patches near water points by mixing dung with soil by hoof action. These nutrient-rich patches support species of annuals that are rare or absent in areas where soils are subjected to low-intensity disturbance.

Key words: boundary locations; Chihuahuan Desert; desert plant communities; livestock grazing; multivariate analysis; semivariogram.

INTRODUCTION

Commercial livestock production is the primary land use in North American desert grasslands. The combination of livestock grazing and periodic drought have produced dramatic changes in the structure of desert grasslands (Buffington and Herbel 1965, Hennessy et al. 1983, Bahre and Shelton 1993). In the Chihuahuan Desert, desertification has resulted in changes from grassland to shrubland and changes in soil texture and distribution, e.g., formation of coppice dunes centered on mesquite (*Prosopis glandulosa* Torr.) (Gibbens et al. 1983, Hennesy et al. 1983). Although none of the remnant grasslands studied on the Jornada Experimental Range (40 km north of Las Cruces, New Mexico) by Buffington and Herbel (1965) are shrub-free, there are patches of grasslands with sparse shrub cover in the Jornada basin.

Within the remnant grasslands, pastures have been established around wells where water can be provided to several pastures from a single well. In desert rangelands, livestock concentrate their activity near these water points. This produces a gradient of soil surface disruption and compaction and changes in composition and cover of perennial vegetation. Disturbance is most intense near the water point and decreases exponentially with increasing distance from water (Lange 1969, Andrew and Lange 1986*a, b,* Fusco et al. 1995, de Soyza et al. 1997). The disturbance gradients emanating from livestock water points are not symmetrical in all directions because cattle modify their foraging direction and time spent grazing in an area in response to water, wind, topography, and heterogeneity of the vegetation (Arnold and Dudzinski 1978, W. G. Whitford, *personal observation*).

Annual plants are an important component of desert rangeland vegetation and are potentially susceptible to the cumulative impacts of livestock on soil properties

PLATE 1. Comparison of grazing effect in the vegetation zones closest to and farthest from the water point. The left photo was taken 10 m from the water point (Camp Well); the right photo was taken 1000 m from the water point.

and perennial vegetation. Despite numerous studies of the physical factors that affect the species composition and abundance of desert annuals (Went 1949, Beatley 1967, Beatley 1974, Halvorson and Patten 1975, Patten 1978, Gutierrez and Whitford 1987a, b, Mun and Whitford 1989, 1990), there have been few studies that examined disturbance by livestock (Waser and Price 1981, Kelt and Valone 1995). The studies of the effects of livestock disturbance on annual-plant assemblages produced conflicting results in part because of the limited number of areas that were available for comparisons. By studying annual-plant communities on livestock disturbance gradients originating from water points, we were able to obtain sufficient replicates to examine the variance in responses of annuals to cumulative, long-term livestock activity.

FIG. 1. Proportion of long-lived vegetation and mean size of bare patches along grazing gradient. Long-lived vegetation $= 6.64 \times 10^{-7}$ (dist.)^2 ($R^2 = 0.93$); mean bare patch $= 19.82$ (dist.)$^{-0.5}$ ($R^2 = 0.96$).

In a study of vegetation cover and size of bare patches along grazing gradients originating at water points, de Soyza et al. (1997) concluded that the impact of grazing animals was greatest at the water point (see Plate 1). We used these data to model the relationships between long-lived vegetation cover and size of bare patches and distance to water. We found that long-lived vegetation cover varies directly as the distance squared while size of bare patches varies inversely as the square root of distances (Fig. 1). Because of these perennial vegetation and soil patterns, we hypothesized that (1) discernable assemblages of annuals would occupy smaller areas close to water points and that the areas occupied by distinct annual assemblages would increase with distance from water, (2) annual plant assemblages close to water points on different gradients would be more similar (clustered together in an analysis of composition) than distant ones and (3) density and species richness of annual plants would be correlated with distance from water and with perennial-plant cover.

We studied the spatial variation of annual-plant communities characterized by sampling along disturbance gradients at equi-spaced locations. Gradients can be partitioned into homogeneous zones by recognizing where the rate of change in composition and abundance of annuals is greatest with respect to distance. This allows the locations of boundaries separating zones where disturbance has affected the composition and abundance of annual plants. Specifically, disturbance might alter soil and environmental variables that influence annuals' germination, establishment, and growth; alternatively, grazing disturbance might directly alter seed variability or composition (e.g., by selective removal of certain species). Several investigators have applied multivariate analysis to locate boundaries in
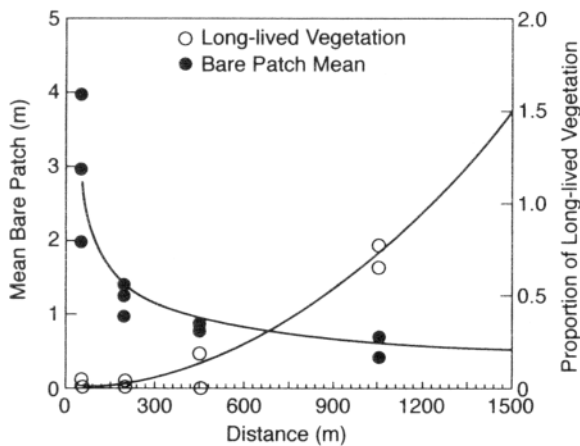
TABLE 1. Location, direction, length, number of quadrats, and grazing regime of annual vegetation transects.

Sites	Transect direction	Transect codes	Transect length (m)		Number of quadrats		Grazing regime
			Winter	Summer	Winter	Summer	
Camp Well	North	CWN	1500	1500	51	51	Winter–spring
	Northwest	CWNW	1500	1500	51	51	Winter–spring
	West	CWW	990	1500	34	51	Summer
	Southwest	CWSW	960	1500	33	51	Summer
Mayfield Well	Southeast	MWSE	1500	1500	51	51	Continuously
	South	MWS	1500	1500	51	51	Continuously
West Well	Southeast	WWSE	1500	1500	51	51	Winter–spring
	South	WWS	1500	1500	51	51	Winter–spring
South Well	North	SWN	1470	1500	50	51	Continuously
	Northwest	SWNW	1500	1410	51	48	Continuously

spatially explicitly biotic and abiotic data (Webster 1973, Ludwig and Cornelius 1987, Wierenga et al. 1987, Nash and Daugherty 1990). In this paper we identify annual-plant communities by locating boundaries of the discontinuity between zones of relatively homogeneous species composition and abundance using multivariate and semivariogram analyses. We used the annual-plant community data to examine responses of annual plants to disturbance gradients produced by livestock.

STUDY SITES

Field studies were conducted at the U.S. Department of Agriculture, Agricultural Research Service (USDA-ARS), Jornada Experimental Range, and the Chihuahuan Desert Rangeland Research Center, New Mexico State University, which are located 48 and 30 km (respectively) NNE of Las Cruces, New Mexico. The long-term average annual precipitation is 225 mm/yr with 60% occurring during July through September as convective storms. Maximum temperatures regularly exceed 40°C and winter minimum temperatures are frequently below 0°C. There are two distinct guilds of annual plants in the northern Chihuahuan Desert: C_3 winter–spring annuals and C_4 summer annuals (Freas and Kemp 1983, Kemp 1983, Cornelius et al. 1991, Guo and Brown 1997). Winter–spring annuals germinate with soil moisture from the frontal winter rainfall that occurs between November and February. Summer annuals are dependent upon the summer monsoonal rains.

Livestock disturbance gradient transects were established at three livestock water points (Mayfield, Camp, and West Wells) that were on the same sandy loams (Wink-Pintura soil series) with an indurated calcic horizon at 0.40–1.00 m depth (U.S. Department of Agriculture, Soil Conservation Service, 1980). Livestock disturbance gradient transects were also established at South Well, which is in an area with a mosaic of soils including Simona-Harrisburg, fine sandy loam with an indurated calcic layer at 0.25–0.50 m, Wink-Harrisburg loamy fine sand with no calcic layer, Onite-Pajarito fine sandy loams, and Berino-Bucklebar sandy loams with

no calcic horizon (U.S. Department of Agriculture, Soil Conservation Service, 1980). The length of transects was determined by the location of water points within pastures and the locations of pasture fences (Table 1). The disturbance gradient transects are identified by the well code and compass direction. These 10 transects had different grazing histories and stocking rates. The vegetation on all disturbance gradients was similar with black-grama (*Bouteloua eriopoda*) grassland and scattered mesquite (*Prosopis glandulosa*) at distances between 700 and 1500 m from water points. The vegetation between the water points and the black-grama grassland was dominated by bunch grasses, *Sporobolus* spp. and *Aristida* spp., with varying densities of snakeweed (*Gutierrezia sarothrae*) and mesquite. Grass cover increased from an average of 0.9% within 100 m of the water point to 24% at 1050 m from the water point. Shrub cover decreased from an average of 10% within 100 m of the water point to 5% at 1050 m. Mean size of unvegetated soil patches decreased from a mean diameter of 2.97 m within 100 m of water to a mean diameter of 0.61 m at 1050 m from the water point (de Soyza et al. 1997). Transect codes in Table 1 are used as abbreviations for transects throughout.

METHODS

The numbers of annual plants of each species within 0.5 m² (50 × 100 cm frames) were recorded. Quadrats were placed at 30-m intervals along each transect. Because of time constraints, we measured the percent cover of perennial species occurring within the quadrats on only a subset of transects (WWSE, CWSW, WWS). In order to investigate the effects of finer scale sample spacing, summer annuals were sampled at 10-m quadrat spacing on selected transects (WWS, SWNW, CWNW) in September–October 1996. Plant taxonomy follows Allred (1997).

Data were collected in March–April 1995 (winter-spring annuals) and September–October 1995 (summer annuals). The November–February rainfall that was responsible for the winter–spring annuals was 110.8 mm. The July–September rainfall that produced the summer annuals was 117.3 mm. The growing season drought

(July–September rainfall = 57.4 mm) in 1994 caused range management to destock most of the pastures. As a result of that destocking, none of the pastures that we studied were being grazed at the time that we sampled.

Statistical analysis

Ludwig and Cornelius (1987) analyzed vegetation along a gradient and used multivariate analysis to locate boundaries between different biotic zones. In their technique, they used a split moving-window and the squared Euclidean distance (SED) simultaneously to locate boundaries. They used different window widths looking for the repeatability of the boundary location. They indicated that sharp peaks define the abrupt changes between biotic communities. Gradual variation in composition and cover on abundance did not produce sharp peaks and that variation was considered to be within community variation.

In that analysis, the window width is unknown and several window widths have to be used to finalize the location of the boundaries. Applying a narrow window results in many peaks and a wide window results in fewer peaks. There is, however, a technique to identify the window widths by examining the spatial variability of the data. Webster (1973) and Nash and Daugherty (1990) used multivariate analysis with the aid of the correlogram and semivariogram to determine the window width.

In this paper, we used principal components analysis using SAS (SAS 1990) to reduce annual plant abundance data from the transects. We used the first principal component, which accounted for most of the variation in the species data. Following Nash and Daugherty (1990), we constructed a semivariogram for the first principal component to determine the range of dependence using Geostatistical Environmental Assessment Software (GEO-EAS 1.2.1; Englund and Sparks, 1991). The range of dependence was an approximation of the width of the split moving-window. Several peaks emerge from moving the window on the principal component, which may not represent the sharp change between biotic zones. Small-sample test statistics were used to find if the resultant peak value from moving the window was significant. The test statistics were calculated as

$$t = (\bar{X}_1 - \bar{X}_2)(0.5n/S_p^2)^{0.5}$$

$$S_p^2 = 0.5(S_1^2 + S_2^2)$$

where $\bar{X}_1$, $\bar{X}_2$ are the sample average values in both halves of the window, S_p^2 is the pooled variance, S_1^2 and S_2^2 are the sample variances, and n is the number of observations in half of the window width.

To test the hypothesis that biotic zones closer to water points are more similar than zones farther from water, we used cluster analysis (Ludwig and Reynolds 1988). For transects in pastures with a particular graz-

TABLE 2. Species richness of winter–spring and summer annuals on livestock disturbance gradients.

Grazing regime	Winter–spring	Summer
Continuous grazing		
SWN	8	5
SWNW	11	13
MWSE	16	5
MWS	18	14
Winter–spring grazing		
CWN	17	14
CWNW	16	14
WWSE	18	13
WWS	18	10
Summer grazing		
CWW	14	12
CWSW	16	13

Note: Long-term grazing regime for the transects is listed above the group of transects subject to that regime.

ing season and intensity, we used cluster analyses for all biotic zones identified by the boundaries from each disturbance gradient transect to investigate variation within clusters and to compare cluster patterns relative to grazing disturbance gradients and landscape position.

In order to obtain an overall estimate of the influence or importance of a plant species in the community, we calculated a partial importance percentage (e.g., Brower et al. 1990) as the average of the relative density and relative frequency of annuals in each biotic zone and used it in the cluster analysis. Relative density is defined as ratio of the number of individual species and total number of individuals of all species. Relative frequency is the ratio of the frequency of occurrence of a species and total frequencies of all species. The importance percentage value is usually calculated with a cover value, which is weighted equally to the density and frequency values. Because our field measurements encompassed a 2-mo period, plant cover values could not be used. Because of temporal effects on the cover values, we excluded cover and used a partial importance percentage value. Finally, densities of annual plants were regressed against perennial cover to examine the relationship between annual plants and the surrounding perennials.

RESULTS

There was large variation in species richness of both winter–spring and summer annuals among transects (Table 2). There were 26 species of winter–spring annuals and 26 species of summer annuals cumulative on all transects. Species richness and abundance of summer annuals were lower than of winter–spring annuals (Fig. 2). There was no pattern of average species richness or average annual density per quadrat with distance from water points (Fig. 2). Average species richness and abundance for winter–spring annuals were lower close to water points. The opposite was observed
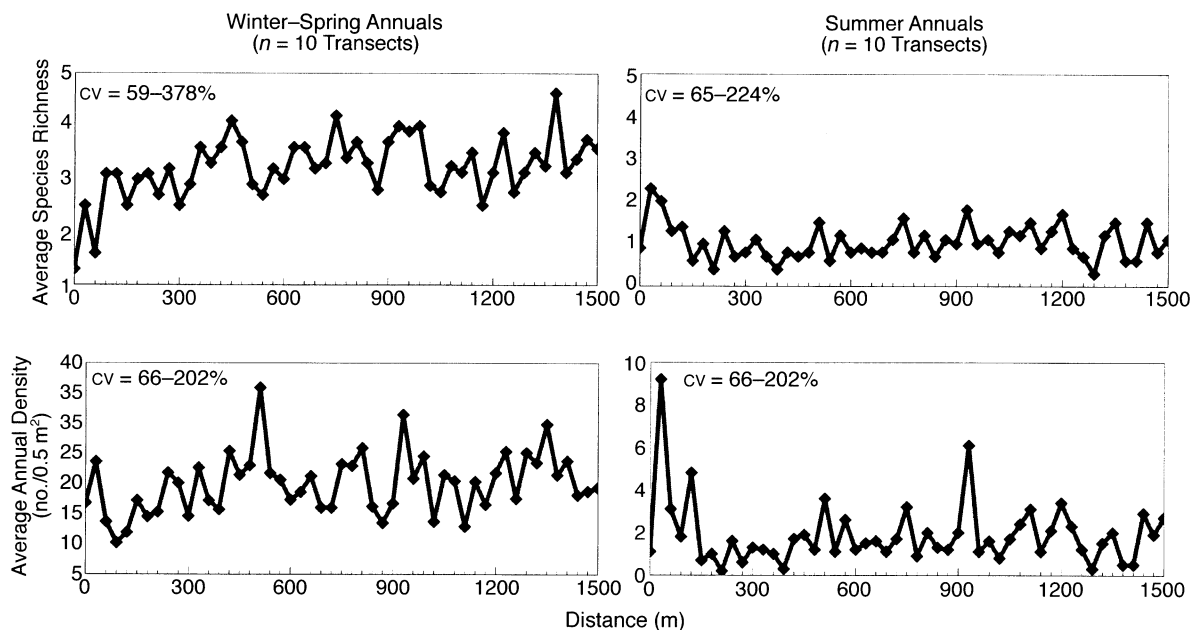
Winter–Spring Annuals
(n = 10 Transects)

Summer Annuals
(n = 10 Transects)

cv = 59–378%

cv = 65–224%

cv = 66–202%

cv = 66–202%

Distance (m)

FIG. 2.   The average richness and abundance for winter–spring and summer annuals (n = 10).

TABLE 3.   Species of summer and winter–spring annuals with partial importance values >10.0.

Species	Trans.	Zones				
		1	2	3	4	5
Summer annuals						
Abronia angustifolia	2	0	0	2		
Amaranthus palmeri	5	5	0	1		
Aristida adscenionis	1	0	1			
Bouteloua aristoides	8	7	5	1		
Bouteloua barbata	6	5	5	1		
Chamaesyce (Euphorbia) serrula	9	5	6	1	0	1
Chamaesyce (Euphorbia) serpyllifolia	1	1				
Gutierrezia sphaerocephala	2	1	0	1		
Helianthus annuus	2	2				
Ipomoea costellata	1	0	0	1		
Kallstroemia parviflora	3	1	1	1		
Panicum hirticaule	2	1	2	1		
Pectis papposa	2	0	1	1		
Portulaca oleracea	4	4				
Portulaca halimoides	3	3	1			
Tidestroemia lanuginosa	2	0	2			
Tribulus terrestris	2	2				
Winter–spring annuals						
Astragalus nutallianus	8	5	7	7	7	5
Aphenostephus ramosissimus	8	2	3	5	5	1
Cryptantha angustifolia	10	7	7	10	8	3
Cryptantha micrantha	1	1	1	1		
Descurainia pinnata	8	6	1	1		1
Dimorphocarpa (Dithyrea) wislizenii	6	4	1	2	3	
Eriogonum abertianum	4	2	3	1	1	1
Lepidium lasiocarpum	5	4	3	2	2	3
Linum vernale	3	2	2	1		
Lesquerella gordoni	6	0	2	5	2	2
Nama hispidum	3	1	2			
Plantago patagonica	0	0	0	0	3	2

Notes: Trans. is the number of transects on which the species occurred at importance values >10.0. Zone numbers (1, nearest the water point; 2, 3, 4, or 5 zones at greater distances from the water point) are dependent upon the number of annual plant zones that characterized a transect. The table entries for zones refer to the number of transects in which the species occurred in that zone with an importance value >10.0.

TABLE 4. Boundary locations for winter–spring flowering and summer flowering annual plants.

Variable	Continuously grazed				Winter–spring grazed				Summer grazed	
	SWN	SWNW	MWSE	MWS	CWN	CWNW	WWSE	WWS	CWW	CWSW
Winter–spring annuals										
No. of zones	3†	4†	7†	5*	5†	4†	4*	4*	5*	4†
Boundary Locations (m)	795	435	315	225	135	345	225	135	75	132
	1005	525	495	555	345	765	405	705	285	555
		1095	735	705	855	1245	555	915	375	675
			855	975	1365				705	
			1125							
			1365							
Summer annuals										
No. of zones	3*	3*	3*	3*	3*	2*	2*	5*	1	2†
Boundary Locations (m)	855	525	315	435	645	735	165	375		1065
	1275	855	1305	555	1205			735		
								885		
								1275		

† $P \leq 0.10$.
* $P \leq 0.05$.

for summer annuals. Variation in numbers of species and abundance along the transects were high. Coefficients of variation for abundance ranged from 66 to 316% (see Fig. 2).

Cumulative species richness curves reached an asymptote at 150–300 m on five of the 10 grazing disturbance gradients and at >1200 m on four of the other gradients. On one gradient the cumulative species richness curve did not reach an asymptote. This variability was also reflected in the importance percentages calculated for both winter–spring and summer annuals. No species of summer annual had partial importance percentage >10.0 on all of the transects (Table 3). There were more species of summer annuals than winter–spring annuals with importance values >10.0 and these species tended to be fairly evenly distributed among zones. On five of the 10 transects, one species of summer annual, *Amaranthus palmeri*, was found only in the high impact zones nearest water points except in a few quadrats that fell on banner-tailed kangaroo rat mounds in zones more distant from water. On the transects where *A. palmeri* occurred, it had very high partial importance percentages (29.2–62.2).

One species of winter–spring annual, *Descurainia pinnata*, had higher partial importance percentages (>10.0) in the zones nearest water points on six of the gradients. On four of the gradients, *D. pinnata* was absent in the zone nearest water and on three of those gradients the highest importance percentages for this species were in the zones most distant from water. On two of those gradients, banner-tailed kangaroo rat mounds were abundant in the most distant zones. There was no species of winter–spring annual that had high partial importance percentages in zones on all 10 grazing disturbance gradients. Although *Cryptantha angustifolia* exhibited high importance value on all of the transects, there was no relationship to the disturbance gradient in the distribution of the importance values. None of the other winter–spring annuals that had high

importance values exhibited any patterns in distribution that could be related to the disturbance gradients.

Disturbance gradient biotic zones

Transects originating from the same water point but oriented in different directions had different numbers of biotic zones. On several disturbance gradient transects the first zone was the smallest (e.g., winter–spring: CWN, WWS, and CWW; summer: WWSE and MWSE; Table 4). At the MWS transect, winter–spring annual biotic zones bounded at 225, 705, and 975 m coincided with three zones of perennial vegetation (coppiced dunes/mesquite shrubland and black-grama grassland) with boundaries at 210, 780, and 970 m, respectively. On the CWN transect substantial surface rock cover appeared at 780 m and increased greatly at 840 m through the end of the transect; these environmental features nearly coincided with winter–spring annual biotic zone boundaries found at 645 and 855 m, respectively. With the exception of the MWS transect, there were fewer summer-annual biotic zones than winter–spring annual biotic zones, and the biotic zone boundaries of summer and winter–spring annuals coincided only at the MWSE transect (Table 4). The average size of biotic zones was 291 m (SD = 167) for winter–spring annuals and 552 m (SD = 364) for summer annuals. No zone boundaries for summer annuals occurred on the CWW transect. Only the WWS transect had more than two boundaries for summer annuals. In a few disturbance gradient transects, winter–spring annual and summer-annual boundaries were similar, but in most cases the first biotic zone (with greatest disturbance) was larger for summer annuals.

Sampling space and boundary locations

When summer-annual plant data collected at 10- and 30-m intervals were compared, a greater number of biotic zones were found with the 10-m spacing (Table 5). On the CWNW and WWS transects, boundaries

TABLE 5. Boundary locations for 1996 summer flowering annual plants for different spatial intervals (all significant at $P \leq 0.05$).

Spatial interval	Boundary locations (m)		
	CWNW	WWS	MWS
10-m interval	235	455	145
	425	885	205
	555		375
	835		655
	935		895
			1365
30-m interval	225	885	0
	945		

located with the 30-m sampling intervals were also found with the 10-m sampling interval. The MWS transect was found to have a single biotic zone (i.e., no boundaries) with the 30-m spacing, but seven biotic zones (six boundaries) were found with the 10-m spaced quadrats. At MWS an area of coppiced dunes began at 240 m and ended at 360 m, and an area of black-grama grassland began at 650 m followed by an increasing frequency of banner-tailed kangaroo rat (*Dipodomys spectabilis*) mounds at 990 m. These features are spatially coincident with some of the summer-annual boundaries found with the 10-m interval samples.

Cluster analyses

Cluster analyses for each individual transect, with the exception of MWSE and MWS, revealed that those winter–spring annual communities in the first zone (closest to the water) were highly dissimilar from other zones. They were separated by chord distances of 0.7 to 1.24 (51 to 13% similarity). The first zones on transects that originated from the same water point and that were subject to the same season of grazing were more similar to each other than to the other zones (Fig. 3a–c, b). Winter–spring annual zones nearest to the water point were clustered together and separated from other zones at a chord distance of 0.45 (68% similarity; Fig. 3a, b). On the Mayfield Well transects, the communities formed clusters according to position on the landscape (Fig. 3c). The same cluster pattern was observed for summer annuals at the Mayfield Well transects. When
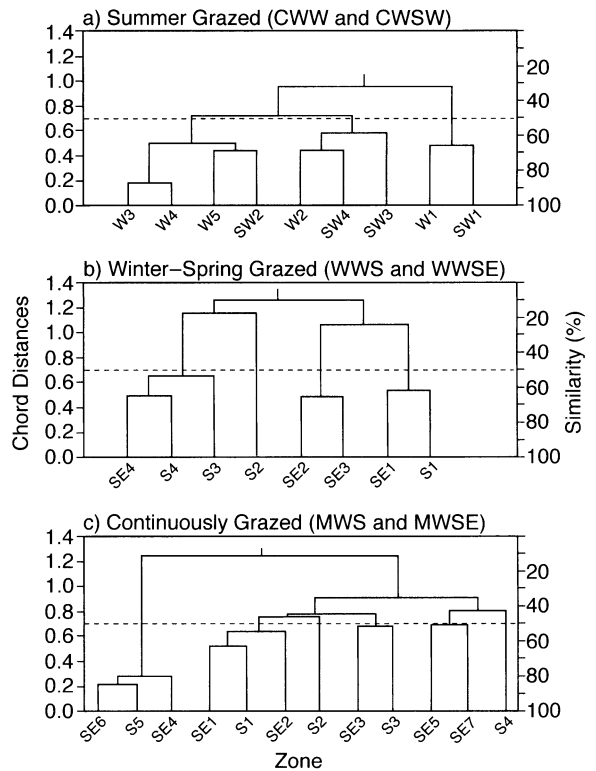

FIG. 3. Dendrograms for the winter–spring annual zones of the (a) summer grazed transects (CWW and CWSW), (b) winter–spring grazed transects (WWS and WWSE), and (c) continuously grazed transects (MWS and MWSE). Letters and numbers on the x-axis denote the number of a biotic zone from a transect, with number 1 being closest to the water point.

transects originated from the same well but were in different grazing season pastures, not all of the zones nearest water clustered together (Fig. 4). The Camp Well (CWNW) zone nearest the water point in the winter-grazed pasture was clearly separated from the other three.

Regression analysis

Regression of annual-plant density and perennial cover on the transects for which we had perennial cover
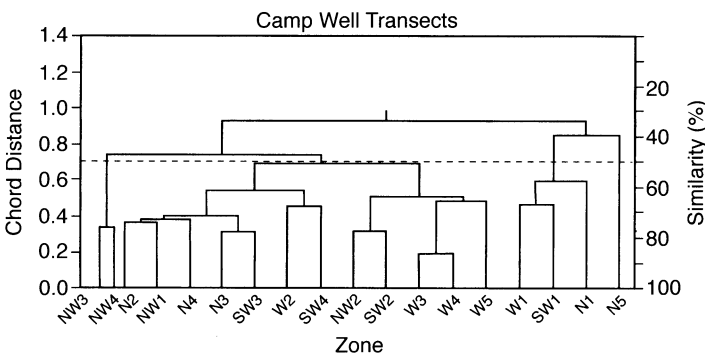

FIG. 4. Dendrogram for the winter–spring annual zone of the Camp Well summer-grazed transects (CWW and CWSW) and winter–spring grazed transects (CWN and CWNW). Letters and numbers on the x-axis denote the number of a biotic zone from a transect, with number 1 being closest to the water point.
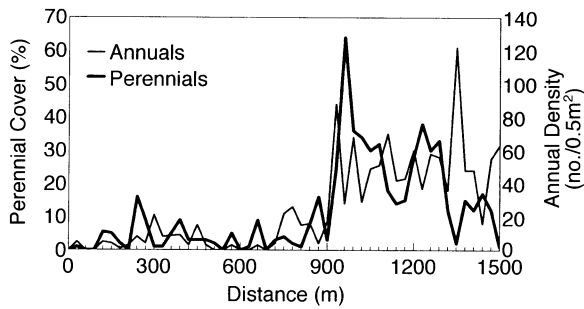
FIG. 5. Percent perennial cover and annual plant density along south West Well (WWS) transect.

measurements yielded an R^2 of 0.05. There was also no correlation between species richness and perennial cover nor of species richness and distance from a water point ($R^2 < 0.1$). Regression analysis of annual-plant abundance on distance from water points yielded an R^2 of 0.02. Plots of the data points for all of these regressions produced clouds of points best fit by a zero slope line. Fig. 5 shows the density of annual plants and percentage of perennial cover along the WWS transect. Both vegetation types were less in areas that are closer to water point. Both vegetation types increased as the distance increased. A simple least-squares regression model yielded low regression coefficients (0.1 to 28.9%) when used to study the relationships among densities or number of annual plants and percent cover of perennial plants.

DISCUSSION

There was considerable variation in the species composition and relative abundances of both winter–spring and summer annuals among the transects that could not be attributed to season of grazing or cover and composition of perennials. The variation in abundance and species richness among quadrats within a zone on a transect, with distance from water points, and with perennial plant cover provides evidence that it is difficult to ascertain patterns attributable to variation in impact of grazing livestock. Species richness was reduced on two of the four transects in continuous grazed pastures. This reduction in species richness might be attributed to livestock consumption of some of the annual species. However the list of "missing" species did not comprise those that are palatable (Jornada Ranch personnel, *unpublished observations*). We attribute the lower species richness on these two transects to soil patch differences and not to the direct impact of cattle.

The patterns of distribution of individual species provide examples of how the activities of livestock affect the species composition and relative abundance of annual plants. Concentrations of dung and urine are greatest close to water points. Soil compaction by trampling is also greatest close to water points. Those species of annuals that exhibited patterns of abundance apparently related to disturbance by livestock were species that

have been documented to reach peak abundance and size in soils that are relatively rich in available nitrogen (Gutierrez and Whitford 1987*b*, Mun and Whitford 1990).

The direct effects of cattle on annuals in the Chihuahuan Desert are minimal. Some species of annuals like *D. pinnata* are toxic to livestock and overall few annuals are consumed by cattle. Livestock compact soil especially where they are concentrated around water points. Although soil compaction reduces infiltration, the average depth of the compaction layer resulting from concentrated activity of livestock near the wells at which our transects originated was at 12 cm (measurements by penetrometer, J. Herrick, personal communication). Rainfall saturating the upper 12 cm of soil is obviously sufficient for germination and establishment of many species of annuals. Thus the primary impact of livestock on annual plants on grazing gradients appears to be one of increasing heterogeneity by changing soil organic matter and consequently soil nitrogen (Whitford et al. 1987). If the primary effect of large herbivores is to increase heterogeneity of soil resources and bulk density due to hoof action, diversity and abundance would be greater in grazed areas. The observed distribution abundance patterns for *D. pinnata* and *Amaranthus palmeri,* based on the partial importance percentages, suggest that livestock affect annual-plant densities and species richness by their effects on soil properties (Guo and Brown 1997). Summer annual plants are less responsive to soil resource differences (Gutierrez and Whitford 1987*b*) and are therefore less affected by distance from water (grazing disturbance). These relationships suggest that cattle influence annuals primarily through their effects on soil resources such as organic carbon and nitrogen.

Summer annuals were more evenly distributed on the disturbance gradients than the spring annuals. There were no clear dominants among the summer annuals and with the exception of *Amaranthus palmeri,* there were no differences in abundance that could be attributed to soil disturbance by livestock. This is probably the result of the germination and establishment differences between winter–spring and summer annuals. Winter–spring annuals germinate over a 4–5 mo period, with some species germinating in November and December that survive as rosettes until warm temperatures in March and April stimulate growth and flowering. Dry periods following the germination of annuals in November or December can result in high mortality of rosettes depending upon the water storage in microsite soils. Other species germinate in late winter and spring. Thus variations in winter rainfall appear to have a greater effect on winter–spring annuals than rainfall variation has on summer annuals. Summer rainfall sufficient for establishment of summer annuals is generally sufficient for those annuals to grow and flower.

Boundary locations may be dependent on the number and spacing of quadrats. Smaller intervals between

sample quadrats resulted in the detection of a greater number of boundaries. However, since the boundaries based on the 30-m sampling distances were also found with the 10-m spacing, the additional boundaries found with the shorter intervals probably reflect microvariability within the larger 30-m intervals. The microvariability evident in the 10-m spacing data was due to scattered coppice dunes and banner-tailed kangaroo rat mounds. Banner-tailed kangaroo rat mounds support high densities of annual plants and a species composition of annual plant assemblages that differ from that in areas away from mounds (Mun and Whitford 1990). Coppice dunes produce patches of unstable soils around the dense coppice of shrub stems. The unstable dune soils are unsuitable as habitat for annual plants. Because these features are scattered and sparse, the probability of encountering one of these features at 30-m spacing of samples is very low. However, since these are small patches embedded in the landscape gradient, the inability to detect them does not detract from using the boundary analysis to address questions concerning the effects of concentrated activity of livestock and distribution of annual plants on grazing gradients. Boundary analysis, therefore, provided an objective means of defining zones of annual-plant communities and allowed us to study spatial differences that may be the result of varying intensities of disturbance.

The analysis of the disturbance gradient biotic zones generally supports the hypothesis that the bounded zones would be smaller near the water points where livestock activity is intense and spatially concentrated. This was true for most but not all the transects and only for winter–spring annuals. One problem encountered in interpreting the data on size of vegetation zones is variation in the gradients within a pasture. Our data show that the zones are not symmetrical on different transects even within the same pasture. This variability is mostly the result of variation in the behavior of grazing animals with respect to wind, topography, and vegetation (Arnold and Dudzinski 1978).

Management implications

Boundary analysis technique did allow demonstration of clear relationships between pattern and composition of the annual community and the influence of grazing livestock. There is no evidence to suggest that direct consumption of annuals by livestock has had an effect on species composition and abundance. The addition of the organic matter and nutrient via dung deposit remains one good candidate for the mechanism of influence. Soil disturbance by livestock has had an effect on the annual-plant community similar to that reported for soil disturbance by banner-tailed kangaroo rats (Mun and Whitford 1990). The other impacts are mostly changes in the spatial extent of assemblages of annuals. Thus we conclude that in the northern Chihuahuan Desert, disturbance by grazing livestock results in only small changes in annual-plant communities and is very different from the effect of intensive livestock grazing on perennial vegetation. Changes in management of domestic livestock would have little effect on annual-plant communities in Chihuahuan Desert rangelands.

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