Multivariate characterization of perennial vegetation in the northern Chihuahuan Desert

A. R. Johnson⋆, S. J. Turner†, W. G. Whitford‡, A. G. de Soyza§ & J. W. Van Zee¶

⋆*Department of Environmental Toxicology, Clemson University, Pendleton, SC 29670, U.S.A.*
†*Department of Biological Sciences, St. Cloud State University, St. Cloud, MN 56301, U.S.A.*
‡*US-EPA, Environmental Sciences Division, P.O. Box 93478, Las Vegas, NV 89195, U.S.A.*
§*Terrestrial Environmental Research Center, Environmental Research and Wildlife Development Agency, P.O. Box 45553, Abu Dhabi, UAE*
¶*USDA-ARS Jornada Experimental Range, Box 30003, 3JER, New Mexico State University, Las Cruces, NM 88003, U.S.A.*

We surveyed vegetation at 100 sites in southern New Mexico to establish a benchmark for monitoring vegetation change. Sites were selected in a stratified random design, based on a classified AVHRR image. Two shrubs (*Larrea tridentata* and *Prosopis glandulosa*) are the most important contributors to perennial cover in the area. Principal components analysis (PCA) and detrended correspondence analysis (DCA) both clearly delineate these shrublands from the smaller number of compositionally-varied grassland sites. A latitudinal trend in DCA axis 1 scores suggests that encroachment of shrubs into grasslands is most pronounced in the southern portion of the study area.

© 2000 Academic Press

Keywords: New Mexico; shrub encroachment; desert grassland; ordination

Introduction

The northern Chihuahuan Desert has been subject to considerable ecological change since the late 19th century (Buffington & Herbel, 1965; York & Dick-Peddie, 1969; Gibbens *et al.,* 1983; Hennessy *et al.,* 1983; Gibbens & Beck, 1988; Grover & Musick, 1990; Gibbens *et al.,* 1992). Descriptions of the region by 19th century botanists typically noted extensive grasslands devoid of shrubs or trees at lower elevations (Buffington & Herbel, 1965). Notes made by surveyors during the original survey of the New Mexico Territory (1858 and sporadically thereafter) have been analysed to reconstruct past vegetation in the study area (Buffington & Herbel 1965; York & Dick-Peddie, 1969). These records indicate extensive grass cover with pockets of *Prosopis glandulosa* Torr. and *Larrea tridentata* (Sess. & Moc. ex DC.) Cov. *P. glandulosa* was found primarily in riparian areas or in association with abandoned Native American

campsites and settlements. *L. tridentata* was restricted to sites with well-drained gravelly soils. In the late 19th century, a dramatic expansion of *L. tridentata* and *P. glandulosa* into former grasslands began (Grover & Musick, 1990). Buffington & Herbel (1965) document the changes for the Jornada Experimental Range, which lies within our study area. In 1858, 58% of the Jornada Experimental Range was entirely free of shrubs. By 1963, all of the Jornada Experimental Range had some shrub cover, and 73% had dense shrub cover (where 55% or more of the total perennial cover consisted of shrubs). More recent studies indicate that the expansion and increase in density of shrubs is continuing (Grover & Musick, 1990; Gibbens *et al.*, 1992). Similar expansion of *P. glandulosa* and *L. tridentata* into former grassland has been documented in south-eastern Arizona, a couple of hundred kilometers west of our study area (Bahre, 1991; Bahre & Shelton, 1993). The causes of this dramatic shift have been the subject of considerable debate. Many researchers have pointed to a combination of heavy grazing by domestic livestock, suppression of grassland fires, and climatic shifts (both the amount and seasonality of precipitation) as causal factors (Buffington & Herbel, 1965; Neilson, 1986; Grover & Musick, 1990; Brown *et al.*, 1997). Experimental studies have documented the important role of kangaroo rats (*Dipodomys* spp.) and other granivores (both vertebrate and invertebrate) in controlling the balance between grasses and shrubs in these systems, suggesting that the role of granivory as a proximate factor in vegetation transitions merits serious attention (Brown & Heske, 1990; Chew & Whitford, 1992).

Although by all accounts grass cover was extensive in the 19th century, the historical species composition of these grasslands is more difficult to ascertain. The Land Office survey notes contain numerous references to 'grama grass'. Many authors have assumed that this corresponds, at least for the most part, to *Bouteloua eriopoda* (Torr.) Torr., which is now commonly called black grama. However, Buffington & Herbel (1965) cite references from 1904 and 1916 which document usage of black grama when referring to *Pleuraphis mutica* Buckley or *Muhlenbergia porteri* Scribn. This terminological ambiguity, coupled with the uncertain and probably variable botanical expertise of the surveyors, limits the precision with which past grassland species composition can be reconstructed (Galatowitsch, 1990). Our results provide a random sample of the varied type of grassland currently existing.

This study focuses on a multivariate characterization of the vegetation of the northern Chihuahuan Desert in south-central New Mexico. Our goal is to document the current extent of shrub dominance in the region, and to describe the composition of the remnant grasslands. An accurate characterization of the current vegetation in our study area serves the dual purposes of enhancing our understanding of the past vegetation dynamics which have shaped the region, and providing a benchmark for monitoring future vegetational change. To ensure a representative sample of the existing vegetation, we employed a stratified randomized sampling design in choosing our study sites. Our multivariate analysis supplements those that of Valverde *et al.* (1996) in their study of southern Chihuahuan Desert vegetation.

Our work provides a snapshot of this dynamically changing arid region. It provides one of the few attempts to quantitatively evaluate the extent of shrub encroachment at a regional scale. Moreover, this study provides a synoptic characterization of plant species composition at a range of sites along the continuum from desert grassland to shrubland. We employ two multivariate ordination techniques (principal components analysis and detrended correspondence analysis) to summarize the compositional variability of the vegetation. These two statistical procedures are based on somewhat different underlying assumptions, and so may be expected to provide somewhat different depictions of the same vegetative data. Despite differences in detail, however, in our analysis both techniques provided a similar overall characterization of the vegetation. The robustness of our main results to different methods of statistical analysis increases our confidence in their validity.

Methods

Site selection

The vegetation data were collected as part of an effort at accuracy assessment (ground-truthing) for a vegetation classification based on remotely-sensed (AVHRR) imagery. This classification has been proposed as a useful tool for assessing degradation (Eve *et al.*, 1999). The study area covered by the classified AVHRR data included much of south-central New Mexico, ranging from 32°00′ to 34°21′ N and from 105°74′ to 107°78′ W. Non-desert areas (including montane forests, woodlands, irrigated agriculture, and urban areas) were not included in the classification.

The classified AVHRR image (Eve *et al.*, 1999) was based on changes in normalized difference vegetation index (NDVI, a measure of surface greenness that correlates with primary production) over the growing seasons of 1990–1993. Pixels were classified according to their similarity to known grass-dominated or shrub-dominated sites. Phenological differences in production of green biomass can be exploited to make this distinction in the vegetation of the northern Chihuahuan Desert because the dominant shrubs are deep-rooted C_3 plants which are evergreen (*L. tridentata*) or deciduous with the production of new leaves in spring (*P. glandulosa*), whereas the dominant perennial grasses are shallow-rooted C_4 plants (e.g. *B. eriopoda*) which are dry and brown in spring, not producing green leaves until summer in response to increased temperature and monsoonal rains. The final classification, based on a composite of multiple AVHRR images spanning 4 years (1990–1993), produced five classes. These classes were defined by the number of years a pixel had displayed an NDVI phenology resembling known shrub-dominated sites, thereby providing a gradient from grassland sites to increasingly shrub-dominated sites.

We selected 20 pixels within each class as sites to conduct vegetation sampling. This number of sites should adequately capture the variability of vegetation within a class, and permits reasonable assessment of the accuracy of the image classification procedure. Sites were selected, to the extent possible, according to a stratified random sampling design. The locations of randomly selected pixels within each class were plotted on the most recent 1:100,000 scale BLM Surface Management Status maps (U.S. Bureau of Land Management, various dates). We chose the first 20 pixels for each numerical class which satisfied our accessibility criteria. Most of the study area was accessible to us, being public lands (U.S. Bureau of Land Management, State of New Mexico), or under U.S. military management (White Sands Missile Range, Fort Bliss) or designated for research (U.S. Department of Agriculture—Jornada Experimental Range). We were also able to work on the largest tracts of patented land in our study area, the Armendaris and Ladder ranches. The few sites that are more than 3·2 km from any mapped road or sites located on small tracts of patented land were considered inaccessible and not included in the study. A few sites initially chosen could not be reached due to eroded roads or locked gates, and five sites were eliminated because of spatial heterogeneity in the vegetation at a scale that would not be adequately characterized by our survey techniques.

The end result of this site selection procedure was a set of 100 sites (20 from each class) ranging from desert grassland through to shrubland. The locations of the sites are shown in Fig. 1. We used a Global Positioning System (GPS) with differential correction to record the location of each of our study sites. This information insures that we will be able to return to the same field sites with a high degree of accuracy for future research.

Data collection

Vegetation surveys were conducted from April through to July of 1996. Most of the study area experienced moderate to severe drought, starting approximately July 1995
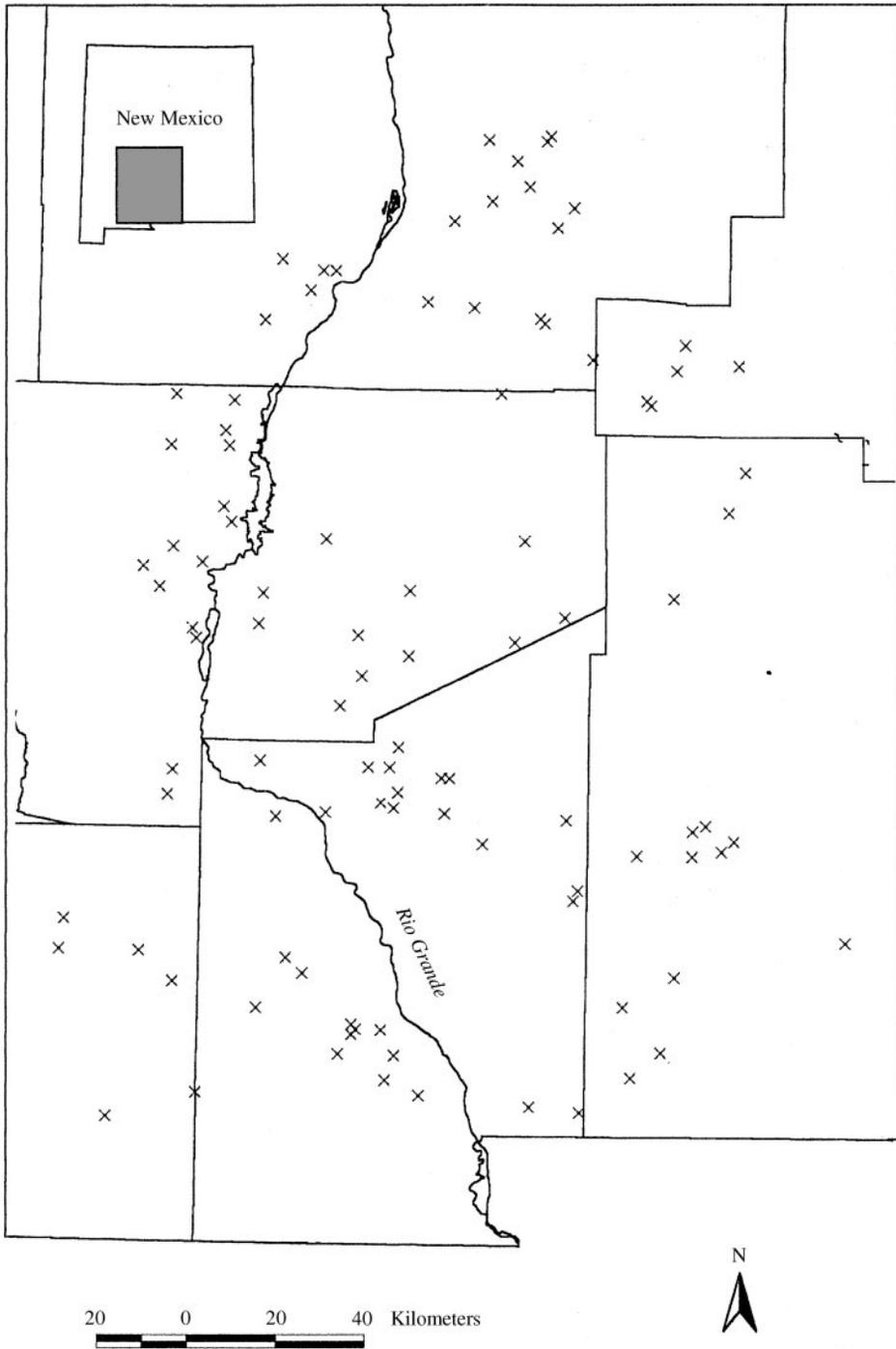
Figure 1. Locations of sites where perennial vegetation surveys were conducted. New Mexico county boundaries and the channel of the Rio Grande are shown. Inset map shows the portion of New Mexico represented by the full map.

and lasting through to May 1996 (NOAA, 1998). Perennial vegetative cover was measured at each site on three transects which radiated out from a central point. We chose a starting direction at random for the first transect and all transects were placed 120° apart. Each of the radiating transects were 100 m long, and intercepts were recorded to the nearest 1 cm. Measurements were made by recording the identity of the plant species (living or standing dead) or bare patch and the horizontal linear dimensions of the plant or bare patch intercepting the transect (Canfield, 1941; de Soyza *et al.*, 1997). Plants could usually be identified to species, but in some cases only genus could be determined. Binomial nomenclature follows that of Allred (1993, 1997). In cases of overlapping canopies (e.g. grass under a shrub), intercepts of both overstory and understory plants were recorded. The present analysis, however, is based solely on overstory cover.

Data analysis

Field data were entered into a computer spreadsheet (Quattro Pro, version 6.0) and proofread to insure accuracy of transcription. Basic univariate statistics were computed using mathematical functions available in the spreadsheet. Cover data by species from all sites were combined to compute weighted average cover values, which represent the relative importance of each species in the regional vegetation. Sites had been selected by a stratified random sampling design which gave equal representation to each class in the classified AVHRR image, but the geographic area (or number of pixels) differed from class to class. So, we computed a weighted mean using the geographic area (number of pixels) as a weighting factor to average the mean percentage cover values computed for each class.

Ordinations of the vegetation data were produced using both principal components analysis (PCA) based on the variance-covariance matrix, and detrended correspondence analysis (DCA) with equal weight given to all variables and 26 segments used in detrending. Species which occurred at less than 5 of the 100 sites were eliminated from the data matrix prior to performing the ordinations. The two ordination techniques employed are attuned to detecting different underlying data structures (Jongman *et al.*, 1995). PCA is most appropriate when vegetative cover of each species is a linear function of an environmental gradient. DCA is most suitable to uncovering patterns in which all species display a unimodal response to an environmental gradient. In actual situations where species may show a complex mixture of responses to environmental gradients, it is often not evident *a priori* which ordination procedure is most appropriate. The simultaneous use of both techniques can be expected to be more informative than the use of a single ordination procedure. Particularly strong patterns are likely to be insensitive to the details of the statistical assumptions, and therefore should be evident in both analyses.

In most cases, the taxa used in the analysis were species. In some cases, congeneric species were lumped together as a single variable. The sagebrushes, *Artemisia bigelovii* Gray and *Artemisia filifolia* Torr. were lumped, as were two of the grama grasses, *Bouteloua gracilis* (Willd. ex Kunth) Lag. ex Griffiths (blue grama) and *Bouteloua hirsuta* Lag. (hairy grama). In both cases, the species lumped together were thought to be ecologically similar, and treating the species separately would have excluded them from the analysis because each species occurred in fewer than five sites. Brickelbush plants identified in the field as *Brickellia* sp. were lumped with those identified as the species *Brickellia laciniata* Gray. Some grasses could be identified to species level if the plant was relatively intact, but could only be identified to genus level if they had been heavily grazed. *Aristida* sp., which was recorded at three sites and never amounted to more than 0·5% cover, was lumped together with *Aristida purpurea* Nutt., which was more prevalent than *Aristida ternipes* Cav. *Sporobolus* sp. is a heterogeneous group,

probably including *Sporobolus airoides* (Torr.) Torr. (alkali sacaton) and *Sporobolus flexuosus* (Thurb, ex Vasey) Rydb. (mesa dropseed) (both included as separate variables in the analyses), but probably also some *Sporobolus contractus* A.S. Hitchc., *Sporobolus cryptandrus* (Torr.) Gray and/or *Sporobolus nealleyi* Vasey (all of which occurred in our sampling, but were identified at fewer than five sites). The decision to retain species-level distinctions within the genus *Sporobolus*, when possible, was made because of ecological differences displayed among these species. In particular, *S. airoides* is a long-lived perennial which exhibits substantial vegetative reproduction, whereas the other *Sporobolus* species are relatively short-lived and display little vegetative reproduction (Van Zee, *pers. obs.*).

Tausch *et al.* (1995) have cautioned that random rearrangements in the order of data can sometimes substantially alter ordination or classification results. DCA is especially vulnerable in this regard. Oksanen & Minchin (1997) have traced the problem to lax convergence criteria and a bug in the rescaling algorithm, for which they provide solutions. Our analyses were conducted using PC-ORD for Windows, version 3·0 (McCune & Mefford, 1997), which incorporates the solutions to the instability problem suggested by Oksanen & Minchin (1997).

Results

Overview of the species

The 40 variables used in the ordinations and classifications are listed in Table 1, along with the number of sites at which each occurred, and the minimum, maximum and median of percent cover values encountered. The most frequently encountered species was the subshrub *Gutierrezia sarothrae* (Pursh) Britt. & Rusby (broom snakeweed), which was present at 88 of the 100 sites. *G. sarothrae* never exceeded 7·97% cover, and had a median cover of 1·51% at the sites where it occurred. The next most ubiquitous species were shrubs *P. glandulosa* and *L. tridentata,* found at 68 and 52 of the 100 sites, respectively.

The species which reached the highest cover value at any one site was the grass *B. eriopoda*, which reached 40·8% cover. Other species with high maximum cover values were the shrubs *P. glandulosa* (35·2%) and *L. tridentata* (33·6%). The top ranking species in median cover (calculated using only non-zero cover values) were the shrubs *L. tridentata* (10·9%), *P. glandulosa* (6·36%) and the grass *S. airoides* (5·76%).

Another way to summarize the percent cover information is to average the percent cover for each species across all 100 sites (i.e. including zero percent cover values in computing the average) (Table 2). Such an average represents the importance of each species to the vegetational cover of the whole region. A simple arithmetic mean would be biased, however, due to the fact that our sampling design gave equal representation to each of the 5 classes in the AVHRR image, but the portion of the study area falling into each class varied. Thus, we computed a weighted mean which weights the cover data for sites drawn from each class in the classified AVHRR image by the number of pixels (i.e. the area) in that class. We expect that this weighted mean gives the best (least biased) estimate of the relative importance of each species. Based on weighted mean cover, the most important species are *L. tridentata* (7·61%), *P. glandulosa* (4·41%) and *S. airoides* (2·12%).

Principal components analysis (PCA)

An ordination of the sites by principal components analysis is shown in Fig. 2. The first three principal components cumulatively explain 68·1% of the variance in the data

Table 1. Taxa included in the multivariate analyses (i.e. perennial vegetation occurring in at least five sites). Frequency of occurrence and percent cover at those sites where present

| Taxon	Number of sites	Percent cover		
		Min	Max	Median
Acacia constricta	5	0·243	26·1	2·61
Aloysia wrightii	6	0·030	2·94	0·49
Aristida purpurea + *Aristida* sp.	47	0·020	10·6	0·34
Aristida ternipes	5	0·68	17·4	4·82
Artemisia bigelovii + *A. filifolia*	11	0·083	19·2	4·46
Atriplex canescens	35	0·040	16·4	2·29
Bouteloua curtipendula	12	0·013	8·98	0·95
Bouteloua eriopoda	37	0·033	40·8	1·16
Bouteloua gracilis + *B. hirsuta*	5	0·18	15·6	2·29
Bothriochloa laguroides	5	0·01	0·43	0·063
Brickellia laciniata + *Brickellia* sp.	5	0·03	4·69	0·22
Condalia warnockii	7	0·06	1·89	0·39
Dalea formosa	15	0·02	2·34	0·31
Dasyochloa pulchella	34	0·036	2·55	0·30
Ephedra torreyana	21	0·13	7·57	1·02
Ephedra trifurca	14	0·06	1·88	0·685
Fallugia paradoxa	6	0·073	1·51	0·75
Flourensia cernua	30	0·08	25·6	2·45
Gutierrezia sarothrae	88	0·007	7·967	1·513
Koeberlinia spinosa	5	0·24	3·31	0·24
Larrea tridentata	52	0·24	33·6	10·9
Lepidium alyssoides	6	0·017	0·76	0·10
Lycium pallidum	15	0·013	3·28	0·45
Mendora scabra	9	0·013	2·31	0·26
Muhlenbergia porteri	41	0·03	6·79	0·46
Opuntia leptocaulis	9	0·047	0·34	0·11
Opuntia santa-rita	16	0·023	1·75	0·08
Parthenium incanum	25	0·033	5·25	0·72
Pleuraphis mutica	40	0·027	19·8	0·87
Prosopis glandulosa	68	0·027	35·2	6·36
Rhus microphylla	17	0·073	11·7	1·08
Scleropogon brevifolius	29	0·01	23·2	0·36
Sporobolus airoides	16	0·07	29·2	5·76
Sporobolus flexuosus	5	0·037	4·58	1·03
Sporobolus sp.	49	0·017	4·79	0·40
Sphaeralcea hastulata	8	0·007	0·08	0·025
Tiquilia canescens	9	0·04	4·5	0·59
Thymophylla acerosa	20	0·013	4·26	0·36
Yucca elata	27	0·113	4·62	0·90
Zinnia acerosa	13	0·01	1·42	0·033

(38·3% in axis 1, 21·8% in axis 2, and 8·0% in axis 3). The first two principal components are highly significant, as the eigenvalues associated with them well exceed the corresponding values for a broken-stick model (Jackson, 1993). The third principal component is probably also significant. Its eigenvalue slightly exceeds the broken-stick

value, and the patterns revealed in the third axis appear sensible, especially since similar patterns are evident in the detrended correspondence analysis reported below. All higher principal components had eigenvalues below the broken-stick value, and were not considered significant.

The first axis is strongly correlated with *L. tridentata* ($+0.60$) and especially with *P. glandulosa* (-0.93). The second axis has a strong negative correlation with

Table 2. *Taxa included in the multivariate analyses (i.e. perennial vegetation occurring in at least five sites). Percent cover averaged over all 100 sites*

Taxon	Percent cover (weighted mean)
Acacia constricta	0·78
Aloysia wrightii	0·050
Aristida purpurea + Aristida sp.	0·53
Aristida ternipes	0·30
Artemisia bigelovii + A. filifolia	0·69
Atriplex canescens	1·12
Bouteloua curtipendula	0·084
Bouteloua eriopoda	1·39
Bouteloua gracilis + B. hirsuta	0·51
Bothriochloa laguroides	0·0037
Brickellia laciniata + Brickellia sp.	0·012
Condalia warnockii	0·058
Dalea formosa	0·11
Dasyochloa pulchella	0·084
Ephedra torreyana	0·29
Ephedra trifurca	0·10
Fallugia paradoxa	0·020
Flourensia cernua	1·08
Gutierrezia sarothrae	1·50
Koeberlinia spinosa	0·056
Larrea tridentata	7·61
Lepidium alyssoides	0·0040
Lycium pallidum	0·16
Mendora scabra	0·041
Muhlenbergia porteri	0·36
Opuntia leptocaulis	0·0112
Opuntia santa-rita	0·032
Parthenium incanum	0·37
Pleuraphis mutica	1·48
Prosopis glandulosa	4·41
Rhus microphylla	0·26
Scleropogon brevifolius	1·16
Sporobolus airoides	2·12
Sporobolus flexuosus	0·046
Sporobolus sp.	0·27
Sphaeralcea hastulata	0·0048
Tiquilia canescens	0·062
Thymophylla acerosa	0·088
Yucca elata	0·23
Zinnia acerosa	0·044
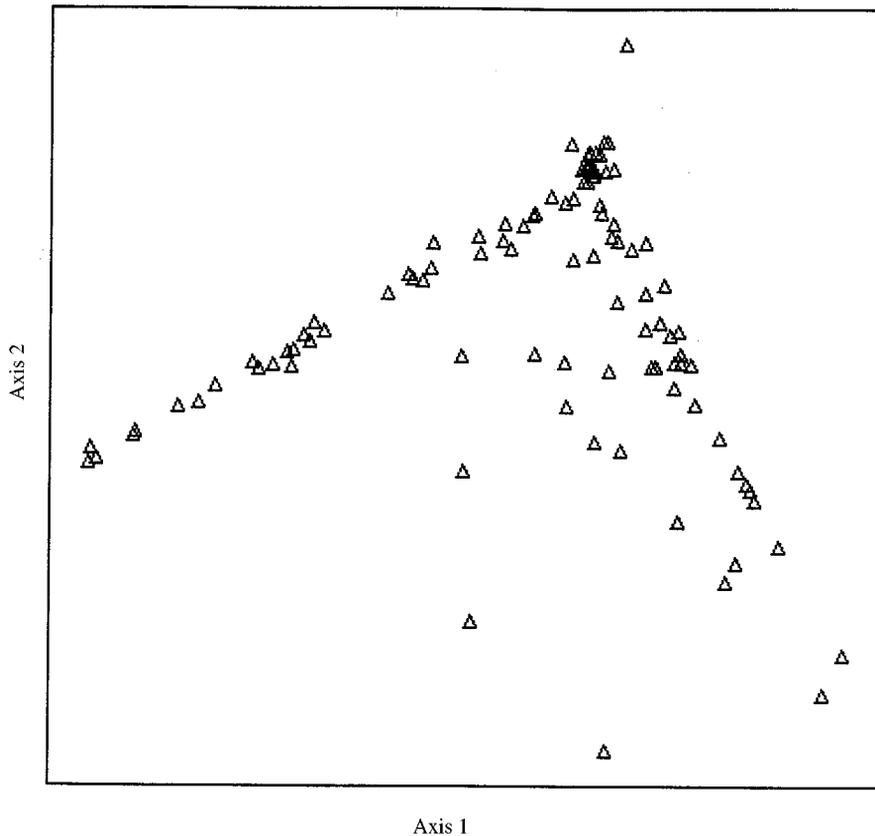
Figure 2. PCA ordination of all 100 sites in the study. Principal components 1 and 2 are shown.

L. tridentata (− 0·80) and weaker negative correlation with *P. glandulosa* (− 0·36). No single variable has a strong positive correlation with axis 2, but as a group grasses tend to be positively correlated (e.g. *B. eriopoda*, + 0·35; *P. mutica*, + 0·26; *S. brevifolius*, + 0·22). If the sites are plotted in the space of the first two principal components, most sites lie along an inverted V shape, or chevron (Fig. 2). Several sites are scattered between the arms of the chevron. Figure 3 shows a series of plots using the first two axes, in which the size of the symbol is proportional to the cover of a particular species. Two shrubs, *L. tridentata* and *P. glandulosa* are shown, as well as four grass variables, *A. purpurea* + *Aristida* sp., *B. eriopoda*, *S. brevifolius* and *S. airoides*. These plots reveal that sites with high cover by *L. tridentata* tend to fall on the right arm of the chevron, while sites with high *P. glandulosa* cover fall on the left arm of the chevron. A number of sites in which both *L. tridentata* and *P. glandulosa* are present at moderate to high cover values occupy the space between the arms of the chevron. Sites with high cover by any of the grasses considered (*A. purpurea* + *Aristida* sp., *B. eriopoda, S. brevifolius, S. airoides*) are clustered near the apex of the chevron.

The third principal component has a strong negative correlation with *B. eriopoda* (− 0·76) and a strong positive correlation with *F. cernua* (+ 0·60). Plotting the sites in the space defined by the first and third principal components, we find the sites arranged approximately in the shape of a plus sign (Fig. 4). Most of the sites lie on the horizontal crossbar. Axis 3 distinguishes only a few sites that lie above or below this horizontal line. Plotting the ordination with symbol size varying in proportion to the cover of a particular species (Fig. 5), we can see that sites with high *F. cernua* cover tend to lie above the line, while sites with high cover by *B. eriopoda* lie below the line. Although the trend is not as
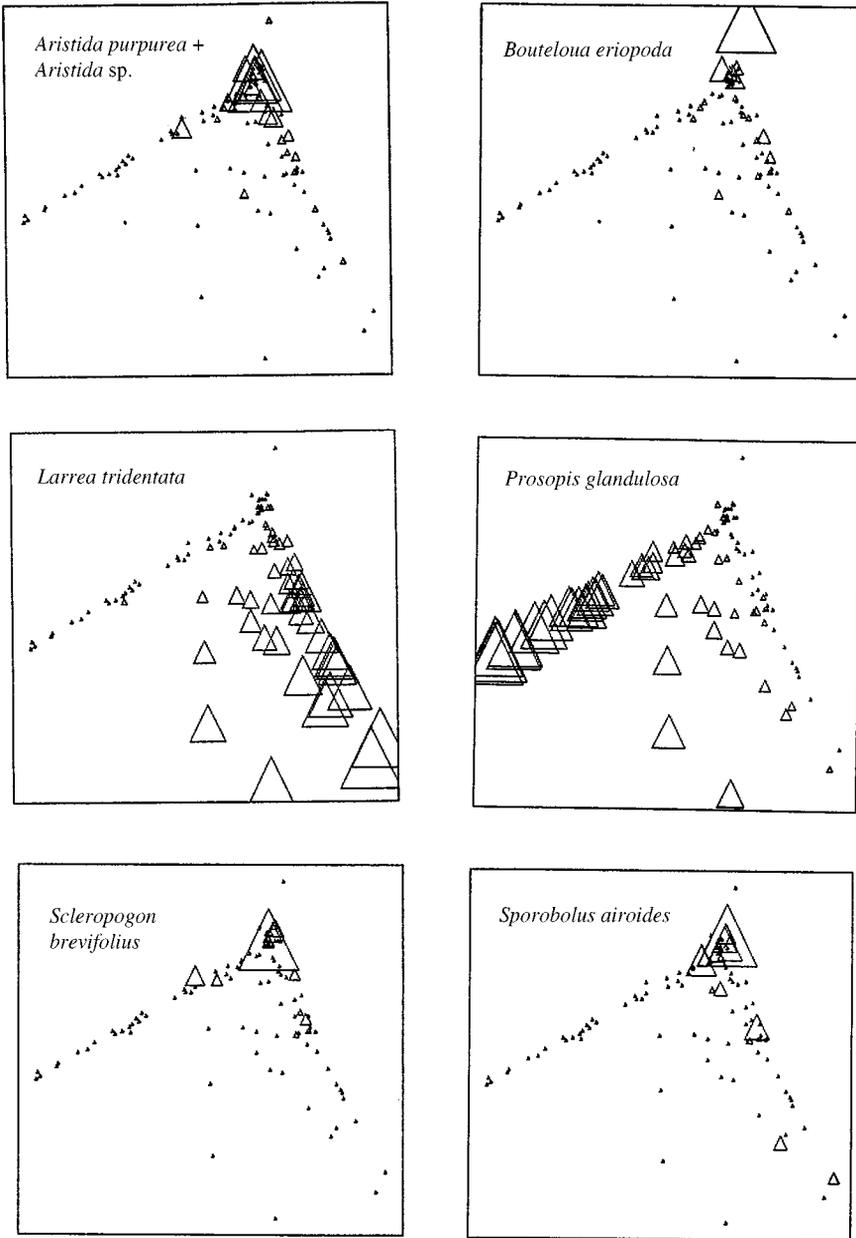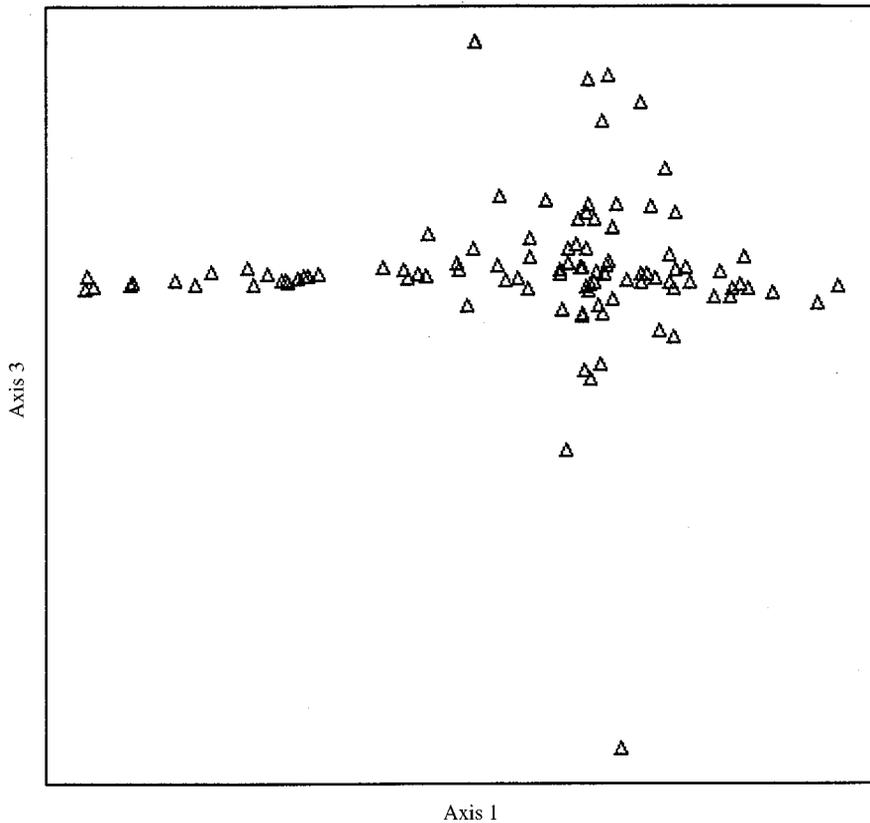
Figure 3. PCA ordination of all 100 sites in the study. Symbol size is proportional to canopy cover by selected species.

strong, we also see that *A. purpurea* + *Aristida* sp. tends to lie below the line while *S. brevifolius* tends to lie above.

Detrended correspondence analysis (DCA)

Another ordination was accomplished using detrended correspondence analysis. An analysis of all 100 sites produced the ordination shown in Fig. 6. The symbol size is
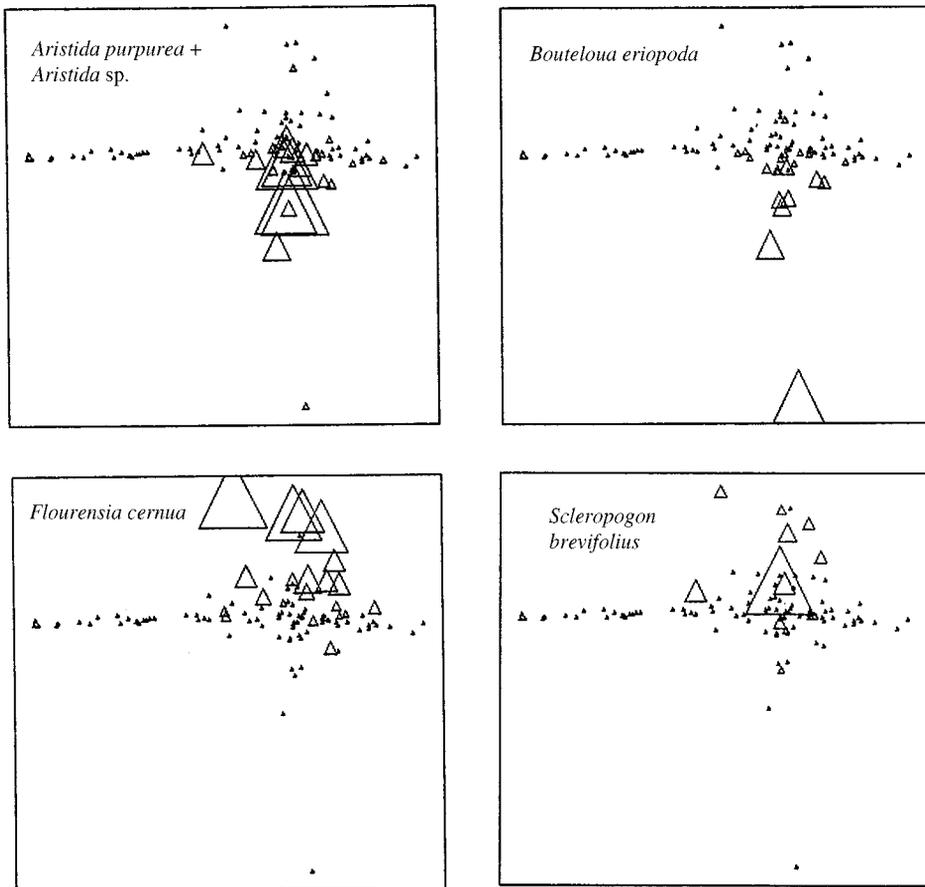
Figure 4. PCA ordination of all 100 sites. Principal components 1 and 3 are shown.

proportional to the cover by a shrub, *Acacia constricta* Gray (whitethorn acacia). It is evident that the first DCA axis is strongly influenced by the single site at which this species reached high abundance. This site becomes an outlier at the far right of the ordination plot. At this unusual site, *A. constricta* was the dominant plant with 26·1% cover out of a total of 30·5% cover by all perennial plants. The highest cover *A. constricta* achieved at any other site was 3·45%. It seems undesirable for the ordination to be so strongly responsive to a single atypical site, hence this site was dropped from the analysis.

The results of an ordination of the remaining 99 sites are shown in Fig. 7. The sites are arrayed in a generally triangular shape of the space defined by the first two DCA axes. Plots in which symbol size reflect the cover by particular species are shown in Fig. 8. Sites with high *P. glandulosa* cover cluster toward the corner of the triangle on the left-hand side (i.e. low scores on DCA axis 1, Fig. 8). Sites with high cover by *L. tridentata* cluster together in the interior of the triangle (Fig. 8). Most sites with substantial grass cover have high scores on DCA axis 1, and thus appear on the right-hand side. DCA axis 1 is strongly correlated with *P. glandulosa* cover (-0.81) but not with *L. tridentata* ($+0.02$). DCA axis 2 differentiates between certain grass variables. Specifically, sites with substantial *B. eriopoda* and/or *A. purpurea* + *Aristida* sp. have low scores on DCA axis 2, and cluster at the bottom right corner of the triangle (Fig. 8). Sites high in *A. ternipes* also occupy the bottom right corner. In contrast, sites with abundant *Scleropogon brevifolius* Phil. and/or *Sporobolus airoides* tend to occupy the upper right portion of the triangular region (Fig. 8). Not shown are the few sites with

high *Sporobolus flexuosus* which clustered tightly with low axis 2 scores, opposite *S. airoides*, and sites with substantial cover that could only be identified as *Sporobolus* sp. are widely scattered through much of the lower portion of the triangular region, mostly separate from *S. airoides*. The principal components ordination also grouped *B. eriopoda* and *Aristida* sites together, while segregating *S. brevifolius* sites to a different region of the ordination space.

The distribution of sites with high cover by several other species also merit inspection (Fig. 9). Sites high in *F. cernua* tend to be near the middle of DCA axis 1, but have relatively high scores on DCA axis 2 (Fig. 9). This places them slightly above the region occupied by *L. tridentata*. Sites with the two species of *Ephedra* ordinate rather differently, with *E. torreyana* Wats. sites having high DCA axis 1 scores, and *E. trifurca* Torr. having moderate axis 1 scores and low axis 2 scores (Fig. 9). Finally, sites with high cover by *Yucca elata* Engelm. (soaptree yucca) cluster in two disjunct regions of the ordination space: on the left in association with *P. glandulosa* shrublands, and in the lower right area, in association with *B. eriopoda/Aristida* grasslands. Similar patterns regarding the *Ephedra* species and *Yucca* were observed in the principal components analysis. Finally, *P. mutica* sites are not shown but fall mostly near the middle of axis 1, but lower on axis 2 than *F. cernua* sites. A separation of *P. mutica vs. F. cernua* sites was also evident in the third PCA axis.

Figure 5. PCA ordination of all 100 sites. Symbol size is proportional to canopy cover by selected species.
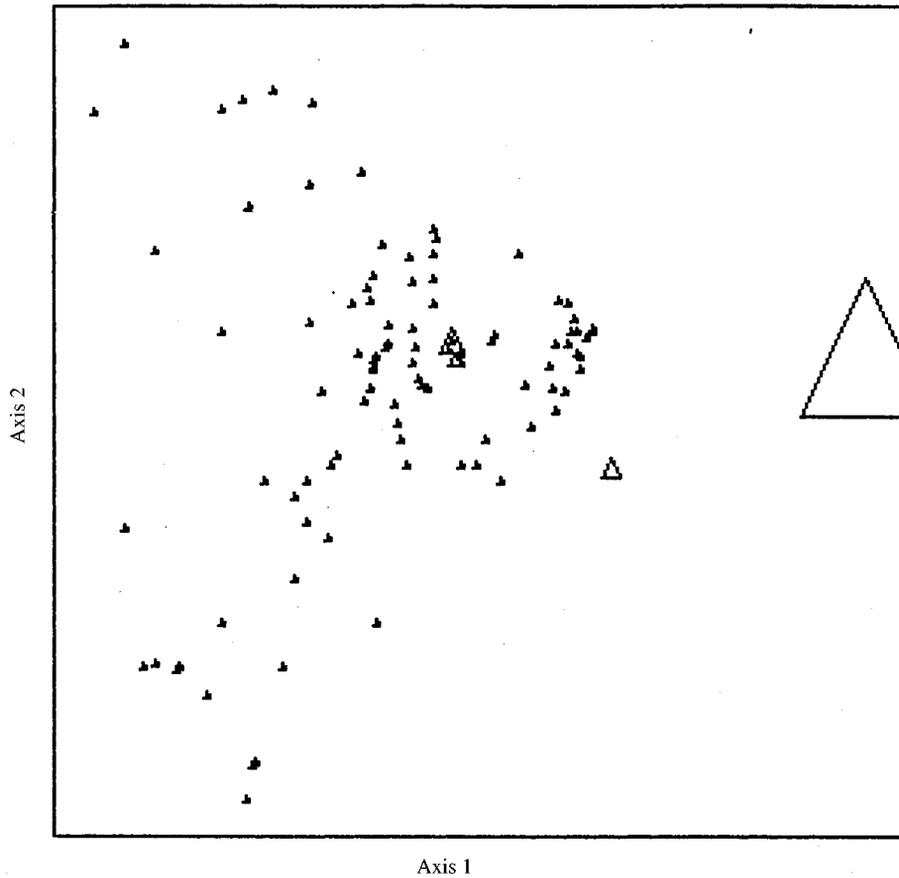
Figure 6. DCA ordination of all 100 sites, axes 1 and 2 shown. Symbol size is proportional to canopy cover by *Acacia constricta*.

Spatial trends

DCA axis 1 scores (from the ordination including 99 sites) were plotted as a function of latitude (Fig. 10). Although there was substantial scatter, a generally increasing trend was apparent. Linear least-squares regression produced a relationship in which the slope of the line differs significantly from zero ($p < 0.001$), and by which 34% of the variance in the DCA axis 1 scores is explained by latitude. No trend was apparent when DCA axis 1 scores were plotted as a function of longitude, and DCA axis 2 scores showed no trend as a function of either latitude or longitude.

Discussion

The results of our analysis are consistent with previous accounts of Chihuahuan Desert vegetation as a whole (e.g. Shreve, 1942; MacMahon & Wagner, 1985; Henrickson & Johnston, 1986; Brown, 1994) and specifically the northern Chihuahuan Desert in New Mexico (Dick-Peddie, 1993). This discussion will place those results in the context of what is known about the ecology of particular species and the historical changes in the vegetation of the northern Chihuahuan Desert over the past century and a half.
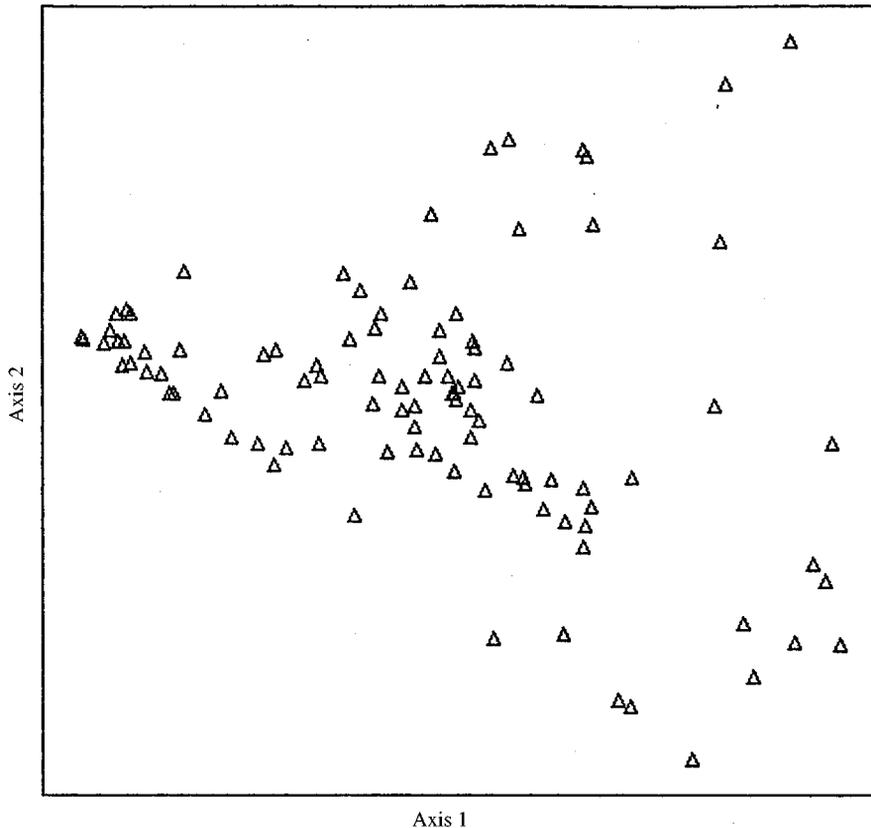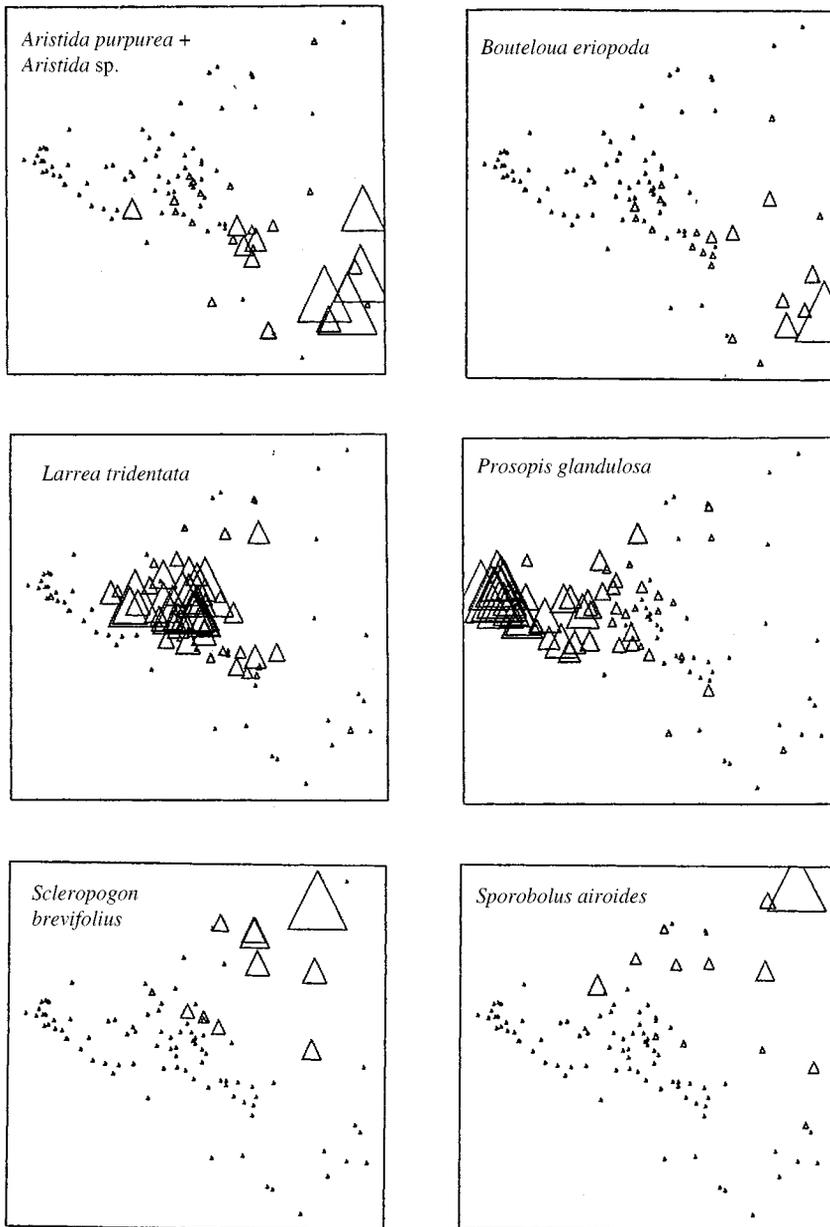
Figure 7. DCA ordination of 99 sites, omitting atypical site dominated by *Acacia constricta*.

The two most important species in the region are *L. tridentata* and *P. glandulosa* based on weighted mean cover values. These species are important in defining the first ordination axis in both principal components and detrended correspondence analysis. PCA clustered *P. glandulosa*-dominated sites to the left-hand side of the first axis, *L. tridentata*-dominated sites on the right-hand side, and sites with a mixture of *P. glandulosa* and *L. tridentata* were scattered in between (Fig. 3). DCA places all shrub-dominated sites to the left on the first axis, with grassy sites on the right, and a gradation from *P. glandulosa*-dominated to *P. glandulosa-L. tridentata* mix to *L. tridentata*-dominated is still apparent (Fig. 8). These results indicate that these two shrubs are now the definitive elements of the regional vegetation.

Although the scatter of sites within the ordination space took on a different shape depending upon whether PCA or DCA were applied, both analytical techniques revealed a clear gradation from shrub-dominated to grass-dominated sites, and within shrubland sites, a continuum related to the relative proportion of *P. glandulosa vs. L. tridentata*. The robustness of this pattern to the different ordination techniques strengthens our confidence that it captures the predominant qualitative features of the vegetative associations found in the region, and is not a statistical artifact.

Bouteloua eriopoda is recognized as a diagnostic species and is usually dominant in desert grasslands (MacMahon & Wagner, 1985; Dick-Peddie, 1993). Among our 100 study sites, 12 had appreciable ($> 2\cdot0\%$) cover of *B. eriopoda*. The two highest cover values measured were $40\cdot8\%$ and $14\cdot6\%$. *B. eriopoda* was frequently associated with

Aristida (8 of the 12 sites also had >2·0% cover of *A. purpurea* or *A. ternipes*). *A. purpurea*, however, could reach high cover values without appreciable *B. eriopoda* (7 sites). Both ordinations tended to cluster *Bouteloua* and *Aristida* sites together. In the DCA they are found in the lower right of the ordination space (Fig. 8). Seven of the sites with >2·0% *B. eriopoda* or *Aristida* cover are actually dominated by shrubs (3 by *L. tridentata*, 2 by *P. glandulosa*, 1 by *L. tridentata*/*P. glandulosa*, 1 by *G. sarothrae*/ *L. tridentata*). These sites cluster with other shrub-dominated sites in the DCA

Figure 8. DCA ordination of 99 sites (atypical site dominated by *Acacia constricta* omitted). Symbol size is proportional to canopy cover by selected species.
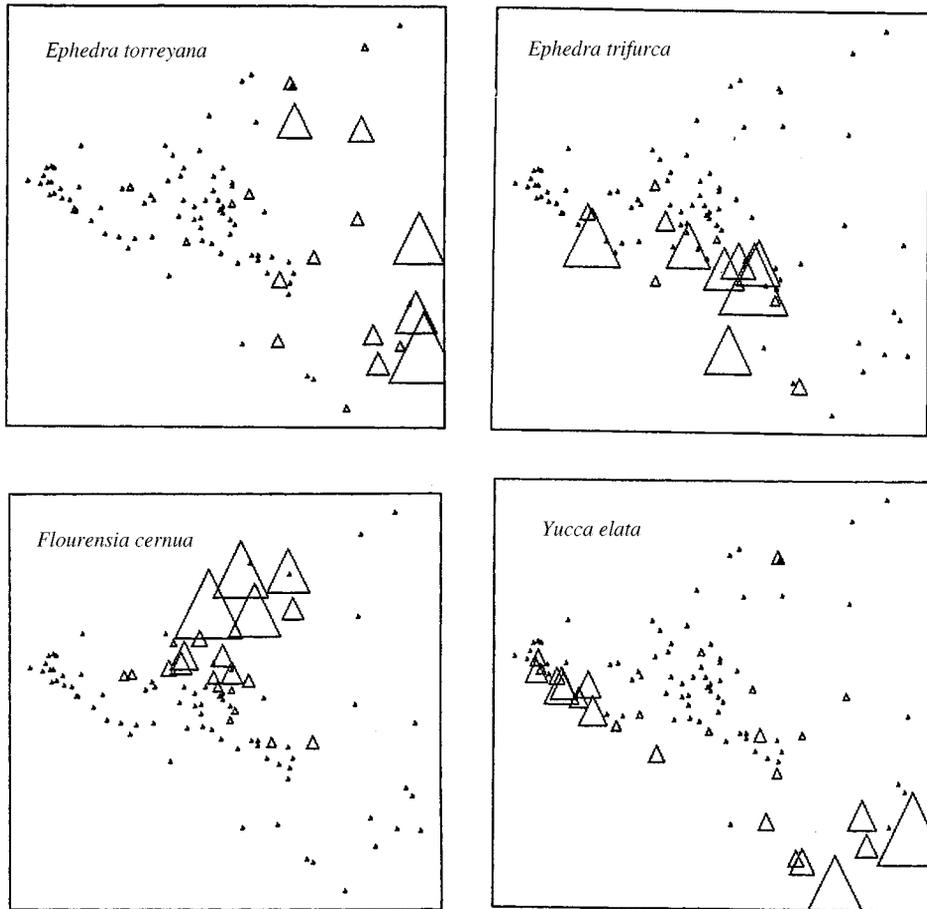
Figure 9. DCA ordination of 99 sites (atypical site dominated by *Acacia constricta* omitted). Symbol size is proportional to canopy cover by selected species.

ordination. They may represent locations of recent shrub encroachment into grasslands, or perhaps shrubland sites that have been recently colonized by grasses. The small number of grass-dominated sites encountered in our survey illustrates the scarcity of the remaining desert grasslands in the study area. The diverse compositions of the grasslands we encountered suggest that *B. eriopoda* may not be as dominant in these remnants as it was in historical grasslands.

The other type of grassland apparent in the DCA has substantial cover by *Sporobolus airoides* and/or *Scleropogon brevifolius* (upper right portion of the ordination space, Fig. 8). Of our 100 study sites, six were dominated by *S. airoides*, two of these also had >5·0% cover by *S. brevifolius*. One site was dominated by *S. brevifolius*. Dick-Peddie (1993) remarks that *S. airoides* can be dominant in swales (local depressions). The fact that *S. airoides* ranks third among all species in weighted mean cover (2·12%) indicates that its importance in the regional vegetation may be greater than is usually recognized. The other species frequently reported as dominant in swales is *Pleuraphis mutica* (Dick-Peddie, 1993), although Neuenschwander *et al.* (1975) comment that it has a higher tolerance for other sites than is generally recognized. We surveyed five sites which were dominated by *P. mutica*. Three of these sites also had appreciable *L. tridentata* or *P. glandulosa* cover. In the DCA, most sites with high *P. mutica* cover were scattered

amongst *L. tridentata/P. glandulosa* sites; the ones with no appreciable shrub cover were far to the right on DCA axis 1, and intermediate between the *B. eriopoda/Aristida* sites and the *S. airoides/S. brevifolius* sites. In the space of the first two principal components, most *P. mutica* sites were near the apex of the chevron, although some were displaced moderately down the *P. glandulosa* or the *L. tridentata* arms. The small number of *P. mutica* sites in our sample make it difficult to characterize its relation to other vegetation types.

Three sites display grass species compositions which do not fit any of the above patterns. One site was dominated by *Bouteloua gracilis* (15·5% cover) with *B. eriopoda* ranking second in cover (9·1%). *B. gracilis* is a common dominant in plains-mesa grassland as identified by Dick-Peddie (1993), which occurs primarily to the north and east of our study area. The site was located on the MacGregor Range of the Fort Bliss Military Reservation, well south of the plains-mesa grassland as mapped by Dick-Peddie (1993). One other site was dominated by *M. porteri* (5·3% cover) and *A. purpurea* (3·3% cover). Total cover by all perennials was very low at this site (13·9%), and slightly over half of the *L. tridentata* cover (which was the predominant shrub) was due to dead plants. We hypothesize that this value was a *L. tridentata* shrubland that had recently been treated with herbicide, a fairly common range management practice (Herbel & Gould, 1995). We also encountered one diverse shrub/grass site in which *Rhus*
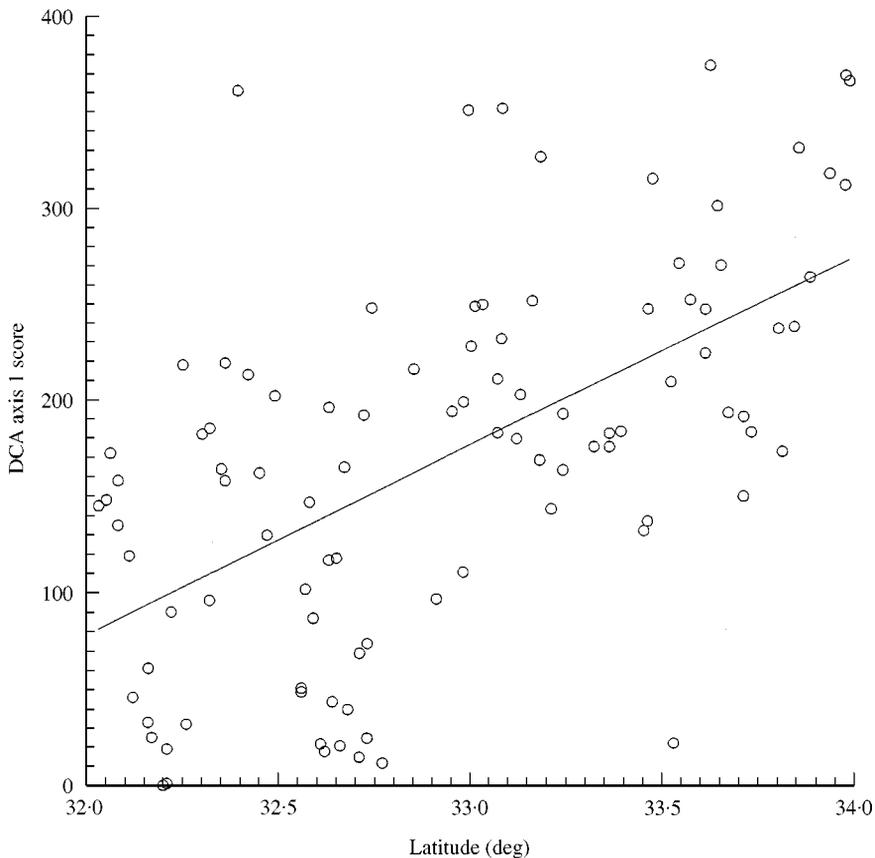
Figure 10. Plot of DCA axis 1 score for 99 sites (atypical site dominated by *Acacia constricta* omitted) as a function of latitude. Linear least-squares regression line is shown ($r^2 = 0.34$, $p < 0.001$ for t-test of the null hypothesis that the slope is zero).

microphylla Engelm, had the greatest cover (9·9%), followed by *Bouteloua curtipendula* (Michx.) Torr. (9·0%) and *S. airoides* (6·0%).

One interesting pattern observed in the ordinations was the presence of two distinct clusters of sites with high cover by *Y. elata*. This is shown for the case of the DCA in Fig. 9, although a segregation of two distinct clusters was also apparent in the PCA. In both ordinations, one cluster is associated with *B. eriopoda/Aristida* grasslands, and the other with *P. glandulosa* shrublands. Several researchers regard *Y. elata* as a characteristic species of desert grasslands, and suggest that *Y. elata* populations found in shrublands are relicts, indicating that grassland occupied the site less than 120 years ago (Smith & Ludwig, 1978; MacMahon & Wagner, 1985; Dick-Peddie, 1993). *Y. elata* is a long-lived plant, but if recruitment of new individuals is not occurring in the populations which are now embedded in a shrubland matrix, a substantial reduction in the abundance of this species in the northern Chihuahuan Desert could be imminent. Such a population decline could have significant implications for a variety of animal species, including yucca moths (*Tegeticula* spp.) which are pollinators and seed parasites, carpenter bees (*Xylocopa californica*) which nest in inflorescence stalks, and a variety of birds (especially raptors) which use the dry stalks as one of the few natural tall perches in this landscape (Kerley *et al.*, 1993).

Two species of *Ephedra* were included in our analysis. *E. torreyana* tended to be associated with grassland sites, while *E. trifurca* was associated with *L. tridentata* or *P. glandulosa* shrublands. This is apparent in the DCA as shown in Fig. 9, and was also evident in the PCA. To our knowledge, no comparative study of the environmental factors controlling the distribution of these species has been conducted. Work on *E. trifurca* indicates that soil moisture availability along an elevational gradient correlates well with the proportion of female plants, but not with the total density of individuals (Brunt *et al.*, 1988). Differential herbivory may also be important in determining the distribution of these species. *E. torreyana* often shows signs of heavy browsing (probably by rabbits and perhaps cattle), while *E. trifurca* does not (Whitford, pers. obs.). Comparative studies of these two species in the field may be complicated by the fact that *E. torreyana* hybridizes readily, and putative crosses with *E. trifurca* have been reported on the margins of our study area (Wendt, 1993).

Gutierrezia sarothrae was identified as the most ubiquitous species in our study (at 88 sites), and it ranked fourth in importance as measured by its weighted mean cover of 1·50% (Table 2). Due to its very ubiquity, it did not cluster into a particular region of the ordination space in either PCA or DCA. Snakeweeds have been noted as conspicuous components of rangeland vegetation in the south-western U.S. since the beginning of the 20th century (Pieper & McDaniel, 1990). Populations of *Gutierrezia* are described as cyclic, where fluctuations between low and high densities often occur in a decade or less (McDaniel, 1990; Torrell *et al.*, 1990). Drought, heavy grazing by livestock, and fire are factors which may enhance *Gutierrezia* establishment by reducing cover of competing grasses (McDaniel, 1990). Although local fluctuations in *G. sarothrae* cover or density have been documented, it is unclear whether there is an overall trend toward increasing (or decreasing) cover in the study area as a whole. Attempts have been made to develop remote sensing methods for assessing *G. sarothrae*, but substantive ground-truthing of these approaches is still lacking (Peters *et al.*, 1992). Our data confirm the importance of this species in the regional vegetation, but repeated surveys would be required to quantify trends or cyclic fluctuations.

The graph of increasing DCA axis 1 scores with latitude (Fig. 10) reveals an interesting regional trend. Approximately one-third of the compositional variation reflected in DCA axis 1 scores can be accounted for by latitude. The fact that two-thirds of the variation is not explained by latitude implies, as would be expected, that other factors are also important in controlling vegetation composition. Yet, given the high statistical significance of the trend ($p < 0.001$), we soundly reject the null hypothesis that DCA axis 1 scores are independent of latitude, suggesting that an ecologically

relevant latitude effect does exist, despite substantial scatter around the trend. By reference to the species which contribute most heavily to DCA axis 1 scores, we interpret this latitudinal effect as a trend toward greater shrub cover in the south and relatively more grass cover in the north. This suggests that the shrub encroachment documented during the past 130 years, particularly with respect to *P. glandulosa*, has been more pronounced in the southern portion of the study area. This could result from a wave of *P. glandulosa* moving northward, but more likely reflects expansion from local pockets, with earlier initiation of the process or greater rates of expansion in the south.

The analysis presented here provides a snapshot of the vegetation in a region that has undergone dramatic change since the 19th century, and which will undoubtedly continue to change in the future. The fact that the study site locations were chosen according to a stratified random sampling design, with equal numbers of sites from a series of classes within a remotely-sensed image intended to provide a gradation from grassland to shrubland vegetation, suggests that our data should provide a good representation of the vegetation types within our study area. Since the locations of our study sites were determined with high accuracy using GPS with differential correction, we can return to the same locations in the future. The fact that most sites contained appreciable cover by *P. glandulosa* and/or *L. tridentata* is consistent with the historical pattern of shrubland encroachment previously described for the region. The relative scarcity of remaining grasslands means that only a minority of our study sites were grass-dominated. We were able to distinguish between a variety of grassland types based on species composition, but we caution that quantitative assessments of the relative importance of various grassland vegetation types probably cannot be inferred from our data due to the limitations of small sample sizes. Overall, however, our data should serve as a useful benchmark against which future vegetation changes can be measured.

References

Allred, K.W. (1993) *A Field Guide to the Grasses of New Mexico*. Las Cruces, NM: Department of Agricultural Communications, New Mexico State University. 259 pp.

Allred, K.W. (1997). *A Field Guide to the Flora of the Jornada Plain* (2nd Edn). Las Cruces, NM: Range Science Herbarium, New Mexico State University. 143 pp.

Bahre, C.J. (1991). *A Legacy of Change. Historic Human Impact on Vegetation of the Arizona Borderlands*. Tucson, AZ: University of Arizona Press. 231 pp.

Bahre, C.J. & Shelton, M.L. (1993). Historic vegetation change, mesquite increases, and climate in southeastern Arizona. *Journal of Biogeography*, **20**: 489–504.

Brown, D.E. (1994). *Biotic Communities. Southwestern United States and Northwestern Mexico*. Salt Lake City, UT: University of Utah Press. 342 pp.

Brown, J.H. & Heske, E.J. (1990). Control of a desert-grassland transition by a keystone rodent guild. *Science*, **250**: 1705–1707.

Brown, J.H., Valone, T.J. & Curtin, C.G. (1997). Reorganization of an arid ecosystem in response to recent climate change. *Proceedings of the National Academy of Science USA*, **94**: 9729–9733.

Brunt, J.W., Conley, M.R. & Cunningham, G.L. (1988). Sex in *Ephedra trifurca* (Ephedraceae) with relation to Chihuahuan Desert habitats. *American Midland Naturalist*, **119**: 137–142.

Buffington, L.C. & Herbel, C.H. (1965). Vegetational changes on a semidesert grassland range from 1858 to 1963. *Ecological Monographs*, **35**: 139–164.

Canfield, R.H. (1941). Application of the line interception method in sampling range vegetation. *Journal of Forestry,* **39**: 388–394.

Chew, R.M. & Whitford, W.G. (1992). A long-term positive effect of kangaroo rats (*Dipodomys spectabilis*) on creosote bushes (*Larrea tridentata*). *Journal of Arid Environments*, **22**: 375–386.

de Soyza, A.G., Whitford, W.G. & Herrick, J.E. (1997). Sensitivity testing of indicators of ecosystem health. *Ecosystem Health*, **3**: 44–53.

Dick-Peddie, W.A. (1993). *New Mexico Vegetation. Past, Present, and Future.* Albuquerque, NM: University of New Mexico Press. 244 pp.

Eve, M.D., Whitford, W.G. & Havstad, K.M. (1999). Applying satellite imagery to triage assessment of ecosystem health. *Environmental Monitoring and Assessment*, **54**: 205–227.

Galatowitsch, S.M. (1990). Using the original land survey notes to reconstruct presettlement landscapes in the American West. *Great Basin Naturalist*, **50**: 181–191.

Gibbens, R.P. & Beck, R.F. (1988). Changes in grass basal area and forb densities over a 64-year period on grassland types of the Jornada Experimental Range. *Journal of Range Management*, **41**: 186–192.

Gibbens, R.P., Tromble, J.M., Hennessy & Cardenas, M. (1983). Soil movement in mesquite dunelands and former grasslands of southern New Mexico from 1933 to 1980. *Journal of Range Management*, **36**: 145–148.

Gibbens, R.P., Beck, R.F., McNeely, R.P. & Herbel, C.H. (1992). Recent rates of mesquite establishment in the northern Chihuahuan Desert. *Journal of Range Management*, **45**: 585–588.

Grover, H.D. & Musick, H.B. (1990). Shrubland encroachment in southern New Mexico, U.S.A.: An analysis of desertification processes in the American Southwest. *Climatic Change*, **17**: 305–330.

Hennessy, J.T., Gibbens, R.P., Tromble, J.M. & Cardenas, M. (1983). Vegetation changes from 1935 to 1980 in mesquite dunelands and former grasslands of southern New Mexico. *Journal of Range Management*, **36**: 370–374.

Henrickson, J. & Johnston, M.C. (1986). Vegetation and community types of the Chihuahuan Desert. In: Barlow, J.C., Powell, A.M. & Timmermann, B.N. (Eds), *Second Symposium on the Resources of the Chihuahuan Desert Region*, pp. 20–39. Alpine, TX: Chihuahuan Desert Research Institute. 172 pp.

Herbel, C.H. & Gould, W.L. (1995). *Management of Mesquite, Creosotebush, and Tarbush with Herbicides in the Northern Chihuahuan Desert.* (Agricultural Experiment Station, Bulletin 775). Las Cruces, NM: New Mexico State University. 53 pp.

Jackson, D.A. (1993). Stopping rules in principal components analysis: A comparison of heuristical and statistical approaches. *Ecology*, **74**: 2204–2214.

Jongman, R.H.G., ter Braak, C.J.F. & van Tongeren, O.F.R. (1995). *Data Analysis in Community and Landscape Ecology.* Cambridge: Cambridge University Press. 299 pp.

Kerley, G.I.H., Tiver, F. & Whitford, W.G. (1993). Herbivory of clonal populations: Cattle browsing affects reproduction and population structure of *Yucca elata*. *Oecologia*, **93**: 12–17.

MacMahon, J.A. & Wagner, F.H. (1985). The Mojave, Sonoran and Chihuahuan Deserts of North America. In: Evanari, M., Noy-Meir, I. & Goodall, D.W. (Eds), *Hot Deserts and Arid Shrublands. Ecosystems of the World 12A*, pp. 105–202. Amsterdam: Elsevier. 365 pp.

McCune, B. & Mefford, M.J. (1997). *PC-ORD: Multivariate Analysis of Ecological Data. User's Guide Supplement (Version 3.0 for Windows).* Gleneden Beach, OR: MjM Software Design. 47 pp.

McDaniel, K.C. (1990). Snakeweed populations in New Mexico, 1979–1989. In: Huddleston, E.D. & Pieper, R.D. (Eds), *Snakeweed: Problems and Perspectives*, pp. 13–25. (Agricultural Experiment Station, Bulletin 751). Las Cruces, NM: New Mexico State University. 225 pp.

Neilson, R.P. (1986). High-resolution climatic analysis and southwest biogeography. *Science*, **232**: 27–34.

Neuenschwander, L.F., Sharrow, S.H. & Wright, H.A. (1975). Review of tobosa grass (*Hilaria mutica*). *Southwestern Naturalist*, **20**: 255–263.

NOAA (1998). Palmer Drought Severity Index data, NOAA NCDC Home Page. [http://www.ncdc.noaa.gov/onlineprod/drought/xmgr.html].

Oksanen, J. & Minchin, P.R. (1997). Instability of ordination results under changes in input data order: Explanations and remedies. *Journal of Vegetation Science*, **8**: 447–454.

Peters, A.J., Reed, B.C., Eve, M.D. & McDaniel, K.C. (1992). Remote sensing of broom snakeweed (*Gutierrezia sarothrae*) with NOAA-10 spectral image processing. *Weed Technology*, **6**: 1015–1020.

Pieper, R.D. & McDaniel, K.C. (1990). Ecology and management of broom snakeweed. In: Huddleston, E.D. & Pieper, R.D. (Eds), *Snakeweed: Problems and Perspectives*, pp. 1–12. (Agricultural Experiment Station, Bulletin 751). Las Cruces, NM: New Mexico. State University. 225 pp.

Shreve, F. (1942). The desert vegetation of North America. *Botanical Review*, **8**: 195–246.

Smith, S.D. & Ludwig, J.A. (1978). The distribution and phytosociology of *Yucca elata* in southern New Mexico. *American Midland Naturalist*, **100**: 202–212.

Tausch, R.J., Charlet, D.A., Wixelman, D.A. & Zamudio, D.C. (1995). Patterns of ordination and classification instability resulting from changes in input data order. *Journal of Vegetation Science*, **6**: 897–902.

Torrell, L.A., Williams, K. & McDaniel, K.C. (1990). Probability of snakeweed die-off and invasion on rangeland. In: Huddleston, E.D. & Pieper, R.D. (Eds), *Snakeweed: Problems and Perspectives*, pp. 71–83. (Agricultural Experiment Station, Bulletin 751). Las Cruces, NM: New Mexico State University. 225 pp.

U.S. Bureau of Land Management (various dates). *Surface Management Status Maps, 30 × 60 Minute Quadrangles (1:100,000)*. Those used include: Carrizozo, NM, 1989 edition; Crow Flats, NM-TX, 1980 edition; Deming, NM, 1984 edition; Hatch, NM, 1984 edition; Las Cruces, NM, 1992 edition; Oscura Mountains, NM, 1984 edition; San Mateo Mountains, NM, 1981 edition; Truth or Consequences, NM, 1981 edition; Tularosa, NM, 1984 edition; White Sands, NM, 1983 edition.

Valverde, P.L., Zavala-Hurtado, J.A., Montaña, C. & Ezcurra, E. (1996). Numerical analyses of vegetation based on environmental relationships in the southern Chihuahan Desert. *Southwestern Naturalist*, **41**: 424–433.

Wendt, T. (1993). A new variety of *Ephedra torreyana* (Ephedraceae) from west Texas and Chihuahua, with notes on hybridization in the *E. torreyana* complex. *Phytologia*, **74**: 141–150.

York, J.C. & Dick-Peddie, W.A. (1969). Vegetation changes in southern New Mexico during the past hundred years. In: McGinnies, W.G. & Goldman, B.J. (Eds), *Arid Lands in Perspective*, pp. 155–166. Tucson: University of Arizona. 421 pp.