Community dynamics of desert grasslands: influences of climate, landforms, and soils

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Abstract. Permanently marked vegetation transects in Big Bend National Park, Texas, USA were monitored to follow temporal dynamics of desert grassland communities on a variety of landforms and soil types over a 26-yr period after the removal of domestic livestock. Historic records indicate that the park area was severely overgrazed prior to its establishment, and our results show that the species present increased in both cover and density after the removal of livestock. However, the timing of recovery corresponded to multi-year periods of above-average precipitation. Little change was observed in between 1955 and 1960, a period dominated by several consecutive years of drought. The cover of two large shrubs common to the Chihuahuan Desert, Larrea tridentata and Fouquieria cernua, increased from 1960 to 1967, a period dominated by summer drought and frequent wet winters. The cover and density of forbs, perennial grasses, and most shrubs increased on nearly all landforms between 1967 and 1981, when summers were wetter than average. In contrast, the cover of Larrea tridentata decreased during this period. Comparisons among the plant communities on each landform showed that they diverged through time after domestic livestock were removed. Presumably, differences in topographic position and soil texture influence water availability which was reflected in the species composition on each soil series.

Unfortunately, we cannot isolate the effects of recovery from grazing on the effects of climate because the study design did not include control plots located within grazed pastures. Certainly, the directional trajectory of change and the regrowth of grasses into inter-shrub spaces, must, at least in part, be the result of recovery from grazing. However, our data also indicate that the desert grassland communities are sensitive to multi-year periods of above- or below-average precipitation. Clearly, the dynamics between shrubs and grasses cannot be explained by a simple successional paradigm that views increased shrub dominance as retrogression from a climax grassland. Many alternate hypotheses have been forwarded to explain the dynamics that control the vegetation composition in the desert and desert grassland region of North America. Experimental tests of these hypotheses are needed to indentify the interactions between biotic and abiotic factors that control dominance by shrubs or grasses.

Keywords: Big Bend National Park; Chihuahuan desert; Desertification; Landform; Livestock grazing.

Nomenclature: Correll & Johnston (1970); Gould (1975) for grasses.

Introduction

Desert grasslands of the southwestern United States and northern Mexico border the Chihuahuan desert and the eastern edge of the Sonoran desert (Brown 1982). Within these deserts, they also occur where precipitation is greater on foothills and piedmont slopes of mountain ranges. Early descriptions of these grasslands indicate that they were once a mosaic of both shrubs and grasses (Hastings & Turner 1965) that apparently resulted from the local effect of topography and landform. Erosional sites on mid-piedmont slopes with shallow, calcareous soils prone to water loss via runoff, usually supported shrub communities dominated by Larrea tridentata. Transport and depositional sites, such as hillslopes or basin floors that receive run-on water, typically supported grasslands (Gardner 1951; York & Dick-Peddie 1969; Stein & Ludwig 1979; McCraw 1985; Wondzell et al. 1987).

Numerous studies in New Mexico and Arizona have shown that the abundance of grasses decreased and the density and cover of shrubs, especially of Larrea tridentata and Prosopis spp., have increased over the last century. These changes have usually been accompanied by extensive sheet and rill erosion, channel cutting, and wind erosion (Thornthwaite et al. 1942; Gardner 1951; Branscomb 1958; Humphrey 1958; Hastings 1959; Buffington & Herbel 1965; Hastings & Turner 1965; York & Dick-Peddie 1969; McCraw 1985; Bahre & Shelton 1993). Fire is generally thought not to have been important for maintaining the desert grasslands because fires were rare (Hastings & Turner 1965) and because the recovery of many shrub species after fire appears to equal or even exceed the recovery of the dominant perennial grasses (Cornelius 1988). Therefore, the cause of the changes in the desert grassland vegetation has been attributed either to grazing of domestic livestock or...
to a warming and drying climate. However, because changes in global climatic patterns after the 'little ice age' (ca. 1900) coincided with a rapid increase in domestic livestock, it has been difficult to separate causes (Neilson 1986). This problem is of more than academic interest. If climatic change is the primary cause of desertification, there may be little potential for reestablishment of desert grasslands; however, if grazing is the primary cause, many desertified areas may still have the potential to support grasslands.

Vegetation changes in the desert grasslands of the Big Bend region in southwestern Texas after settlement in about 1850 are thought to have been similar to those of southern New Mexico and Arizona, although documentation is slight. Certainly, by 1944, most of what was to become Big Bend National Park, the locale of this study, was severely overgrazed (H.M. Ratcliff 1944, unpubl. memorandum, United States Park Service). However, desertified areas were expected to return to grassland once the areas were protected from livestock grazing. In order to determine "the successional trends of plant communities" in the park, permanently marked vegetational transects were established in 1955 and 1957 (The Ecological Survey of the Big Bend Area 1957, unpubl. report, Big Bend National Park).

We expand on that earlier work to investigate the long-term dynamics of the desert grasslands after the removal of domestic livestock following the establishment of Big Bend National Park in 1944. Specifically, we examined (1) temporal dynamics within each plant community, and (2) divergence among plant communities. We hypothesized that native perennial grasses would increase in cover and density given the size of the area and the length of time that the desert grasslands had been protected from grazing. Of course, the establishment and growth of perennial grasses would be dependent on favorable climatic patterns and would occur only if soil conditions following decades of grazing could still support perennial grasses. Because large desert shrubs are long-lived, we expected little change in cover or density of these species over the course of the study.

The permanent transects were located on five soil series which represent distinct combinations of landforms, topographic position, and soil texture that presumably influence water availability in arid and semi-arid locations (Noy-Meir 1973; Olsvig-Whittaker et al. 1983; Wierenga et al. 1987; Wondzell et al. 1987). We hypothesized that these factors would be reflected in vegetation patterns such that each soil series would have supported a distinct plant community before grazing. Extended grazing of domestic livestock has been a severe disturbance to these grasslands and may have blurred distinctions among plant communities supported on the different soil series because of decreased grass cover and subsequent dominance by a few species of desert shrubs. If recovery occurred following the removal of domestic livestock, the desert grassland plant communities should become increasingly heterogeneous (i.e., divergent) through time as each recovered toward its former condition (Inouye & Tilman 1988).

**Study sites**

The central portion of Big Bend National Park is a sunken fault block, or graben, bordered by fault block mountains to the west and east. This basin was partially filled with sediments eroded from adjacent highlands. Subsequently, igneous intrusions during the Cenozoic era formed the Chisos Mountains and the nearby Paint Gap and Grapevine Hills. Rhyolitic sediments from these hills and mountains have since been deposited over earlier basin fills (Maxwell 1968). These sediments have been deposited in several landforms known collectively as piedmont slopes. Ephemeral stream channels dissect the surface of the piedmont slopes, and terraces have been constructed within the channels during past episodes of sedimentation. These channels drain onto nearly level basin floors, where they deposit fine-grained sediments in alluvial flats (Peterson 1981). The 17 study sites, all within the desert grassland zone of the park, encompassed five soil series (Table 1) - Chilicotol, Lajitas, Pantera, Solis, and Tornillo (Cochran & Rives 1985) - that broadly conform to the dominant landforms.

**Table 1.** Selected characteristics of each soil series / landform; ? = not available.

<table>
<thead>
<tr>
<th>Soil series</th>
<th>Landform</th>
<th>Slope (%)</th>
<th>Depth to bedrock (cm)</th>
<th>Depth to calcic horizon (cm)</th>
<th>Texture</th>
<th>Parent material</th>
<th>Number of study sites</th>
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<td>Chilicotol</td>
<td>Piedmont slope</td>
<td>0-6</td>
<td>?</td>
<td>15-50</td>
<td>Gravelly loam</td>
<td>Rhyolitic alluvium</td>
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<tr>
<td>Lajitas</td>
<td>Hill slope</td>
<td>8-47</td>
<td>10-50</td>
<td>?</td>
<td>Very cobbly loam</td>
<td>Fractured rhyolite</td>
<td>4</td>
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<tr>
<td>Pantera</td>
<td>Alluvial terrace</td>
<td>6-8</td>
<td>?</td>
<td>?</td>
<td>Gravelly/sandy loam</td>
<td>Rhyolitic alluvium</td>
<td>2</td>
</tr>
<tr>
<td>Solis</td>
<td>?</td>
<td>3-8</td>
<td>shallow</td>
<td>?</td>
<td>?</td>
<td>Sandstone and Clay</td>
<td>1</td>
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<tr>
<td>Tornillo</td>
<td>Alluvial flat</td>
<td>0</td>
<td>?</td>
<td>?</td>
<td>Clay loam</td>
<td>Rhyolitic alluvium</td>
<td>1</td>
</tr>
</tbody>
</table>
of the Basin and Range physiographic province described by Peterson (1981).

Annual precipitation in the desert grasslands of Big Bend National Park averaged 338 mm (Panther Junction weather station - 1956-1981). The annual pattern of precipitation is seasonal. The wet season receives 80% (268 mm) of the average annual precipitation and lasts from May through October. The dry season receives only 20% (70 mm) of the annual precipitation and lasts from November through April.

Large-scale ranching began in the Big Bend region during the 1850s and expanded rapidly in the 1880s. Livestock numbers within the park area (3190 km²) were estimated to be 10,000 to 15,000 cattle and horses in the late 1800s and 30,000 animals in 1936-1937. Sheep and goats, first introduced around the time of World War I, comprised nearly half of the total number of livestock by 1936, and considerably more than half by 1944 (R.A. Maxwell 1947, unpubl. memo, United States Park Service). Numerous accounts attest to the severe impact of grazing, and in 1944, at the time of its establishment the entire park area was considered 'seriously overgrazed' (W.P. Taylor, W.B. McDouggall & W.B. Davis 1944, unpubl. report, USPS) and 'thoroughly damaged' by livestock (W.B. McDouggall 1944, unpubl. memo, USPS). An estimated 40,000 head of cattle, horses, sheep, and goats were removed from the newly established park in 1944 and 1945 (R.A. Maxwell 1947, unpubl. memo, USPS). Immediately after the removal of livestock, vegetation began to recover (S.T. Carlson, & H.M. Ratcliff 1946, unpubl. memo, USPS) and many 'climax' grasses began reestablishing (H.M. Ratcliff & P.L. Bauch 1947, unpubl. memo, USPS).

Methods

Vegetation sampling

62 permanently marked transects were established in 1955, and an additional 15 in 1957 (Ecological Survey of the Big Bend Area 1957, unpubl. report, Big Bend National Park). Each transect consists of a belt 6.10 m (20 ft) long and 0.31 m (1 ft) wide. Three parallel transects spaced ca. 12 m apart, constitute a single site. Scale drawings of the plant cover on each transect were made, and the transects were photographed. Copies of the original reports, transect drawings, and photographs are archived at Big Bend National Park, Texas. All transects were redrawn and photographed during the winter of 1960-1961. A single transect at each site was redrawn and all transects were photographed in August 1967 (unpubl. vegetation survey 1967, unpubl.). We remeasured 51 transects within the desert grassland zone of Big Bend National Park in September 1981.

Plant cover was drawn to scale on each measurement date. However, documentation of the original sampling methods was confusing. Since we were unable to determine the original methods clearly, we recorded both basal area and canopy cover. Thus, scale drawings made in 1981 show root crowns of grasses, forbs, and ferns (basal area) and the vertical projections of the canopy outlines of shrubs and succulents (canopy cover). Ocular estimates of the canopy covers of all plants, including grasses, forbs, and ferns, were recorded at the same time. Later, comparisons between the historical photographic series and the summarized data from each transect convinced us that the original scientists actually measured canopy cover of grasses, even though it was called basal area. Thus, the analyses reported here used the ocular estimates of canopy cover for 1981 (analyses reported in Wendzell 1984; Ludwig et al. 1986 used basal-area data for 1981).

Canopy cover was estimated from the scale drawings of the plants on each transect. However, ephemerals were not included because we felt that the time between observations would not allow the resolution necessary for interpreting changes in abundance. Densities were estimated from the scale drawings by counting the number of distinct outlines of each species on the transect. These values for density may be misleading because individuals of the same species, with overlapping canopies, may have been counted as a single individual. Further, we drew outlines of the basal areas of grasses and forbs in 1981, and this change in method may have led to increased density estimates for those growth forms. However, because total cover was low, especially at the first three sampling times, density estimates should be reasonable.

Climate analysis

Long-term annual and seasonal mean precipitation for Panther Junction was calculated for the period of record (1956-1981). The only nearby weather station in operation for the years preceding the earliest vegetation sample was located in the Chisos mountains, 500 m above the Panther Junction station where precipitation is greater (Anon. 1949-1981). To predict precipitation for the years 1949-1955 at Panther Junction we fit annual and seasonal precipitation totals for both stations to a simple linear regression. Annual and seasonal departures of precipitation from the long-term mean (1956-1981) were calculated for the 33 years of data. Moving split-window distances were calculated for the resulting 'temporal gradient' of precipitation with the program BOUNDARY (Ludwig & Cornelius 1987) to identify multi-year periods with distinctive precipitation.
patterns. Averages for annual, cool-season, and warm-season precipitation were then calculated for each period.

Data analysis

Species occurring on less than 10% of the transects on each soil series (all sample dates combined) were omitted to minimize effects of rare species. To simplify our analyses, data collected from the nine transects established in 1957 were designated 1955, since we expected little change to have occurred during the drought year of 1956. Data collected during the winter of 1960-1961 were designated 1960. All multivariate analyses were based on cover data because of limitations in the density data.

We believed that individual soil series would support distinctive assemblages of plant species, or plant communities. Because the original study was not stratified by soil series, we tested for overall differences among the vegetation types supported on each soil series in 1981 using a multivariate analysis of variance model with individual transects nested within sites. Our results indicated that distinctive communities were present on each soil series. Thus, we choose to stratify our analysis by soil series. However, the limited number of replicates located on the Panteria, Solis, and Tornillo soil series in the original study, combined with only a partial sample in 1967, has resulted in small sample sizes and unbalanced data which weakens the analysis for these soil series. Despite these problems, our results were consistent across soil series and with the changes visible in the fixed-point photographs. Thus, we include them here.

Community dynamics on each soil series

One-way repeated-measures multivariate analysis of variance (Huitema 1980; Anon. 1985) was used to test for overall time effects. Data for canopy cover on the three transects within a single site were averaged to avoid problems of unbalanced sampling resulting from the partial 1967 sample. Plant communities showing significant time-effects ($P < 0.1$) were analyzed with canonical discriminate analysis (Anon. 1985), and the mean positions of all transects within a soil series on each sample date were plotted to show the overall trajectory of change through time in the discriminant space. Mahalonobis distances (Johnson & Wichern 1982) were used to test for significant separation through time within the discriminant space. Plots of species loadings were compared to plots of the temporal trajectory to identify species with high discrimination between years. The changes in cover and density are shown for a subset of these species. Species shown had high loadings on canonical variates and were selected to represent a suite of growth forms. Because missing values for unread transects may have led to apparent changes for 1967, we calculated mean cover and density twice. Once with only those transects for which data were available in 1967, and again with data for all transects. Trends in both cover and density were similar (exceptions noted in results) so we presented means calculated from all transects sampled.

We also tracked the demographics for all shrub species over the study period using the transect drawings in conjunction with the photographs. Apparent changes in density could result from change in canopy size due to the way density was estimated. Thus, recruitment was categorized as either reproduction or canopy in-growth; loss was categorized as either death or canopy

Fig. 1. Departures from mean precipitation for cool and warm seasons at Panther Junction, Big Bend National Park. Values for 1949-1955 are predicted; values for 1956-1981 are measured. Asterisks indicate dates of transect surveys. Vertical broken lines delineate multi-year climatic periods.
die-back. The relative effect of change in canopy size versus reproduction and mortality for each species of shrub present was calculated.

**Divergence among plant communities**

Canonical discriminant analysis (Johnson & Wichern 1982) was used to test for the similarity of plant communities on different soils through time. Plots of species loadings were compared to plots showing the location of transects within the discriminant space to identify species with high discrimination between soil series. We present separate plots for each sample date even though the results are from a single analysis, and the discriminant space shown in each plot is identical. Mahalanobis distances (Johnson & Wichern 1982) were used to test for significant separation within the discriminant space. We performed the analysis twice, once with only those transects for which data were available in 1967, and again with data for all transects because missing values for unread transects in 1967 may have distorted the discriminant space. Both analyses showed similar trends and only the results of the latter are reported.

**Results**

**Climate**

Total annual precipitation, and both warm- and cool-season precipitation at Panther Junction and at Chisos Basin were highly correlated ($r^2 = 0.96, 0.95,$ and $0.95$, respectively). Moving split-window analyses of predicted (1949 - 1955) and actual (1955 - 1981) precipitation for Panther Junction separated groups of years with similar precipitation: 1951 - 1957, 1958 - 1965, and 1966 - 1981 (Fig. 1). Warm and cool season precipitation was below average from 1951 through

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<tr>
<td>Chilicotal - Lajitas</td>
<td>1.86</td>
<td>2.13</td>
<td>3.55</td>
<td>7.05***</td>
</tr>
<tr>
<td>Chilicotal - Pantera</td>
<td>1.76***</td>
<td>3.82***</td>
<td>3.20***</td>
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<td>Chilicotal - Solis</td>
<td>1.92</td>
<td>2.28</td>
<td>3.12</td>
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<td>2.70</td>
<td>7.00</td>
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<tr>
<td>Lajitas - Pantera</td>
<td>2.80**</td>
<td>4.77***</td>
<td>4.70</td>
<td>13.02***</td>
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<tr>
<td>Lajitas - Solis</td>
<td>2.94</td>
<td>3.15</td>
<td>4.22</td>
<td>9.32***</td>
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<tr>
<td>Lajitas - Tornillo</td>
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<td>3.62</td>
<td>7.98</td>
<td>13.39***</td>
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<td>4.44</td>
<td>1.93</td>
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<tr>
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<td>2.69</td>
<td>4.73</td>
<td>7.06</td>
<td>15.98***</td>
</tr>
<tr>
<td>Solis - Tornillo</td>
<td>1.86</td>
<td>1.23</td>
<td>7.07</td>
<td>11.48***</td>
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</table>

(* = significant at $P < 0.1$; ** = $P < 0.01$; *** = $P < 0.001$.)

**Fig. 2.** Temporal changes in plant communities on the four sampling dates, by soil series. Large symbols indicate the mean position of transects sampled on a given date. Small symbols indicate the position of individual transects on a given date. Lines represent the overall trajectory of change through time.
1957, and total annual precipitation averaged 60% of the long-term mean. There were several consecutive years of summer drought between 1958 and 1965 and warm-season precipitation averaged 85% of the long-term mean. However, cool-seasons tended to be wetter, averaging 110% of the long-term mean over this period. Rainfall was highly variable after 1965, but in general, wetter conditions prevailed during this period, especially during summers, when precipitation was above average in 10 out of 16 years and in six summers, precipitation exceeded 400 mm. Half of the cool-seasons were wetter than average. For this period as a whole, warm seasons received 112% and cool seasons 107% of their respective long-term mean precipitation.

**Community dynamics**

The plant communities supported on each soil series in 1981 were significantly different from each other, with only two exceptions (Table 2), suggesting that each soil series supported a different plant community. Therefore, data were stratified by soil series for all subsequent analyses.

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**Table 3.** Percent cover of plant species present on three transects in 1955 and 1981. Transect 021 is on the Chilicotal soil series, transect 031 is on the Lajitas soil series, transect 024 is on the Solis soil series. Photographs of these transects are shown in Fig. 3.

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<td>Aristida spp.</td>
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<td>14.75</td>
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<td>Erioneuron pulchellum</td>
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<td>B. brevisea</td>
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<td>12.45</td>
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<td>B. hispida</td>
<td>0.00</td>
<td>0.65</td>
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<td></td>
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<td>0.25</td>
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<td>Leptoloma congestum</td>
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<td>Croton spp.</td>
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<td></td>
<td>Psilotrophe tajamontana</td>
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<tr>
<td>Total</td>
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<td>Total</td>
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<td>0.40</td>
<td></td>
<td>Croton spp.</td>
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<td>Shrub</td>
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<td>Parthenium incanum</td>
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<td>3.30</td>
<td></td>
<td>Opuntia phaeocantha</td>
<td>0.25</td>
<td>0.00</td>
<td></td>
</tr>
<tr>
<td>C. greggii</td>
<td>0.00</td>
<td>3.75</td>
<td></td>
<td>Total</td>
<td>0.02</td>
<td>3.40</td>
<td></td>
<td>Total</td>
<td>0.60</td>
<td>5.20</td>
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</tr>
<tr>
<td>Larrea tridentata</td>
<td>12.69</td>
<td>18.75</td>
<td></td>
<td>Forreroxus saxatinus</td>
<td>2.02</td>
<td>18.80</td>
<td></td>
<td>Forreroxus saxatinus</td>
<td>0.25</td>
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<tr>
<td>Total</td>
<td>2.86</td>
<td>9.25</td>
<td></td>
<td>Total</td>
<td>2.47</td>
<td>18.80</td>
<td></td>
<td>Total</td>
<td>0.25</td>
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</table>

**Chilicotal soil series.** The plant community on the Chilicotal soil changed little between 1955 and 1960 (Fig. 2). By 1967 the plant community had changed somewhat from that in 1955, and by 1981 was significantly separated ($P < 0.001$) from the 1955 vegetation. In general, the canopies of shrubs increased in size while sub-shrubs and perennial grasses established and began to fill inter-shrub spaces (Fig. 3, Table 3). Mean cover values of all species showed relatively little change between 1955 and 1960, although a few species of grasses increased in density (Fig. 4). Between 1960 and 1967, the cover of shrubs increased, mostly due to a large increase in the cover of the common desert shrub, *Larrea tridentata*. *Bouteloua eriopoda* increased in cover during this period, possibly as a result of recruitment during the previous period. After 1967, there were large increases in cover and density of most grasses and sub-shrubs, and the density of most forbs. The cover of *Larrea tridentata* decreased after 1967, in clear contrast to other shrubs.

The density of all large shrubs combined doubled over the study period; ca. 50% of this increase resulted from in-growth of shrub canopies. Even though the cover of *Gymnosperma glutinosum* was low on every
Fig. 3. Typical transects on the Chilicotal, Lajitas, and Solis soil series in 1955 and 1981. Actual measurements for these transects are in Table 2. Upper: Transect 21, Chilicotal; Middle: Transect 31, Lajitas; Lower: Transect 24, Solis.
CHILICOTAL SOIL SERIES

Fig. 4. Average cover (solid line) and density (broken line) of selected plant species averaged over all transects on the Chilicotal soil series at each measurement date. G = grasses, F = forbs, SS = sub-shrubs, Sh = shrubs, Su = succulents. Data points indicate dates of transect surveys: 1955, 1960, 1967, 1981.

Sample date, this species accounted for over 60% of the total reproductive recruitment of all shrubs here. The change in density of Gymnosperma glutinosum resulted from reproduction and mortality. In contrast most of the change in density of Larrea tridentata resulted from canopy in-growth or die-back, with little reproduction or mortality. Reproduction and mortality were equally as important as change in canopy size in changes in the measured densities of Acacia spp., Zexmenia brevifolia, and Flourensia cernua.

Lajitas soil series. The plant community on the Lajitas soil series changed little before 1960 (Fig. 2). By 1981 it was significantly separated (P < 0.001) from the 1955 vegetation. Perennial grasses were common on the Lajitas series in 1955 in comparison to the other soil series and increased in both cover and density by 1981 (Fig. 3, Table 3). Bouteloua breviseta accounted for 60% of the total grass cover in on the Lajitas soil 1981. The cover and density of large shrubs increased during the period of wet summers between 1967 and 1981 (Fig. 5).

LAJITAS SOIL SERIES

Fig. 5. Average cover (solid line) and density (broken line) of selected plant species on the Lajitas soil series (see Fig. 4).
Shrub density increased nearly three-fold over the study period, and only 20% of this increase resulted from in-growth of shrub canopies. *Gymnosperma glutinosum*, *Zea mays* breviliria and *Viguiera stenoloba* accounted for 71%, 19% and 14%, respectively, of the total reproductive recruitment of all shrubs combined. Nearly all of the change in density of these species resulted from reproduction and mortality.

Panthera soil series. The plant community on the Panthera soil series changed between 1955 and 1960 on the second canonical variate (Fig. 2), probably due to a five-fold increase in the cover of *Eriococcum pulchellum* by 1960. Little change occurred between 1960 and 1967. The cover of *Larrea tridentata* peaked in 1967 (Fig. 6), however the decrease in cover between 1967 and 1981 was an artifact of the reduced sample in 1967, because means calculated for only those transects measured in 1967 show a sharp increase by 1967 but no change in cover between 1967 and 1981. Large increases in the cover of perennial grasses, especially *Bouteloua eriopoda*, after 1967 led to significant separation (P < 0.01) of the 1981 vegetation from that of 1955. *Eriococcum pulchellum* decreased in density during the study period from 23.1 to 2.2 individuals/m²; during the same period, density of all other perennial grasses increased from 7.0 to 47.4 individuals/m².

The total density of large shrubs increased four-fold over the study period; only 14% of this increase resulted from in-growth of shrub canopies. The change in density of both *Gymnosperma glutinosum* and *Viguiera stenoloba* were dominated by reproduction and mortality, and accounted for 72% and 17%, respectively, of the total reproductive recruitment of all shrubs combined.

Solis soil series. The plant community supported on the Solis soil did not show a significant time effect. Only a single site was located on this soil series, and little change is visible in the photographic record (Fig. 3, Table 3). Perennial grasses were uncommon, and the cover of the evergreen shrub *Larrea tridentata* and several species of short-lived perennial forbs was low, and changed little during the study period. Some regrowth of shrub canopies is apparent in the background of the transect photographs.

Tornillo soil series. The multivariate analysis of variance of the plant community on this soil series indicated that time effects were significant and large changes were evident in the photographic record. However, the canonical discriminant analysis did not identify significant separation between 1955 and the vegetation at later sampling dates. We include the results because the vegetation dynamics on this soil series were unique, driven by changes in the cover of shrubs and cacti rather than cover of grasses. By 1967, a strong divergent trend was apparent along the first and second canonical variate (Fig. 2), a trend that continued through 1981.

The total cover of shrubs changed little between 1955 and 1960, increased from 1960 to 1967, and declined slightly thereafter (Fig. 7). The peak covers of *Echinocereus* spp. and *Opuntia leptocaulis* in 1967 appear to be an artifact of the reduced sample size in that year, because the data for the single transect measured in 1967 showed a broad peak with maximum cover in 1960 and a sharp decline between 1967 and 1981. Between 1960 and 1967, the cover of shrubs increased; this was mostly due to a large increase in the cover of the common desert shrubs, *Larrea tridentata* and *Flourensia cernua*. Between 1967 and 1981 the cover of *Larrea tridentata* decreased, as it did on the Chilicotal soil series. However, the decrease in cover of *Flourensia cernua* between 1967 and 1981 appears to be an artifact of the reduced sample size in 1967. The total density of
large shrubs nearly doubled over the study period, but all of this increase resulted from in-growth of shrub canopies, mainly *Larrea tridentata*. Both the cover and density of *Parthenium incanum*, the dominant sub-shrub in this community, increased between 1967 and 1981.

*Divergence among plant communities*. There were few significant differences among plant communities in 1955, 1960, and 1967 (Fig. 8, Table 2). By 1981, only the plant communities on the Chilicotal and Solis soil series and the Chilicotal and Tornillo soil series were not significantly separated. Although the plant community on the Tornillo soil series appears similar to that of the Lajitas soil series (Fig. 8), they were significantly separated on canonical variate III (not shown).

The comparison between species loadings (Fig. 9)
and the locations of transects plotted in discriminant space (Fig. 8) showed that the divergence of the Lajitas soil series on variate I resulted from high cover of *Bouteloua breviflora* and *Agave lecheguilla*; divergence of the Pantera soil series on variate II resulted from high cover of *Bouteloua eriopoda*, *Digitaria californica*, and *Leptoloma cognatum*. The Tornillo soil series diverged on variate III because of the high cover of *Flourensia cernua*, *Parthenium incanum*, and *Bahia absinthifolia* (not shown). In 1981, Chilicotal soils had the least clearly defined plant community of any soil series. High covers of *Larrea tridentata*, *Zexmenia brevifolia*, and *Eriophyton pulchellum* tended to position transects on this soil series statistically near the origin. Transects with low cover were similar to transects on the Solis soil series. Transects with relatively high covers of *Agave lecheguilla* and *Bouteloua breviflora* were similar to transects on the Lajitas soil series. Transects with relatively high cover of *Flourensia cernua* were similar to those on the Tornillo soil series, and those with relatively high cover of *Bouteloua eriopoda* became more similar to transects on the Pantera soil series.

**Discussion**

*Community dynamics on each soil series*

The directional trajectories of change shown in discriminant space (Fig. 2) for the desert grassland plant communities of Big Bend National Park and the increase in relative cover of perennial grasses in these plant communities are relatively uncommon. Many similar studies in southern Arizona (Griffiths 1901, 1910; Brown 1950; Glendening 1952; Parker & Martin 1952; Humphrey 1953; Glendening & Paulsen 1955) and in southern New Mexico (Gardner 1951; Wright 1982; Hennessy et al. 1983) have found no evidence for directional recovery of former desert grasslands after protection from grazing. Several studies (Griffiths 1910; Brown 1950; Glendening 1952; Wright 1982; Hennessy et al. 1983) even document continued replacement of perennial grasses by shrubs after the exclusion of domestic livestock. Historic records indicate that the park area was severely overgrazed prior to its establishment. We conclude that the directional trajectory of change, especially the regrowth of grasses into inter-shrub spaces, must, at least in part, be the result of recovery from grazing.
We believe that the differences between our results and the results of other studies conducted in Arizona and New Mexico may be explained by regional climatic differences. There are strong gradients in the length of the summer rainy season, and the proportion of cool- vs. warm-season precipitation across the desert grassland region (Neilson 1987). Big Bend National Park lies at the eastern edge of the region, where the rainy season is longest, and receives at least 80% of the total annual precipitation during the warm season. In contrast, regions further west have shorter summer rainy seasons and receive proportionately more cool-season precipitation. The long summer rainy season in Big Bend may have favored the maintenance of perennial grass species over decades of heavy grazing and facilitated their recovery following the establishment of the park.

Unfortunately, we cannot isolate the effects of grazing from the effects of climate because the study design did not include control plots located within grazed pastures. Our data indicate that climatic patterns, including a severe drought immediately prior to the establishment of this study, and a period of above-average precipitation influenced the vegetation communities. The intervals between sample dates loosely matched multi-year periods of distinctive precipitation patterns (1951-1957, 1958-1965, and 1966-1981). Trajectories of changes in plant communities between sample dates were not linear (Fig. 2), indicating that different species responded during each time interval. Specifically, there was little change when rainfall was below-average during both summer and winter. The cover of the common Chihuahuan desert shrubs had increased by 1967, after the period of above-average cool-season precipitation between 1958 and 1965. The cover of perennial grasses, subshrubs, and most other shrubs increased during a wetter-than-average period between 1967 and 1981. In clear contrast to these species, the cover of the common desert shrub, Larrea tridentata declined between 1967 and 1981.

Several authors have suggested that the response of shrubs and grasses to cool-versus warm-season precipitation may explain the differences in these growth forms. Specifically, Walker et al. (1981) hypothesized that reductions in the ratio of shallow to deep soil moisture would favor tap-rooted plants such as shrubs over grasses with fibrous root systems. An alternative hypothesis proposed by Neilson (1986) is that shrub species, such as Larrea tridentata, that have a C3 photosynthetic pathway are favored by cool-season precipitation, while perennial grass species having a C4 photosynthetic pathway are favored by warm-season precipitation. Our data fail to support either of these hypotheses, even though the study period included distinct periods of cool-season and warm-season precipitation. First, little shrub establishment was observed, and most of the establishment that did occur was by a single species, Gymnopuspera glutinosum, during the period dominated by warm-season precipitation. Secondly, changes in the cover of this species, and several other common shrubs paralleled the changes observed in the native warm-season perennial grasses. Most of the increase in shrub cover during periods of cool-season precipitation was accounted for by Larrea tridentata, and to a lesser extent, F. cerua, and Larrea tridentata was the only shrub that decreased in cover during periods dominated by warm season precipitation. Clearly, simple models based on growth form or photosynthetic pathway, alone, cannot account for the observed changes in the cover and density of grasses and shrubs.

The failure of the long-lived desert shrub, Larrea tridentata to establish during the course of this study could be indicative of competitive exclusion (Glendening & Paulsen 1955; Williams & Hobbs 1989; Harrington 1991). Certainly, many authors have hypothesized that shrub seedlings are excluded from established stands of grasses because of competition. However, the cover of perennial grasses on most of our study sites was low. Little is known about the grass density necessary to exclude shrubs, the effect of grasses on already established shrubs, or the influence of existing shrubs on the establishment of either grasses or other shrubs. Additionally, we do not know if climatic conditions have precluded shrub establishment. Certainly, many shrub species are long-lived, and climatic conditions that drive episodic establishment may not have occurred in the last 26 years. These results highlight the need to identify both the abiotic and biotic factors that regulate the response of both desert and desert-grassland species to climatic patterns.

**Divergence among plant communities**

We believe that grazing and drought reduced plant cover and led to dominance of a few species of shrubs in the vegetation communities present in 1955. Our data show that plant communities on individual soil series diverged through time after removal of domestic livestock. Resource-based models of community structure (Tilman 1982, 1988; Inouye & Tilman 1988) predict that areas differing in the rate or availability of resources should support different plant communities at equilibrium. Spatial vegetation patterns are often strongly correlated with environmental gradients (e.g. Stein & Ludwig 1979; Olsvig-Whittaker et al. 1983; Wierenga et al. 1987; Wondzell et al. 1987; Burke et al. 1989; Wondzell et al. 1990). We suggest that water availability so strongly controls production and composition in
these ecosystems that differences in soil texture and topographic position among landforms account for the vegetation patterns even though equilibrium may never occur.

For example, the surface of the Lajitas soil series is very rocky, and localized runoff from rock surfaces should increase the moisture available for plant growth (Olwig-Whittaker et al. 1983), even from relatively small storms, which might favor grass dominance. In contrast, the small, isolated alluvial plain of the Tornillo soil series was undisturbed by arroyo channels, and water pooled on the surface following heavy rains (pers. observ.). We suggest that moisture from small storms would evaporate from these fine textured soils, reducing moisture availability throughout most of the year. However, large storms would flood the alluvial plain and recharge deep soil moisture, which should favor shrub dominance (Walker et al. 1981; Archer 1989). The gravelly loam sediments of the Pantera soil series should have rapid infiltration rates and small evaporative losses (Noy-Meir 1973). Thus, more water may be available for plant growth throughout the growing season, favoring perennial grasses.

Clearly, not all landforms support plant communities that diverge through time. For example, the vegetation on the stony pavements of the Solis soil series changed little after 1955. It seems unlikely that the study areas on Solis soils had an unusual grazing history since nearby transects on the Chilicotal soils did change following 1955. Nor do these sites show evidence of recently accelerated erosion, as do some locations on the Tornillo soils. Thus, it seems reasonable to conclude that these poorly developed soils originally supported a naturally occurring shrubland.

Our results suggest that landform, topography, and soil affect both species composition and community dynamics. However, the relationships between these factors and soil moisture availability may not be consistent between wet and dry years or between large and small storm events. The ways in which species of the desert grasslands respond to these differences remain highly speculative. Yet the differences have clear implications for the composition and persistence of plant communities through time and warrant further study.

Acknowledgements. We thank the scientists who initiated the Ecological Survey of the Big Bend Area in 1955, especially B.H. Warnock, and Big Bend National Park for permission to remeasure permanent plots and the use of their facilities. We thank E.F. Aldon of the United States Forest Service; M.R. Fletcher of the United States Park Service; and Park Naturalist, M. Flemming; and J. Meents and M. Serena for help with the field work. D. Bachelet, J.M. Cornelius, G.L. Cunningham, R.L. DeVelice, W.A. Dick-Peddie, E. Muldavin, and R.P. Neillson, contributed helpful discussions. W. Boekland suggested appropriate statistical analyses. J.A. Lattin, D. Goldberg, and four reviewers suggested changes which greatly improved this manuscript. This work was supported by Cooperative Research Grant #RM-81-189-CR from the U.S. Man and the Biosphere Program. Additional support was provided by the United States Department of Agriculture Forest Service Rocky Mountain Forest and Range Experiment Station, the United States Department of the Interior National Park Service.

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Received 4 October 1994; Revision received 22 February 1995; Accepted 1 March 1995.