What is the Gran Chaco vegetation in South America? : II. A redefinition ; contribution to the study of the flora and vegetation of the Chaco, VII

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What is the Gran Chaco vegetation in South America? II. A redefinition
Contribution to the study of the flora and vegetation of the Chaco. VII

DARIÉN E. PRADO

ABSTRACT

PRADO, D. E. (1993). What is the Gran Chaco vegetation in South America? II. A redefinition. Contribution to the study of the flora and vegetation of the Chaco. VII. *Candollea* 48: 615-629. In English, English and Spanish abstracts.

The twenty-three more relevant woody communities of the Gran Chaco are studied following classical phytosociological and numerical analysis techniques (PCA and CLINK), in an attempt to redefine the present concept of the Chaco province in South America. The congruence between the different results is striking. On this basis, the communities Gallery Forest, "Selva de Ribera", "Tipa-Pacará" Forest, "Palo blanco" Forest and the Calcareous Forest of Mato Grosso do Sul cannot be regarded as chaquenian, while the Austro-Brazilian Transitional Forest and three different communities from Mato Grosso are considered transitional. A new map of the Chaco *sensu stricto* is presented, with a wide belt of transitional vegetation on the east of the region, whereas gallery forests and hills vegetation are completely excluded.

RESUMEN

PRADO, D. E. (1993). ¿Qué es la vegetación del Gran Chaco de Sudamérica? II. Redefinición. Contribución al estudio de la flora y de la vegetación del Chaco. VII. *Candollea* 48: 615-629. En español, resúmenes en inglés y en español.

Las veintitrés comunidades leñosas más relevantes del Gran Chaco fueron estudiadas siguiendo técnicas de análisis fitosociológico clásico y numérico (PCA y CLINK), tratando de redefinir el concepto actual de la provincia del Chaco en Sud América. La congruencia entre los distintos resultados es sorprendente. Sobre esta base, las comunidades Bosque en Galería, Selva de Ribera, Bosque de Tipa y Pacará, Bosque de Palo Blanco y los Bosques Calcáreos de Mato Grosso do Sul no pueden ser aceptadas como chaqueñas, mientras que el bosque Transicional Austro-Brasileño y tres comunidades diferentes de Mato Grosso son consideradas transicionales. Se presenta un nuevo mapa del Chaco *sensu stricto,* que muestra una amplia faja de vegetación transicional en el este de la región, al tiempo que los bosques en galería y la vegetación de los cerros son totalmente excluídos.

KEY-WORDS: Chaco — Classical phytosociology — Floristics groups — Numerical analysis — Vegetation — Woody communities.

Introduction

In a previous contribution a review of the available knowledge on the Gran Chaco vegetation of Bolivia, Paraguay and Argentina was presented (PRADO, 1993). In studying this problem the need of a thorough analysis of the present day notion of the Chaco arose, since in the literature available the concept of the Chaco as a phytogeographical province has simply been equated with the Chaco as a geographical region (see review in PRADO, 1993), an established view that has prevailed unchallenged so far. The comparative study showed that the geographical region known as

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the "Gran Chaco" in fact includes rather different kinds of vegetation, and there is a number of floristic elements of widely different lineages in the woody communities still regarded as chaquenian. Such studies then provide the basis for an attempt to redefine the "Chaco proper" by more objective techniques.

The twenty-three woody vegetation units encompassed in the analysis have been regarded as pertaining to the Gran Chaco by different authors. These include the Gallery Forests in the islands of the river Paraná and tributaries, considered chaquenian by RAGONESE (1941) and RAGONESE & CASTIGLIONI (1970), and often confused with the next one, the "Selva de Ribera" (SCHULZ, 1967; PRADO & al., 1989), as in REBORATTI & NEIFF (1986). The Subandean Piedmont Forests of NW Argentina and SW Bolivia (PRADO, 1991), bordering the western limit of the Chaco and included in it by HUECK (1959, 1972) and UNZUETA (1975), consists of two different units: the "Tipa-Pacará" and the "Palo blanco" forests. The Austro-Brazilian Transitional Forest (PRADO, 1991) and the nearby "quebrachales" of *Schinopsis balansae* have, more often than not, been confused as a single vegetation type (e.g. HUECK, 1972; CABRERA, 1976). Also arguable is the phytogeographical position of the five communities described by PRADO & al. (1992) for a sector of alleged Chaco vegetation in Mato Grosso do Sul (HUECK, 1955). There is little argument, in contrast, about the chaquenian character of the "quebrachales" of three "quebrachos" dominated by *Schinopsis quebracho-colorado,* of white "quebracho" *(Aspidosperma quebracho-blanco),* and of two "quebrachos" in the drier western Chaco; the same is true for the "Palosantales" of *Bulnesia sarmientoi,* the white "quebracho" dominated Arid Chaco Woodland of SW Chaco (SARMIENTO, 1972), together with the main four azonal woody communities ("Algarrobales", "Cardonales", two variants of "Palmares", and "Vinalares"; PRADO, 1993). Also enclosed in the analysis are the Pampean and Subandean varieties of the Sierra Chaco Forests.

Methods

In order to assess to what an extent the woody chaquenian communities and neighbouring seasonal formations are interrelated, reliable floristic lists were selected from the available literature and worked out in phytosociological tables on a basis of presence-absence of species. These data were then analyzed following three different techniques:

a) Classic phytosociological analysis of the Zürich-Montpellier school, in the more modern version modified by MUELLER-DOMBOIS & ELLENBERG (1974). This consists essentially in listing all the species (rows) occurring in certain areas or localities (columns), and then mechanically search for species with common patterns of distribution in the columns. Subsequent reshuffling of columns and rows generally results in the grouping of some species which seem to be exclusive to a determined group of localities, exclusive to a single area, or common to most or all of them. These species groups are taken to indicate the presence of common environmental factors by which they are restricted in their phytogeographical distribution. Therefore, such groups have an ecological indicator value, and they are referred to as "floristic groups (FG)" (MUELLER-DOMBOIS & ELLENBERG, 1974). Because of the subjective nature of this analyses it is necessary to compare the results with those of more objective statistical studies, as the following.

b) Multivariate numerical methods:

b.1. CLINK (Complete Linkage) algorithm from WISHART's (1987) package, employing SØRENSEN's (1948) similarity index (also known as Czekanowski-Dice coefficient). This agglomerative technique of classification fuses the individuals (localities/areas) into increasingly larger discrete groups, based on their similarity matrix, and a dendrogram is provided to show their relationships. The fusion is interrupted according to a subjective criterion, generally when recognizable clusters of ecologically-floristically related individuals are formed, or when no individual is left isolated (MATEUCCI & COLMA, 1982).

b.2. PCA (Principal Components Analysis) from the JMP IN™ statistical software. This ordination technique, contrary to the classificatory ones, does not establish discrete classes but

displays the individuals under study in a hyper-dimensional space along axes of continuous variation. The axes ("principal components") are numbered according to the decreasing percentage of accumulated variation they concentrate. Thus, Axis I always comprises the highest value of variation absorbed by any possible axis, which can be interpreted as representing one particular environmental or ecological factor. The individuals are then displayed in succesive two-dimensional plots ("scattergrams"), of which only the Axis I-Axis II coordinates are shown and discussed here.

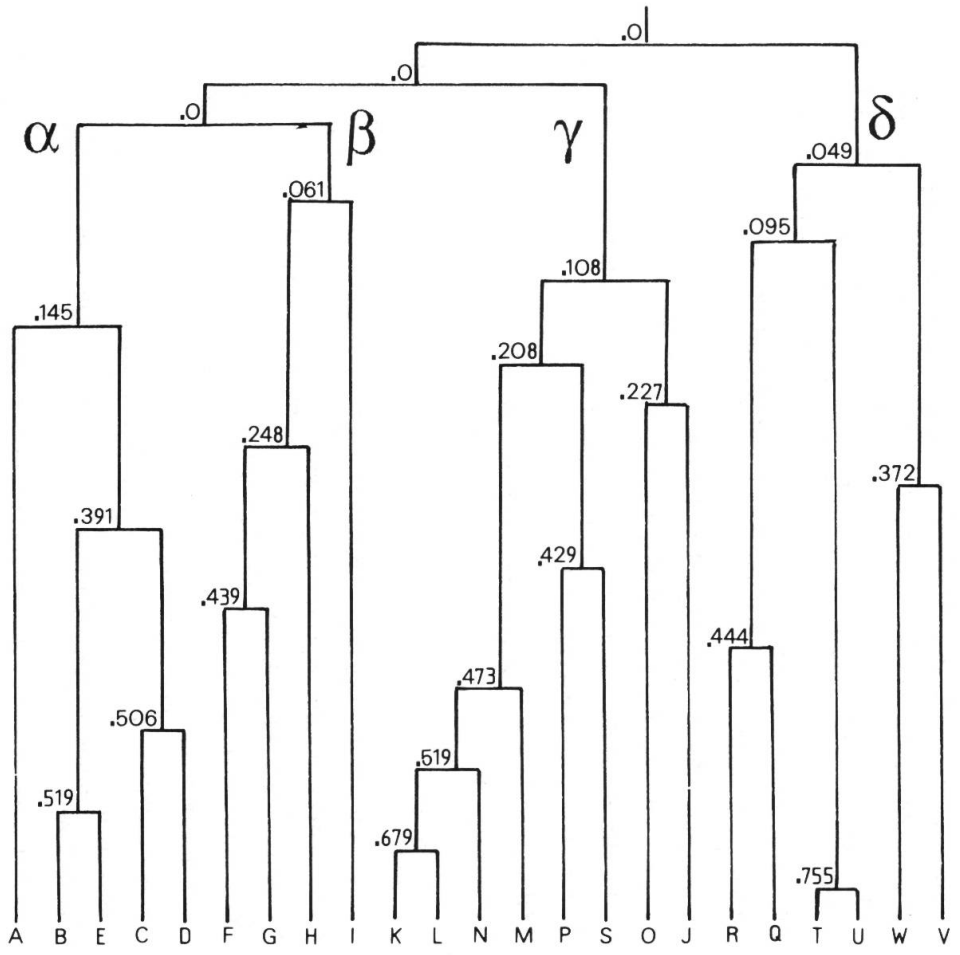


Fig. 1. — Dendrogram resulting from Clink classification analysis of the main woody communities of the Chaco and neighbouring formations. Letters at the bottom indicate the communities studied (see Table 1 for key), and figures in the horizontal lines the similarity index value at each level of fusion.

Results

All the vegetation types described by PRADO (1993) and usually regarded as part of the Gran Chaco region have been analyzed in Table 1. A number of FG, namely II, V, VI and XII amongst others, indicate very close links between those woody communities of wetter and less frost-affected areas, such as A (Gallery Forest), B ("Selva de Ribera"), C ("Tipa-Pacará" Forest), D ("Palo blanco" Forest) and the Austro-Brazilian Transitional Forest (E), alongside the communities described by PRADO & al. (1992) for Mato Grosso do Sul (F, G, H, I and J). Apart from FG XXI, which comprises species with a wide ecological plasticity, there are scarce connections between communities A to J and what will be here regarded as Chaco s.s. (communities K to W). The FG XXII comprises the species that relate the Austro-Brazilian Transitional Forest (E) to the Chaco proper, which are on the one hand of scarce importance here and sometimes accidental, and on the other

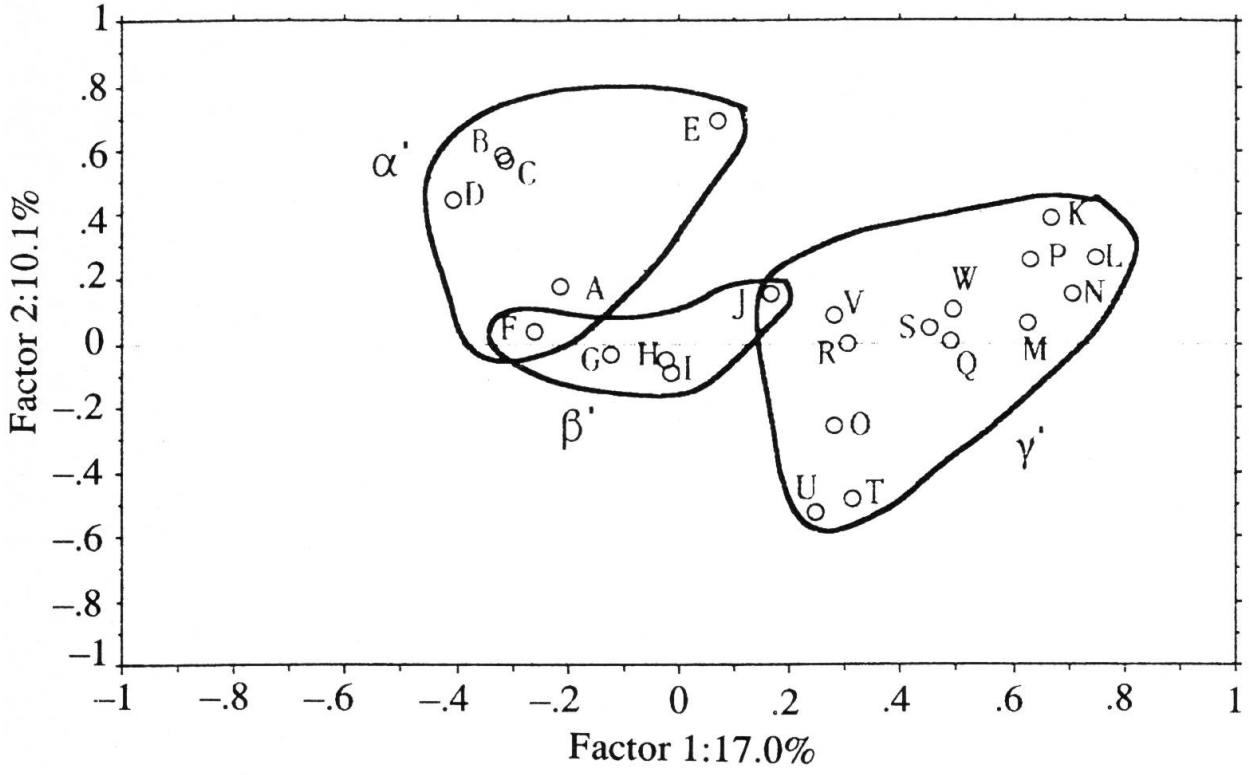


Fig. 2. — Scattergram from PCA analysis of the main woody communities of the Chaco and neighbouring formations.

are overweighed by the much more relevant links to communities A to D. The Chaco forest at Porto Murtinho (J) is the only one between the communities of Mato Grosso do Sul that can be regarded as truly chaquenian, as shown by Table 1 and coinciding with PRADO & al. (1992). The FG XXIII, XXIV, XXV, XXVI, XXVII, XXVIII, XXXIII and XXXIV illustrate the strong internal homogeneity of the Chaco s.s. woody communities.

Fig. 1 shows the dendrogram resulting from the CLINK classification analysis applied to the same set of communities shown in Table 1. It is noteworthy that the order of the communities rendered by CLINK is basically very similar to that proposed in the phytosociological table, save for the position of the Chaco at Porto Murtinho (J). Group α comprises communities A to E, while β those of Mato Grosso do Sul (F to I). Meanwhile, groups γ and δ consist of all the communities of the Chaco s.s., separated into two groups probably because of an east-west floristic gradient within the province.

The results of the PCA analysis shown in Fig. 2 present three basic clusterings of communities: the wetter ones (A to F) are together in cluster α', the Mato Grosso do Sul communities are grouped in another one (β'), while the bulk of the Chaco s.s. in cluster γ' shows stronger links within itself than with the rest of the neighbouring formations. Once again the Chaco of Porto Murtinho (J) is in a transitional position and could pertain to either of two clusters, while the Austro-Brazilian Transitional Forest (E) unmistakably joins the group of wetter communities.

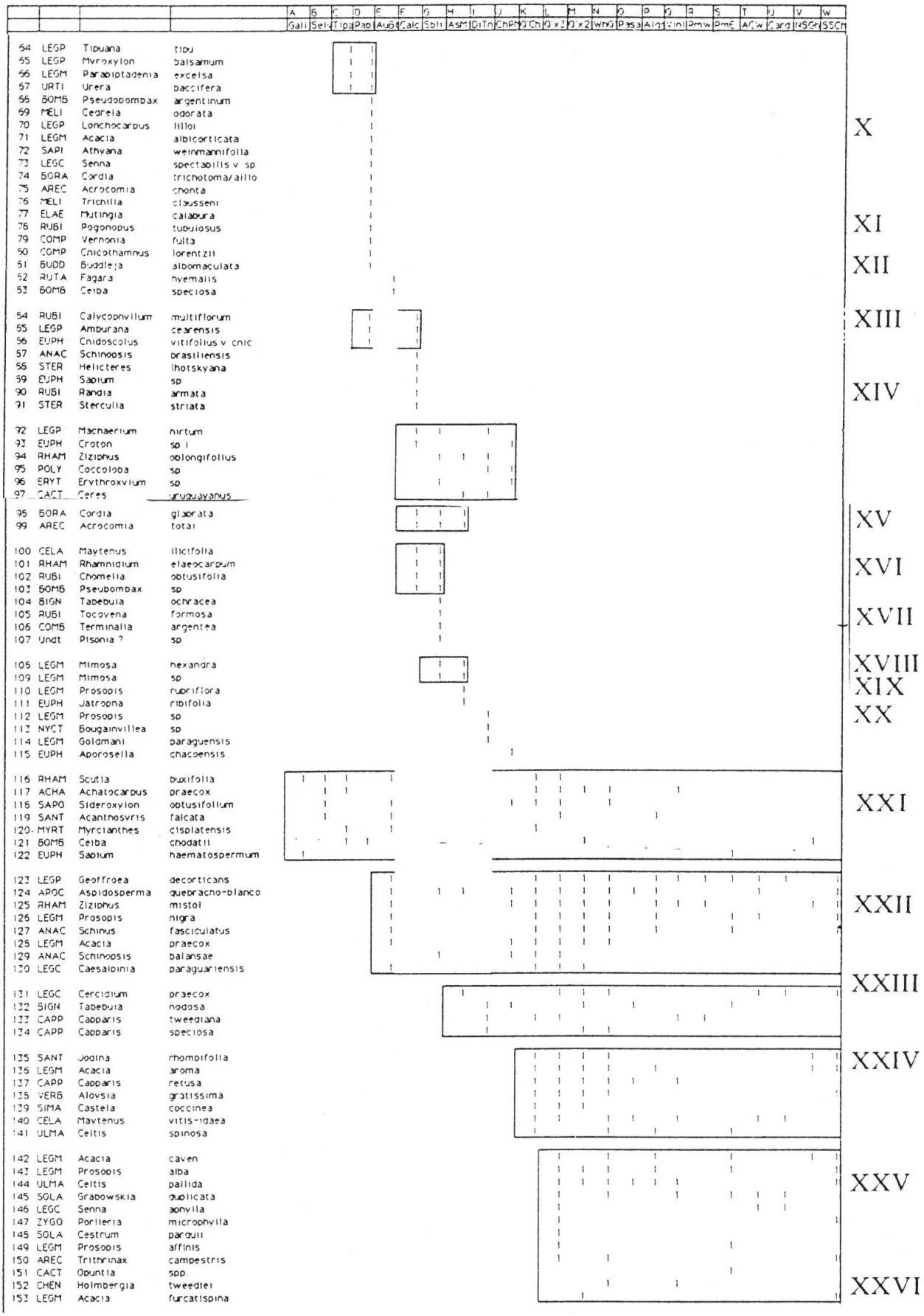
Discussion

The results of three different types of analysis applied to the Gran Chaco vegetation have been presented: the classical phytosociological approach and, as a more objective yardstick to evaluate this, two numerical analyses were performed, one to classify (CLINK) and one to ordinate (PCA) the samples. The congruence between the different results is striking. Out of the 23 vegetation units that had been regarded as chaquenian by different authors (see PRADO, 1993 and Table 1), five

Table 1. — Classical phytosociological analysis of the main woody communities of the Chaco and neighbouring formations. Source of the floristic lists is indicated.

Column: **A,** Gallery forest, Paraná River (FRANCESCHI & LEWIS, 1979). **B,** "Selva de Ribera" (PRADO & al., 1989; MORELLO & ADÁMOLI, 1974). **C,** "Tipa-Pacará" forest (MEYER, 1963; DIGILIO & LEGNAME, 1966; BROWN & al., 1985). **D,** "Palo blanco" forest (MEYER, 1944; CORO, 1956; ADÁMOLI & al., 1972; CABRERA, 1976). **E,** Austro-Brazilian Transitional Forest (LEWIS & PIRE, 1981, and author's field experience; also MORELLO & al., 1971, MORELLO & ADÁMOLI, 1974, and CABRERA, 1976). **F,** Calcareous woodlands, Mato Grosso do Sul (PRADO & al., 1992). **G,** *Schinopsis balansae* parkland, M. Gr. do Sul (PRADO & al., 1992). **H,** *Aspidosperma-Mimosa* scrubland, M. Gr. do Sul (PRADO & al., 1992). **I:** *Diplokeleba-Tabebuia-Capparis* scrubland, M. Gr. do Sul (PRADO & al., 1992). **J,** Chaco forest, Pto Murtinho, M. Grosso do Sul (PRADO & al., 1992). **K,** "Quebrachal" of *Schinopsis balansae* (LEWIS & PIRE, 1981, and author's field experience). **L,** "Quebrachal" of 3 "quebrachos" (RAGONESE, 1941; LEWIS & PIRE, 1981, and author's field experience). **M,** "Quebrachal" of 2 "quebrachos" (MORELLO & ADÁMOLI, 1968; ADÁMOLI & al., 1972, and author's field experience). **N,** "Quebrachal" of white "quebracho" (MORELLO & al., 1971; LEWIS & PIRE, 1981). **O,** "Palosantal" of *Bulnesia sarmientoi* (MORELLO & al., 1971, and ADÁMOLI & al., 1972). **P,** "Algarrobal" of *Prosopis* spp. (MORELLO & al., 1971). **Q,** "Vinalar" of *Prosopis ruscifolia* (MORELLO & al., 1971). **R,** "Palmar" of *Copernicia australis,* Western Chaco (CABRERA, 1976). **S,** "Palmar" of *Copernicia australis,* Eastern Chaco (CABRERA, 1976; LEWIS & PIRE, 1981, and author's field experience). **T,** Arid Chaco woodland (SAYAGO, 1969). **U,** "Cardonal" of *Stetsonia coryne* (SAYAGO, 1969). **V,** North Sierra Chaco (MARLANGE, 1972). **W,** South Sierra Chaco (SAYAGO, 1969).

	Family	Genus	Species	A Gall	B Sali	C Tipa	D Pabl	E Aub1	F Calc	G Sbil	H AcM	I DiTn	J ChPM	K QCh	L Q x3	M Q x2	N vNQ	O Pasa	P Algt	Q vin	R Pmw	S PmE	T ACW	U Card	V NSCh	W SSCh	
1	LAUR	Nectandra	falcifolia	1																							
2	LEGM	Albizia	polyantha	1																							
3	MYRT	Hexachlamis	edulis	1																							
4	CAPP	Crateva	tapia	1																							
5	APOC	Peschiera	australis	1																							
6	LEGM	Inga	uruguensis	1																							I
7	LEGM	Acacia	monacantha	1																							
8	ULMA	Celtis	iguanaea	1																							
9	EUPH	Croton	urucurana	1																							
10	FLAC	Banara	arguta	1																							
11	AREC	Arecastrum	romanzoffianum	1																							
12	LEGP	Geoffroea	striata	1																							
13	ANNO	Rollinia	emarginata	1																							
14	POLY	Ruprechtia	laxiflora	1	1	1	1	1																			II
15	LEGM	Enterolobium	contortisiliquum	1	1	1	1	1																			
16	MYRT	Eugenia	uniflora	1	1	1	1	1																			
17	RUTA	Fagara	naranjillo	1	1	1	1																				III
18	COMB	Terminalia	triflora	1		1	1																				
19	MYRS	Rapanea	laetevirens	1	1	1																					
20	SAPO	Pouteria	gardneriana	1	1																						
21	LEGC	Holocalyx	balansae		1																						
22	MORA	Ficus	luschnathiana		1																						
23	SAPI	Sapindus	saponaria		1																						
24	MORA	Sorocea	sprucei		1																						
25	MELI	Trichilia	elegans		1																						IV
26	NYCT	Pisonia	aculeata		1																						
27	CEL	Schaefferia	argentinensis		1																						
28	PTER	Acrostichum	aureum		1																						
29	CECR	Cecropia	adenopus		1																						
30	RUTA	Pilocarpus	pennatifolius		1																						
31	STER	Guazuma	ulmifolia		1																						
32	TILI	Luehea	divaricata		1																						
33	LEGC	Peltophorum	dubium		1																						
34	ULMA	Phyllostylon	rhamnoides		1	1	1	1	1			1		1													V
35	ULMA	Celtis	sp		1	1	1	1	1																		
36	BIGN	Tabebuia	impetiginosa		1	1	1	1	1	1																	
37	LEGM	Anadenanthera	colubrina v cebil		1	1	1		1																		
38	ANAC	Astronium	urundeuva				1		1	1	1																
39	RUTA	Fagara	rhoifolia			1	1	1		1				1													
40	CAPP	Capparis	aff retusa ?		1								1	1													
41	SAPI	Diplokeleba	floribunda					1					1														
42	BORA	Patagonula	americana		1	1	1	1																			VI
43	MYRT	Myrcianthes	pungens		1	1	1	1																			
44	SAPI	Allophylus	edulis		1	1	1	1																			
45	NYCT	Pisonia	zapallo		1	1	1	1																			
46	LEGC	Gleditsia	amorphoides		1		1	1																			
47	SAPO	Chrysophyllum	gonocarpum		1		1	1																			
48	MORA	Maclura	tinctoria		1		1	1																			
49	LEGM	Pithecellobium	scalare				1	1																			
50	ARAL	Pentapanax	angelicifolius		1	1	1																				
51	CARI	Carica	quercifolia		1	1		1																			
52	PHYT	Phytolacca	dioica		1			1																			
53	SOLA	Brunfelsia	australis		1			1																			
54	ANAC	Astronium	balansae		1			1																			VII
55	LEGC	Pterogyne	nitens		1		1																				
56	SAPI	Cupania	vernalis			1	1																				VIII
57	SAPO	Chrysophyllum	marginatum			1	1																				
58	ULMA	Trema	micrantha			1	1																				
59	BIGN	Jacaranda	mimosifolia				1																				
60	MYRT	Myrcianthes	mato				1																				
61	BIGN	Tecoma	stans				1																				IX
62	PIPE	Piper	tucumanum				1																				
63	TILI	Heliocarpus	popayanensis				1																				


A B C D E F G H I J K L M N O P Q R S T U V W
Gali Sely Tipa Pasb Aub6 Calc Spli AsM DiTn ChPt MO Ch Ox1 Ox2 Ox3 wnO Pasa Alig Vini Pmw PmE ACw Carg NSCr SSCr
54 LEGP Tipuana tipu
55 LEGP Myroxylon balsamum
56 LEGM Paraoptadenia excelsa
57 URTI Urera baccifera
58 BOMB Pseudobombax argentinum
59 MELI Cedrela odorata
70 LEGP Lonchocarpus lilloi
71 LEGM Acacia albicorticata
72 SAPI Athyana weinmannifolia
73 LEGC Senna spectabilis v. sp
74 BORA Cordia trichotoma/aillo
75 AREC Acrocomia chonta
76 MELI Trichilia claussenii
77 ELAE Mutingia calabura
78 RUBI Pogonopus tubulosus
79 COMP Vernonia fulta
80 COMP Gnicothamnus lorentzii
81 BUDD Buddleja albomaculata
82 RUTA Fagara hyemalis
83 BOMB Ceiba speciosa
84 RUBI Calycophyllum multiflorum
85 LEGP Amburana cearensis
86 EUPH Cnidoscolus vitifolius v. cnic
87 ANAC Schinopsis brasiliensis
88 STER Helicteres lhotskyana
89 EUPH Sapium sp
90 RUBI Randia armata
91 STER Sterculia striata
92 LEGP Machaerium hirtum
93 EUPH Croton sp 1
94 RHAM Ziziphus oblongifolius
95 POLY Coccoloba sp
96 ERYT Erythroxylum sp
97 CACT Cereus uruguayanus
98 BORA Cordia glaborata
99 AREC Acrocomia total
100 CELA Maytenus ilicifolia
101 RHAM Rhamnidium elaeocarpum
102 RUBI Chomelia obtusifolia
103 BOMB Pseudobombax sp
104 BIGN Tabebuia ochracea
105 RUBI Tocoyena formosa
106 COMB Terminalia argentea
107 Undt Pisonia ?
108 LEGM Mimosa hexandra
109 LEGM Mimosa sp
110 LEGM Prosopis ruboriflora
111 EUPH Jatropha ribifolia
112 LEGM Prosopis sp
113 NYCT Bougainvillea sp
114 LEGM Goldmani paraguensis
115 EUPH Aporosella chacoensis
116 RHAM Scutia buxifolia
117 ACHA Achatocarpus praecox
118 SAPO Sideroxylon obtusifolium
119 SANT Acanthosyris falcata
120 MYRT Myrcianthes cisplatensis
121 BOMB Ceiba chodatii
122 EUPH Sapium haematospermum
123 LEGP Geoffroea decorticans
124 APOC Aspidosperma quebracho-blanco
125 RHAM Ziziphus mistol
126 LEGM Prosopis nigra
127 ANAC Schinus fasciculatus
128 LEGM Acacia praecox
129 ANAC Schinopsis balansae
130 LEGC Caesalpinia paraguariensis
131 LEGC Cercidium praecox
132 BIGN Tabebuia nodosa
133 CAPP Capparis tweediana
134 CAPP Capparis speciosa
135 SANT Jodina rhombifolia
136 LEGM Acacia aroma
137 CAPP Capparis retusa
138 VERB Aloysia gratissima
139 SIMA Castela coccinea
140 CELA Maytenus vitis-idaea
141 ULMA Celtis spinosa
142 LEGM Acacia caven
143 LEGM Prosopis alba
144 ULMA Celtis pallida
145 SOLA Grabowskia duplicata
146 LEGC Senna aphylla
147 ZYGO Porlieria microphylla
148 SOLA Cestrum parquii
149 LEGM Prosopis affinis
150 AREC Trithrinax campestris
151 CACT Opuntia spp.
152 CHEN Holmbergia tweediei
153 LEGM Acacia furcatispina
X
XI
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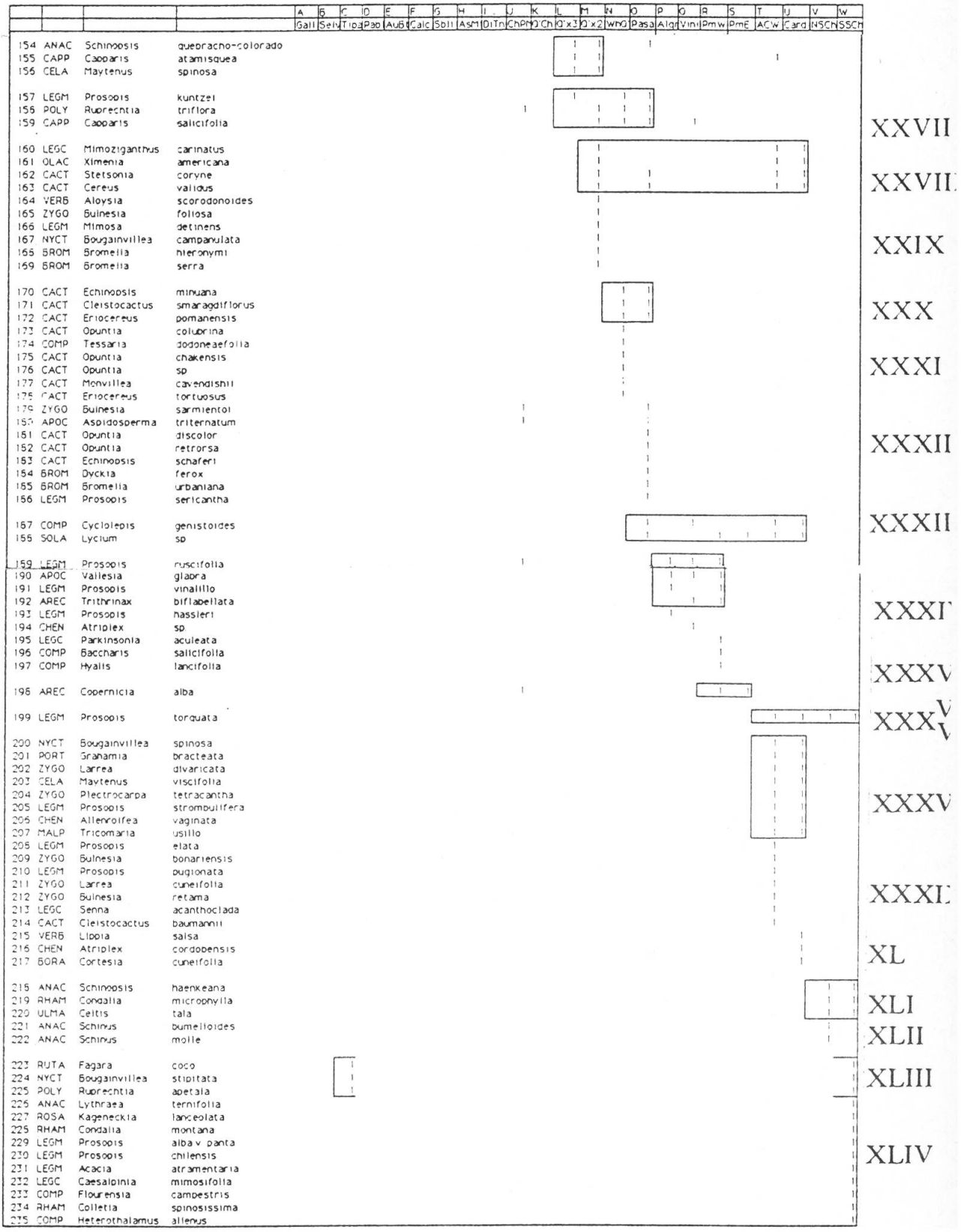
A Gall
B SelV
C TipA
D Pab
E AuB
F Calc
G SbII
H AsM
I DiTn
J ChPM
K Ch
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M 0°x2
N WhG
O Pasa
P Algr
Q VinI
R Pmw
S PmE
T ACw
U Card
V NSCh
W SSCh
154 ANAC Schinopsis quebracho-colorado
155 CAPP Capparis atamisquea
156 CELA Maytenus spinosa
157 LEGM Prosopis kuntzei
158 POLY Ruprechtia triflora
159 CAPP Capparis salicifolia
160 LEGC Mimoziganthus carinatus
161 OLAC Ximenia americana
162 CACT Stetsonia coryne
163 CACT Cereus validus
164 VERB Aloysia scorodonoides
165 ZYGO Bulnesia foliosa
166 LEGM Mimosa detinens
167 NYCT Bougainvillea campanulata
168 BROM Bromelia hieronymi
169 BROM Bromelia serra
170 CACT Echinopsis minuana
171 CACT Cleistocactus smaragdiflorus
172 CACT Eriocereus pomanensis
173 CACT Opuntia colubrina
174 COMP Tessaria dodoneaefolia
175 CACT Opuntia chakensis
176 CACT Opuntia sp
177 CACT Monvillea cavendishii
178 CACT Eriocereus tortuosus
179 ZYGO Bulnesia sarmientoi
180 APOC Aspidosperma triternatum
181 CACT Opuntia discolor
182 CACT Opuntia retrorsa
183 CACT Echinopsis schaferi
184 BROM Dyckia ferox
185 BROM Bromelia urbaniana
186 LEGM Prosopis sericantha
187 COMP Cyclolepis genistoides
188 SOLA Lycium sp
189 LEGM Prosopis ruscifolia
190 APOC Vallesia glabra
191 LEGM Prosopis vinalillo
192 AREC Trithrinax biflabellata
193 LEGM Prosopis hassleri
194 CHEN Atriplex sp
195 LEGC Parkinsonia aculeata
196 COMP Baccharis salicifolia
197 COMP Hyalis lancifolia
198 AREC Copernicia alba
199 LEGM Prosopis torquata
200 NYCT Bougainvillea spinosa
201 PORT Grahamia bracteata
202 ZYGO Larrea divaricata
203 CELA Maytenus viscifolia
204 ZYGO Plectrocarpa tetracantha
205 LEGM Prosopis strombulifera
206 CHEN Allenrolfea vaginata
207 MALP Tricomaria usillo
208 LEGM Prosopis elata
209 ZYGO Bulnesia bonariensis
210 LEGM Prosopis pugionata
211 ZYGO Larrea cuneifolia
212 ZYGO Bulnesia retama
213 LEGC Senna acanthoclada
214 CACT Cleistocactus baumannii
215 VERB Lippia salsa
216 CHEN Atriplex cordobensis
217 BORA Cortesia cuneifolia
218 ANAC Schinopsis haenkeana
219 RHAM Condalia microphylla
220 ULMA Celtis tala
221 ANAC Schinus bumelioides
222 ANAC Schinus molle
223 RUTA Fagara coco
224 NYCT Bougainvillea stipitata
225 POLY Ruprechtia apetala
226 ANAC Lythraea ternifolia
227 ROSA Kageneckia lanceolata
228 RHAM Condalia montana
229 LEGM Prosopis alba v. panta
230 LEGM Prosopis chilensis
231 LEGM Acacia atramentaria
232 LEGC Caesalpinia mimosifolia
233 COMP Flourensia campestris
234 RHAM Colletia spinosissima
235 COMP Heterothalamus alienus
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XLIV

are definitely non-chaquenian (Gallery Forest, "Selva de Ribera", "Tipa-Pacará" Forest, "Palo blanco" Forest, and Calcareous Forest), four are here considered transitional with neighbouring formations (the Austro-Brazilian Transitional Forest and three of the communities of Mato Grosso do Sul), and 14 correspond to what is here defined as Chaco *sensu stricto:* the four "Quebrachales", the "Palosantal", "Algarrobal", "Vinalar", "Cardonal", the two "Palmares", both Sierra Chaco variants, the Arid Chaco Woodland and the Chaco Forest at Porto Murtinho. A brief discussion on the excluded and transitional communities follows.

a) Excluded communities

Between the communities listed in Table 1, none of the Gallery Forest (A), "Selva de Ribera" (B), "Tipa-Pacará" Forest (C), "Palo blanco" Forest (D) and the Calcareous Forest of Mato Grosso do Sul (F) can be regarded as chaquenian in character. Climate, soils and water regime are entirely different from that which prevails in the Chaco s.s., and as a result their flora is essentially of Amazonian lineage (*sensu* CABRERA & WILLINK, 1980). All of these vegetation types are well defined, each characterized by a floristic group comprising the species which are exclusive to them within the scope of this study. Moreover, the numerical analyses (Figs. 1 & 2) have shown that they are more closely inter-related, and linked to what has been called "Austro-Brazilian Transitional Forest" (PRADO, 1991), than to the Chaco s.s. communities. Therefore, none of these five vegetation types should be included in the Chaco phytogeographical province, as the more modern treatments have indicated (e.g. CABRERA, 1976; PRADO, 1991).

b) Transitional communities

The four transitional units consist of three from the Mato Grosso do Sul area studied by PRADO & al. (1992): the *Schinopsis balansae* parkland (G), the *Aspidosperma-Mimosa* scrubland (H), and the *Diplokeleba-Tabebuia-Capparis* scrubland (I), and finally the "Austro-Brazilian Transitional Forest" (E). The first three communities contain a very low percentage of true Chaco species (PRADO & al., 1992), along with a number of cerrado and semi-deciduous forest elements, and none of the three can be fully ascribed to any of the major phytogeographical units which converge in the Pantanal, i.e. Cerrados, Amazonian, Paranense and Chaco provinces (ADÁMOLI, 1982). Furthermore, the numerical analyses (Fig. 2) show these communities in a clear transitional position between the Chaco s.s. and the wetter vegetation units.

The Austro-Brazilian Transitional Forest (E) is undoubtedly the climax community in the east of the Gran Chaco area (LEWIS & PIRE, 1981, *sub* "bosque chaqueño"), i.e. the sector referred to as "Eastern Chaco" in all phytogeographical classifications (MORELLO & ADÁMOLI, 1968; RAGONESE & CASTIGLIONI, 1970; CABRERA, 1971 & 1976). Four true Chaco communities also manage to extend into this eastern area. These are the *Schinopsis balansae* "quebrachal" (K), *Prosopis* spp. "algarrobales" (P), *Copernicia australis* "palmares" (S), and *Stetsonia coryne* "cardonales" (see PRADO, 1993). They are evidently edaphic-dependent, and their presence in an area of over 900 mm yearly rainfall is allowed only by the physiological drought caused by the high salt content of the soil and consequent higher osmotic potential. Consequently, and contrary to the position sustained by RAGONESE & CASTIGLIONI (1970) and CABRERA (1976), the "quebrachal" of *Schinopsis balansae* should not be regarded as a climax community, since it rather thrives on non-climatogenic saline soils, with high clay level, periodical waterlogging, elevated Na^{++} concentration and very strongly alkaline subsoils (ESPINO & al., 1983). Thus, true Chaco vegetation is found in a strip of some 100 km wide, parallel to the Paraguay and Paraná rivers, in an area where climatic, edaphic and geomorphological conditions are different from those in the center and west of the Chaco s.s. Presumably, the salinity factor is responsible for this outlying representation, since Chaco elements can survive in edaphic conditions which are hostile for the subtropical humid forests species of the Austro-Brazilian Transitional Forest. This hypothesis is exactly the opposite to HUECK's (1972), who postulated that chaquenian species would occur on higher, drier ground within the floodable, water-modelled Eastern Chaco. On the contrary, such drier areas are covered by a different kind of forest dominated by species such as *Patagonula*

americana, Phytolacca dioica, Ruprechtia laxiflora, Gleditsia amorphoides, Tabebuia impetiginosa, Pisonia zapallo, and *Enterolobium contortisiliquum.* All of these species occur elsewhere in subtropical humid forests in S Brazil, E Paraguay and N Argentina. Indeed, the species listed above are all widespred in South American forests, and extend to NE Brazil or humid Atlantic forests (KLEIN, 1967), or even to Central America and Mexico in similar ecosystems (e.g. *Tabebuia impetiginosa,* in GENTRY, 1979).

Most species of the Austro-Brazilian Transitional Forest are elements which are common to the five vegetation types here excluded altogether from the Chaco s.s., such as the species listed above together with *Diplokeleba floribunda, Astronium balansae, Chrysophyllum gonocarpum, Pithecellobium scalare* and *Brunfelsia australis* (see Table 1, FGs II, V and VI). Seven of the most typical Chaco species[1] may also occur in this transitional unit, but they are never dominant trees and seem to be at the extreme of their ecological range in this area. Hardly any of these chaquenian intruders can be found further east in wetter areas either in Argentina, Paraguay or Brazil, and it is likely that their existence in this unit could be due to anthropogenic alteration of the environment (overgrazing, selective felling), or even brought in by cattle. Therefore it is proposed that this vegetation type, which has received several different names by different authors, and has generally been included in the Chaco province (CABRERA, 1971 & 1976), is better called Austro-Brazilian Transitional Forest and should be excluded altogether from the Chaco s.s.

This forest is basically a very impoverished version of the Brazilian Subtropical Forests (sensu ANDRADE-LIMA, 1966, and KLEIN, 1972), which is here at the extreme western limit of its distribution. Furthermore, and despite the presence of some chaquenian elements in it, the Austro-Brazilian Transitional Forest should be regarded as a component of the Paranense province of the Amazonian Dominium (sensu CABRERA & WILLINK, 1980), since the dominant trees are species which are mainly distributed in other districts of this province where, however, they may be of lesser importance. Thus, of the Paranense province floristic stock, these species are probably those that can tolerate a few frosts each year, and can still compete successfully against the chaquenian species pushing east in areas with less alkaline and less waterlogged soils.

This interpretation is reinforced by the fact that most of the dominant species of the Austro-Brazilian Transitional Forest reappear further west, jumping over 700 km of dry Chaco plains, in the Yungas province (SMITH, 1962; RAGONESE & CASTIGLIONI, 1970; CABRERA, 1976) in the "Tipa-Pacará" (C) and "Palo blanco" (D) Forests. There is a very close relationship between those three vegetation units, as shown by several floristic groups of Table 1 and strongly supported by the numerical analysis. However, although units C & D also include some widespread chaquenian species, it is of interest that few authors tried to include these two forest types in the Chaco (e.g. HUECK, 1972), whilst virtually all phytogeographers have merged without hesitation the Austro-Brazilian Transitional Forest with the Chaco, with perhaps the sole exception of CASTELLANOS & PÉREZ-MOREAU (1944) in their map of vegetation of Argentina.

c) The Eastern Chaco problem

The fact that the so-called "Eastern Chaco" is in effect a meeting point of quite diverse floristic elements, i.e. true xerophytic chaquenian communities and humid subtropical and tropical species, has been perceived by some previous authors. Thus, CABRERA (1970) was aware that the boundary between the Chaquenian and Amazonian Dominia, which meet in the Eastern Chaco, is confused, and he remarked that the whole of the river Paraguay basin is an immense transition area with a very complicated intermingled pattern. A striking example of such intermingling is that the current concept of "Eastern Chaco" even includes "paratodales" of *Tabebuia caraiba* in floodable localities associated with the river Pilcomayo valley in SE Paraguayan Chaco region and NE Formosa in Argentina (CHODAT & VISCHER, 1977; FIEBRIG, 1933; RAGONESE & CASTIGLIONI, 1970; MORELLO & ADÁMOLI, 1974, p. 42). *T. caraiba* can hardly be accepted

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[1]These are: *Geoffroea decorticans, Aspidosperma quebracho-blanco, Ziziphus mistol, Prosopis nigra, Schinus fasciculatus, Acacia praecox* and *Caesalpinia paraguariensis* (see Table 1, FG XXII). Sometimes even *Schinopsis balansae* may appear in this forest, but its occurrence is very occasional and marginal to the unit (LEWIS, J. P., in litt.).

as Chaco species (see distribution map in PRADO & GIBBS, in press) since it also occurs in NE Brazil in the "sertão" and "agreste" (ANDRADE-LIMA, 1960 & 1989), is also an abundant species in the Cerrados (HERINGER & al., 1977; FURLEY & RATTER, 1988; RATTER & al., 1988), and the "paratodales" are one of the main features of the Pantanal landscape (RATTER, 1984; ALLEM & VALLS, 1987)!

Although edaphic factors can explain the eastward expansion of some Chaco taxa, the reason why southern or central Brazilian hygrophilous elements can expand westwards to interdigitate with chaquenian communities must be climatic. In Chaco vegetation maps the line drawn to separate the so-called "Eastern Chaco" from the rest of the province (see subregions map in MORELLO & ADÁMOLI, 1968; also HUECK & SEIBERT, 1981) seems to coincide roughly with a rainfall isoline somewhere between 950 to 1000 mm per year (PRADO, 1991), and also with the alleged limit between humid and dry climates, the MI(Moisture Index) = 1 line (BOX, 1986). In RAGONESE & CASTIGLIONI's map (1970), where their concept of "Eastern Chaco" covers the eastern half of the Gran Chaco region, this line coincides roughly with the western boundary of the "Pilaguense" and "Bosque Chaqueño" districts.

The climate classification systems of Koeppen and the two systems proposed by Thornthwaite have been compared for Argentina by BURGOS & VIDAL (1951), who concluded that Thornthwaite's Second System is the most fitted to the distribution of the natural vegetation. For the Argentine Chaco, this correlation is very good: the transitional belt proposed here (Fig. 4) matches very well with an equivalent narrow band along the river Paraná with C_2B_4'ra' climate (Fig. 3), and so does the zero isoline for the MI according to Thornthwaite's Second System (BURGOS & VIDAL, 1951, Fig. 7D). The similarities extend even to most of the chaquenian districts proposed by RAGONESE & CASTIGLIONI (1970), such as the "Pilaguense", "Matacense", and "Santiagueño" districts, to which the corresponding climate types are C_1A'da', DA'da' and DB_4'da' respectively, and the districts "Campestre", Mixed Forests & Savannas and Chaquenian Forest as a group with the corresponding climate type C_1B_3'da'. It is noteworthy that a very similar kind of climate to that of the eastern Transitional Belt appears to the west of the Chaco in areas occupied by both the "Tipa-Pacará" and "Palo blanco" Forests!

Given the weight of floristic and correlated climatic and edaphic evidence, the question could be posed now why the "Eastern Chaco" has traditionally been considered as truly chaquenian, as in MORELLO & ADÁMOLI (1968), RAGONESE & CASTIGLIONI (1970), CABRERA (1976), HUECK & SEIBERT (1981), RAMELLA & SPICHIGER (1989), SPICHIGER & RAMELLA (1989), and ZELLWEGER & al. (1990). The reasons are more historical than botanical. The rainforests or thorny dry woodlands formed a barrier to an eastward expansion for centuries with the result that most of the exsiccata collected on the eastern side of the Paraná and Paraguay rivers have simply the locality "Chaco", whether they are xerophytic or humid forest species, just because the collector ferried the river or sailed along the tributaries. The NE Argentine Chaco region and the Paraguayan Chaco region were cautiously explored by naturalists in a narrow fringe parallel to the big rivers or their tributaries, mainly the Pilcomayo (see the picturesque account by KERR, 1968), at the beginning of this century. HOCHREUTINER (1923) remarked that the Paraguayan Chaco was known only along the banks of the Paraguay and Pilcomayo rivers, and FIEBRIG (1933) was honest enough to admit that up to that time scientific exploration extended only for 100 to 150 km west of the river Paraguay (though the present author still believes that is an overestimate)[1]. Geographically speaking the term Chaco will continue as the denomination of the whole of the region, but from a phytogeographical point of view the name must have a more restricted usage.

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[1]The first botanical collector to cross the Paraguayan Chaco by land was Teodoro Rojas, who followed the Paraguayan lines during the "Chaco War" and reached the Parapetí river in Bolivia in 1935. More evidence comes from the zoological field; the endemic peccary genus *Catagonus,* considered for long as extinct and known only from fossils, was rediscovered as late as in 1972 in the heart of the Paraguayan Chaco (WETZEL & al., 1975).

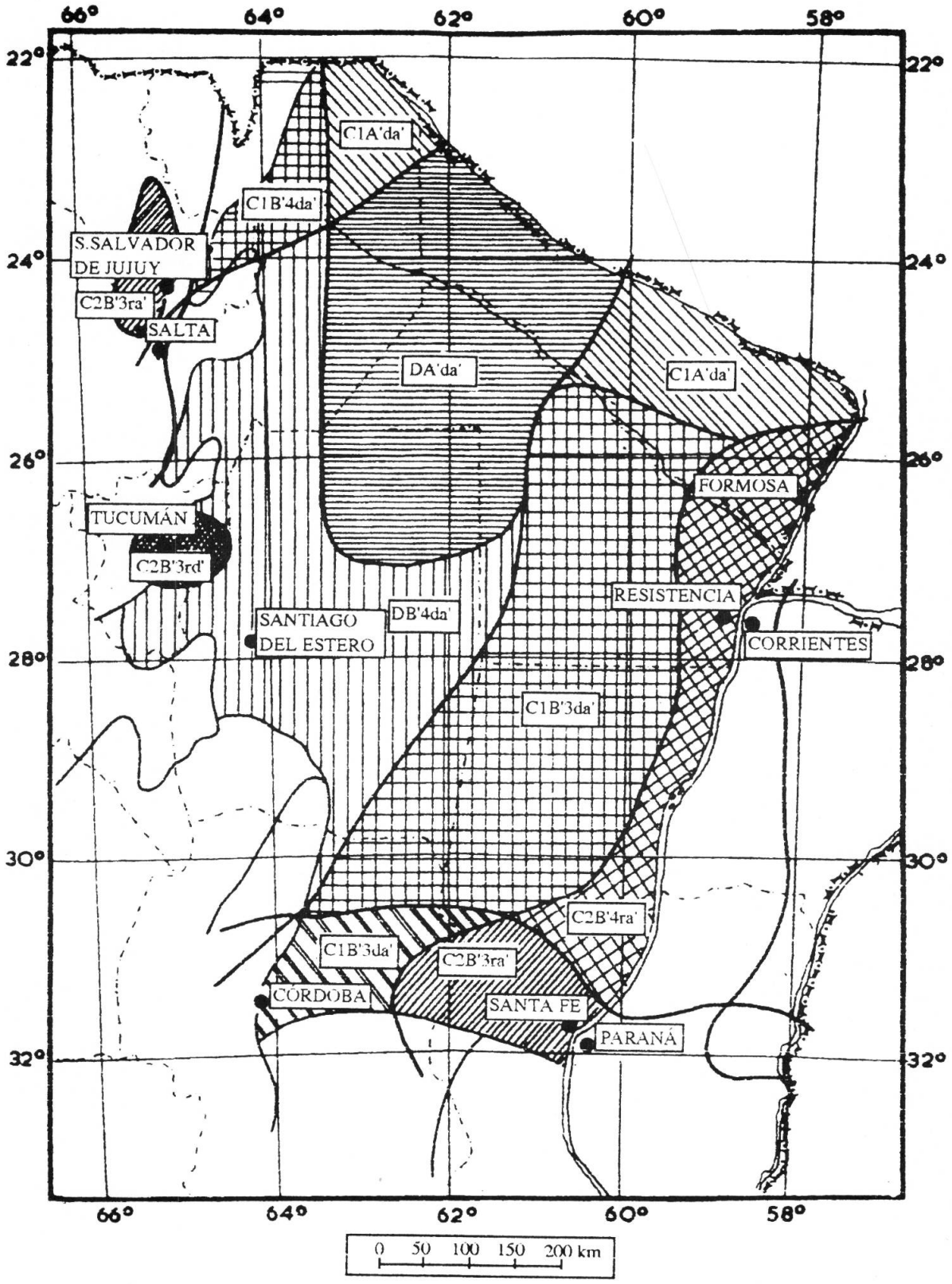

Fig. 3. — Climate types for the Argentine Chaco, according to the Second System of Thornthwaite. Modified from GALMARINI & R. DEL CAMPO, 1964.

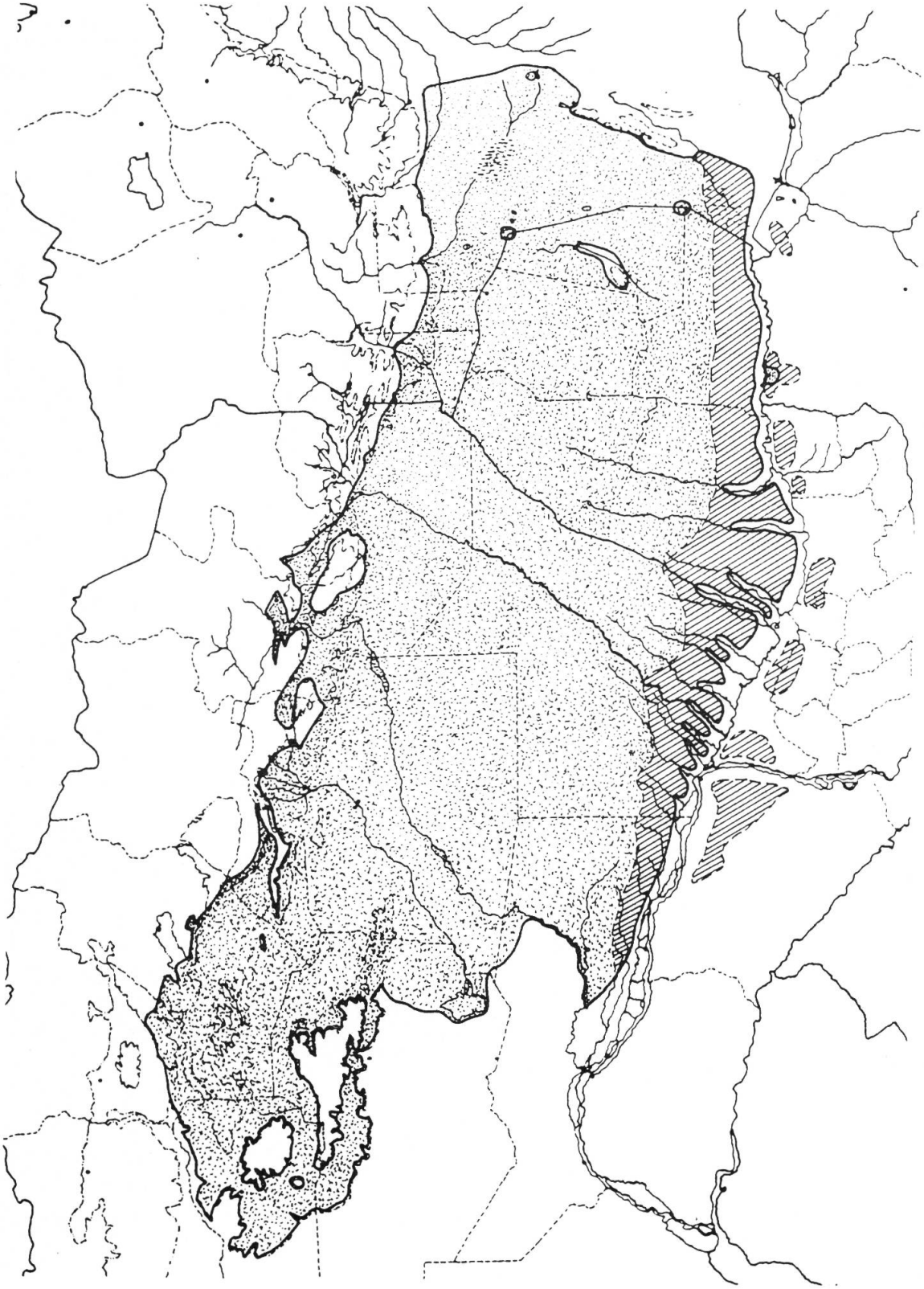

Fig. 4. — A new proposal for the geographical limits of the Chaco sensu stricto. The transitional belt is indicated by oblique hatching.

d) The Chaco sensu stricto

By excluding these extraneous communities it is now possible to re-establish the geographical limits of the Chaco as a phytogeographical province. On the basis of a strict floristic list of woody and succulent species (PRADO, 1991), phytosociological study of the more relevant plant communities in the region both in classical and numerical analyses, and putting the vegetation of this area against the background of similar formations in South America (PRADO, 1991), a map of what is here regarded as Chaco *sensu stricto* is presented (Fig. 4). It must be noted that the Sierra Chaco, although taken as a separate entity throughout the analysis, is accepted as part of the Chaco s.s.; however, the *Polylepis australis* woodlands are not to be regarded as chaquenian, as in CABRERA (1976). In the construction of this new map some previous vegetation maps have been employed; i.e. CORO (1956) and ELLENBERG (1981) for the Bolivian Chaco, VERVOORST (in HAWKES & HJERTING, 1969) for NW Argentina up to La Rioja province, RAGONESE & CASTIGLIONI (1970) for SW Chaco in the provinces of La Rioja, San Juan, San Luis and Córdoba in part, SAYAGO (1969) and LUTI & al. (1979) for the Córdoba province, and D'ANGELO & al. (1987) together with LEWIS (1981) for the southern and eastern limit in the Santa Fe province. Also taken into consideration were the maps of the neighbouring phytogeographic provinces Monte (MORELLO, 1958) and Espinal (LEWIS & COLLANTES, 1973).

The extremely patterned vegetation in the east of the Chaco s.s. cannot be mapped with any precision at this stage with the knowledge available to date. A wide belt of transitional vegetation (Fig. 4) has been left open to further studies which could determine the exact localities where true Chaco vegetation can be found. However, to delimit this belt, information was taken from maps in CASTELLANOS & PÉREZ-MOREAU (1944), MORELLO & ADÁMOLI (1967), RAGONESE & CASTIGLIONI (1970), LEWIS (1981), ESSER (1982), and PRADO & al. (1989 & 1992), together with the present author's field experience and the plant distribution maps presented elsewhere (PRADO, 1991; PRADO & GIBBS, in press). Other differences with previous concepts of the Chaco shown in this new map consist in the exclusion of the vegetation of some of the "cerros" of Paraguay, such as the Cerros León, Cabrera and Chovoreca, clearly linked to the Subandean Piedmont Forests (RAMELLA & SPICHIGER, 1989) and also to the arboreal forms of Caatingas of NE Brazil (PRADO, 1991). Also excluded are the gallery forests on the rivers crossing the Chaco, particularly in their lower courses close to the Paraguay and Paraná rivers, and the vegetation of the Río Timane in the Paraguayan Chaco. Of the alleged Chaco vegetation in SW Brazil only a reduced sector remains as such (Fig. 4), together with some limited neighbouring transitional areas. It is noteworthy as well that the expansion of the Chaco s.s. beyond the line Santa Cruz de la Sierra-Chiquitos is here dramatically limited with respect to previous maps.

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