# Environmental factors and community dynamics at the southernmost part of the North American Graminetum

*I. On the contribution of climatic factors to temporal variation in species composition*

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## Abstract

Compositional patterns of vegetation and their relationship to temporal and spatial environmental variation, with emphasis on climatic factors, were investigated in plant communities located in the southernmost portion of the North American *Graminetum*, in central México. Data from 353 samples, obtained in four ecologically contrasting plant communities during 11 years, were analyzed by partial canonical correspondence analysis. Eight climatic variables and eighteen covariables (seventeen edaphic and one resource management) were included in the ordination. A relationship between floristic change and weather variation, once covariables effects were fitted, was examined. Despite a strong contrast in ecological conditions among study sites, a set of four climatic variables was finally found in which each variable contributed independently and statistically ($P < 0.01$) to the total variance in the vegetation data. Thus, environmental variables other than climatic could not conceal the important role of weather as a mediator of floristic change through time. Summer precipitation and summer maximum temperature showed the highest correlations with the first two species axes, 0.77 and –0.39, respectively. Contribution of these two climatic variables to variance in the vegetation data explained by environmental variables was approximately 81%. Annual species were abundant during rainy years, while abundance of perennial grasses and shrubs showed no clear relationship to weather variation. This study explicitly probes the important role of rain patterns in shaping structure and composition of semiarid communities and considers how other environmental factors can affect plant communities at the southernmost part of the North American *Graminetum*.

## Introduction

The North American *Graminetum* extends from southern Canada to central México. It is comprised of the tallgrass, mixed and shortgrass prairies (Coupland 1979). These grasslands are present in Canada and the United States. The semiarid grassland of México may be regarded as a southern extension of the short-grass prairie, which extends from Alberta and Saskatchewan to Arizona, New Mexico and Texas (Shelford 1963). Many physiognomic and ecological similarities exist between the shortgrass prairie and the Mexican semiarid grassland, including dominance by species of *Bouteloua*. México is considered a probable center of diversification for this genus (Rzedowski 1975).

Grassland comprises 17% of the Mexican territory (Beetle 1987), and its existence seems to date from the middle or even from the early Tertiary (Rzedowski 1975). The bulk of this vegetation (more than 80%) is located in the Mexican Altiplano in the form of semiarid grassland, which extends like a continuous belt along the mountainous system known as the Sierra Madre Occidental from northeastern Sonora to Los Llanos de Ojuelos physiographic subprovince in northeastern Jalisco. It develops mainly on igneous soils of shallow to medium depth. The climate is temperate and dry, with an annual median temperature ranging from 12 to 20 °C and 300–600 mm of annual precipitation, with most of the precipitation occurring in the summer (June-September; Rzedowski 1981).

The Los Llanos de Ojuelos region, in northeastern Jalisco, México, represents the southernmost portion of the North American *Graminetum*. Open grassland and shrubland represent grazing lands at this region. The *Bouteloua gracilis* grassland is considered to be the climax community (García-Moya & Villa 1977; Aguado-Santacruz 1987). *B. gracilis* occupies most of this region, although *Bouteloua scorpioides* seems to dominate in previously plowed grasslands. Extensive shrublands dominated by *Acacia schaffneri* are found in overgrazed areas with deeper soils.

The introduction of livestock into México occurred in 1521, marking the beginning of this industry, which reached maximum development between 1562 and 1680 (Brand 1961). As in many other countries, the initial lack of conservative grazing practices led to serious degradation of the land resource (González 1965). A study carried out at Los Llanos de Ojuelos indicated that 84.6% of the ranges sampled were overgrazed; of these, 63.6% were strongly eroded, 9.0% moderately eroded, and 27.3% slightly eroded (DGDUT 1982). The plowing of vast areas leaving them exposed to wind erosion (Gentry 1957; Hernández X. 1970; García-Moya & Villa 1977; Hernández X. 1979) has intensified deterioration of Mexican rangelands. Tovar-Soto (1986) found that eolic erosion redistributed up to 150 t ha$^{-1}$ of soil over a three-month period in plowed lands of this region.

Natural environmental agents also play a significant role in shaping plant community structure and composition in the Los Llanos de Ojuelos physiographic subprovince. An aridity gradient running in a north-south direction, with rain decreasing and temperature increasing northward toward the *Larrea tridentata* desert shrubland, is especially important.

Although anthropogenic and non-anthropogenic environmental factors are known to be important in the Mexican semiarid grassland, little has been done to analyze or partition the effects attributable to each. An attempt is made in this paper to analyze the net correlation of temporal floristic variation to weather patterns, by fitting the effects of some other relevant environmental factors as covariables.

**Materials and methods**

*Study area*

The study area is located in the Los Llanos de Ojuelos physiographic subprovince, which is located within the Mexican Altiplano (Figure 1). Its climate is typical for the region; annual mean temperature fluctuates between 12 and 18 °C, while annual precipitation ranges from 400 to 500 mm (CETENAL 1970). Exclosures (one hectare in size) were established at four different sites to study vegetation dynamics under livestock and livestock plus minor fauna exclosure conditions. Records for adjacent grazed pastures at every site are also available. Sites characteristics according to CETENAL (1973), Aguado-Santacruz (1987) and Aguado-Santacruz et al. (1989a; 1989b) are summarized in Table 1. The La Colorada site, located in a foothill (Figure 2), shows soil and vegetation characteristics that differ from the rest of the study sites. Although grazing regimes at the sites have been highly variable, grazing is known to have been severe at the La Presa site (Table 1). The contrast between exclosed and grazed vegetation at this site is remarkable. Original vegetation was a *Bouteloua gracilis*-dominated grassland, but overgrazing has induced a large increase in the cover of the half-shrub *Haplopappus venetus*, to the point that this species dominates in grazed pasture. Forage production has been severely affected. During 1988 (annual precipitation 444.1 mm), the standing crop within the exclosure was 1303 kg DM ha$^{-1}$, while outside the standing crop amounted to 252 kg DM ha$^{-1}$. Aboveground net primary production of *Bouteloua gracilis* was 267.8 kg DM ha$^{-1}$ (4.0 g DM per plant) inside the exclosure, but only 29.2 kg DM ha$^{-1}$ (1.08 g DM per plant) outside the exclosure (unpublished results). Past land use at the La Colorada and Vaquerías sites has included possible plowing from 1925 to 1940.
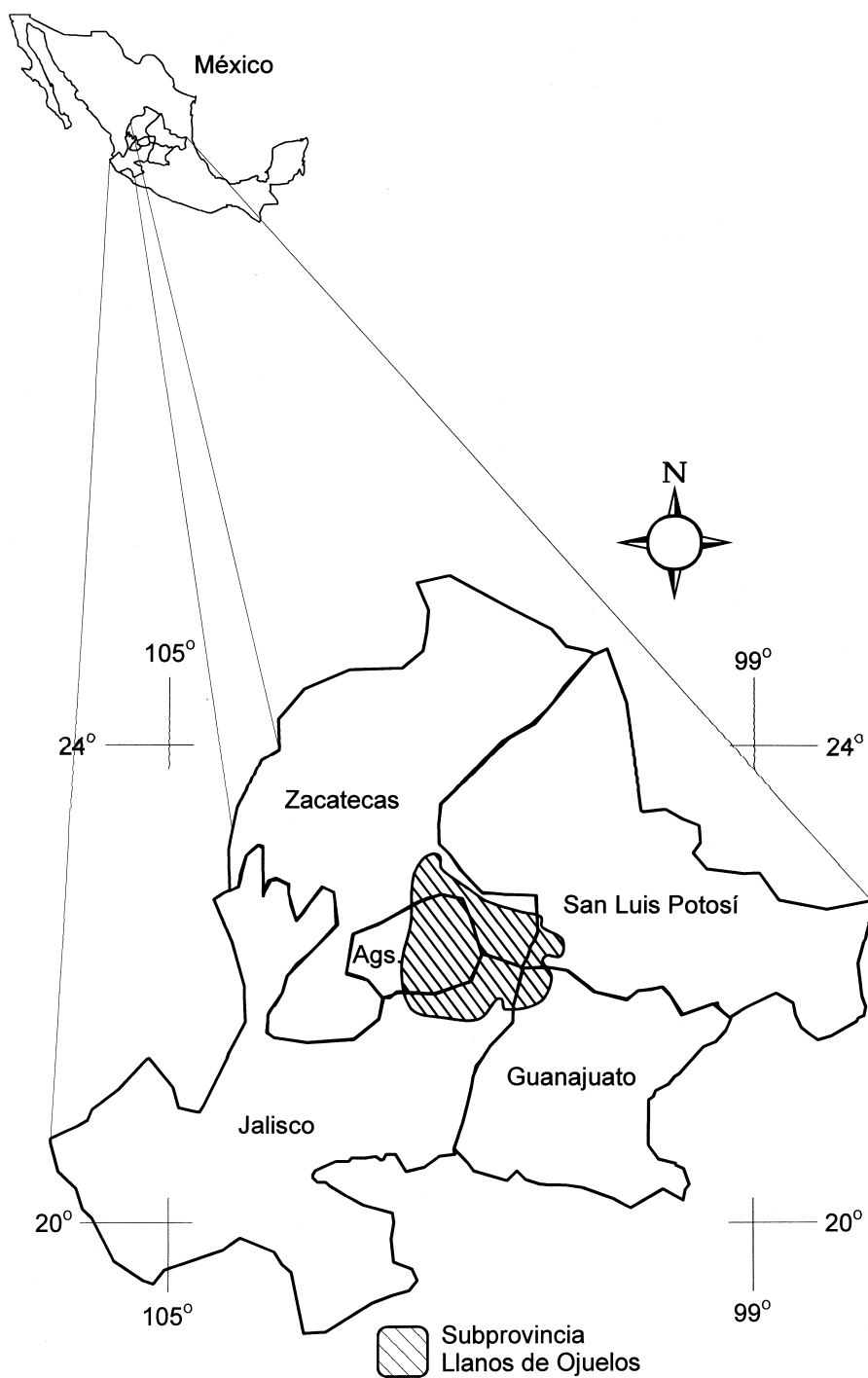
*Figure 1.* Study area location within the Los Llanos de Ojuelos physiographic subprovince, in the Mexican Altiplano.
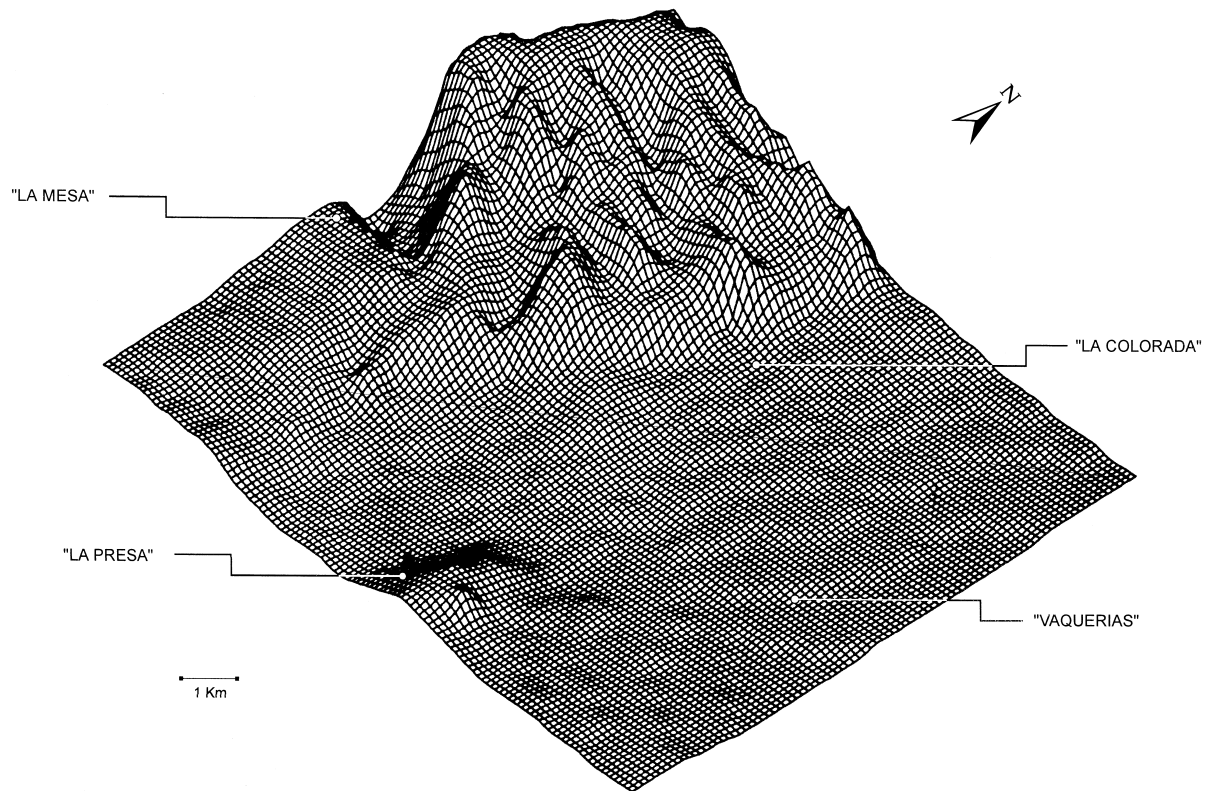
*Figure 2*. Topography and relative position of the study sites.

*Plant records*

Floristic composition and plant cover were determined annually on twenty-meter-long permanent lines using the line intercept method (Canfield 1941). This method is based on the measurements of all plants intercepted by the vertical plane of a transect line placed at or near ground level. Measurements of grasses, grass-like plants and forbs were taken on the line at the ground surface (basal diameter). Shrubs and half-shrubs were measured by crown intercept. Both exclosed and grazed pastures at the different sites were sampled during September-November, at the end of the rainy (growing) season. Number of available records (number of transects and years of sampling) varied for both exclosed and grazed pastures (Table 1).

*Climatic records*

Information was obtained from a weather station established in 1979 and located 1 km southwest from Vaquerías site. Annual and aestival average temper-ature (mean, maximum and minimum), precipitation and evaporation were used in the analysis.

*Edaphic records*

Soil sampling was carried out at all sites during June 1992. A profile description was made outside exclosed areas to determine the type and number of soil composite samples and subsamples to be taken within exclosures. Accordingly, 5 subsamples/treatment for each identified horizon were taken with a 'California' type auger at the Vaquerías and La Mesa sites, and 3 and 10 subsamples/ treatment were taken at the La Presa and La Colorada sites, respectively. Samples from grazed pastures were obtained directly from soil profiles. Soil properties were determined for each horizon-treatment combination at each site using standard methods. These included pH, electrical conductivity, organic matter, total nitrogen (calculated from organic matter), extractable phosphorus, exchangeable potassium and textural analyses.

*Table 1.* Characteristics of the study sites

| | Sites | | | |
| --- | --- | --- | --- | --- |
| | Vaquerías | La Mesa | La Colorada | La Presa |
| Vegetation | *Bouteloua scorpiodes* grassland | *Bouteloua gracilis* grassland | *Acacia schaffneri* shrubland | *Bouteloua gracilis* grassland |
| Elevation (m) | 2200 | 2380 | 2270 | 2280 |
| Soil type[1] | Haplic xerosol | Haplic phaeozem | Eutric fluvisol | Haplic xerosol |
| Exclosure establishment | 1979 | 1980 | 1979 | 1980 |
| Historical grazing regime | Heavy | Moderate (at least since 1925) | Heavy | Heavy |
| Current level of grazing | Moderate | Moderate | Heavy | Heavy |
| No. permanent lines inside exclosure | 12 | 8 | 6 | 6 |
| No. permanent lines outside exclosure | 12 | 20 | 20 | 12 |
| Years sampled for excluded (ex.) and grazed areas (gr.) | ex.= 11 gr.= 4 | ex.= 8 gr.= 1 | ex.= 8[2] gr.= 1 | ex.= 2 gr.= 1 |

[1] According to FAO/UNESCO classification
[2] Only seven years for 3 of the lines

*Data analysis*

Tridimensional floristic data matrices ($q \times t \times s$) were transformed to bidimensional ($qt \times s$; Williams et al. 1969). Climatic, edaphic and floristic information were subjected to a partial canonical correspondence analysis (Ter Braak 1988a), an option available in the CANOCO program (Ter Braak 1988b, 1990), in order to establish the relationship of community change to weather variation, eliminating partially the effects of edaphic and management factors. Accordingly, weather variables were considered as explanatory environmental variables, whereas first two horizon (A and B) soil properties, soil depth and pasture management were entered as covariables. Global (353 line transects) and individual (site) analyses were performed. In the individual analyses, previous grouping by TWIN-SPAN (Hill 1979) was used to reduce variation among sampling units (permanent lines). After this process, the Vaquerías, La Mesa and La Colorada analyses were based on 155, 64, and 65 sampling units, respectively. For the La Presa site, where just two records in time were available, no individual ordination was performed. Values of <0.01 in species cover were eliminated to reduce variation in the data, and cover data was relativized to 100%. Each climatic variable added to the model was statistically tested by a Monte Carlo permutation test. An overall test and a test for the first canonical axis were also made. Multivariate analysis of variance under a split plot design (Stroup & Stubbendieck 1983) was performed for each study site using the SAS statistical package in order to obtain a partial verification of the ordination results. Because rare species increased variance in data greatly, only species with at least two years of occurrence were considered. The working hypothesis for each site was: 'Community composition varies among years, with at least one year different from the others'.

**Results**

*Weather conditions during study*

Weather conditions during the study were highly variable among years (Figure 3). On an averaged monthly basis, however, weather fluctuation closely matched the study area climate description available from CETENAL (1970). Precipitation was concentrated in the summer (June–September), showing an
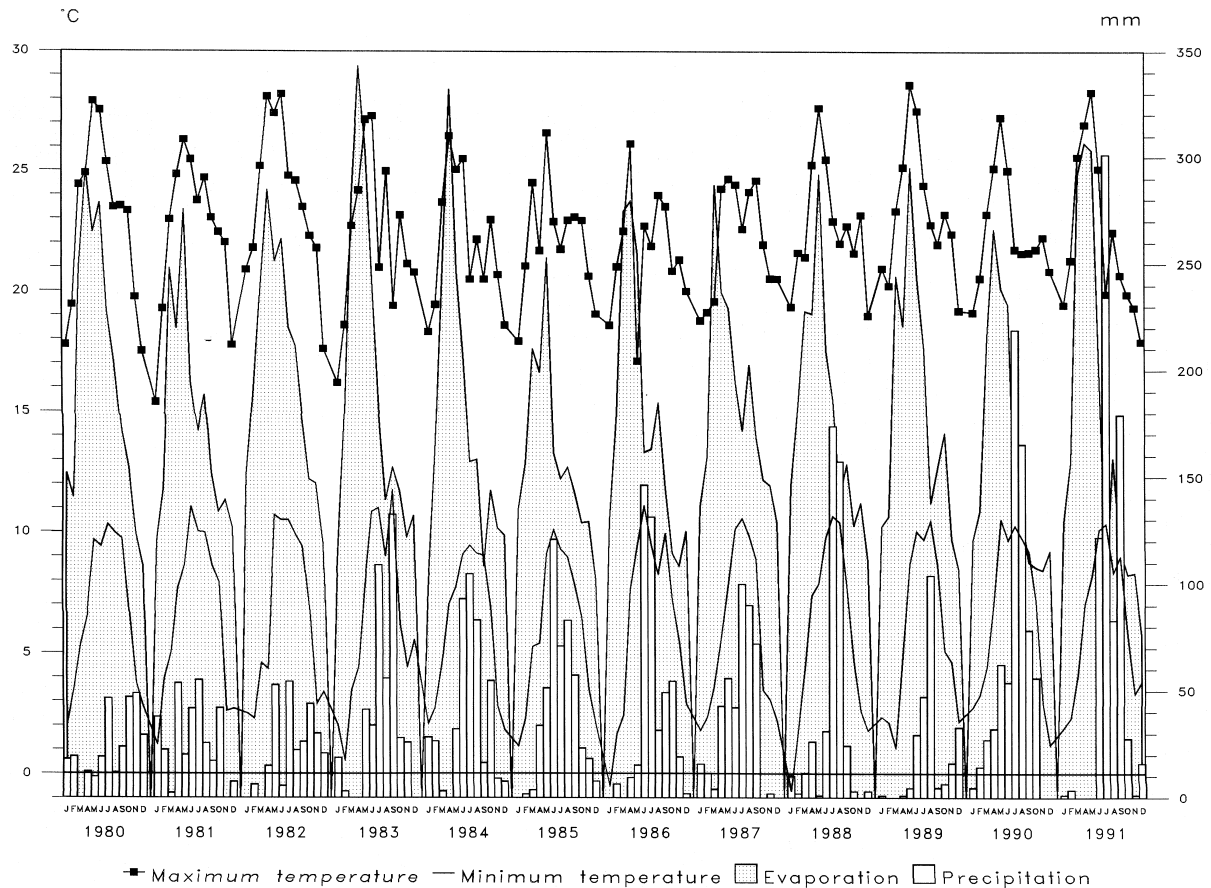
*Figure 3.* Monthly weather patterns during the course of the study (1980–1991).

annual mean of 450.9 mm, the highest evaporation occurred during the March-May period, annual mean temperature was 14.4 °C, January and February were the coldest months (minimum temperatures 1.7 and 2.4 °C, respectively), and May was the hottest month (maximum temperature 26.9 °C).

The rainiest years in terms of annual and aestival averages were 1990 and 1991 with 264 mm (58.5%) and 285 mm (63.2%) above the aestival mean, respectively (Figure 4). The driest years were 1982 (aestival averages) and 1989 (annual averages) with 212.2 mm (66.1%) and 202.8 mm (45.0%) below the aestival mean, respectively. Highest evaporations occurred during 1980 and 1982 with 214 and 247 mm above the mean. The hottest year was 1982, while 1985 (aestival averages) and 1988 (annual averages) were the coldest years.

*Changes in plant cover in exclosed areas*

Fluctuation in total plant cover showed a similar trend at three sites (Figure 5a). This similarity in cover fluctuation was more marked for the open grasslands of the Vaquerías and La Mesa sites. At the La Presa site, where just two records in time were available, the change in cover from 17.8% in 1987 to 27.2% in 1991 was similar to the change observed over the same period at the other sites.

A better understanding in plant cover fluctuations can be reached by differentiating the trends for different functional groups (shrubs, herbs including an unidentified moss, and grasses), and relating these trends to weather during the period when conditions are more favorable for plant growth. In the study area, this period corresponds to the summer season, when most of the rain occurs (Figure 4). Plant growth is mainly observed during this season, although some species like *Lupinus sparsiflorus*, *Argemone mexicana*, *Ipomoea longifolia*
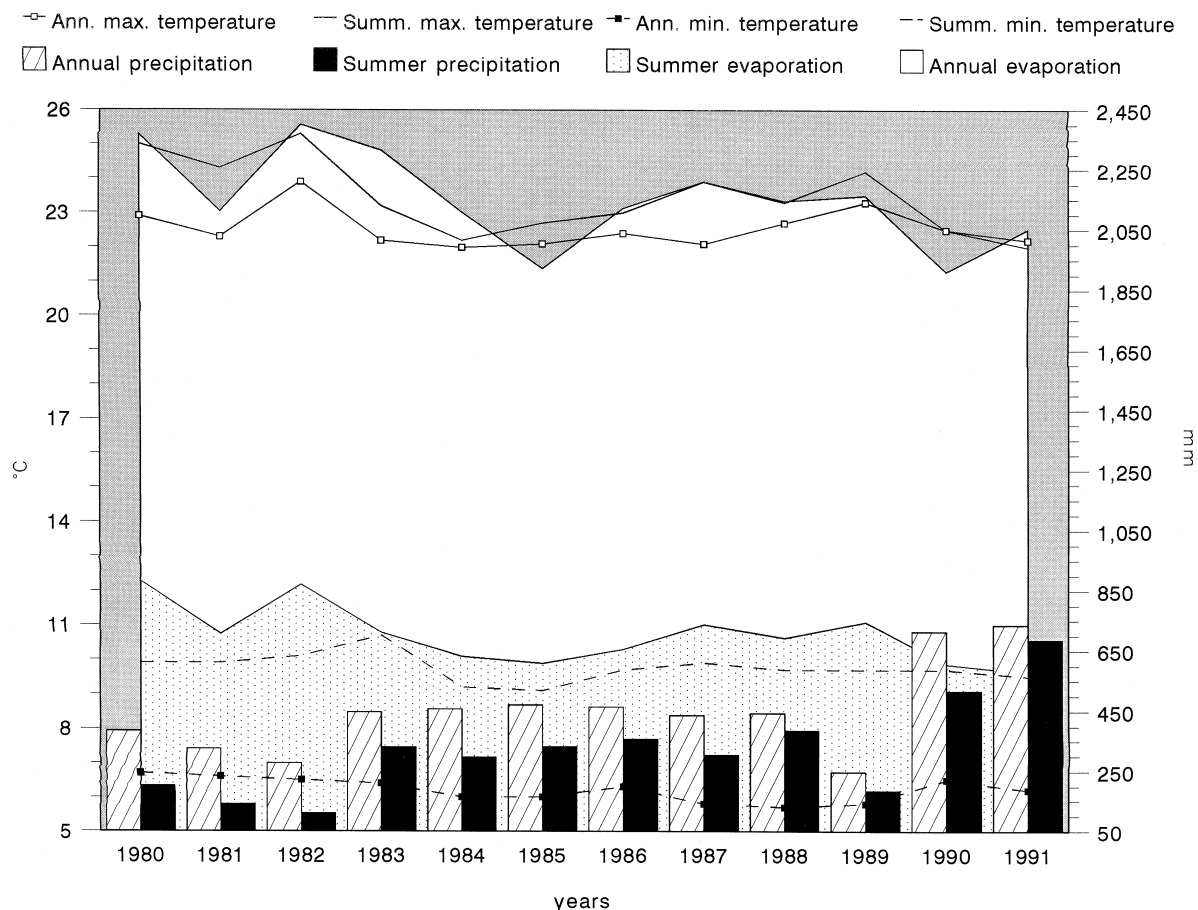
*Figure 4.* Summer and annual weather conditions during course of the study (1980–1991).

and *Astragalus mollissimus* have developed mechanisms which allow them to blossom during the dry season.

Similarity in cover fluctuation among sites was higher for grasses (Figure 5b) than for shrubs (Figure 5c) or herbs (Figure 5d). With the exception of the 1985–1986 period, when an increment in grass cover at the La Colorada site was observed *versus* decrements at the Vaquerías and La Mesa sites, the trend in cover change was the same. Maximum grass cover was attained at all three sites in 1987, a year of average precipitation (aestival 304.9 mm; annual 436.9 mm). The highest precipitation was observed in 1991 (aestival 686.1 mm; annual 736.2 mm); this did not correspond with the highest grass cover value (Figure 5b).

At the La Colorada site, shrub cover was highest during the years in which the highest aestival precipitation occurred (1988 and 1991) and lowest in the driest year for which plant records are available (Figure 5c).

Little can be said about the other sites because of the scarcity of woody components.

Herbs showed a remarkable increase in cover during the last year of the study, when the highest precipitation occurred (Figure 5d). This increase was highly influenced by the cover of a moss. No clear relationship with rain patterns was evident the rest of the study, although the second highest value in herb cover was attained during the second rainiest year at the La Mesa site.

### Soil characteristics

Two horizons were identified at Vaquerías and La Presa sites corresponding to depths 0–25 and 25–40 cm. At La Mesa and La Colorada sites three horizons were present with depths of 0–15, 15–30 and 30–38, and 0–18, 18–59 and 59–77, respectively. pH values ranged from 5.1 to 8.5 (Table 2). Organic matter and total
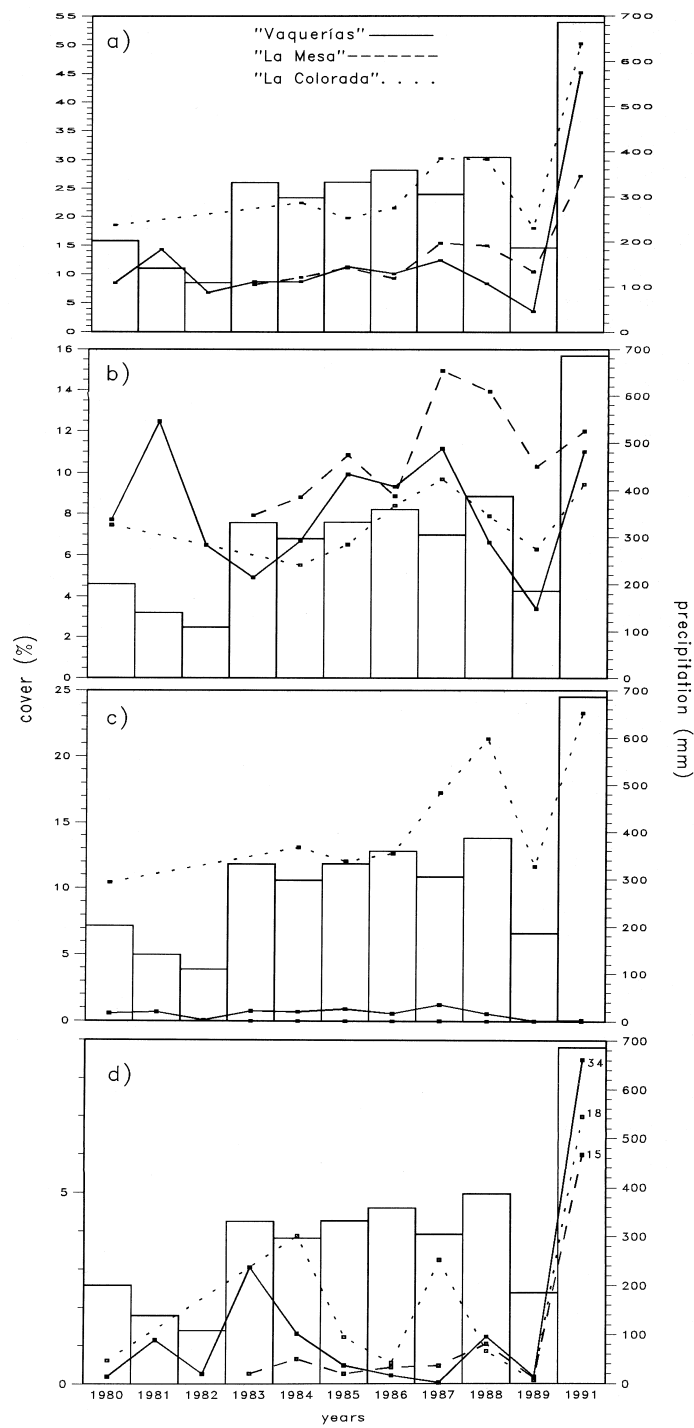
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*Figure 5.* Plant cover under livestock exclosure conditions at three sites and summer precipitation totals during the study period: (a) total cover, (b) grass cover, (c) shrub cover , and (d) herb cover.

*Table 2.* Soil characteristics shown as averages for horizons A and B at each site

| Site | Treatm. | Horiz. | Edaphic variables | | | | | | | | |
|------|---------|--------|------|--------------|--------|---------|-----|--------------|-----------|-----------|-----------|
| | | | pH | E.C. mmho/cm | O.M. % | Total N % | P ppm | K meq/100g | Sand % | Silt % | Clay % |
| Vaquerías | EX | A | 6.8 | 0.29 | 1.0 | 0.05 | t | 1.26 | 41 | 39 | 20 |
| | | B | 7.8 | 0.07 | 0.7 | 0.04 | t | 2.52 | 51 | 25 | 24 |
| | GR | A | 7.7 | 0.10 | 1.0 | 0.05 | t | 1.54 | 54 | 23 | 22 |
| | | B | 8.5 | 0.31 | 0.6 | 0.03 | t | 2.61 | 48 | 25 | 26 |
| La Mesa | EX | A | 6.6 | 0.15 | 2.0 | 0.10 | t | 1.77 | 33 | 39 | 28 |
| | | B | 7.1 | 0.08 | 1.1 | 0.05 | t | 1.92 | 32 | 35 | 33 |
| | GR | A | 6.0 | 0.19 | 2.3 | 0.12 | 1 | 1.50 | 34 | 38 | 28 |
| | | B | 6.9 | 0.09 | 1.4 | 0.07 | t | 1.71 | 38 | 34 | 28 |
| La Colorada | EX | A | 5.9 | 0.05 | 1.0 | 0.05 | 1 | 1.21 | 48 | 30 | 22 |
| | | B | 6.6 | 0.07 | 1.0 | 0.05 | 1 | 1.51 | 41 | 23 | 36 |
| | GR | A | 6.0 | 0.07 | 2.2 | 0.11 | 1 | 0.95 | 20 | 44 | 36 |
| | | B | 6.3 | 0.08 | 1.3 | 0.06 | 1 | 1.50 | 18 | 46 | 36 |
| La Presa | EX | A | 6.5 | 0.08 | 0.6 | 0.03 | 2 | 1.20 | 46 | 29 | 24 |
| | | B | 7.8 | 0.13 | 0.6 | 0.03 | 2 | 2.78 | 54 | 29 | 16 |
| | GR | A | 5.1 | 0.04 | 1.3 | 0.07 | 1 | 0.84 | 48 | 29 | 22 |
| | | B | 7.5 | 0.13 | 0.7 | 0.04 | 1 | 1.50 | 46 | 31 | 22 |

* EX, grazing exclosure; GR, grazing; *t*, <1 ppm.

nitrogen contents tended to be higher in horizon A as opposite to potassium which had higher values in horizon B. Phosphorus concentrations were always low in all sites. Sand content showed a comparatively greater variability at La Colorada site (Table 2).

*Ordination*

Prior to running ordination, four properties related to the B horizon and site management were excluded from analysis because of multicollinearity effects. Because summer evaporation showed negligible variance, it was also omitted from the environmental variables group. Other environmental (climatic) variables had to be intentionally removed in order to eliminate some of residual collinearity, which generated high variance inflation factors. One of the strongest correlations occurred between annual and summer precipitation ($r = 0.9595$); the former was discarded because it was less important in terms of explained variance in species data. Ultimately, the ordination was performed using four environmental variables (summer maximum temperature, summer precipitation, annual maximum temperature and annual evaporation), 12 covariables (soil depth, seven soil properties related to A horizon and four to B horizon), 353 samples and 101 species.

Because part of the information is already explained by the effects that covariables have on the response variables, the eigenvalues (Table 3) showed that the extracted gradients were quite short when compared to those obtained by standard CCA in other studies (Purata 1986; Cramer & Hytteborn 1987; Avila 1992), but similar to those attained in a study approached with partial CCA (Ter Braak 1988a).

Cumulative percentage variance of the species-environment relationship for axes 1 and 2 was 91.6, indicating that most of the information was concentrated on the first two axes. Covariables explained a higher percentage (43.4) of the species data variance than climatic variables, which by themselves explained 6.3%; the remaining 50.3% of the variation was due to other environmental factors.

From the canonical coefficients and correlations between climatic variables and species and environmental axes shown in Table 4, it can be inferred that the first species axis was shaped by a summer precipitation gradient in time, while second axis was defined by summer maximum temperature. This fact is also evident in the ordination diagram (Figure 6). Contribution of summer precipitation and summer maximum temperature to variation in species data by weather was ca. 81% of the whole set of environmental variables.

*Table 3.* Summary for the partial CCA ordination of the sites data in relation to four climatic variables with edaphic and management effects fitted.

| Axes | 1 | 2 | 3 | 4 | Total inertia |
|---|---|---|---|---|---|
| Eigenvalues: | 0.335 | 0.050 | 0.020 | 0.015 | 6.666 |
| Species-environment correlations: | 0.852 | 0.531 | 0.394 | 0.371 | |
| Cumulative percentage variance of species data: | 8.9 | 10.2 | 10.7 | 11.1 | |
| of species-environment relation: | 79.7 | 91.6 | 96.4 | 100.0 | |
| Sum of all unconstrained eigenvalues (after fitting covariables) | | | | | 3.775 |
| Sum of all canonical eigenvalues (after fitting covariables) | | | | | 0.420 |

*Table 4.* Canonical coefficients and correlations of climatic variables with the first two ordination axes (intraset-correlations) and with the samples scores (interset-correlations).

| Variable | Canonical coefficients | | Intraset-correlations | | Interset-correlations | |
|---|---|---|---|---|---|---|
| | Axis 1 | Axis 2 | Axis 1 | Axis 2 | Axis 1 | Axis 2 |
| Annual maximum temperature | 0.50 | –0.14 | –0.09 | –0.68 | –0.07 | –0.36 |
| Annual evaporation | –0.07 | 1.02 | –0.29 | –0.18 | –0.25 | –0.10 |
| Summer maximum temperature | 0.13 | –1.94 | –0.49 | –0.73 | –0.41 | –0.39 |
| Summer precipitation | 1.29 | –0.75 | 0.90 | 0.32 | 0.77 | 0.17 |

It is noteworthy that the samples group by years in response to climatic patterns, with those records taken during the wettest year (1991) positioned in the right-hand part of diagram, near the tip of the arrow standing for summer precipitation (Figure 6). This relationship was especially important for the La Presa site, whose records from 1987 and 1991 were located close to the two ends of this gradient (PEX91 and PEX87). A similar pattern was noted for the temperature gradient, with samples from the warmest years (1982 and 1989) occurring at the bottom, and those taken during one of the coldest years (1984) at the top of the ordination diagram.

A separation between samples from exclosed and grazed areas was also evident within the ordination field. For example, samples taken during 1983 under exclosure conditions were separated from samples taken under grazing conditions at the Vaquerías site (VGR83 vs. VEX83; top of Figure 6). Additionally samples from livestock exclosure at the La Colorada site were separated from the livestock and minor fauna exclosure samples (e.g., CFE91 vs. CLE91, to the right of diagram). For the remaining study sites, the points representing these two treatments remained together within the ordination field (e.g., points 49–53, located at the top of Figure 6, representing the 1984 sampling at the Vaquerías site). This difference between La Colorada and the other sites seems to be the result of strong floristic heterogeneity present at La Colorada.

Species varied in their response to the climatic gradients (Figure 7). At the high end of the precipitation gradient (wettest years), less abundant components of grasslands (principally annual species) were located: *Chloris virgata, Cosmos parviflorus, Digitaria ternata, Physalis cordata, Tagetes lunulata, Trisetum kochianum, Verbena gracilis* and one unidentified moss. Some perennial species found in this group were *Cerdia congestiflora, Cyperus seslerioides, Eryngium heterophyllum, Gaura hexandra* and *Piqueria trinervia*. Correlation with the temperature gradient was less evident, with *Agrostis* sp. and *Solanum elaeagnifolium* at the higher end of gradient and *Buddleia scordioides, Castilleja lithospermoides, Gomphrena decumbens* and *Stevia micrantha* at the lower end.

In accordance with examination of the cover data by life form, perennial grasses were positioned to the center of the diagram, which indicated that they were either indifferent to or have their optima at intermediate levels of the evaluated environmental factors. To test this, we reordered species and samples according to their scores on the first canonical axis for one of the study sites (Vaquerías; Table 5). Herbs like *Cyperus seslerioides, Borreria verticillata, Euphorbia prostrata, Bulbostylis juncoides, Eleocharis acicularis* and an unidentified moss (BRYO) showed a preference for rainy years, while grasses varied in their response to precipitation patterns. *Bouteloua hirsuta, Lycurus phleoides* and *Aristida divaricata* spread over the

*Table 5.* Ordering of species and samples for *Vaquerías* site, according to scores on the first CCA axis obtained in global ordination. Just two central sample scores of each year are considered. Species abundances were transformed by taking square roots. Precipitation values were divided by 100 and rounded.

| Species | 126 | 128 | 101 | 100 | 116 | 112 | 001 | 038 | 083 | 012 | 075 | 088 | 051 | 095 | 070 | 037 | 061 | 058 | 021 | 014 | 027 | 034 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Moss cover | 4 | 5 | 0.4 | | 0.5 | 0.5 | | | | | | | | | | | | | | | | |
| Cyperus seslerioides | 0.4 | | 0.2 | | | | | | | | | | | | | | | | | | | |
| Borreria verticillata | 2 | 0.9 | | | | | | | | | | | 0.1 | | | | | | | | | |
| Euphorbia prostrata | 3 | 2 | 0.8 | 0.3 | | | 0.2 | | 0.5 | | 0.1 | | | 0.5 | | 0.5 | | 0.1 | | | | |
| Bulbostylis juncoides | 0.5 | 0.6 | 0.3 | 0.1 | | | | 0.2 | 0.2 | | 0.1 | | 0.2 | | | 0.3 | | | | | | |
| Eleocharis acicularis | 0.3 | 0.7 | 0.1 | | | | | | | | | | | | | 0.2 | | | | | | |
| Bouteloua hirsuta | 1 | 2 | 1 | 2 | 1 | 0.6 | 0.9 | 0.9 | 2 | 1 | 2 | 2 | 1 | 2 | 0.9 | 0.3 | 1 | 0.6 | 2 | 1 | 2 | 0.8 |
| Lycurus phleoides | 1 | 0.6 | 0.7 | | | 1 | 1 | 0.2 | 0.6 | 0.1 | 0.9 | 1 | 0.4 | 0.4 | 0.8 | 0.2 | 1 | 0.7 | 0.6 | 0.7 | 0.4 | 0.5 |
| Microchloa kunthii | 0.6 | 0.4 | 0.6 | 0.3 | | | 1 | | 0.6 | 1 | 0.4 | 0.6 | | 0.9 | 0.2 | | 0.4 | 0.4 | 1 | 2 | | |
| Bouteloua gracilis | | | 0.2 | 0.3 | | 0.7 | 0.8 | | 1 | | 0.6 | 0.8 | 0.4 | 0.8 | | 0.6 | 0.3 | | | | | |
| Bouteloua scorpioides | 2 | 1 | 1 | 1 | 0.8 | 0.6 | 0.8 | 1 | 2 | 0.9 | 2 | 2 | 1 | 2 | 2 | 0.6 | 2 | 2 | 2 | 2 | 1 | 1 |
| Aristida divaricata | 1 | 1 | 0.4 | 0.4 | 0.9 | 0.5 | 0.8 | 3 | 0.7 | 0.9 | 0.8 | 1 | 0.3 | 0.8 | 1 | 0.5 | 1 | 0.7 | 1 | 1 | 0.8 | 0.9 |
| Dichondra argentea | | | | | | | | | | | | | | | 0.2 | 3 | 0.5 | | | 2 | | |
| Precipitation | 7 | 7 | 4 | 4 | 2 | 2 | 2 | 3 | 4 | 2 | 4 | 3 | 3 | 3 | 3 | 3 | 3 | 3 | 1 | 1 | 1 | 1 |
| Year | 91 | 91 | 88 | 88 | 89 | 89 | 80 | 83 | 86 | 80 | 86 | 87 | 84 | 87 | 85 | 83 | 85 | 84 | 81 | 81 | 82 | 82 |

Sample number

*Figure 6.* Biplot obtained by partial CCA of vegetation samples in relation to four climatic variables: summer precipitation (SPRE), summer maximum temperature (SMAT), annual maximum temperature (AMAT) and annual evaporation (AEVA). First two axes and representative plots are shown. Records labeled in accordance with the following codes: first three letters indicate site (V, Vaquerías; m, La Mesa; C, La Colorada; and P, La Presa) and pasture management (EX, grazing exclosure; GR, grazing), respectively. Digits represent year of sampling. An additional distinction is made for La Colorada grazing exclosure conditions into livestock (LE) and livestock and minor fauna (FE) exclosure treatments.

entire range of precipitation with no clear relationship to summer rain patterns. *Microchloa kunthii* tended to increase during dry years, and *Bouteloua gracilis* to be absent from years of extreme precipitation.

Little can be said about any shrub cover shift because a conspicuous change in density has not been evident since the establishment of the experiment. Shrub cover fluctuations are mainly related to can-

opy variation rather than net recruitment or mortality phenomena.

The ordination presented in Figures 6 and 7 accounted for 92% of the variance for 101 species weighted averages with respect to the four climatic variables. Permutation tests overall, for the first axis eigenvalue ($\lambda_1 = 0.335$), and for each variable added to model, were all significant ($P < 0.01$). It follows that
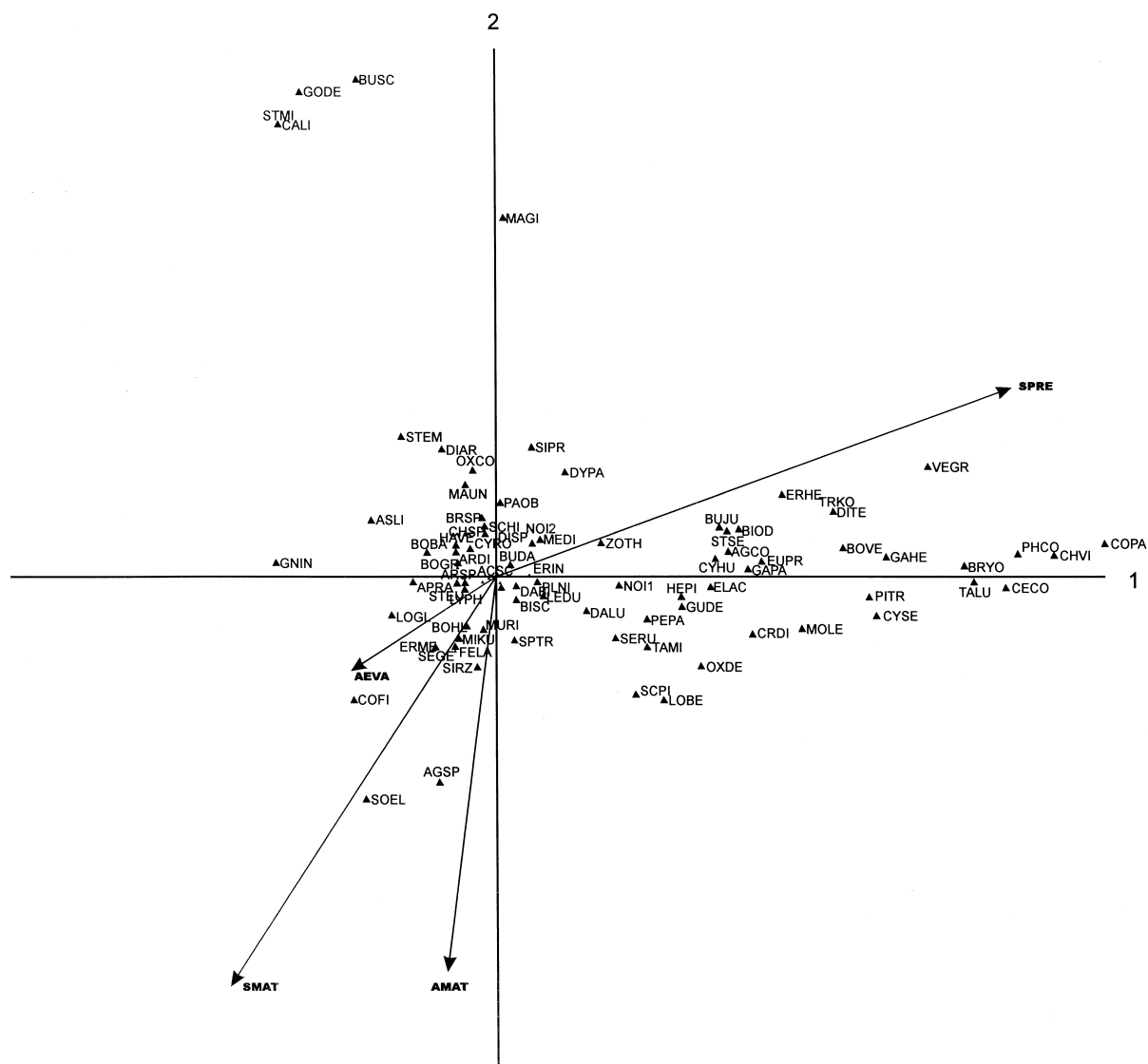
*Figure 7.* Biplot obtained by partial CCA of species in relation to four climatic variables: summer precipitation (SPRE), summer maximum temperature (SMAT), annual maximum temperature (AMAT) and annual evaporation (AEVA). First two axis are shown. Acronyms of species are: ACSC, Acacia schaffneri; AGCO, Ageratum corymbosum; ARDI, Aristida divaricata; BIOD, Bidens odorata; BOGR, Bouteloua gracilis; BOHI, Bouteloua hirsuta; BOSC, Bouteloua scorpioides; BOVE, Borreria verticillata; BRYO, unidentified moss; BUJU, Bulbostylis juncoides; CALI, Castilleja lithospermoides; CECO, Cerdia congestiflora; CHVI, Chloris virgata; COFI, Conyza filaginoides; COPA, Cosmos parviflorus; CYHU, Cyperus humilis; CYSE, Cyperus seslerioides; DIAR, Dichondra argentea; DITE, Digitaria ternata; ELAC, Eleocharis acicularis; ERHE, Eryngium heterophyllum; EUPR, Euphorbia prostrata; FELA, Ferocactus latispinus; GAHE, Gaura hexandra; GAPA, Galinsoga parviflora; GODE, Gomphrena decumbens; LOBE, Lobelia berlandieri; LYPH, Lycurus phleoides; MAGI, Macroptilium gibbosifolium; MAUN, Mammillaria uncinata; MIKU, Microchloa kunthii; MURI, Muhlenbergia rigida; PHCO, Physalis cordata; PITR, Piqueria trinervia; SEGE, Setaria geniculata; STMI, Stevia micrantha; TALU, Tagetes lunulata; TRKO, Trisetum kochianum; VEGR, Verbena gracilis.

the community variation observed at the different sites (once the edaphic and management effects are fitted) is significantly related to the evaluated climatic variables, particularly to summer precipitation patterns.

Single site ordinations produced similar results to those obtained in the previous global ordination, with summer precipitation as the main climatic factor affecting community composition over time, although for the

26

La Colorada site the result of the permutation test for the first canonical axis was nonsignificant ($P < 0.25$).

The multivariate split plot analysis supported the ordination results only for the Vaquerías study site, because enough repetitions in time were not available for the other sites to run the analyses. The calculated value of Wilk's statistics test for Vaquerías was significant ($P < 0.0001$), supporting the hypothesis that community composition varied among years.

## Discussion

*Climatic influences*

Miles (1981) mentioned that plant fluctuations in response to climatic variation are regarded as universal, although causes are not always so obvious as in droughts, because complex interactions are involved. Our study confirms this assertion for Mexican Altiplano conditions and supports previous research on both dryland farming (Carrillo 1979; Quintero 1987) and rangelands (González et al. 1981, 1988; Rivas 1988; Gutiérrez & Velásquez 1989; Del Hoyo et al. 1991). Floristic change occurring at the population level alters the balance existing among species abundances, and this in turn changes community composition and structure. Environmental factors considered in this research explained part of this floristic variation, with precipitation patterns being especially important. The significance of rain patterns in floristic fluctuations across years has been demonstrated using different approaches and plant response attributes. On an experimental basis, Van der Maarel (1981) demonstrated the relationship of floristic fluctuations to rain variation, while Goldberg and Turner (1986) explained cover and density changes in Sonoran Desert vegetation with precipitation patterns prevailing over a 72-year investigation.

Climate-biomass production relationships have been intensively studied because of their usefulness for predictive adjustments in resource management. Thus, several studies have confirmed the importance of temperature and rain patterns on fluctuation in a variety of vegetation attributes (Albertson & Tomanek 1965; Melvin et al. 1989), even though precipitation seems to be more influential in forage production on rangelands than temperature (Stoddart et al. 1975). Coupland (1979) concluded that, at least for biomass, amount of precipitation during the growing season seems to be the most important factor. In a 50-year study, Smoliak (1986) proved this assertion, finding higher correlations between precipitation and forage production than between temperature and forage production. Conversely, Savage (1937) and Powell et al. (1986) concur in considering high temperatures more influential than precipitation, except for very dry years.

Under a multivariate approach and assuming an unimodal response between species and environmental variables, our study shows that aestival precipitation is the climatic factor that most influences among-year floristic (community) variation. A secondary role is ascribed to (aestival) temperature. Austin et al. (1981) using PCA found precipitation and trend to be more important factors affecting community variation over time than soil or grazing influences, whereas Borchert et al. (1991) and Bassett (1980) discuss the effect of regional temperature and precipitation gradients.

Semiarid regions are characterized by a highly variable environment where water is the major limiting factor, so it is not surprising that floristic fluctuations track rain patterns. Plant fluctuations in general are known to be conditioned by the availability of resources (Fowler 1988).

A highly variable climate imposes a great stochasticity on vegetation, in terms of population as well as community processes (Collins & Glenn 1991). In spite of the set of common species that can be used to characterize plant communities, no plant assemblage occurring in a given year can be considered strictly equal to some other, because of the numerous and particular environmental and biotic processes operating under specific temporal circumstances. This results in a series of typical plant communities (assemblages) appearing over the course of time.

Unpredictability, with recurrent droughts and rainy years occurring over time, makes it difficult to conceive of climate as a major successional force (at least on a human time scale). However concepts have been engendered such as a rate of succession being increased or decreased by precipitation patterns (Holechek et al. 1989).

In the long term, climate could define the kind of species to survive in an specific environment, while autogenic factors might be involved in determining community directional change. Which autogenic factors are more important in this respect is a topic of controversy. However, an important role should also be conceded to some other allogenic factors varying in a less stochastic way, thus permitting directional change to proceed (Cramer & Hytteborn 1987 ).

The consistent cover responses of grasses, as a group, to weather variation in this study was remarkable, despite contrasting environmental factors (elevation, soil, grazing intensity) among sites. Although climate drives (nondirectional) floristic change, factors such as grazing or soil seem to modulate vegetation response (Pitt 1975). Moderate grazing, while increasing to some extent the unfavorable effect of droughts on plants, seems to be a factor less important than climate in modifying vegetation cover (Coupland 1958).

Broadly, two groups of species were identified in this study as a function of their distribution in time: constant species, occurring consistently over the entire study period, and occasional species, appearing mainly during rainy years. Our findings agree with the satellite-core species hypothesis of Hanski (1982), with a few satellite species varying within a stable matrix of constant species. Core species are essentially in equilibrium, while satellite species exhibit a great variability in distribution and abundance over time (Glenn & Collins 1990). The equilibrium points would be settled by independent factors such as soil or climate. This theory has found support in studies like that of Collins and Glenn (1991).

In our study area, the main structure of core species would consist of perennial grasses, while annual plants would conform to satellite species behavior. When testing response population models, Huisman et al. (1993) found that annual species were more affected by weather fluctuation than perennials, thus exhibiting lower coefficients of multiple determination ($R^2$). Floret (1981) observed a great among-year floristic variability in a steppe, chiefly attributable to changes in abundance of annual species. Both amount and seasonal distribution of rain affected cover of these plants. Aronson & Shmida (1992) for annual plants in general, and Pitt & Heady (1978) for annual grasses, have also illustrated the positive response of these plants to rainy years. Milchunas et al. (1989) suggest that short-term weather cycles exert a greater influence on less abundant components than on the main components of grasslands, whereas Borchert et al. (1991) found that interannual differences in plot ordination scores were mainly influenced by species with less than 1% cover rather than by dominant species.

These contrasting patterns arise from particular plant strategies. Grasses withstand droughts by assuming a condition of drought dormancy, while ephemerals escape or evade moisture restrictions imposed by the environment by completing their life cycles in brief mesic conditions as a result of occasional rains and sur-viving critical periods as seeds. Germination of seeds of these plants is mainly controlled by soil moisture and secondarily by temperature (Tevis 1958).

*Edaphic influences*

Arredondo (1984) has shown how some chemical soil properties can affect species composition and structure in grasslands in the study area. Aguado-Santacruz et al. (1989b) working at the La Presa site, found some essential soil properties to be similar between exclosure and grazing conditions. Conversely, Dormaar et al. (1990a) report differences among exclosed, lightly grazed, and heavily grazed pastures in some nitrogenated compounds for a fescue grassland. While the present investigation did not attempt to evaluate the edaphic influences on vegetation through time (cf., Vasek & Lund 1980; Dormaar et al. 1990b), the effect of soil influence on spatial floristic variation was quite evident within the ordination. Upper soil horizon properties were especially important, e.g., pH and electrical conductivity at the Vaquerías site, phosphorus at La Mesa, and pH, organic matter content and sand percentage at La Colorada. Deeper horizons evidenced importance only when sites were jointly analyzed (global ordination). Although subsoil affects surface soil properties, most of the interrelationships between plants and soil take place in the first layers. This is the zone of maximum root development and contains most of the nutrients and water available for plants.

The strong floristic heterogeneity detected at the La Colorada site could be influenced by shrubs and sediment deposition. Sand percentage was an important edaphic variable within the La Colorada ordination analysis. Alluvial depositions at La Colorada coming from neighboring hills (Figure 2) were evident in the soil profile description and during sampling using the auger. This spatial heterogeneity could have masked the climatic influence on temporal floristic variation.

28

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