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Plant communities and phytogeographical position of a large depression in the Great Chaco, Argentina

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Abstract

A survey is presented of the vegetation of the central region of the Santafesinian Chaco (Argentina), a scarcely populated flat area of 20 000 km^2, with seasonal flooding. Soils have a strong halo-hydromorphic character and vegetation is basically halophilous. Trees are scarce and most communities are savannas, grasslands or swampy vegetation. Twenty-three communities are described, some of them with several variants. The most widespread communities are *Spartina argentinensis* grasslands, *Elyonurus muticus* savannas and a complex of hygrophilous communities. The most important communities are distributed in relation to a topographical gradient, and their structure is shaped by recurrent flooding and fire disturbance. Most of the area is virgin land with very little human interference. The phytogeographical position of the area is discussed.

Nomenclature: Burkart, A. 1969, 1974, 1979. Flora ilustrada de Entre Rios, INTA, Buenos Aires, and Cabrera, 1963, 1965a, b, 1967, 1968, 1970. Flora de la Provincia de Buenos Aires, INTA, Buenos Aires.

Introduction

The Great Chaco comprises SE Bolivia, W Paraguay and N Argentina and can be divided in an eastern humid sector and a western drier one. The flora is characterized by endemic species of *Schinopsis*, and the vegetation in general by subhumid and xerophytic forests and savannas (Cabrera & Willink 1980).

The study area is situated in the SE of the Great Chaco, 28° S–30° S, 60° W–61° 30′ W, and almost confined to the province of Santa Fe (Argentina). The northern boundary runs along parallel 28° S and the river Salado is the southern limit. A sharp topographic scarp separates the region from the eastern 'Cuña Boscosa' (Forest Wedge) of the Santafesinian Chaco. The western limit is not well defined; there is a large transitional zone with the Subhumid Western Dorsum of the Santafesinian Chaco.

The region, which is know locally as the Submeridional Lowlands, is a huge depression of ca 20 000 km^2 with no rivers, brackish ground water, very few roads and only 2000 inhabitants. The area is alternatively flooded and dry so that the vegetation ranges from very hygrophilous to rather xerophilous. General reviews of the vegetation of the Submeridional Lowlands are included in accounts of Argentinian or Santafesinian vegetation (Ragonese 1941; Cabrera 1976; Lewis & Pire 1981).

The aim of this paper is to present a detailed analysis of the plant communities and their distribution in relation to environmental factors, and a discussion of the phytogeographical position of the region in comparison with neighbouring and similar areas of the world.

The study area

The Submeridional Lowlands are a sedimentary basin which began to be formed in the Paleozoic. During the late Tertiary the river Salado ran across the northern limit towards the river Paraná, but subsequently changed its course several times, shaping the sedimentary surface (Castellanos 1968). In the Quaternary there were several marine ingressions and important changes in the climate. During one of the dry periods the wind reshaped the surface. At the same time tectonics reassumed and the crystalline bedrock of the western and eastern dorsa of Santa Fe moved, uplifting their sediments and then tilting eastwards. As a consequence the river Salado was prevented from entering the Submeridional Lowlands across the north, and the water within the region was unable to move eastwards across the eastern dorsum. In addition internal depressions were formed here and there (Popolizio *et al.* 1978a, b).

As a result of this morphogenesis, the Submeridional Lowlands are a very flat depression between two elevated areas, with a very gentle slope from NW to SE (1.10‰). The area is hardly drained, mainly through two poorly developed river systems (Golondrinas and Calchaquí) on the eastern edge, and the river Salado on the south.

The climate is warm temperate humid, more subhumid towards the west. There are no complete series of meteorological data from the Submeridional Lowlands; those from the four nearest stations are given in Table 1. Rainfall shows an east-west gradient and is mainly aestival. As a result of local rainfalls, run-off from neighbouring regions, and very slow drainage, the area is often flooded at the end of the summer. The winter can be very dry.

The soils have developed on loess or loessic silts deposited during the Quaternary. The parent materials, the proximity of a very saline water table (at 1 m depth or less), and frequent flooding give them a very strong halo-hydromorphic character with heavy texture. The most important types present are Solonetz and Solodized Solonetz (typic albic natracualfs and typic natracuols, with salinity and neutral to strong alkaline reaction). On the transitional zone with the western dorsum there are also Soloths or transitional types (typic natralbols) and some Plano-

Table 1. Yearly temperature and rainfall data for the period 1961–1970. Data from Servicio Meteorológico Nacional (Argentina), 1985. Station 1 situated NE of the area, 2 at the northern edge, 3 at the southeasterm edge, 4 at near the southwestern edge.

Meterological stations	Temperature (°C)				Rainfall (mm)
	Mean annual minimum	Absolute minimum	Mean annual maximum	Absolute maximum	
1. Resistencia	15.6	−2.8	27.4	42.3	1211
2. Villa Angela	14.6	−5.5	28.2	45.8	1002
3. Reconquista	14.5	−3.7	26.4	43.9	1211
4. Ceres	13.0	−4.1	26.6	43.7	792

sols (typic argiacuic argialbols). There are occasional Planosols and Gley subhumic soils (udolic ocracualf) with accumulation of organic matter on the surface and acid reaction. As a whole their agricultural value is very low (Espino *et al.* 1983).

An important feature of the landscape is formed by ant-hills, 0.5 to 1.0 m high of *Camponotus punctulatus* Mayr. The great density (an average of 500 ant-hills per ha) of mounds of this size in such a flat area is a major topographical feature. Another peculiar feature of the landscape is the 'mogotes of Palo Azul' which are oval mounds of 25 m diameter and 0.4–0.5 m high. In a way these 'mogotes' resemble the North American 'mima mounds' which are the results of long term fossorial rodent activity (Dalquest & Scheffer 1942; del Moral & Deardoff 1976; Brotherson 1982; Cox 1984). Mima-type mounds have been reported for Peru (Scheffer 1985) and Argentina (Cox & Roig 1986). However, the 'mogotes' may have another origin than the mima mounds.

The principal human activities in the region are primitive cattle raising and hunting. Agricultural development schemes have so far not been successful. The region is frequently disturbed by fires. The Submeridional Lowlands presumably undergo less human interference than most other pristine regions of the world.

Methods

Vegetation was sampled in 671 quadrats, in spring 1981 and autumn 1982. The quadrats were laid out so as to represent the conspicuous variation in vegetation and always far from big trees in order to avoid cattle impact (Andrew & Lange 1986). Random sampling was not considered realistic since communities covering a very small area have a very low chance of being represented (Pignatti 1980), especially in view of the enormous size of the area surveyed. Moreover many sites are not accessible and stands may be burnt unexpectedly before sampling.

In species-rich communities species were counted in nested quadrats of increasing size. Since the number of species did not increase substantially beyond 16 m^2, this size was chosen as a standard. Smaller sizes were accepted in very small stands like in perilacunar communities arranged as narrow rings around the open water, or covered by homogeneous pure rush populations, or in the case of 'mogotes'.

In each quadrat a Braun-Blanquet (1979) relevé was made and the environment briefly described. In addition the presence of trees in the stand, and if present their height and type of distribution was recorded. Physiognomical characters (height, coverage and dominant species) of each layer were measured. When ant-hills were present in the quadrat species occurring on them were noted separately.

Similarity between spring and autumn aspects of each quadrat was measured by means of the Sørensen (1948) index. Then the two season's lists for each quadrat were combined in one relevé while taking the higher cover-abundance value attained by each species in any list. Those quadrats with a seasonal similarity below a treshold ($\bar{X} - \sigma_{n-1}$, where $\bar{X}$ is the mean value of the similarity index of the community and σ_{n-1} its standard deviation) were rejected from further analysis.

Data were analysed by tabular comparison following Mueller-Dombois & Ellenberg (1974). As the communities are characterized mainly by their physiognomic dominats they may be called associations *sensu* Beard (1980) or dominance-types (Whittaker 1980). Communities were then grouped subjectively in order to facilitate description.

Results

Physiognomy and structure of the vegetation

The scarcity of trees is the outstanding characteristic of the vegetation. The dominant physiognomy of the Submeridional Lowlands is the 'tall grass savanna' or 'tropical grassland' as defined by Mueller-Dombois & Ellenberg (1974).

Table 2. Submeridional Lowlands communities: structural data.

Communities*	3.3	3.1	3.2	3.9	3.8	6.2	3.4	3.5	3.7	3.6	1.2	1.3	1.1	2.2	2.1	2.3	6.1	7.1	5.1	5.2	4.1	4.2	1.4
Number of relevés	10	60	8	38	26	24	9	26	18	5	6	6	152	21	34	15	5	5	12	5	10	6	5
Coverage (%)																							
Spring	63	46	65	65	54	67	72	68	71	55	63	66	67	61	58	59	48	90	86	16	64	16	55
Autumn	76	57	60	66	63	56	62	69	80	68	75	75	64	72	76	56	61	69	90	19	61	13	71
Height tree layer (m)												6.0		5.3	6.5	4.9	3.4	6.1	4.7		5.5		
shrub layer (m)														1.4		1.5	1.9		1.8	2.3			
Main herb layer (cm)																							
Spring	28	191	212	13	6	11	31	27	26	30	82	147	72	57	51	43	20	98	45	36	20	13	86
Autumn	41	174	141	15	8	10	37	30	42	37	82	197	96	77	58	51	53	99	43	37	20	14	112
Total number of species																							
Spring	42	73	22	52	46	91	22	43	54	32	51	72	225	118	166	102	61	71	115	51	41	18	11
Autumn	29	78	26	58	56	91	26	46	48	28	50	45	209	98	152	98	61	60	111	53	35	18	7
Total	48	96	36	73	65	116	27	56	68	36	68	80	266	144	197	122	79	93	146	72	49	24	12
Average number of species per relevé																							
Spring	9	7	5	6	8	11	6	6	8	11	16	21	15	24	24	25	22	21	26	25	9	7	5
Autumn	8	8	7	6	8	11	7	7	9	10	16	17	13	19	22	23	24	17	23	27	8	6	4
Average seasonal similarity	59.7	67.1	48.9	67.6	59.4	58.5	84.2	74.4	67.5	67.5	55.5	53.5	61.4	59.4	58.2	59.4	62.1	51.1	57.6	55.4	68.6	59.3	74.7

* The order is derived from Table 3.

Table 3. Condensed constancy table of the herbaceous layer of the Submeridional Lowland's communities. Species spread over several communities.

Communities	3.3	3.1	3.2	3.9	3.8	6.2	3.4	3.5	3.7	3.6	1.2	1.3	1.1	2.2	2.1	2.3	6.1	7.1	5.1	5.2	4.1	4.2	1.4
Species																							
Spartina argentinensis	II	II	II	II	II	III		II	II	III	II	V	V	V	II	IV	III		IV	III	II	III	II
Cynodon dactylon	II	II		II	IV	V	II	II	I	III	III	IV	III	III	IV	III	V	II			IV	II	
Diplachne uninervia	V	II	II	II	III	IV	II	III	II	III	III	III	II			II			II		II	II	
Aster squamatus	II	II	II	II	II	III			III	II	III	V	IV	IV	III	IV	V	III	III		II		
Mikania periplocifolia	III	IV	V			II			III			V	IV	II		II	V	II	III				II
Cyperus corymbosus						II		III	IV	II	V	V	III	II	II	II		II					
Setaria geniculata			II			II			II	II	V	V	IV	V	V	III	III	III	II				
Eriochloa punctana		II	IV		II	III				II	III	III	III	III	II	II	III						
Euphorbia serpens	IV	II		III	IV	III					II	III	IV	V	III	IV				V			
Eclipta prostaoa	II				II			II	II	II	IV	IV	II		II								
Vernonia incana										II	II	II			II		II						
Ambrosia elatior						II			II			III	II				II						
Chenopodium macrospermum	IV	III	III	II	II	II			II				II						II		II	III	V
Paspalum vaginatum	II	II		V		III		III				II										IV	IV
Heliotropium curassavicum				II	II	III							II	II	II	III	III	II		III	IV	II	
Salicornia ambigua				II									II	II		IV				V	II	V	V
Sesuvium portulacastrum						II							II	II		III		II		V		V	
Distichlis spicata																III	II	II	III		V	III	
Sporobolus pyramidatus																III	II			III	III	IV	
Eryngium coronatum															III		IV				II		
Paspalidium paludivagum	V	IV	V	III	IV	II	II	III	II	II		II	II										
Paspalum lividum	IV	II	II			II	II	II	V	V	V	IV	II	II									
Scirpus californicus	III	V	IV	III	II	II		II	II			II											
Ludwigia peploides	II	II			II	II	V	IV	IV	II	IV												
Paspalum distichum	II	II			V	II	II																
Malvella leprosa		II		II	II	II																	
Polygonum hydropiperoides					II		II				III												
Nymphoides indica					II		III																
Borreria verticillata	II				II																		
Leersia hexandra							III	II	III	V	V												
Echinochloa helodes							III	V	IV	III		II											
Alternanthera philoxeroides							III		III	III	II												
Cyperus digitatus							II	II	II									II					
Sorghastrum agrostoides										II	III												
										II	II												
Echinodorus grandiflorus					II	II					III	IV	II	IV	V								
Neptunia pubescens									II		II	IV	II	II	II								
Desmanthus chacoensis											II	V		II									
Solidago chilensis												IV		II	II								
Dolichopsis paraguariensis												II		II									
Spergularia platensis														II	II								
Bothriochloa hassleri														II	II								
Bothriochloa saccharoides														II	II								
Hypochoeris sp.					II	II					II	III	II	IV	IV	IV	III	II					
Plantago myosurus											II	II	III	IV	IV	IV		II					
Eryngium ebracteatum											IV	II	II	IV	III								
Eupatorium candolleanum												II	II	III	IV	IV	II	II	II	II			
Panicum bergii			II									III	III	IV	IV	IV	III	III	III	III	II		
Conyza bonariensis													II	IV	IV	IV	II		II	IV			
Pluchea sagittalis												II	II	IV	IV	III							
Cyperus reflexus												II		III	III	II							
Stemodia lanceolata												II		II	III	III	II						
Bothriochloa laguroides												II		II	II	II	II						
Ruellia tweediana						II						II	II	III	III	IV	IV	II				II	
Phyla canescens												II	II	III	III	II	III		II				
Gamochaeta subfalcata														II	III	II	III	II	II				
Apium leptophylum														III	III	II	II		II				
Cienfuegosia drummondii												II	II	V	V	IV	III	II		III			
Elyonurus muticus												II		II	II	II		II		IV			
Heimia salicifolia												III	II	III	III	IV	III	II		V			
Holocheilus hieracioides													III	III	II	IV	V	III		II			
Lepidium sp.														II	IV	III	IV	II		IV			
Chloris canterae														III	II	IV	IV	II		II			
Leptochloa chloridiformis														III	III	II				V			
Pterocaulon subvirgatum														II	II	II				II			
Conyza chilensis						II							II	II	II		III			V			
Hymenoxys anthemoides																II	II			IV			
Baccharis pingraea															II			II		II			
Verbena intermedia															II	IV	II	IV	IV	III			
Nicotiana longiflora																		II	IV	II			
Physalis viscosa											II							II	III				
Boopis anthemoides												III				II	II		III				
Ambrosia tenuifolia												II							IV				
Chaetotropis chilensis																III	III						
Spergularia ramosa																		II	III				
Clematis montevidensis																		II	II				
Sphaeralcea laciniata																		II	III				
Scolymus sp.																			III	II			
Limonium brasiliense																			II	II			
Wahlenbergia linarioides																			II	IV			
Trichloris crinita																			II	V			
Pterocaulton lorentzii																							

Table 4. Condensed constancy table of the herbaceous layer of the Submeridional Lowlands' communities. Species restricted to one community.

Communities	3.3	3.1	3.2	3.9	3.8	6.2	3.4	3.5	3.7	3.6	1.2	1.3	1.1	2.2	2.1	2.3	6.1	7.1	5.1	5.2	4.1	4.2	1.4
Species																							
Typha domingensis			V																				
Ammannia friesii			II																				
Eleocharis macrostachya					III																		
Polygonum aviculare						II																	
Echinochloa crusgalli							III																
Solanum glaucophyllum							II																
Thalia multiflora							II																
Luziola peruviana										II													
Jaborosa integrifolia										II													
Paspalum intermedium											V												
Aeschynomene rudis											III												
Eleocharis elegans											III												
Eleocharis parodii											II												
Eleocharis contracta											II												
Rhynchospora scutellata											II												
Panicum milioides											II												
Marsilea concinna											II												
Vernonia sp.											II												
Sida rhombifolia											II												
Cortaderia selloana												V											
Schyzachirium sp.															III								
Paspalum plicatulum															II								
Eupatorium squarroso-ramosum															II								
Rhynchosia senna															II								
Pappophorum pappiferum																III							
Eragrostis lugens																II							
Chenopodium ambrosioides																	IV						
Chenopodium album																	II						
Iresine diffusa																	II						
Morrenia odorata																	II						
Tweedia brunonis																	II						
Cyperus sp.																	II						
Pennisetum frutescens																		V					
Setaria pampeana																		II					
Melilotus sp.																		II					
Solanum sp.																		II					
Petunia parviflora																		II					
Glandularia peruviana																		II					
Centaurea tweediei																		II					
Cirsium vulgare																		II					
Abobra tenuifolia																			IV				
Comelina sp.																			IV				
Apium sellowianum																			IV				
Samolus valerandi																			III				
Baccharis coridifolia																			III				
Parietaria debilis																			II				
Eupatorium ceratophyllum																			II				
Hordeum stenostachys																			II				
Pappophorum mucronulatum																				V			
Melilotus alba																				III			
Baccharis notosergila																				III			
Senecio argentinus																				II			
Sporobolus phleoides																				II			
Cortesia cuneata																				II			
Cressa truxillensis																						V	
Heterostachys ritteriana																						II	
Euphorbia sp.																						II	
Spartina densiflora																							V

There were 23 main communities distinguished. In Table 2 structural characteristics of these communities are summarized.

The tree layer is discontinuous and sparse if not absent altogether. The most widespread species are *Prosopis alba* and *Geoffroea decorticans*, but *Prosopis affinis*, *P. nigra*, *P. nigra* var. *ragonesei* and their hybrids with *P. alba* are also frequent. *Acacia caven*, *A. aroma* and the small palm *Trithrinax campestris* are very rare; in the NE of the region the palm *Copernicia australis* is fairly abundant. Some lakes are surrounded by a natural levee covered in places by thick woody vegetation where *Celtis* spp. may be abundant.

Shrubs are usually scarce; however, there is one community which has a dense and almost continuous layer of *Tessaria dodoneaefolia*. Also the 'mogotes' are covered by scrubby vegetation.

The most important communities have a very dense, tall layer of tussock grasses, in some cases accompanied by lower herbaceous layers. Some communities consist fo low dense turfs of rhizomatous or stoloniferous grasses.

Plant communities

The 23 communities are grouped into 7 broader types. Tables 3 and 4 present constancy figures for the common and the diagnostic species respectively. Table 5 presents constancy figures for the woody layer species. The communities are indicated by their vernacular name or their physiognomy and dominant species.

1. Spartina *and related communities*
These occur on low halomorphic soils, normally flooded at the end of summer and usually very dry during winter and early spring. Trees are almost absent.

1.1 Spartina argentinensis *'espartillar' (Fig. 1).* The most widespread and characteristic community of the region with a tall layer of the constant and dominant *Spartina argentinensis*, with *Aster squamatus*, *Mikania periplocifolia*, *Setaria geniculata* and *Euphorbia serpens* as additional constant species. Five variants can be distinguished:

Table 5. Condensed constancy table of the tree and shrub layer of the Submeridional Lowlands' communities.

Communities	1.3	2.2	2.1	2.3	6.1	7.1	5.1	5.2	4.1
Tree layer species									
Geoffroea decorticans	II	III	IV	II	V				III
Prosopsis alba		III	III	IV		III	III	II	II
Prosopsis affinis			III						
Prosopis sp.			II						
Shrub layer species									
Lycium americanum		II		IV	II		IV	V	
Tessaria dodoneaefolia				V			III	V	
Maytenus vitis-idaea				II			V	IV	
Prosopis reptans				II			IV	III	
Cyclolepis genistoides							V	V	
Holmbergia tweedii							II	II	
Schinus polygamus							III		
Suaeda divaricata							III		
Opuntia sp.							II		
Allenrolfea vaginata								V	
Prosopis vinalillo								V	
Opuntia pampeana								V	
Grabowskia duplicata								VI	
Prosopis kuntzei								II	
Lippia salsa								II	
Cactaceae (unidentified)								II	

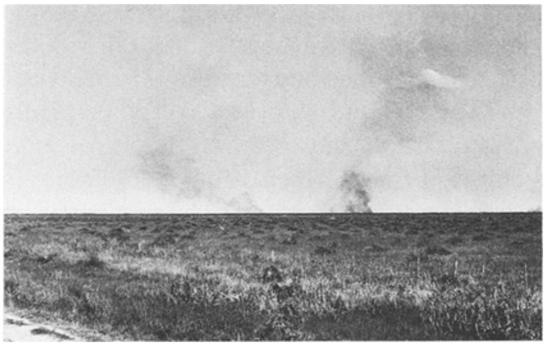

Fig. 1. Panoramic view of a *Spartina argentinensis* grassland. Road 98, 25 km west of river Golondrinas. On the background smoke from burning vegetation.

a) Poor, variant often with only the dominant *Spartina* present. Possibly induced by fire.
b) With an intermediate layer of *Salicornia ambigua* and *Chenopodium macrospermum* and sometimes a lower creeping layer of *Distichlis spicata* and *Paspalum vaginatum*. On strongly halomorphic soils.
c) With a lower layer of *Paspalum lividum*, and frequently also *Leersia hexandra*, *Paspalidium paludivagum*, *Ludwigia peploides* and *Echinochloa helodes*. On humid soils flooded for long periods.
d) Tussocks of *Elyonurus muticus* and frequent occurrence of *Panicum bergii* and *Stemodia lanceolata*. Floristically richer than the three previous variants. On relatively higher and less halomorphic soils.
e) With an open tall layer, and the intertussock space covered by *Cynodon dactylon*. The halophytes *Heliotropium curassavicum*, *Hymenoxis anthemoides* and *Sesuvium portulacastrum* are frequent. On disturbed soils.

1.2 Paspalum intermedium *tall grassland.* Tall layer of the dominant, many hygrophytes. In small circular usually flooded depressions within the previous community.

1.3 Cortaderia selloana *tall grassland.* Very similar to 1.1 but floristically richer and with an emergent layer of *Cortaderia selloana*.

1.4 Spartina densiflora *'espartillar'.* Similar to variant b of 1.1 but floristically poorer, with a tall, relatively open layer of *Spartina densiflora* in stead of *S. argentinensis*. Intertussock space covered by a turf of *Paspalum vaginatum* or *Distichlis spicata*. Narrow stands between large stands of 1.1 and rivers or waterlogged depressions.

2. Savannas of Elyonurus muticus *and related communities*

On relatively higher and better drained soils than those of the former group. Tree layer is sparse in the east and center of the region and denser and sometimes clustered towards the west. *Geofroea decorticans* is more abundant on lower soils than *Prosopis* spp., particularly *P. affinis*, occurring on the highest and less saline soils.

2.1 'Aibal' (Fig. 2). The most important community of the group. Upper herbaceous layer of *Elyonurus muticus* ('aibe') accompanied by *Setaria geniculata*, *Chloris canterae*, *Bothriochloa* spp., *Pterocaulon subvirgatum*. Lower layer of *Cynodon dactylon* accompanied by *Eryngium coronatum*, *Cienfuegosia drummondii*, *Plantago myosurus* and *Gamochaeta subfalcata*. Floristically very rich. There are two variants:
a) Floristically richer than b, with *Phyla canescens*, *Euphorbia serpens*, *Holocheilus hieracioides* and *Heliotropium curassavicum*.
b) With sparse tussocks of *Spartina argentinensis* and *Cyperus corymbosus*.

Fig. 2. Savanna of *Elyonurus muticus* and *Prosopis* spp. Near San Bernardo.

2.2 'Aibal-Espartillar'. A transitional community between 2.1 and 1.1 over a very large area. In the upper herbaceous layer *Spartina argentinensis* and *Elyonurus muticus* share the dominance.

2.3 'Chilcal'. A savanna with a dense shrub layer of *Tessaria dodoneaefolia.* Upper herbaceous layer with *Spartina argentinensis*, *Elyonurus muticus*, *Leptochloa chloridiformis* and *Chloris canterae*; lower herbaceous layer of either *Cynodon dactylon*, *Distichlis spicata* or *Phyla canescens.*
Towards the west of the region there are a few Savanna stands with *Leptochloa chloridiformis* and *Chloris canterae* as dominants.

3. Hygrophilous communities
In internal depressions of variable size or in drainage areas. Soils are flooded for very long periods, sometimes the whole year round. Trees are absent or very rare. Floristically very poor, frequently pure populations of dominant species occur.

3.1 'Juncal' or 'Pirisal' (Fig. 3). The most widespread community of the group. Stand size ranges from a few sq.m to several sq.km. Upper layer of the rush *Scirpus californicus*, when flooded with a conspicuous pleuston layer of *Azolla* spp. and *Salvinia* spp. Depth of water and density of upper layer determine several variants:

a) Pure dense *Scirpus californicus* in the deepest part of depressions.

Fig. 3. A temporary pond with *Scirpus californicus* surrounded by *Ludwigia peploides* meadows. Near Fortín Charrúa.

b) Lower density of *Scirpus* in large depressions within 1.1 with a low layer of *Paspalum vaginatum*, developing during summer.
c) In smaller depressions within 1.1 a variant similar to 3.1b but with a lower layer of *Paspalum distichum.*
d) With a low layer of *Paspalidium paludivagum* and *Paspalum lividum*, sometimes with *Distichlis spicata* and *Typha domingensis* in the upper layer.
e) In small depressions with less saline soil, *Solanum glaucophyllum*, *Ludwigia peploides* and *Echinochloa helodes* are frequent.

3.2 'Espadañal' or 'Totoral'. In environments similar to 3.1, often mixed with it. Dense upper layer of *Typha domingensis* and a lower layer of *Paspalidium paludivagum* and *Paspalum lividum.*

3.3, 3.4 Wet meadows. Surrounding 3.1 and 3.2 where the water is not deep enough for *Scirpus californicus* and *Typha domingensis.* a) *Paspalidium paludivagum* is the dominant of 3.3, a high constancy of *Diplachne uninervia* and halophytes suggests that the substrate is more saline than in 3.4, where b) *Ludwigia peploides* is the dominant (Fig. 3).

3.5–3.7 Flooded prairies. In relatively large and flat areas where the water can be very deep at times; spatially arranged according to water level:

3.5 occurs where the water level is highest and has a dense layer of *Echinochloa helodes*, often with *Ludwigia peploides* and *Paspalidium paludivagum*; next to it occurs, 3.6 with a dense layer of *Leersia hexandra* and sometimes *Luziola peruviana*; 3.7 has a dense layer of *Paspalum lividum* with *Cyperus coryumbosus*, *Ludwigia peploides* and *Echinochloa helodes.*

3.8, 3.9 Wet turfs. On wet soils, flooded for shorter periods than those of the flooded prairies. 3.8 is a turf of *Paspalum distichum* which spreads on the edge of *Scirpus* ponds. *Cynodon dactylon*, *Paspalidium paludivagum* and *Ludwigia paploides* are frequent, and sometimes there is an upper layer of *Eleocharis* spp. 3.9 is a turf of *Paspalum vaginatum* found over large areas between *Scirpus* and *Spartina* communities.

4. Halophilous communities
These communities are on halomorphic soils over restricted areas.

4.1 Grassy halophilous community. Within 1.1 there are patches with drier and more alkaline soils covered by a short and dense turf of *Distichlis spicata*, with *Heliotropium curassavicum* and *Sporobolus pyramidatus*.

4.2 Open Succulent halophyte community with *Salicornia ambigua*, *Heterostachys ritteriana* and *Sesuvium portulacastrum*, accompanied by *Cressa truxilensis*, *Sporobolus pyramidatus*, on the oveflow areas of the rivers Salado and Golondrinas. When water runs off and the soil dries out, a salt layer remains on the surface.

5. 'Mogotes' and 'Jumeales'
Scrubby almost impenetrable thickets covering small oval-shaped areas within the matrix of *Spartina argentinensis* or *Elyonurus muticus* communities.

5.1 Mogotes of 'Palo azul', covered by dense *Cyclolepis genistoides* (palo azul) accompanied by *Maytenus vitis-idaea* and *Lycium americanum*.

5.2 'Jumeal'. Similar to 5.1 more halophilous. *Allenrolfea vaginata* ('jume') is dominant, *Cyclolepis genistoides* is abundant and *Salicornia ambigua* is the dominant of the herbaceous layer.

6. Anthropic communities
On soils which have been ploughed and, after several crop failures, abandoned. Some hygrophilous communities may be replaced by the 'gramillar' (6.2) when overgrazed.

6.1 'Chañar' islets. They are small islets or groves with a continuous layer of *Geoffroea decorticans* ('chañar') within the matrix of *Spartina argentinensis* communities. The herbaceous layer is very heterogeneous, usually dominated by *Cynodon dactylon*.

6.2 'Gramillar'. A turf of *Cynodon dactylon*, very often accompanied by *Diplachne uninervia*. The presence of *Spartina argentinensis*, *Paspalum vaginatum* or *P. distichum*, indicates which community has been found here before grazing started.

7. 'Simbolar'
Common in the Chaquenian forests, but very rare in the Submeridional Lowlands. It has a very dense upper herbaceous leyer of *Pennisetum frutescens* ('simbol').

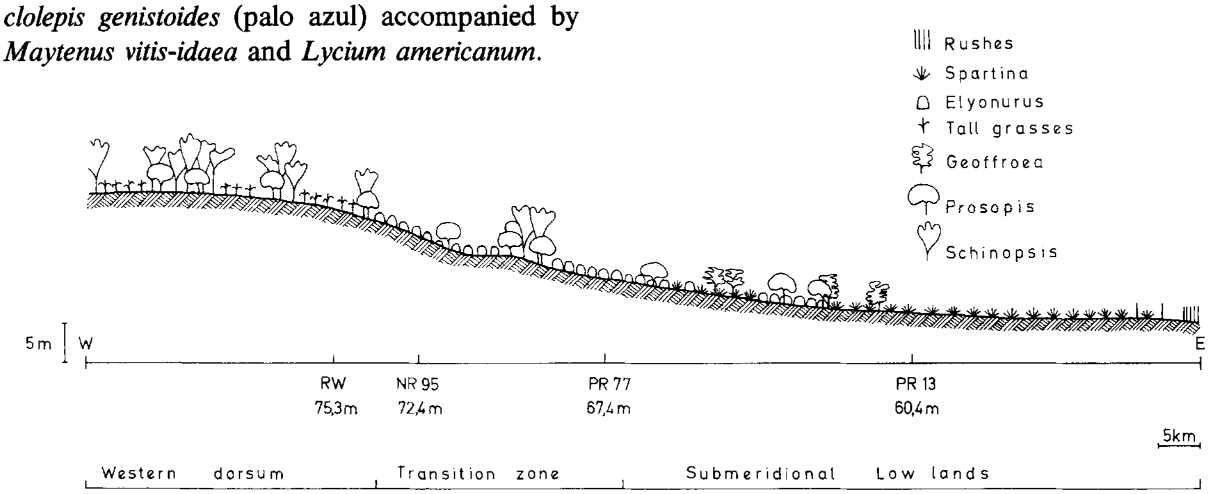

Fig. 4. Vegetation diagram along a transect from the western subhumid dorsum (near Villa Minetti) down to the center of the Submeridional Lowlands (near lake La Tigra). RW: Railway Tostado-Villa Minetti, NR: national road, PR: provincial road.

Spatial distribution of plant communities

Fig. 4 shows the vegetation of a transect from the western subhumid dorsum of Santa Fe down to the center of the Submeridional Lowlands. The slope along this transect is very gentle. On the dorsum there are forests of *Schinopsis balansae*, *S. lorentzii*, *Aspidosperma quebracho blanco* and *Prosopis* spp. and different types of savannas. Towards the center of the region trees become scarce and the communities are arranged according to an elevation gradient; from higher to lower parts we find *Elyonurus muticus* savannas, *Spartina argentinensis* espartillares, *Paspalum vaginatum* turfs and *Scirpus californicus* rushes or *Typha domingensis* populations. From the center to the east *Spartina argentinensis* is spread over kilometers of very flat land, alternating with rushes and wet turfs on relatively lower soils.

Within the region there are many lakes and temporary ponds of variable size. The vegetation pattern around them varies considerably but in general it fits the diagram of Fig. 5. In the center there are rush populations surrounded by rings of different hygrophilous communities, meadows of *Paspalidium paludivagum* or *Ludwigia peploides*, wet turfs of *Paspalum vaginatum* or *P. distichum*, and then the prevailing major community of the area: *Spartina argentinensis* or *Elyonurus muticus* communities.

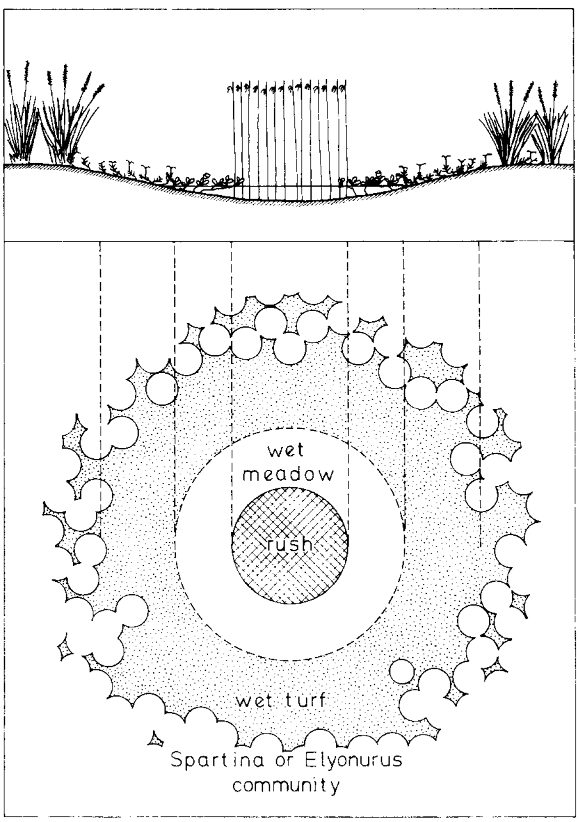

Fig. 5. Plant communities distribution around small temporary ponds.

Discussion and conclusions

Along the elevation gradient the major communities, and their variants and transitional communities form a continuous range of floristic variation in response to variation in soil salinity and water logging conditions. Floristic richness of the herbaceous layer of the *Elyonurus muticus* savannas is relatively high, but decreases down the gradient where the communities tend to be monospecific; under extreme environmental conditions the community only consists of a pure population of the dominant. Apparently such conditions are beyond the tolerance range of most species (Grubb 1985).

Most species of the communities in the regularly flooded areas are stoloniferous gramineae that extend or retreat according to the fluctuating water depth. When water runs off hygrophilous annuals such as *Diplachne uninervia* become abundant, and when the water level rises the stoloniferous grasses are flooded and the surface is colonized by a aquatic (pleuston) species: *Azolla* spp., *Salvinia* spp. and *Pistia stratiotes*.

The communities appearing around ponds depend largely on depression size, substrate characteristics and water depth. When the water fills the ponds the communities of the inner rings expand and encroach those of the outer rings. When the ponds dry out the *Paspalum* spp. turfs spread to the center and invade the more hygrophilous communities which decay or even disappear if the pond remains dry for long periods.

The most important and characteristic communities of the Submeridional Lowlands are the 'espartillares' and the most widespread species in *Spartina argentinensis*, which Mobberley (1956) considered as identical with *Spartina spartinae* of the northern hemisphere. *Spartina* species are widespread and frequently dominant in coastal and estuarine marshes at both sides of the Atlantic. On S. American Atlantic shores *Spartina coarctata* is present on sand dunes (Eskuche 1974) and *S. alterniflora* and *S. densiflora* (Vervoorst 1967) as well as *S. longispica* occur in tidal and estuarine marshes. On the Gulf of Mexico and the Atlantic coast of N. America the most important species are *S. alterniflora* and *S. patens* (White 1983; Clark 1986; Roberts & Robertson 1986), though Johnston (1963) mentions *S. spartinae* as well. On European shores *S. maritima*, *S. alterniflora* and *S. townsendii* are dominant (Kortekaas *et al.* 1976) and *S. anglica* (Hubbard 1970). However, in S. America only *S. densiflora* and *S. argentinensis* occur in inland marshes, and in the northern hemisphere *S. pectinata* and *S. gracilis* are the only species which have many inland stations (Mobberley 1956; Brotherson 1983). In Central America and the Gulf of Mexico, *S. spartinae*, which probably is the same species as *S. argentinensis*, is more frequent in coastal marshes than in inland stations.

Communities of *S. argentinensis* have been reported south from the Submeridional Lowlands in subchaquenian and pampean vegetation in Santa Fe (Argentina) (D'Angelo *et al.* 1987; Lewis *et al.* 1985) and also around Mar Chiquita lake (Province of Córdoba, Argentina) (Sayago 1969). They are also present in depressions of the 'Cuña Boscosa' (Lewis & Pire 1981). Morello & Adámoli (1974) who consider *Spartina argentinensis* communities as pampean, reported such communities from more than 500 km north from our region in the Patiño swamps (Formosa, Argentina). The species has also been collected in Paraguay, but communities have not been described there. From further north, Prance & Schaller (1982) did not mention this community in the Brazilian Pantanal. South of latitude 33° S, *S. argentinensis* is replaced by *S. densiflora* (Lewis & Collantes 1975). Though *S. densiflora* communities are also present in the Submeridional Lowlands, here they are not frequent, therefore both species, *S. argentinensis* and *S. densiflora* can be considered as largely vicarious species, the former chaquenian, the latter pampean.

Contrary to what has been stated by Ragonese (194) and Cabrera (1976) *Elyonurus muticus* savannas are far less widespread in the Submeridional Lowlands, and almost confined to the edges. However, they are very common in the whole chaquenian region (Adámoli *et al.* 1972; Morello & Adámoli 1974) and NE Argentina (Eskuche 1984), and even in the Brazilian Cerrado (Cabrera & Willink 1980). *E. muticus* grasslands have been reported on sandy soils far SW from this region, in the province of San Luis (Anderson *et al.* 1970). They are absent altogether from the eastern Pampa, but *E. muticus* is present in some communities of the western Pampa (Cabrera 1945). Although León & Anderson (1983) considered the *E. muticus* grasslands of San Luis as pampean, they are more typical of the chaquenian region. Instead, the typical pampean communities are *Stipa* prairies and steppes.

Both *Scirpus californicus* and *Typha* spp. are widespread in wetlands all over the Americas. *Scirpus* communities are common in the Pampa (Vervoorst 1967; Lewis *et al.* 1985), the river Paraná flood plain (Burkart 1957; Franceschi & Lewis 1979), the chaquenian region (Morello & Adámoli 1974; Lewis & Pire 1981), and even in the high Andes (Heiser 1979) and elsewhere further north. *Typha* communities are not common in the Submeridional Lowlands, but Vervoorst (1967) mentioned a similar community of *Typha latifolia* in the Salado depression of the Pampa, and *Typha domingensis* is widespread in the Chaco as far as the Brazilian Pantanal (Prance & Schaller 1982) and even further north in the United States.

Halophilous prairies of *Distichlis spicata* and *Paspalum vaginatum* are fairly common in the Pampa region (Vervoorst 1967; León *et al.* 1979). *Distichlis* spp. with *Salicornia* spp. communities have a very wide range all over America, both on seashores and in inland marshes. In N. America the equivalent marsh meadows are of *Distichlis* *stricta* and *D. spicata* with *Salicornia pacifica* or *S. rubra* in stead of *S. ambigua* (Coupland 1961; Shay & Shay 1986). In the Submeridional Lowlands, where *Paspalum vaginatum* turfs are frequent, *D. spicata* communities are rare. Halophilous chenopod communities are very common around the whole world, but in this region only *Salicornia ambigua* and *Chenopodium macrospermum* are widespread.

According to Ragonese & Castiglioni (1970) and Cabrera (1976) the Submeridional Lowlands are a district of the Great Chaco; but in that case their southern limit should be placed further south than the river Salado, as the neighbouring subchaquenian space has the same physiographic characteristics and plant communities (D'Angelo *et al.* 1987). However, most depressions of the Chaco have the same or very similar communities, and the only difference is the size of the area. There are no important endemics in the Submeridional Lowlands; the only species almost confined to this area is *Zizaniopsis villanensis* (Quarín 1976), a restricted endemic (Rabinowitz 1981) which is the extreme case of rarity, as it is also rare within this region. Therefore only geomorphology and size permit consider the Submeridional Lowlands a distinct unit;but its flora places it within the eastern Chaco.

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