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MAJOR VEGETATIONAL TRENDS RELATED TO RELIEF AND HYDROLOGY IN THE MAR CHIQUITA WETLANDS

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Abstract. Spatial variation of vegetation was analyzed in relation to the hydrological and geomorphological features of the Mar Chiquita Depression. Sampling was made at 30° S along an E-W transect of nearly 100 km length. Elevation, water table depth, conductivity and the presence of surface water were considered to provide an environmental description of the variability of vegetation. The floristic analysis shows a major trend from hygro-halophyllous grasslands and prairies, through halophyllous scrublands, xero-halophyllous woodlands and xerophyllous forests along an increasing elevation gradient, positively correlated with the first ordination axis. This trend is opposite to that of water influence. The vegetation also has a secondary trend in variability, related to local heterogeneity in relief and water dynamics. There are sharp floristic and physiognomic changes between the margins and lower areas of the depression, and inside, between upper and shallow zones. The textural complexity, species richness and life forms have shown hydro-topographic variation trends. The higher diversity value was detected in middle elevations, and greater local variability at the lower end. From these results some hypotheses on dominant processes shaping the plant communities are suggested.

Resumen. La variación espacial de la vegetación fue analizada en relación a la heterogeneidad hidro-geomorfológica de la depresión de Mar Chiquita. Los censos florísticos fueron realizados a 30 °S, a lo largo de una transecta E-W de 100 km. La altura sobre el nivel del mar, la profundidad de la freática, la conductividad y la presencia de agua en superficie fueron considerados para la interpretación ambiental de la variabilidad de la vegetación. El análisis florístico muestra una tendencia principal de variación desde praderas y pastizales halófilos e higrófilos, hacia matorrales halófilos, bosques xero-halófilos y bosques xerófilos a lo largo de un gradiente de elevación, positivamente correlacionado con el primer eje de ordenación. Dicha tendencia es opuesta a la de la influencia hídrica. La vegetación muestra una variabilidad secundaria, presumiblemente relacionada con la heterogeneidad local del relieve y con el dinamismo hídrico. Se observan cambios fisonómicos y florísticos nitidos entre los márgenes y zonas más bajas de la depresión, y entre las zonas relativamente elevadas y las saturadas. La riqueza de especies, la complejidad estructural y las formas de vida muestran una tendencia hidro-topográfica. Los valores máximos de diversidad se presentan en puntos intermedios del gradiente de elevación, y la mayor variabilidad hacia el extremo inferior. A partir de estos resultados surgen algunas hipótesis relativas a los procesos dominantes que estructuran las comunidades en el área estudiada.

Introduction

The spatial variation of vegetation in periodically flooded inland areas has been a matter for investigation for a long time. Common environmental features of these wetlands are the highly variable soil-salinity and seasonal and yearly hydric variability. Some vegetation types remain under water during the rainy season, followed by periods of desiccation.

Many authors report the influence of these environmental features on vegetation structure, and describe its variability along topographic and edaphic gradients (Malmer 1986, Lewis *et al.* 1990, Carnevale *et al.* 1987, Dirschl & Coupland 1972, Burchill & Kenkel 1990, Roberts & Robertson 1986), as well as along groundwater flow patterns interacting with superficial flows and with relief (G. Bernaldez *et al.* 1985, 1987, G. Bernaldez & Montes 1989, Shay & Shay 1986, Wassen *et al.* 1989, Rey Benayas *et al.* 1990, Rey Benayas & Sheiner 1993, Wassen & Barendregt 1992, Glaser *et al.* 1981).

Earlier studies in the region give physiognomical descriptions at large scale, based on visual inspection, aerial photographs and satellite images (Luti *et al.* 1979, Sayago 1969, Herrera & Orueta 1981, Menghi *et al.* 1991). In these works relationships between vegetation variability, geomorphological gradients, soil salinity and flooding are described, but none have been based on quantitative approaches nor have used multivariate analysis to detect vegetation types and trends of spatial variation.

Fernandez *et al.* (1992) have recently delimited environmental units according to geomorphology, and regional, intermediate and local systems of water recharge and discharge. Differences in substrate nature and in the length of underlying flows between west and east zones from river course were also considered.

The aims of this study were:

1) to detect the major spatial vegetation patterns related to hydro-geomorphological variation in the Mar Chiquita depression,

2) to analyze structural and floristic changes on a coarse grain scale, and

3) to suggest biotic and abiotic processes affecting the structural organization of plant communities.

Study area

The study area lies in the Mar Chiquita Depression northeast Córdoba province (Argentina, Fig. 1). The depression is a flat plain, 90-100 km wide between its eastern ("Bordo de los Altos") and western ("Barranca del Saladillo") limits. It rises to 70 m.a.s.l. with a southward gently sloping topography (9 m/100 km).

The lowest area is occupied by the Mar Chiquita Lagoon; a huge inland water body, shallow and saline, with a surface varying from 100.000 to 600.000 ha depending on season. Its expansion or retraction affects mainly the northern areas.

The depression is seasonally flooded by regional discharge (Sali-Dulce river basin) and underlying flows. Pineda (1991), Pineda *et al.* (in press) and Fernandez *et al.* (1992) provide a description of the environmental features. The following characteristics are pointed out. The climate is temperate and subhumid. The mean temperature is 25°C in January and 10°C in July. There is water deficit (100-200 mm) at the end of summer. Mild winters are characteristic. Rain falls in summer; the mean value increases from west (594 mm) to east (845 mm).

The sediments are fluvio-lacustrine in origin on which strongly halo-hydromorphic, poorly drained soil develops. The river has changed its course many times, and reshaped the surface. The former river beds remain as narrow linear depressions relatively elevated by sediment deposits. Slightly elevated plain areas, temporary flooded small depressions and permanent shallow lagoons are also common. The flood-

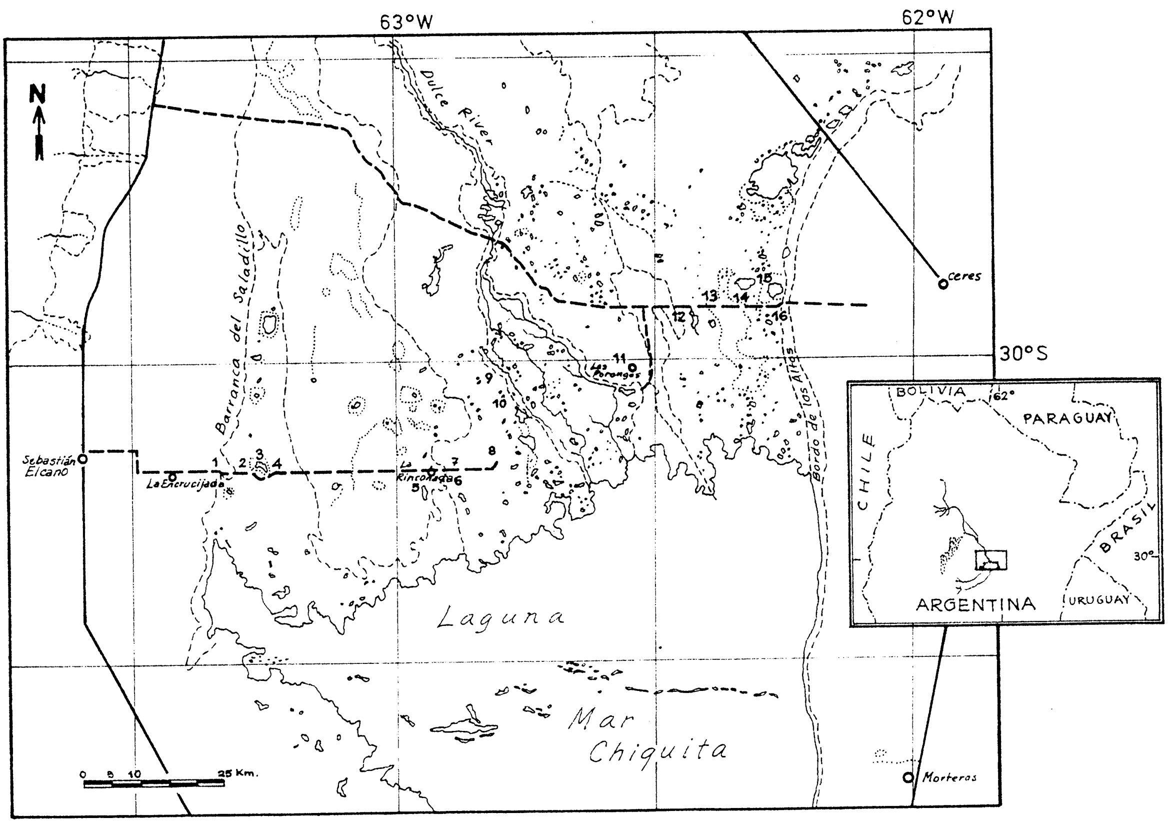

Figure 1. Study area. The numbers indicate sites sampled. The hydrological and relief conditions follow Fernandez et al. (1992). Legend: Regional recharge in western margin (21). Regional discharge on inclined planes slightly elevated (2, 4). Regional discharge on temporary ponds, out of current river floodplain (3). Regional discharge with local recharge, over plain areas slightly elevated (1, 6, 11). Regional discharge with temporary fluvial recharge, over second flooding level. Plain areas (7, 8), and shallow lagoons (14, 15, 17). Regional discharge with maximun fluvial recharge over first flooding level. River bank (9, 20, 19); temporary ponds (10, 12, 13). Intermediate discharge (16). Intermediate recharge, with lineal recharge, in eastern margin (18).

drought cycles vary between years. The residence time and dynamics of surface water vary also, according to relief.

The vegetation is basically halophyllous: shrublands, grasslands, rush communities and low prairies are common, while trees are scarce. The phytogeographical aspects have been discussed by others (Kurtz 1904, Parodi 1945, Cabrera 1953, Morello 1958, 1968, Sayago 1969, Ragonese & Castiglioni 1970, Luti *et al.* 1979, Lewis *et al.* 1990). Most of the authors consider the area as a transition, with a mix of global chacoan and pampean components.

The most common land-use is cattle, horse and sheep grazing over native vegetation. Itinerant burning is practiced to improve forage quality. Human settlements and roads are scarce. Landscape and native fauna give a unique natural environment for scientific work.

Methods

Sampling

The field sample comes from 30° S from a W-E transect 100 km long. The elevation range is from 72.5 to 94 m.a.s.l.

Twenty one sites were analyzed from the depression margins towards the Dulce river course. Ten of these represent elevated areas with no or occasional fluvial influence (sites # 1, 2, 4, 5, 6, 8, 11, 16, 18, 21), and eleven (sites # 3, 7, 9, 10, 12, 13, 14, 15, 17, 19, 20) with river flooding and greater groundwater influence (Fig. 1).

Three stands, homogeneous with respect to plant physiognomy, were selected within each site, avoiding the proximity of roads and recent disturbances such as fire and grazing. Woody and herbaceous communities were sampled fulfilling for each one the minimal area criterion. In each stand the woods were analyzed in five 16 m^2 randomly placed quadrats. In the almost pure populations of grass species, forbs and rushes of lower areas, ten 1 m^2 plots were used. In total 495 plots were recorded during the dry period (springs 1991, 1992 and 1993) when all units were accessible.

The vegetation relevés used the six point cover-abundance scale (Mueller-Dombois & Ellenberg 1974). The scores were replaced by the average class values for numerical analysis. Plant life-form (*sensu* Raunkiaer), cover and height of the dominant layer were also recorded.

Conductivity and water table depth values were taken from previous studies (Fernandez *et al.* 1992). The flooding frequency was calculated from a temporal sequence of satel-

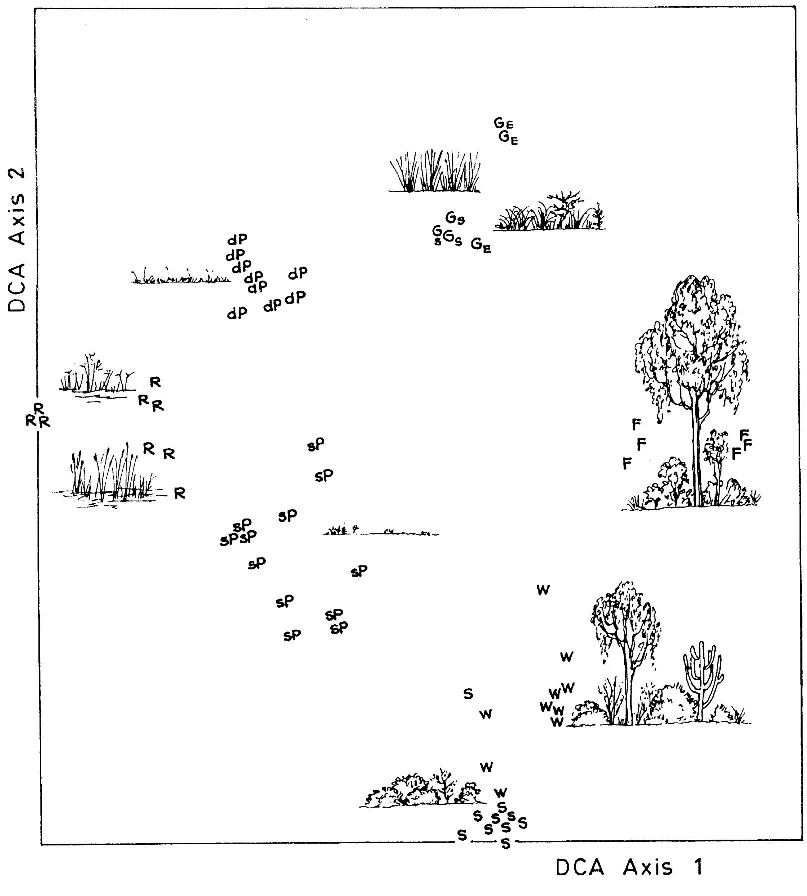

Figure 2. DCA of 63 relevés from the 21 sites sampled. The first axis accounts for 45% and the second for 36% of the total variation. I. Hygro-halophyllous herbaceous communities: R: "totorales" of *Typha latifolia*, "uncales" of *Scirpus californicus* and *S. americanus*. dP: low dense prairies of *Cynodon dactylon* and *Distichlis spicata*. sP: low sparse praires of *Salicornia ambigua, Sesuvium portulacastrum, Cressa truxillensis*. G grasslands tall sized, dominated by *Spartina argentinensis*(Gs), or *Elyonurus viridulus* (Ge). II. Halophyllous succulent scrublands: S: *Allenrolfea vaginata, A. patagonica, Cyclolepis genistoides, Atriplex cordobensis, Prosopis reptans, Lycium spp.* III. Xerophyllous, low open woodlands with halophyllous shrubs: W: *Zizyphus mistol, Prosopis nigra, Celtis spinosa, Jodina rhombifolia, Larrea divaricata, Opuntia quimilo, Condalia microphylla, Allenrolfea* spp., *Lycium spp. IV.* Xerophyllous, tall closed forest: F: *Aspidosperma quebracho-blanco, Bumelia obtusifolia, Z. mistol, Prosopis alba, P. sericantha, Cereus coryne, Geoffroea decorticans.*

lite images, and the altitude above sea level from topographic charts.

Data analysis

A data matrix of 151 spp x 63 relevés was analyzed, removing rare species for multivariate analysis. Detrended correspondence analysis (DCA, Hill & Gauch 1980) and TWINSPAN (Hill 1979) were used to detect the major trends and to pick out major groupings. The vegetation and environmental relationships were analyzed using correlations with DCA ordination axes on elevation, water-table depth, flooding frequency and conductivity values.

The vegetation textural changes of the groups were described by the average number of plant species (S), Shannon-Wiener diversity index (H') and evenness (E). For other numerical exploration the Wildi & Orlóci (1990) program package was used.

Dominant life strategies were studied through biological spectrum, using both the number and the relative abundance of species within each life-form.

Results and discussion

Physiognomic and floristic analysis

The first two axes of DCA (81% of total variance, Fig. 2) point up a major vegetation trend from the lowest and more humid areas to those drier and elevated. A main mosaic pattern is displayed, although a continuous variation is recognized within major groupings.

The data structure shows a complex pattern, which suggests the interference of frequency of hydrological procceses operating at different spatial and temporal scales (Allen 1987).

The first axis is significantly correlated with elevation ($r=0.76$, $p\leq..0005$), water-table depth ($r=0.92$, $p\leq0.0001$), and with flooding frequency ($r=-0.84$, $p\leq..0001$). When these environmental variables are plotted over the vegetation ordination, a correspondence of vegetation pattern with a regional trend in hydrological and topographic spatial variation is observed (Fig. 3).

There is no clear trend in conductivity variation along the major elevation gradient. The variable land-form and related water level fluctuation and salt concentration account for much of the local vegetation variability detected by the second axis, within definite elevation ranges.

Table 1 provides plant species composition and their constancy in the detected groups.

Sharp floristic changes are detected between the margins and lower areas, and inside the depression between lower and relatively higher areas. Halophyllous and hygro-halophyllous plant species restricted to the depression, as well as the glicophyllous salt tolerants (Fig. 4) identify ranges in the

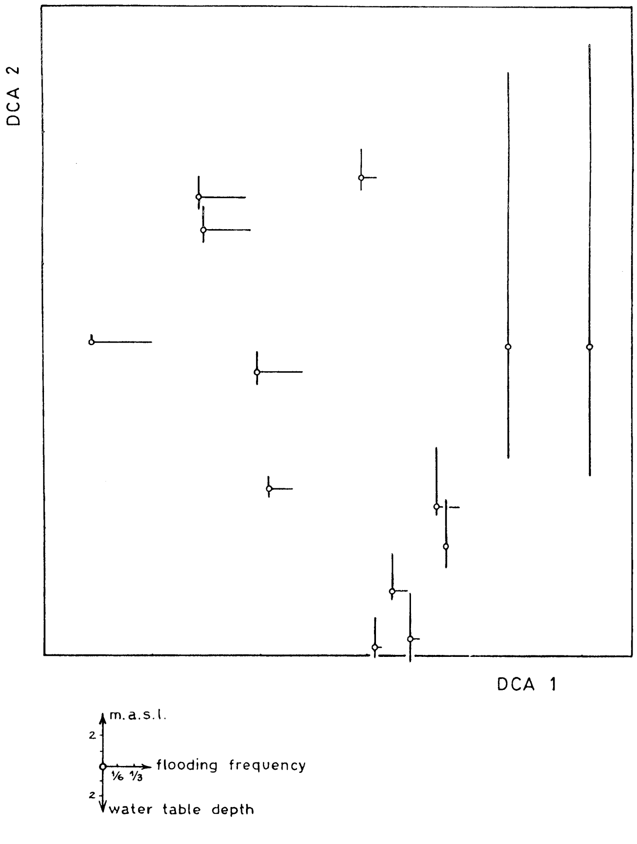

Figure 3. Correlation of environmental variables with DCA axes. Line lengths are proportional to the magnitude of frequency. A complex elevation-moisture gradient from lower periodically flooded areas (left) towards drier, elevated margins is apparent.

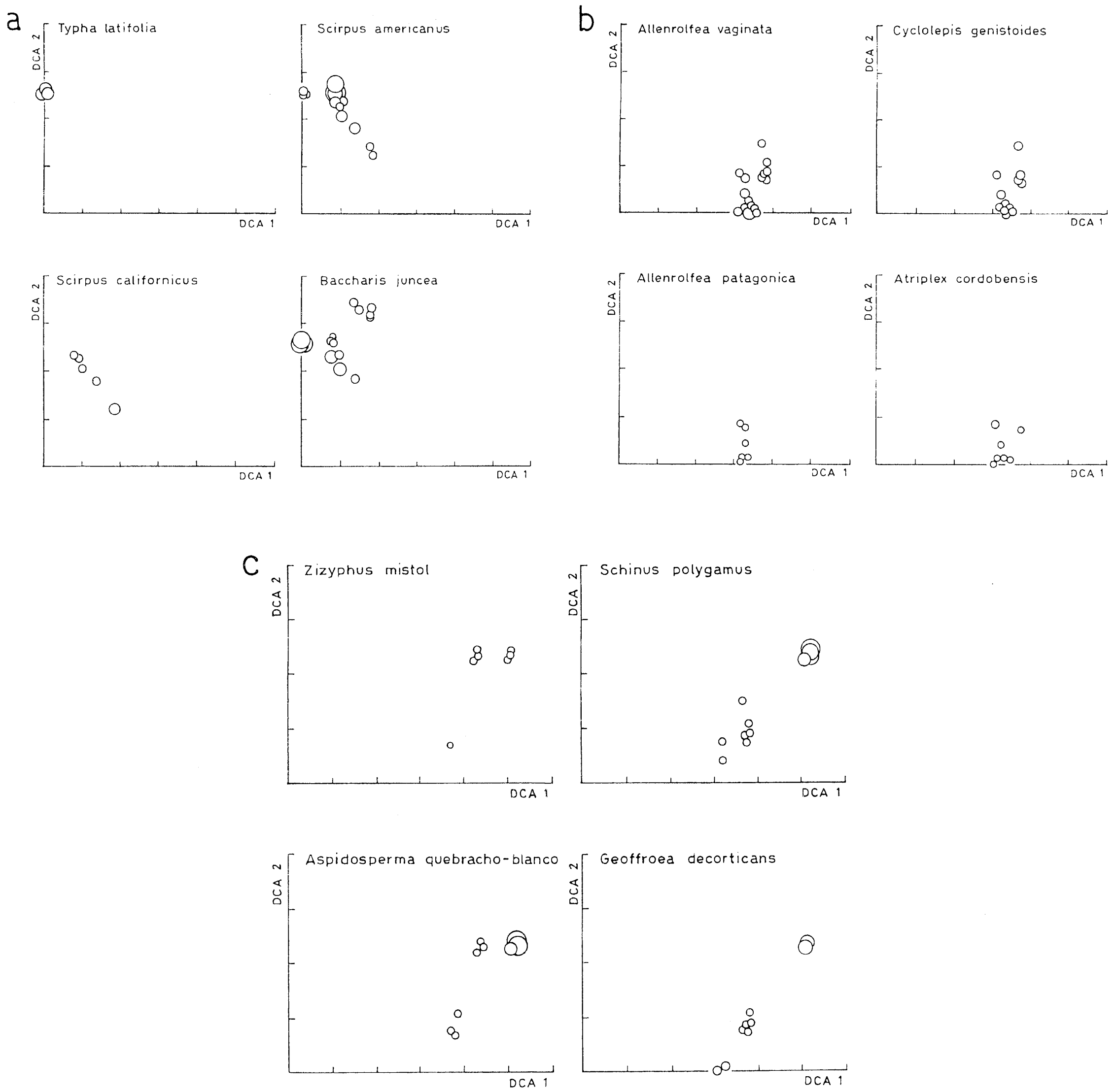

Figure 4. Abundance of plant species associated with definite ranges of the moisture-elevation gradient, given by species in the DCA ordination diagram. The size of the circles is proportional to abundance. Small circle: up to 5 %;medium circle: 5 to 50 %; large circle: over 50 %. a: Hygro-halophyllous plant species restricted to humid, lower areas. b: Halophyllous plant species restricted to elevated areas inside the depression, greatly affected by water-table. c: Xerophyllous plant species tolerant to low salinity and mesic conditions of elevated areas inside the depression.

elevation-moisture gradient. Eight dominant plant physiognomy types were detected. These show variation in plant cover. Canopy height, average number of species (Table 1) and variety of life forms (Fig. 5) increase from humid to dry ends. The herbaceous vegetation fully dominates the current floodplain (sites #7, 9, 10, 12, 13, 14, 15, 17, 19, 20), and cover greater areas eastward from the river course.

Associated with distinct local relief and water influence, rush and sedge communities (R), low density (dP) and sparse prairies (sP) and tall grass communities (G) can be discerned (Fig. 2). There are hygro-halophyllous plant-species, exclusive to this portion of the moisture-elevation gradient (Fig. 4a).

Halophyllous succulent scrublands (S) are the typical vegetation associated with elevated areas of middle topography, occasionally subject to river flooding, but greatly affected by water table rise at or near the surface (sites # 2, 4,

Table 1. Structural features and floristic composition of groups detected by DCA (Fig. 2). Roman numerals (I-IV) refer to the constancy class scale of Braun-Blanquet (1950).

	HUMID LOWER ZONES				MESIC UPPER PLAINS			DRY MARGINS
Altitude range (m.a.s.l)	72.5 to 74.0				74.0 to 76.0			76 to 94
Sample sites (Fig. 1)	13 14 17	9 19 20	3 10 12 15	7	6	2 4 8 5	11 1 16	18 21
No. sample plots	90	90	120	30	30	60	45	30
Physiognomic group	R	dP	sP	Gs	Ge	S	W	F
Canopy height (m)	1.8	.15	.15	1	.65	1.5	6	8
Canopy cover (%)	100	90	30	100	100	70	80	100
S	5 to 9	11 to 19	4 to 9	6	20	16 to 20	19 to 37	23
E	.201 to .631	.404 to .716	.615 to .827	.183	.446	.871 to .875	.812 to .993	.383 to .911
H'	.359 to 1.330	.937 to 1.612	1.075 to 1.363	.376	1.376	2.425 to 2.644	2.400 to 3.351	1.195 to 2.835
Scirpus californicus	II							
Typha latifolia	II							
Scirpus americanus	V							
Baccharis juncea	V	III						
Chenopodium macrospermum	IV	V	V	II		I		
Distichlis spicata	IV	V	III	II		II		
Malvella leprosa		II	I					
Melilotus indicus		IV						
Frankenia pulverulenta		IV	III					
Ambrosia tenuifolia		IV						
Aster squamatus		V						
Polypogon monspeliensis		III						
Diplachne univervia		III	I	IV				
Spergularia levis		IV	I					
Eleocharis macrostachya		II						
Polygonum aviculare	II	IV	III			I		
Rumex obtusifolius		V	I					
Lepidium bonariense		V						
Cynodon dactylon	IV	V	II		IV		II	
Sesuvium portulacastrum	II		V	II			III	
Spartina argentinensis				V		III	III	
Salicornia ambigua	V	III	V	IV		IV	IV	
Heliotropium curassavicum		III	II				II	
Cressa truxillensis	II	II	IV	V		III		
Petunia parviflora		II				I		
Boopis anthemoides		IV			V	I	V	
Sphaeralcea miniata			III		IV	II		II
Sporobolus phleoides			III		V	II	II	
Phyla canescens		III			IV		III	
Baccharis salicifolia						II	I	
Bothriochloa saccharoides						II		
Holocheilus hieracioides						III	II	
Allenrolfea patagonica						I	II	
Lepidium aletes						III		
Lycium americanus						I	II	
Parietaria debilis						IV	IV	I
Atriplex cordobensis						IV	III	
Lycium infaustum						III	II	
Harrisia pomanensis							III	
Lippia salsa						III	V	I
Cyclolepis genistoides						V	IV	
Allenrolfea vaginata						V	V	
Sporobolus pyramidatus					II	II	II	
Prosopis reptans					V	V	II	

	HUMID LOWER ZONES				MESIC UPPER PLAINS			DRY MARGINS
Physiognomic group	R	dP	sP	Gs	Ge	S	W	F
Aloysia gratissima						I	II	
Hybanthus parviflorus						I	II	
Spergularia marina						I	III	
Mollugo verticillata							IV	
Parthenium hysterophorus						I	II	
Larrea divaricata							II	
Leptoglossis linifolia						III	III	
Cleistocactus baumanii						II	II	I
Lycium chilense						I	III	
Opuntia quimilo						I	IV	
Schizachyrium microstachyum					IV	II		
Trichloris crinita				IV	V	IV	V	I
Plantago myosuros		II			V	V	IV	
Ruellia tweedi					V			
Heimia salicifolia					V	II		I
Euphorbia serpens					IV	I		
Eragrostis lugens					VI		II	
Elyonurus viridulus					V	I		
Cardus sp.						II		I
Geoffroea decorticans						III	II	II
Grabowskia duplicata						III		I
Maytenus vitis-idaea						IV	IV	III
Setaria spp.						V	III	III
Prosopis nigra							II	III
Relbunium bigeminum						II	II	II
Clematis sp.						II	I	I
Cortesia cuneifolia						I	III	II
Pappophorum mucronulatum						IV	I	III
Gnaphalium sp.			II			III	IV	
Stipa eriostachya							II	III
Prosopis sericantha							II	III
Cereus coryne							II	II
Bothriochloa laguroides					V		II	III
Solanum pygmaeum							II	
Ephedra triandra							II	
Lycium tenuispinosum							III	III
Gamochaeta sp.						II		III
Passiflora mooreana					IV			
Bumelia obtusifolia								III
Maytenus spinosa								IV
Zizyphus mistol							I	V
Solanum glaucum								V
Celtis spinosa								V
Condalia microphylla							I	III
Jodina rhombifolia							I	V
Prosopis alba								III
Capsicum chacoense							I	III
Capparis atamisquea							II	IV
Porliera microphylla							I	V
Aspidosperma quebracho-blanco							II	V
Dichondra microcalyx								III
Oxalis sp.							I	III
Rhynchosia senna							II	III
Chaptalia nutans						II		III
Schinus polygamus						II	III	III

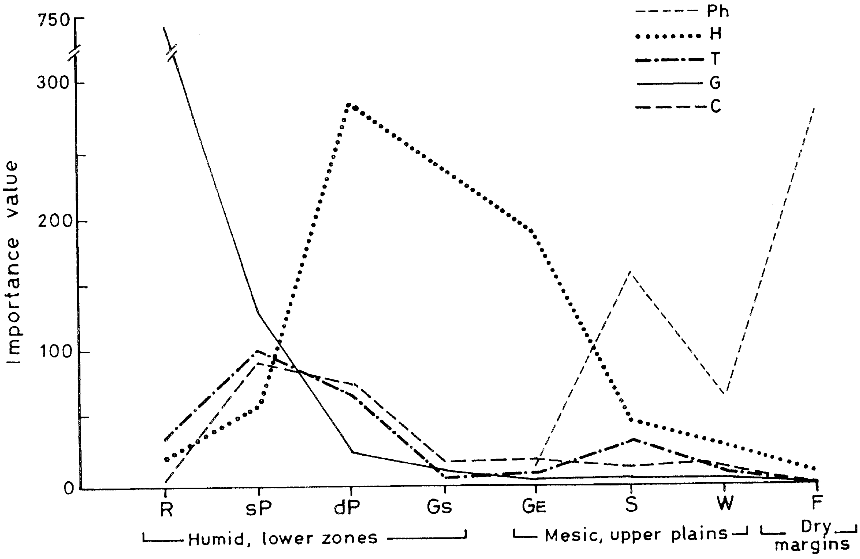

Figure 5. Life forms spectra of humid, mesic and dry sites. Legend: P phanerophytes; H hemicriptophytes; T terophytes; G geophytes; C chamaephytes. The importance value was calculated by summing up average cover values (5=87. 5; 4=62. 5; 3=37. 5; 2=15; 1=3; +=0, 5) for species, in all samples of each physiognomic group.

8). Most of the dominant shrub species are restricted to these environmental conditions (Fig.4b).

Xero-halophyllous, low open woodlands (W) cover plane areas, relatively high and with deeper water table (rising up to 1 m, sites # 1, 5, 11, 16). Many xerophyllous "Chaco" plant species (*A. quebracho-blanco; Zizyphus mistol; Geoffroea decorticans; Schinus polygamus*; etc.) tolerant to mesic and low saline conditions, enter into the depression through these areas (Fig.4c), and coexist with succulent halophyllous species. Also, a typical "Monte" floristic component (*Larrea divaricata*) occurs.

The low woodlands are well represented in areas of reduced extent in the depression, locally named as islands: "Isla de los Chorros" (point 1, Fig. 1), "Isla Negra", "Isla Larga", "Isla Grande" and "El Mistolar", which stand out over the surrounding halophyllous grasslands or shrublands, northward and southward of the transect.

Xerophyllous, closed forests (F) characterize the depression margins. These are elevated areas, up to 94 m.a.s.l., never flooded, and with ground water table at a depth of 7 to 8 m (sites # 18, 21). The dominant plant structure corresponds to a "Chaco" forest with lower height and impoverished in tree species. The results indicate no influence of soil salinity and watertable on the floristic composition. In agreement with Sayago's (1969) descriptions, some floristic and structural differences were detected between the forests on the two margins. Our results show the same floristic average richness (23), but on the eastern margin a higher dominance was found (E .383).

In the "Barranca del Saladillo" margin (over 500 mm of rainfalls), the forest, although lower in tree height, showed floristic similarity to the mesic end of the pluviometric gradient described by Cabido *et al.* (1993). While in the "Bordo de los Altos" (845 mm) *Bumelia obtusifolia* and *Trithrinax campestris* were present, they were absent in our sample sites of the occidental margin.

We believe that the pluviometric increment from west to east, as well as human use outside the depression, could have influenced the forest structure. More detailed and extensive sampling would be required to elaborate this point further.

Diversity patterns and life forms spectrum

The results in Table 1 indicate a decreasing trend in species richness and evenness toward the lower areas, and some variability within physiognomic groups. The greater diversity values correspond to middle elevations with mesic conditions (sites # 1, 5, 11, 16). These areas concentrate 60% of the recorded species, representing a mixture of xerophyllous and halophyllous componentes. This finding agrees with the general prediction which expects higher diversity values to be related to middle conditions of environmental gradients.

Although the low species richness in the shallow zones should be attributed to a harsher environment, the diversity patterns (Table 1) and morphological features observed in dominant life forms suggest that the biotic processes are important in shaping the community (Menghi *et al.* 1992).

All the life forms presented a clear moisture and elevation pattern (Fig. 5). Many plant species are amphiphytes, and in agreement with Menges and Waller (1983), they are present in different points of the elevation gradient. The proportion of cryptophytes (geo- and helophytes), therophytes and chamaephytes peaks in the humid, lower areas. Combinations of stress and disturbance typical of that sector of the elevation gradient allow the categorization of life strategies according to three main environmental conditions.

Chronically disturbed but potentially productive environments in the river bank are dominated by fast growing annuals and chamaephytes. The greater abundance of low caespitose hemycriptophytes (*Cynodon dactylon, Polypogon semiverticillatus, Hordeum compressum*) is favoured by severe grazing after the river recedes. Nearby, in small ponds subject to high salinity and to flood-drought cycles, a stress condition dominates. Chamaephytes, therophytes, geophytes and hemicriptophytes appear equally affected. From the diversity patterns a sharing of resources (E .615 to .827) is concluded, at a high level when compared with the shallow zones. Low competitive capacity and the harsh conditions should account for this trend. In small shallow lagoons, with water at the surface almost all the year and up to 0.60 cm deep, or even deeper during rainy periods, the cryptophytes (geo- and helophytes) dominate. The environmental conditions are tolerated by few species (# 6 to 9), but do not limit biomass production.

Tall, fast-growing clonal non-forbs (*Typha latifolia, Scirpus californicurs, S. americanus*), seem to play an important role in eliminating competitors. Although water moves slowly during flooding, the grass morphology and strongly anchored roots of these species should confer mechanical tolerance against water level fluctuations and enable efficient regrowth.

Hemicriptophytes were of greater relative importance in plain areas regularly flooded for brief periods and low depth. Distinct dominant growth forms are specific to the environmental conditions. While in a river bank low caespitose grasses resist frequent flooding and severe grazing, the forbs (*Sesuvium portulacastrum, Heliotropium curassavicum, Rumex obtusifolius*) are more adapted to conditions in temporary ponds, where the water remains stagnant. *R. obtusifolius* is abundant also in the river bank and should survive floods, producing great quantity of seeds and elongating the stems to keep their leaves over the water level (Bloom *et al.*1990).

At middle, better drained elevations, tall competitive tussock grasses, such as *Spartina argentinensis* and *Trichloris crinita* in the Gs (# 6; H'.376; E .183), or *Elyonurus viridulus* in the Ge (# 20; H' 1.284; E .647) respectively, dominate the coarse grasslands. Fire and grazing pressure plays there a critical role in structuring the community.

Phanerophytes dominate the drier uplands, out of river flooding, where both water table depth and probably soil texture allow deeper root growth. Slight differences in the two physical features influence the distinct elevation range of nano-, micro-, mesophanerophytes and cacti.

Inside the depression, low sized shrubs have shown greater relative importance (77-98%) among the phanerophytes. Small leaves, succulence, multistemmed and creeping growth forms, are very common morphological features of plant species in elevated areas inside the depression. The differences detected in their relative abundances could be caused by biotic interactions. The proportion of mesophanerophytes (91%) peaks in the dry, elevated margins

Conclusions

1. Multivariate analysis shows a main mosaic structure in vegetational pattern, strongly correlated with a regional topographic-moisture complex gradient.

2. The secondary local trends in variation displayed in definite ranges of the environmental gradient suggest the influence of more frequent hydrological effects which require further study to be interpreted.

3. Three major physiognomic groups were recognized:
a. xerophyllous forests on the dry, elevated margins;
b. woody vegetation low to medium sized, characterized by xero-halophyllous plant species, in elevated areas inside the depression, under watertable effects; and
c. herbaceous vegetation, with higro-halophyllous plant species, dominant on lowlands under fluvial and watertable influences.

4. In terms of life form spectra, geophytes, therophytes and chamaephytes dominate under more dynamic and limiting environmental conditions. Hemicryptophytes are found in areas with higher productivity, subject to short fluvial flooding and under some form of anthropogenic pressure. Nanophanerophytes appear in saline habitats, out of the river influence, but greatly affected by groundwater fluctuation up to or near to the ground surface.

5. With respect to physiognomical features it can be concluded that the regional pattern agrees, in general terms, with that reported by Sayago (1969) and Herrera & Orueta (1981). Present work contributes details mainly on vegetation and environmental features of the shallow zones.

6. From the results we conclude that the vegetation-environment relationship is very complex. Two aspects, scale and the nature of the processes appear related in structuring the vegetation. While the environmental control on the vegetation pattern is clear at large scales, its influence in localized areas within definite moisture-elevation sectors is masked by biotic interaccions.

7. At the same time the influence of regional hydrological differences at the east and west margins on vegetation pat-

terns remain obscure with respect to the characteristics that we analyzed. The floristic and physiognomic resemblance detected between the vegetation (sP) of temporary ponds (sites # 3, 10, 12, 13, Fig. 1), should emphasize the greater influence of local processes, mainly determined by land form and stagnant water dynamics.

8. To analyze local variability in spatial pattern, it is neccesary to consider separately the major physiognomic groups. Morphoecological features and vegetation dynamics as well as mineralogical and water level fluctuation, and edaphic properties not considered here should also provide interesting details, to elucidate the hypothesis about the dominant processes, and the scale at which they operate.

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