



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

II. Temporal plant assemblages determined by rainfall patterns

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Abstract

We have delineated the spatio-temporal plant assemblages prevailing under contrasting environmental conditions at the southernmost part of the North American Graminetum in central México and discuss the relative importance of these factors in determining plant community structure and composition. 353 line-transect samples were collected during 11 years from exclosures and adjacent grazed areas within three *Bouteloua*-dominated grasslands and one *Acacia schaffneri* shrubland and analyzed using TWINSPLAN. In addition, eight edaphic variables were utilized to evaluate similarities in soil properties among sites, using unweighted-pair groups method. Results from TWINSPLAN were translated into mosaic patterns to show the distribution of communities as a function of environmental factors over time. Under no or moderate grazing, summer precipitation promotes an initial differentiation of vegetation into high, low or average rainfall communities. This situation is altered in grasslands degraded by intensive grazing pressure, where rainfall patterns play a subordinate role to that of livestock herbivory. Soil influences are secondary to those of precipitation and grazing in affecting grassland structure and composition. In shrubland, community stability is related to high floristic and edaphic spatial heterogeneity in the face of climatic variability.

Nomenclature:

Grasses follow Hitchcock (1971); other families in accordance with De la Cerda & Siqueiros (1984).

Introduction

Plant community change over time is driven by environmental and autogenic factors, the importance of each determined by the particular conditions and interrelationships prevailing for the ecosystem in question. Arid and semiarid regions are characterized by a highly variable environment, where precipitation patterns exert a fundamental influence on interannual floristic fluctuations (Rabotnov 1985). Plant communities include a great variety of life forms, each adapted to persist in the face of the climatic stochasticity of the semiarid environment; some plants evade, others tolerate unfavorable periods (Solbrig & Oriens 1977). Although a set of species can be used to characterize the communities prevailing at a specific site and time, these plant assemblages are distinctive entities resulting from spatial and temporal phenomena operating under specific circumstances.

Previously (Aguado-Santacruz & García-Moya 1998) we showed that among climatic variables, summer precipitation has the most influential role in shaping community structure and composition at the southernmost part of the North American *Gramine-*

tum. We here now define the spatio-temporal plant assemblages prevailing for the highly variable environmental conditions of this region and discuss their relative importance. Specifically, we evaluate the effects of exclosure from grazing, both moderate and heavy grazing pressure and soil variability on community structure and composition in both space and time.

Material and methods

Study area

This study was conducted over an eleven-year period within a region known as ‘Los Llanos de Ojuelos’ at the southernmost part of the Chihuahuan Desert in the Mexican Altiplano. Four study sites, Vaquerías, La Mesa, La Colorada and La Presa were considered in this research. La Mesa and La Presa are *Bouteloua gracilis*-dominated grasslands. Vegetation at the Vaquerías site consists of grassland dominated by *B. scorpioides*, while an *Acacia schaffneri*-shrubland is present at La Colorada. Site elevations range from 2200 to 2380 m. One exclosure (one hectare in size) was established at each site. In addition, sites differ in historical and current grazing regimes, soil types and temporal extent of available floristic records (Table 1).

Floristic, edaphic and climatic records

Floristic composition and plant cover were determined annually on twenty-meter-long permanent line transects using the line intercept method (Canfield 1941). This method is based on the measurement 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 using 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).

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 using a California type auger. Accordingly, five subsamples/treatment for each identified horizon were taken at Vaquerías and La Mesa sites, and three

and ten at La Presa and La Colorada sites, respectively. Samples from grazed pastures were obtained directly from soil profiles. Soil properties determined for each horizon/treatment/site included: pH (Jackson 1976), electrical conductivity (Richards 1973), organic matter (Jackson 1976), total nitrogen (calculated from organic matter), phosphorus (Olsen & Dean 1965) and exchangeable potassium (Chapman 1965). Information also included textural analyses (Bouyoucos 1962).

Climatic information was obtained from a weather station established in 1979 and located 1 km southwest of the Vaquerías site (Figure 1).

Data analysis

Plant communities (spatio-temporal assemblages) at each site were defined using TWINSPAN (Hill 1979); the term ‘community’ is used here without any connection to the levels of any established phytosociological hierarchy. Global (353 line transects) and individual (site) analyses were carried out.

For the site analyses, preliminary classifications were carried out in order to reduce floristic variation among sampling units (transects). After this process, Vaquerías, La Mesa, La Colorada and La Presa analyses were based on 155, 64, 65 and 24 sampling units, respectively. Pseudospecies were considered as community indicators using the cut levels 0, 2, 5, 10 and 20%, so that 1, 2, 3, 4 and 5 represented the species cover percentages 0.02–1, 2–4, 5–9, 10–19 and above 20, respectively. Thus, ‘BOUT GRAC5’ operated as indicator species when *Bouteloua gracilis* was present with a cover value $\geq 20\%$. Levels of pseudospecies had the same weight and all were used as potential indicators. The minimum group size for division varied according to the number of line transects established at each treatment/site to allow assemblages to fall into their own treatment group.

Using the edaphic variables, similarity of soils among sites was evaluated by unweighted pair group cluster analysis from an Euclidean distances matrix (UPGMA; Sneath & Sokal 1973). Soil clustering was based on the properties of the first two soil horizons; values were standardized to zero mean and unit variance *prior* to data processing. The beta constant value in clustering was -0.25 .

Table 1. Characteristics of the study sites.

	Sites			
	Vaquerías	La Mesa	La Colorada	La Presa
Vegetation	<i>Bouteloua scorpioides</i> grassland	<i>Bouteloua gracilis</i> grassland	<i>Acacia schaffneri</i> shrubland	<i>Bouteloua gracilis</i> 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.

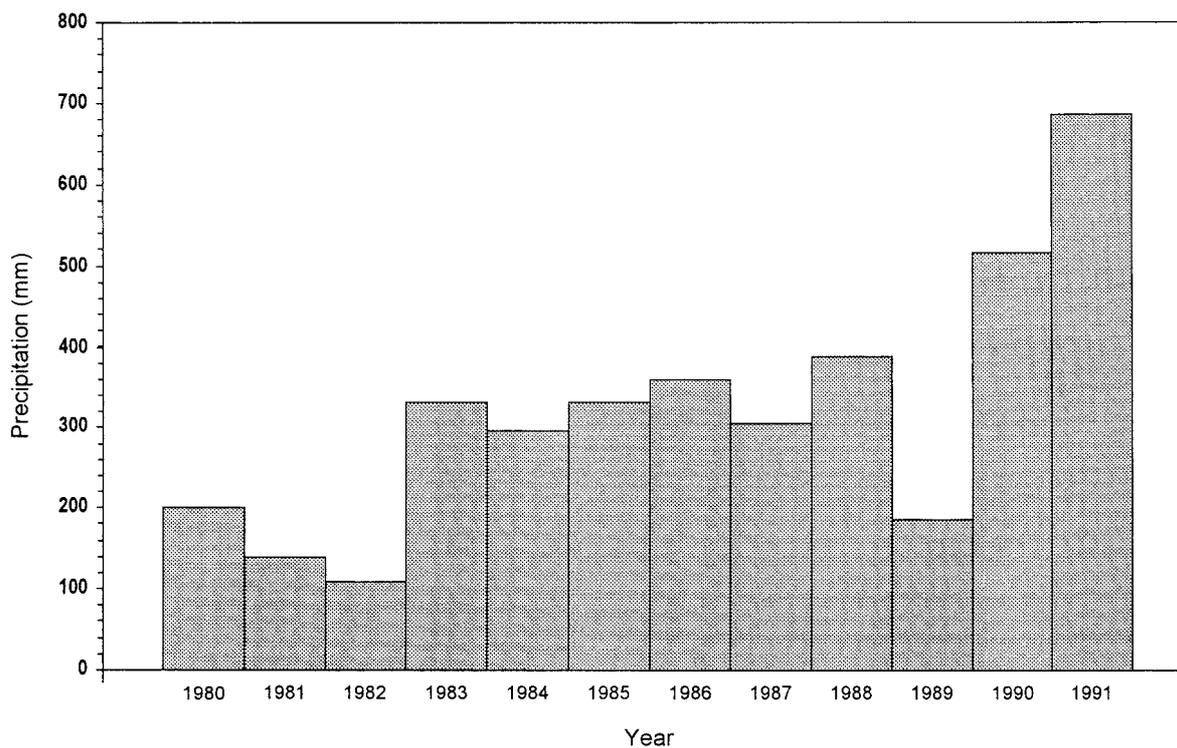


Figure 1. Summer precipitation during course of study.

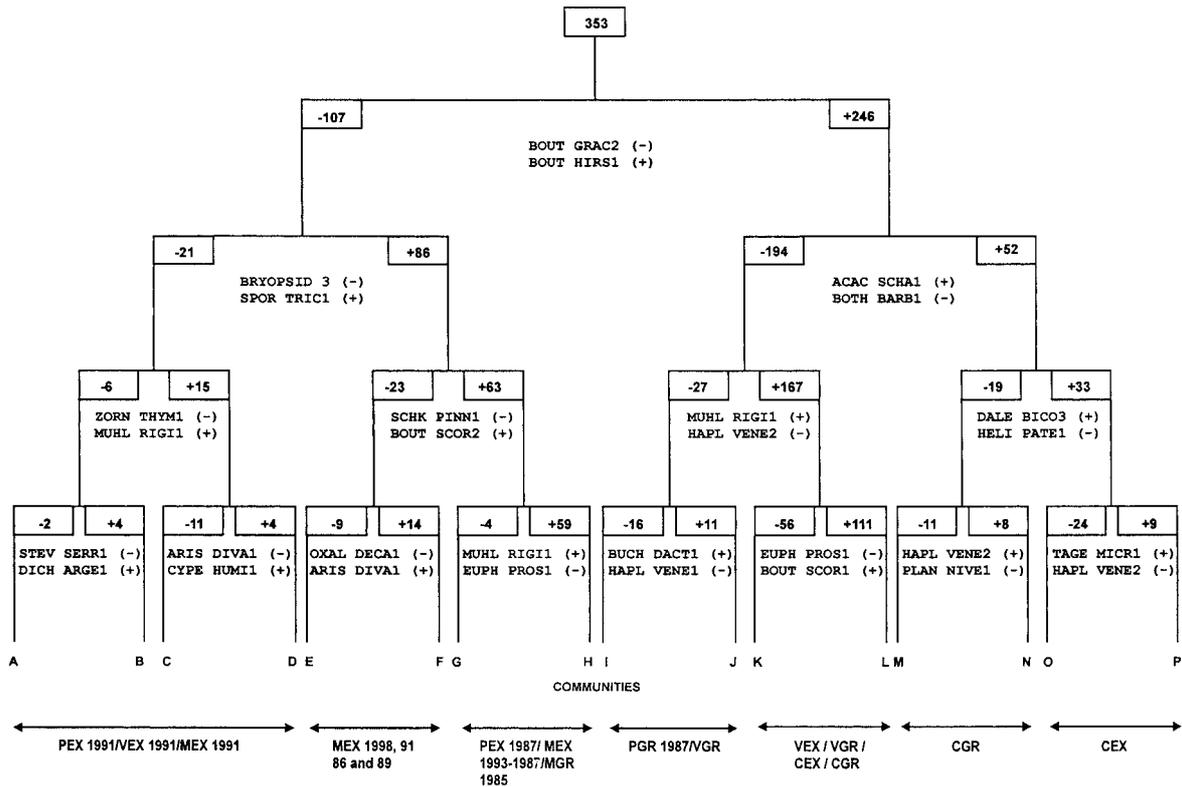


Figure 2. Global classification of sites. Acronyms for species are: ACAC SCHA, *Acacia schaffneri*; ARIS DIVA, *Aristida divaricata*; BOTH BARB, *Bothriochloa barbinodis*; BOUT GRAC, *Bouteloua gracilis*; BOUT HIRS, *Bouteloua hirsuta*; BOUT SCOR, *Bouteloua scorpioides*; BRYOPSISID, moss complex including *Campylopus* sp, *Archidium* sp, *Didymodon* sp, and *Pseudocrossidium* sp; BUCH DACT, *Buchloë dactyloides*; CYPE HUMI, *Cyperus humilis*; DALE BICO, *Dalea bicolor*; DICH ARGE, *Dichondra argentea*; EUPH PROS, *Euphorbia prostrata*; HAPL VENE, *Haplopappus venetus*; HELI PATE, *Helianthemum patens*; MUHL RIGI, *Muhlenbergia rigida*; OXAL DECA, *Oxalis decaphylla*; PLAN NIVE, *Plantago nivea*; SCHK PINN, *Schkuhria pinnata*; SPOR TRIC, *Sporobolus trichodes*; STEV SERR, *Stevia serrata*; TAGE MICR, *Tagetes micrantha*; ZORN THYM, *Zornia thymifolia*. Digits 1 to 5 denote the following cover categories: 1, 0.02–1%; 2, 2–4%; 3, 5–9%; 4, 10–19%; and 5, 20–100%. First three letters indicate site (V, Vaquerías; M, La Mesa; C, La Colorada; and P, La Presa) and pasture management (EX, grazing enclosure; GR, grazing). Year of sampling is indicated when required.

Results

Global Classification

A first dichotomy from TWINSPAN was observed which separated disturbed (heavily grazed grassland and shrub-invaded grassland) from undisturbed pastures (exclosed grassland and lightly to moderately grazed grassland; Figure 2). At 'Los Llanos de Ojuelos' physiographic subprovince, undisturbed grasslands are dominated by *Bouteloua gracilis* and have a high productive level in terms of grass biomass. Conversely, disturbed grassland is degraded, or shrub- or half-shrub invaded grassland with lower grass cover and productivity (Aguado-Santacruz et al. 1990). The undisturbed grassland indicator species was *Bouteloua gracilis* with 2–4% cover, while the disturbed grass-

land group was characterized by *Bouteloua hirsuta* with 0.02–1% cover.

Subsequent divisions showed other environmental effects including site and time; such divisions were not clear cut. Indicator species for communities (plant assemblages) 'A'-'D' was a moss complex (cover 5–9%) constituted by at least four species, *Campylopus* sp, *Archidium* sp, *Didymodon* sp, and *Pseudocrossidium* sp, with the first one representing the more abundant moss within collected samples. This moss complex occurred during the rainiest year of the study (1991) within exclosed grasslands at the La Presa, La Mesa and Vaquerías sites. Notably, for Vaquerías only the 1991 records were situated among the undisturbed rangelands; the remaining records fell within community 'K' in the deteriorated-grassland group. Remaining records from La Presa and La Mesa ex-

closures were located in 'E'-'H' communities characterized by *Sporobolus trichodes* (cover 0.02–1%); the sole year sampled from grazed conditions at La Mesa (1985) also occurred in this group. The most conspicuous element at La Colorada, *Acacia schaffneri* (cover 0.02–1%), was the indicator species for this shrubland, while *Bothriochloa barbinodis* (cover 0.02–1%) operated as indicator for the open grasslands of La Presa (grazed) and Vaquerías (grazed and exclosed); and for a few records from La Colorada (grazed and exclosed; Figure 2).

Initial classifications for individual sites were carried out in order to obtain more homogeneous groups of plant assemblages for a clearer partitioning of environmental effects other than resource condition. Accordingly, the Vaquerías and La Mesa classifications excluded samples clearly defined by grazing at the second level of division, after a first delineation of plant assemblages as a function of summer precipitation patterns. For the La Colorada and La Presa analyses, both exclosed and grazed conditions were considered due to a lack of rainfall-induced floristic variation at the first site, and to a clear and sharp definition of plant assemblages in terms of the environmental factors at the second one, as shown later.

La Presa site

At this site, where pasture condition under grazing is the poorest among all sites, the first dichotomy was defined by the resource management condition (Figure 3). The moss complex mentioned above (cover 0.02–1%) was the indicator for exclosed conditions, while a perennial composite, *Haplopappus venetus* (cover 2–4%), was the indicator for grazed conditions. The second division showed temporal and spatial heterogeneity effects for exclosed and grazed conditions, respectively. Influences of spatial heterogeneity were evident up to the third level of division for exclosed conditions (Figure 3). This difference in data behavior was due to a lack of 1991 records for the grazing treatment.

Divisions were almost perfect at this site. From the 24 available sampling units, all grazing records (12) were clustered jointly from the first level of division; just one sample from exclosed conditions was included within this group (Figure 3). This sample showed compositional characteristics of both grazed and exclosed conditions. Non-grazing properties included an absence of components varying highly in their abundances throughout the study (mainly annu-

als) such as *Conyza filaginoides*, *Digitaria ternata*, *Dyssodia papposa*, *Eragrostis mexicana* and *Tagetes micrantha*. Pseudospecies attributes related to grazing were the presence of *Haplopappus venetus* with a relatively high cover and a sparse cover of *Bouteloua gracilis*.

In relation to exclosed conditions, the six 1991 samples were clustered into the same group as those from 1987 (with the exception of the above-mentioned borderline transect). Samples obtained during 1991 (the rainiest year; Figure 1) were characterized by a perennial Asteraceae, *Bidens schaffneri* (cover 0.02–1%); and those samples taken in 1987 by another member of this family, *Gnaphalium inornatum* (cover 0.02–1%; Figure 3).

Vaquerías site

Two initial groupings were obtained, corresponding to average to low summer rainfall years, and to high summer rainfall years (1988 and 1991; Figure 4). The first cluster included eight communities characterized by a perennial member of the Convolvulaceae, *Dichondra argentea* (cover 0.02–1%); the second cluster had four communities with the *Campylopus*-moss complex (cover 2–4%) as indicator.

Rain patterns (Figure 1) resulted in characteristic communities for particular years. The 'I' community was distinctive to the wettest years (1988 and 1991); 'B', 'A' and 'F' communities were also present during 1988, although the two latter were considerably less important. Communities 'J', 'K' and 'L' were restricted to 1991, with 'J' being the more important community during this year (Figure 5). 'D' was the best spatially represented community for particular years (1980 and 1983) throughout the study period; this community also occurred mainly in those years. 'A' and 'C' communities also showed a limited distribution in time being mostly restricted to 1983 and 1985, respectively (Figure 5).

La Mesa site

A clearer differentiation of communities in terms of summer rain patterns through time was observed at this site (Figures 6 and 7). Communities 'A', 'B' and 'C', initially characterized by *Bouteloua scorpioides* and *Sporobolus trichodes* (cover 2–4%), were found in the year with the lowest summer precipitation for which floristic records were available (1989). Communities 'A' and 'B' were restricted to 1989, while 'C' was also present in 1983 (Figure 7); 'B' was the

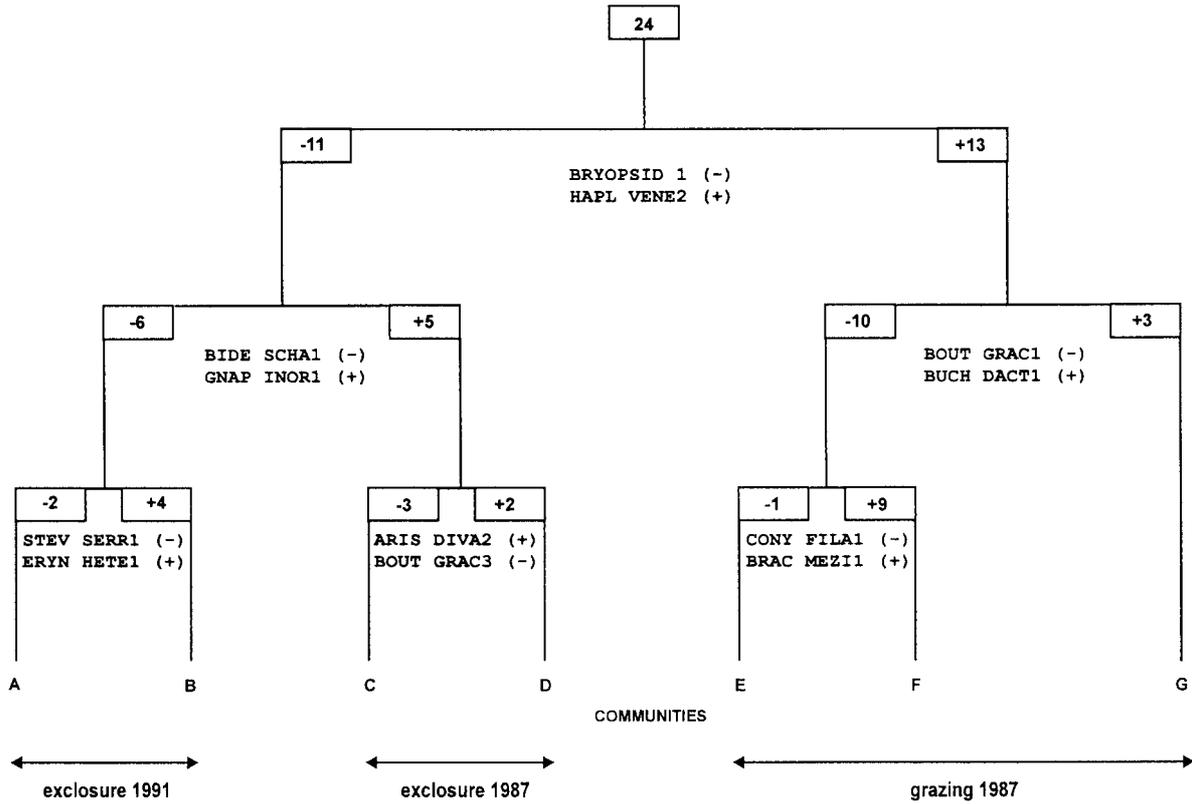


Figure 3. La Presa site classification. Acronyms of species are: ARIS DIVA, *Aristida divaricata*; BIDE SCHA, *Bidens schaffneri*; BOUT GRAC, *Bouteloua gracilis*; BRAC MEZI, *Brachiaria meziana*; BRYOPSID, moss complex including *Campylopus* sp, *Archidium* sp, *Didymodon* sp, and *Pseudocrossidium* sp; BUCH DACT, *Buchloë dactyloides*; CONY FILA, *Conyza filaginoides*; ERYN HETE, *Eryngium heterophyllum*; GNAP INOR, *Gnaphalium inornatum*; HAPL VENE, *Haplopappus venetus*; STEV SERR, *Stevia serrata*. Cover categories as in Figure 1.

community best represented during 1989. *Schkuhria pinnata* communities, ‘H’ to ‘M’, were found during the wettest years, with a split for community ‘J’ between 1988 and 1991; the most important communities during these two wet years were ‘H’ and ‘I’, and ‘L’, respectively. Community ‘G’ was largely limited to 1986, where ‘F’ community showed higher importance (Figure 7).

La Colorada site

In contrast to the other sites, it was not possible to establish a rain pattern-induced community differentiation at La Colorada site due to a more even distribution of communities in both time and space, although a greater heterogeneity of plant assemblages was observed (sixteen communities; Figures 8 and 9). This was the result of a strong floristic spatial heterogeneity, in which each sampling unit was more similar to itself over time (temporal trajectory) than to its ho-

mologues for a specific year (as was the case at the other sites). Thus, in general, groups were constituted by the line transect trajectories over time. The strong floristic spatial heterogeneity present at this site had been previously detected by partial CCA of these data (Aguado-Santacruz & García-Moya 1998).

Groups were formed in terms of their management (Figures 8 and 9). One was assembled from sampling units from ungrazed conditions and included eight communities initially characterized by *Acacia schaffneri* (cover 10–19%). A second group containing units from grazed conditions included four communities characterized by *Helianthemum patens* and *Haplopappus spinulosus* (both with cover 0.02–1%). A third ill-defined group included units from both grazed and exclosed conditions, with *Helianthemum patens* (cover 0.02–1%) and *Bouteloua scorpioides* (cover 2–4%; Figures 8 and 9) as indicators.

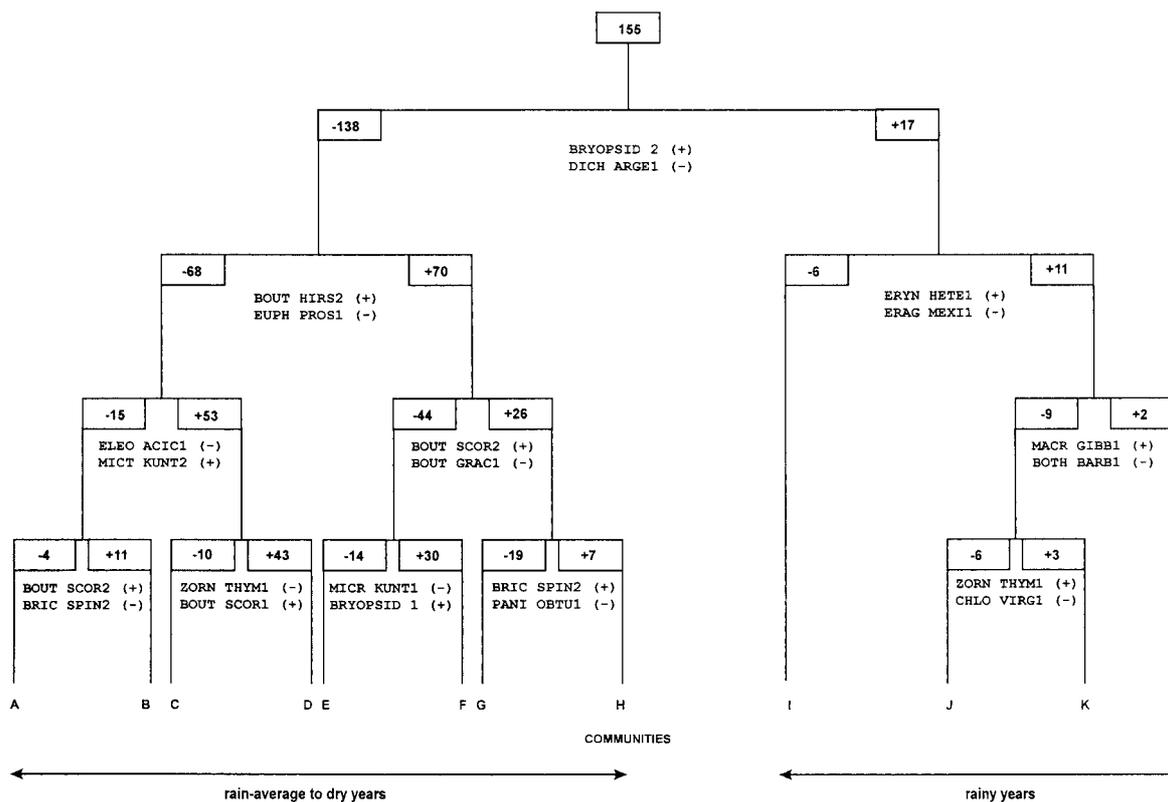


Figure 4. Vaquerías site classification. Acronyms of species are: BOTH BARB, *Bothriochloa barbinodis*; BOUT GRAC, *Bouteloua gracilis*; BOUT HIRS, *Bouteloua hirsuta*; BOUT SCOR, *Bouteloua scorpioides*; BRIC SPIN, *Brickellia spinulosa*; BRYOPSISID, moss complex including *Campylopus* sp, *Archidium* sp, *Didymodon* sp, and *Pseudocrossidium* sp; CHLO VIRG, *Chloris virgata*; DICH ARGE, *Dichondra argentea*; ELEO ACIC, *Eleocharis acicularis*; ERAG MEXI, *Eragrostis mexicana*; ERYN HETE, *Eryngium heterophyllum*; EUPH PROS, *Euphorbia prostrata*; MACR GIBB, *Macropodium gibbosifolium*; MICR KUNT, *Microchloa kunthii*; PANI OBTU, *Panicum obtusum*; ZORN THYM, *Zornia thymifolia*. Cover categories as in Figure 1.

Soil classification

Interesting relationships were derived from soil classification (Figure 10). A first dichotomy separated all of the La Mesa samples, and some of those from La Colorado from the other two sites (groups 'd' and 'e'). Next, clusters 'a' and 'b' tended to group soil samples from horizons A and B, respectively, coming from La Presa and Vaquerías sites. Certain samples from La Colorado showed no clear affinity, possibly as a consequence of edaphic heterogeneity, and appeared within groups 'a', 'b' and 'c'; the last cluster reminiscent of La Colorado's similarity to La Mesa's soil.

Discussion

Using TWINSPLAN we have defined in this study spatio-temporal assemblages resulting from the highly

variable environmental conditions prevailing at the southernmost part of the North American *Gramineum*. These results confirm our previous findings using an ordination technique (Aguado-Santacruz & García-Moya 1998) and illustrate the non-equilibrium condition of grassland communities, which have been shown to be highly variable in time and space (Collins & Glenn 1991; Glenn & Collins 1993; Herben et al. 1993; van der Maarel & Sykes 1993). Both analyses reveal the importance of rainfall patterns (summer precipitation in our case) in shaping community structure over time. Using a classification technique (Divisive Information Analysis), Austin et al. (1981) also differentiated wet year communities from average-precipitation-communities verifying their results through an ordination analysis (PCA), in which precipitation and trend were identified as more important than soil or grazing in determining community composition over time.

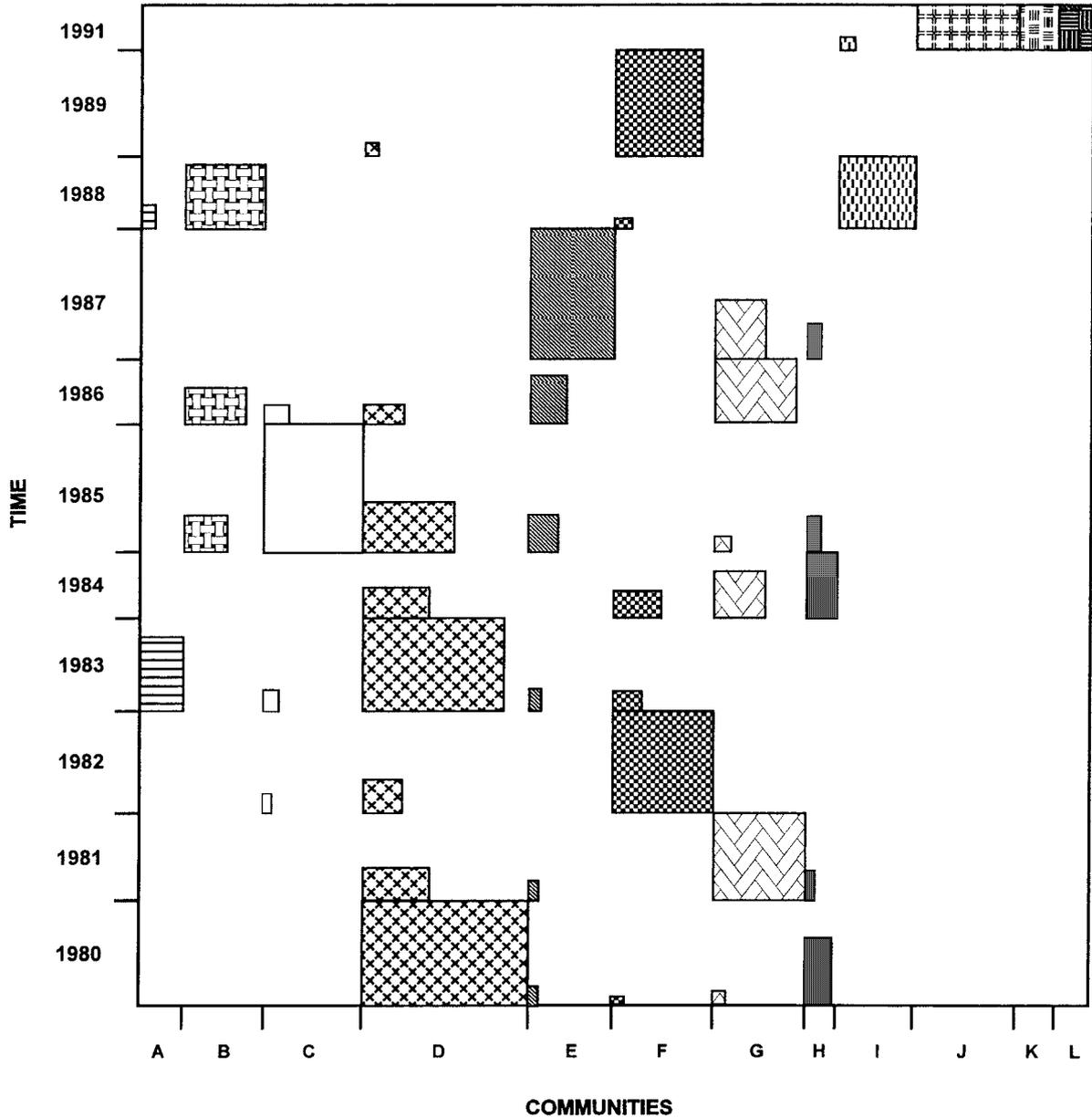


Figure 5. Community spatio-temporal relationships at the Vaquerías site obtained as the relative frequency of a given community as related to: (a) study period (time), and (b) all plant assemblages present for a particular year (communities).

A great part of this differentiation between wet year communities and average-precipitation year communities can be explained by fluctuations in abundance of annual herbs. Wet year grassland communities are characterized by components exhibiting high interannual variability; i.e. the satellite elements in the Hanski hypothesis (Hanski 1982), while plant assemblages prevailing during average precipitation years

are demarcated by the core species. Therefore, very dry or wet years increase both community specificity in time and the importance of a given assemblage's contribution to global floristic spatial heterogeneity (Vaquerías and La Mesa sites).

In our preliminary analyses of individual sites we could detect the effects of moderate grazing (Vaquerías and La Presa sites) up to the second level of

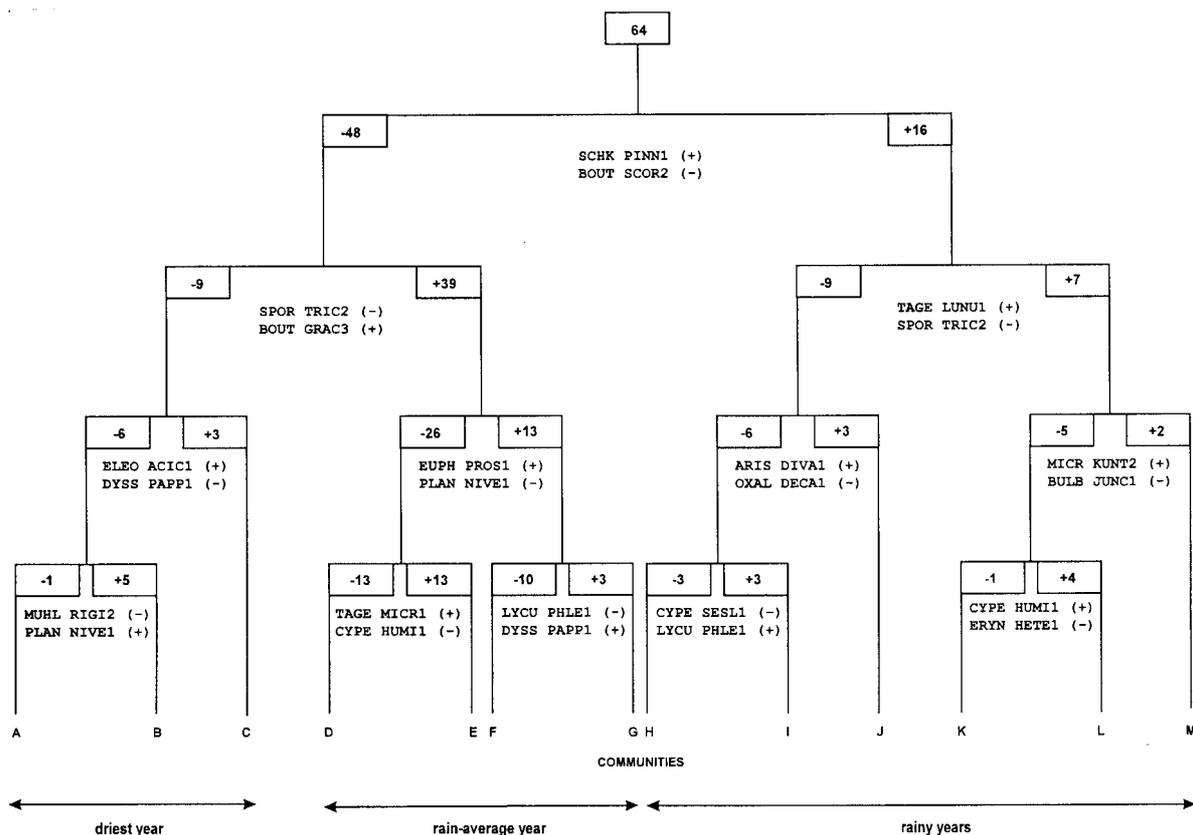


Figure 6. La Mesa site classification. Acronyms of species are: ARIS DIVA, *Aristida divaricata*; BOUT SCOR, *Bouteloua scorpioides*; BOUT GRAC, *Bouteloua gracilis*; BULB JUNC, *Bulbostylis juncoides*; CYPE HUMI, *Cyperus humilis*; CYPE SESL, *Cyperus seslerioides*; DYSS PAPP, *Dyssodia papposa*; ELEO ACIC, *Eleocharis acicularis*; ERYN HETE, *Eryngium heterophyllum*; EUPH PROS, *Euphorbia prostrata*; LYCU PHLE, *Lycurus phleoides*; MICR KUNT, *Microchloa kunthii*; MUHL RIGI, *Muhlenbergia rigida*; OXAL DECA, *Oxalis decaphylla*; PLAN NIVE, *Plantago nivea*; SCHK PINN, *Schkuhria pinnata*; SPOR TRIC, *Sporobolus trichodes*; TAGE LUNU, *Tagetes lunulata*; TAGE MICR, *Tagetes micrantha*. Cover categories as in Figure 1.

division after a first dichotomy based upon precipitation fluctuation. Thus, moderate grazing can be considered as secondary to precipitation in shaping grassland structure and composition on these sites. Conversely, results from the La Presa site analysis show that extreme grazing pressure can play a more important role than rainfall in determining vegetation change. In this respect, Milchunas et al. (1989) consider grazing intermediate between soil and weather influences in shaping community structure. In the La Presa site analysis, TWINSPAN clearly and progressively showed grazing, weather (precipitation) and soil effects on vegetation. At this site, grazing impact is apparently high enough to overcome weather and soil induced floristic variation. Animal unit/hectare ratio at this site reached 1 during certain periods of time, with horses an important fraction of the grazing livestock (DGDUT 1982). Forage utilization of

92% for *Bouteloua gracilis* was found at this site in 1987 (Aguado-Santacruz et al. 1989a). Consequences of this overuse are now evident, so that the contrast between excluded and grazed conditions is sharp at the La Presa site.

Above ground production was found to be much higher for excluded conditions (1303 kg DM ha⁻¹) than for grazed areas (252 kg DM ha⁻¹; Aguado-Santacruz et al. 1989b). Diversity (H') was lower under grazing due to both *Haplopappus venetus* dominance and low plant density at La Presa site. Conversely, diversity was higher under grazing at the other three sites (Aguado-Santacruz 1987; Aguado-Santacruz et al. 1989a). Grazing can increase plant diversity (Watt 1957; Thomas 1960; Johnston 1961; Duffey et al. 1974; García 1988; Aguado-Santacruz & Fierro 1988; Molina 1990), however if prolonged intensive grazing persists, a general decrease in plant

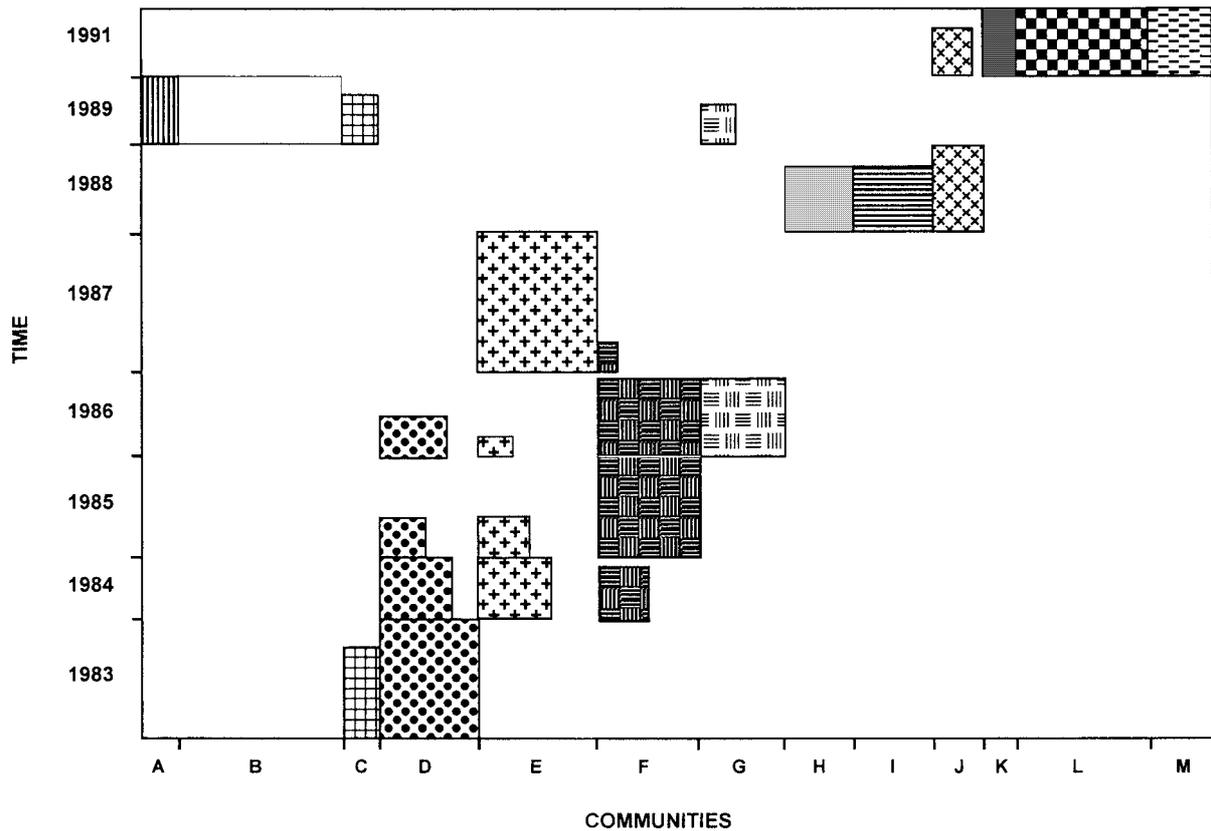


Figure 7. Community spatio-temporal relationships at the La Mesa site obtained as the relative frequency of a given community as related to: (a) study period (time), and (b) all plant assemblages present for a particular year (communities).

density occurs, followed by a reduction in diversity (Aguado-Santacruz 1994).

Indicator species identified by TWINSPLAN agreed quite well with field observations and results from other studies. For example, it is well-known that the half-shrub *Haplopappus venetus* increases under over-grazing on the southernmost part of the Mexican High Plateau (Arredondo 1982). On the other hand, increase in moss carpets under grazing exclusion (Turner 1971; Rice & Westoby 1978; Kleiner 1983) is also well documented. These observations were clearly confirmed by the La Presa site classification.

A more heterogeneous vegetation was observed at La Colorada's shrubland. Shrub invasion favors the formation of islands of fertility under the canopies of these plants (García-Moya & McKell, 1970), leading to an increase in the spatial and temporal heterogeneity of soil resources in former grassland (Schlesinger et al. 1990). Failure to detect a rain induced community differentiation at the La Colorada site suggests that complete site dominance by long-lived perenni-

als can prevent the climate-driven interannual floristic fluctuation typical of herbaceous-dominated semiarid systems (Rabotnov 1985). It was not possible to distinguish wet year from average precipitation or dry year communities at the La Colorada site due to a relatively even distribution of plant assemblages in both time and space. Some assemblages were year specific ('I', 'K', 'L', and 'P' communities; Figure 9), but their appearance could not be explained by the rainfall patterns. In particular, the 'P' community was characteristic of a rainy year (1991) but it only included one transect (Figure 8). Conversely, sixteen and seventeen transects represented the rainy plant assemblages for La Mesa and Vaquerias sites, respectively (Figures 4 and 6).

This floristic stability found at La Colorada site was, in part, a function of the shrubby component of the vegetation. In our previous work using partial canonical correspondence analysis (Aguado-Santacruz & García-Moya 1998), we could not correlate temporal floristic change with weather (summer precipitation) at this site as we did at the other three

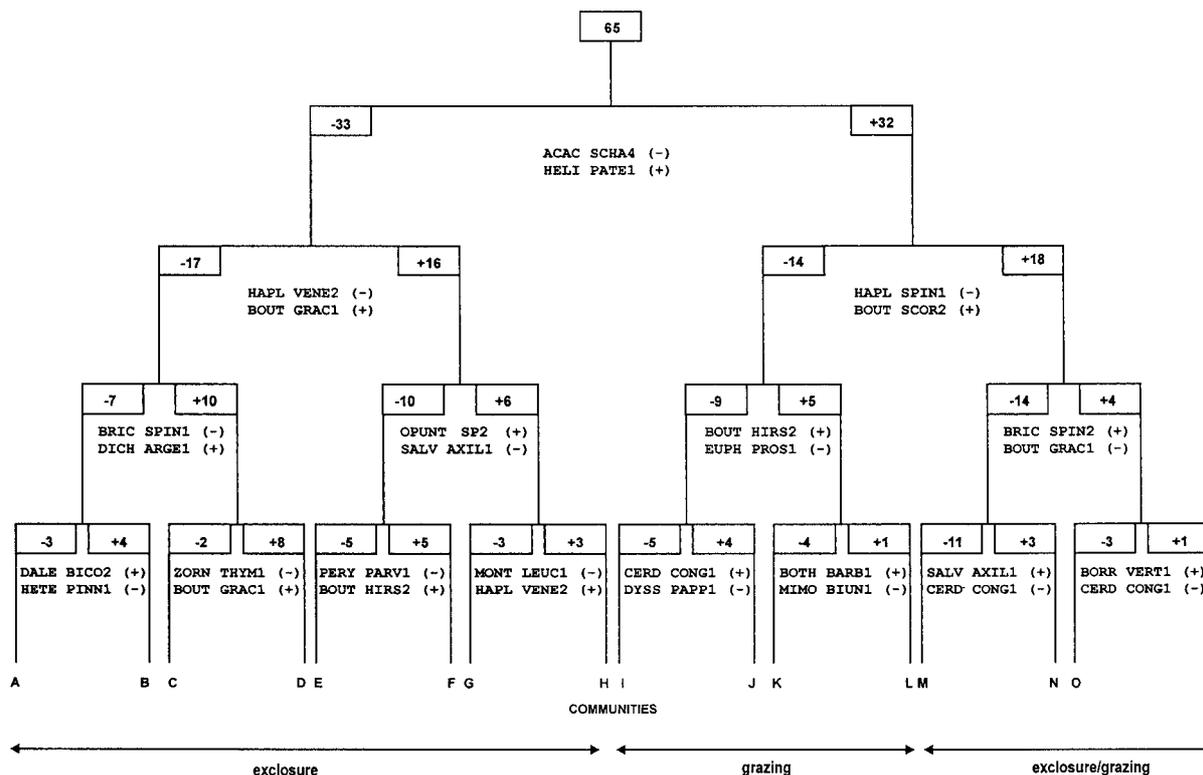


Figure 8. La Colorado site classification. Acronyms of species are: ACAC SCHA, *Acacia schaffneri*; BERR VERT, *Borreria verticillata*; BOTH BARB, *Bothriochloa barbinodis*; BOUT GRAC, *Bouteloua gracilis*; BOUT HIRS, *Bouteloua hirsuta*; BOUT SCOR, *Bouteloua scorpioides*; BRIC SPIN, *Brickellia spinulosa*; CERD CONG, *Cordia congestiflora*; DALE BICO, *Dalea bicolor*; DICH ARGE, *Dichondra argentea*; DYSS PAPP, *Dyssodia papposa*; EUPH PROS, *Euphorbia prostrata*; HAPL SPIN, *Haplopappus spinulosus*; HAPL VENE, *Haplopappus venetus*; HEMI PATE, *Helianthemum patens*; HETE PINN, *Heterosperma pinnatum*; MIMO BIUN, *Mimosa biuncifera*; MONT LEUC, *Montanoa leucantha*; OPUNT SP, *Opuntia* sp.; PERY PARV, *Perymenium parvifolium*; SALV AXIL, *Salvia axillaris*; ZORN THYM, *Zornia thymifolia*. Cover categories as in Figure 1.

sites. In a ten-year study conducted at La Colorado exclosure, Aguado-Santacruz et al. (1990) found no significant differences in among-year cover and basal diameter for the main herbaceous and shrubby species, nor in bare ground and litter accumulation, i.e., vegetation of this shrubland remained essentially without change during the 10 year study. Although some plant assemblages could be year-specific, they may be the product of environmental factors (biotic or abiotic) not necessarily correlated to rainfall.

Undoubtedly shrubs exert fundamental direct and indirect effects on the herbaceous component of vegetation altering its abundance and spatial distribution pattern. Shrubs create microclimatic conditions differing from open areas and favor the establishment and growth of certain species or even the arrival of small herbivores, which in turn can modify vegetation patterns and development (Hobbs & Mooney 1986). Islands of fertility affect the distribution of soil mi-

crobial populations (Herman et al. 1995) and there is increased rainfall infiltration beneath shrubs due to an increase in canopy interception by and stem-flow from these plants (West & Gifford, 1976; Mauchamp & Janeau 1993). Reynolds et al. (1999) found evidence suggesting that *Prosopis glandulosa* and *Larrea tridentata* islands of fertility can reduce the impact of drought periods on cover of plants associated with these shrubs, which supports our findings.

One of the most evident shrub effects on soil and floristic spatial patterns is related to litter accumulation. Most important debris accumulation areas at La Colorado are located under the crowns of *Acacia schaffneri* (Aguado-Santacruz 1987; Aguado-Santacruz et al. 1989a). This has drastic effects on community spatial heterogeneity because few species can grow beneath this shrub due to both litter layer thickness and shade. Among those plants whose distribution is restricted to these sub-canopy areas are *Ox-*

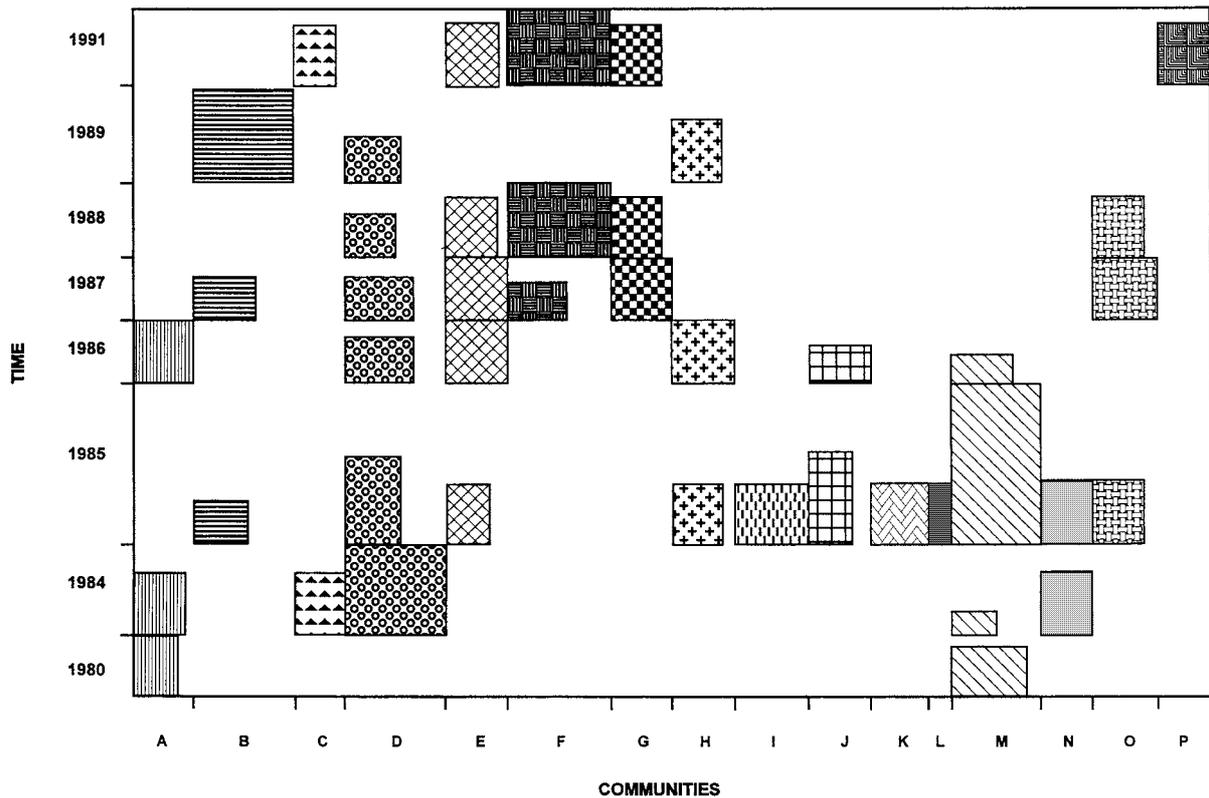


Figure 9. Community spatio-temporal relationships at the La Colorada site obtained as the relative frequency of a given community as related to: (a) study period (time), and (b) all plant assemblages present for a particular year (communities).

alis corniculata, *Selaginella rupicola*, *Chenopodium graveolens* and *Montanoa leucantha*. Hobbs and Mooney (1986) found that cover of herbaceous species was low under the shrub *Baccharis pilularis* and in a zone 50 cm out from the edge of the canopy. They also mentioned a drop in biomass of herbaceous species from 490 to 60 g m⁻² due to the effect of this shrub's invasion of California grassland. In brush control studies under exclosure conditions, Aguado-Santacruz et al. (1990, 1989c) reported an almost three-fold decrease in grass cover, and a 73% reduction in grass production, due to the shrubby component in the *Acacia schaffneri*-dominated shrubland of the La Colorada site.

Other effects of shrubs on soil spatial heterogeneity are less obvious. García-Moya and McKell (1970) and West and Skujins (1977) noted the effect of shrubs on soil nitrogen distribution in desert and semi-desert communities, respectively, while Tiedemann and Klemmedson (1973) observed that litter and soluble salts accumulations were higher under a *Prosopis* species than in the areas outside of their canopy in-

fluence. Allelopathic compounds released by some shrubs are also known to have a strong influence on spatial pattern of vegetation (Mueller 1966; 1969).

The soil classification did not correspond with our global floristic classification (Aguado-Santacruz & García-Moya 1998) which, as discussed previously, progressively showed the effects of management, site and time. Broadly, La Presa (exclosed) and La Mesa (exclosed and grazed) sites were grouped separately from La Presa (grazed), Vaquerías (exclosed and grazed) and La Colorada (exclosed and grazed) sites. Conversely, the UPGMA classification, in general terms, grouped together La Mesa and La Colorada soils separating them from La Presa and Vaquerías soils (more details given below).

As expected, floristic heterogeneity was related to soil heterogeneity at the La Colorada site (Figure 10). Shrubs and sediment deposition could contribute to this variability in edaphic characteristics. In our earlier work (Aguado-Santacruz & García-Moya 1998), we found sand percentage in soil to be an important edaphic variable within the La Colorada or-

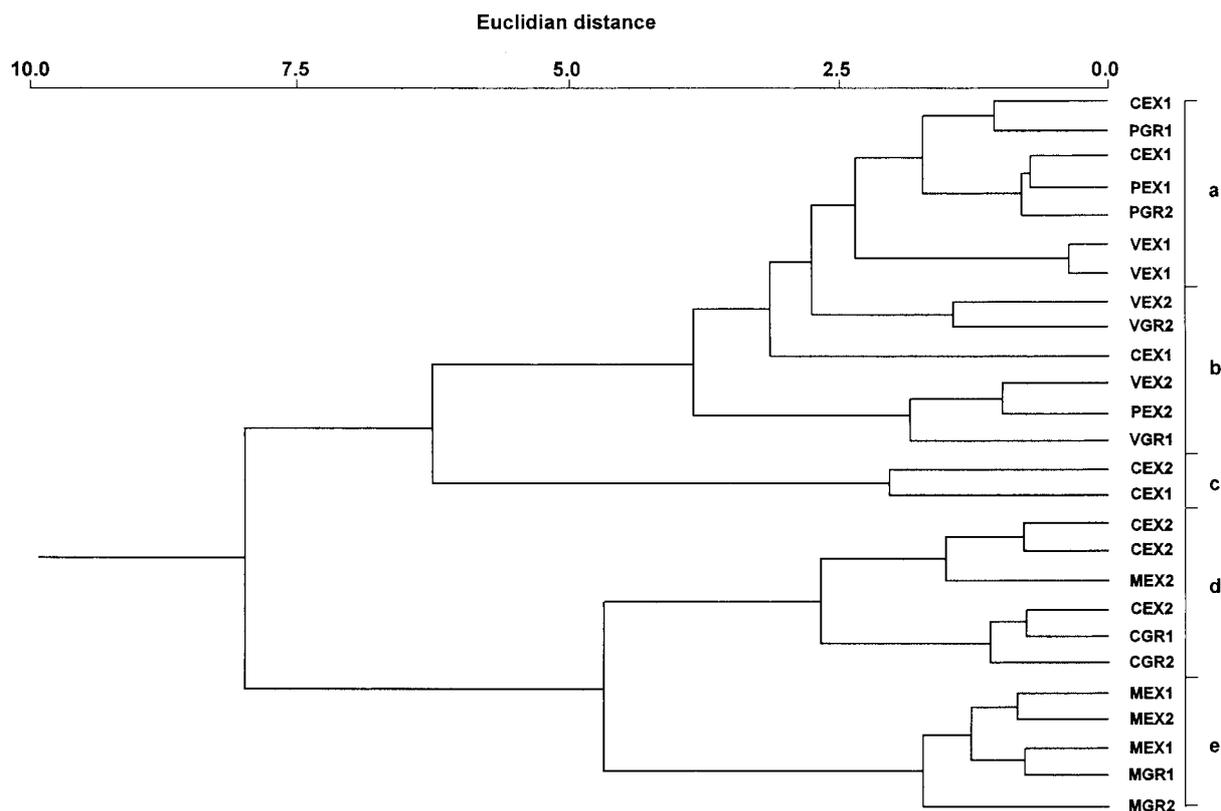


Figure 10. Soil classification obtained by UPGMA from an Euclidian distance matrix of first two soil horizons of sites. Samples labeled in accordance with the following codes. First three letters indicate site (V, Vaquerías; M, La Mesa; C, La Colorada; and P, La Presa site) and pasture management (EX, grazing exclosure; GR, grazing). Digits represent soil horizon (1 = A, and 2 = B). Cophenetic correlation coefficient = 0.759.

dination analysis. Alluvial deposits at La Colorada coming from neighboring hills were evident in both the soil profile description and the soil samples. Consequently, some samples from La Colorada showed more similarity with soils from the other three sites.

Cartography from CETENAL (1973a, b) indicated Haplic phaeozem or Xerosol as the predominant soil types for Vaquerías, La Mesa and La Presa, and Eutric fluvisol for La Colorada. Surprisingly, the soil from the open grassland of La Mesa, a *Bouteloua gracilis* community with a long history of proper management, showed more similarity to the soil of the shrub-invaded rangeland of La Colorada, than with soils from the other two grasslands. However, this analysis was based on the first two horizons; a third well-defined horizon at 59–77 cm depth at the La Colorada site was not considered in the soil classification. The presence of this extra horizon is assumed to profoundly affect plant-soil relationships and may be a condition for

successful establishment and propagation of *Acacia schaffneri*.

Prior land tillage at Vaquerías and La Presa sites could also contribute to the separate clustering of La Mesa and La Colorada soils. This manipulation was evident in soil profile descriptions and it could date from at least 74 years before soil sampling for this study, when these sites were used for corn production (Aguado-Santacruz 1987). McIntyre and Lavorel (1994) found that soil disturbance had the most influential role in shaping community structure in temperate grasslands, with grazing and water making similar contributions to variation in species composition. Time since soil disturbance at Vaquerías and La Presa sites was probably long enough to allow recovery of vegetation, as edaphic influences were found to play a lesser role than weather and grazing impact.

In this and earlier work (Aguado-Santacruz & García-Moya 1998) we have explored the relative importance of environmental factors in shaping com-

munity structure and composition of grasslands over time. In the Mexican semiarid grasslands located at the southernmost part of the North American *Graminetum*, weather (summer precipitation) is the fundamental force driving temporal floristic change when influences from other factors such as grazing, soil disturbance or the presence of shrubby components are not too extreme. Thus, weather effects on vegetation should never be defined without reference to these factors. The effect of environmental factors on floristic variation is expected to be a function of their relative intensities and complex biotic and abiotic interactions.

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