Phytocoenologia	**36** (4)	473–508	Berlin–Stuttgart, December 15, 2006

Classification of the forests of the northern Paraguayan Chaco

by Gonzalo Navarro, Cochabamba (Bolivia), José A. Molina, Madrid (Spain) and Lidia Pérez de Molas, Asunción (Paraguay)

with 4 figures and 7 tables

Abstract. The forests of the northern Paraguayan Chaco are described and classified using phytosociological methods and numerical analysis. Forest types are based on the close relation between the different floristic combinations detected and the variations in soil, bioclimate and biogeography of the northern Paraguayan Chaco. Seven main groups are recognized: 1) Forests on sandy soils of the Médanos; 2) Xerophytic forests on well- to fairly well-drained soils of the old alluvial plains; 3) Forests on poorly-drained soils of the north-western Chaco; 4) Chaco to Chiquitanía transitional forests; 5) Forests of the eastern Chaco of the Alto Río Paraguay; 6) Chiquitanía to Chaco transitional forests and shrublands; 7) Hygrophytic and floodable forests. On a more detailed level 26 forest types are identified, with the different types of Quebracho forest being the most common in the territory. From a biogeographical viewpoint the Chacoan forests are the most extensive while the Chiquitanian forests are restricted to the far north-east of the northern Paraguayan Chaco. Within the Chacoan forests in turn two large transitional groups can be seen: towards the Chiquitanía (the Cerrado) and towards the Pantanal. From an ecological viewpoint, the processes related with the degree of drainage of the soils and the possibility of flooding are the main factors in the floristic and structural characterization and distribution of the Chacoan forests.

Keywords: dry Chaco, phytosociology, soil drainage factor, floodable lands, Paraguayan forests, classification.

1. Introduction

The Chaco is one of the most interesting and original eco-regions in South America (www.worldlife.org). Its range, approximately 1 million square kilometres, covers a large part of the centre of the continent and includes a great diversity of ecological systems with different kinds of forests and dry, deciduous shrublands (Cabrera & Willink 1980, NatureServe 2003).

The dry woods are considered to be the most endangered ecosystem in the neotropics (Gentry 1977, Janzen 1988, Linares-Palomino et al. 2003). Their structure and composition have also been seriously affected by a variety of human activities: overgrazing by cattle, forest fires, massive deforestation in order to cultivate oil-producing species, among others (soy,

DOI: 10.1127/0340-269X/2006/0036-0473 0340-269X/06/0036-0473 $ 9.00

sunflower, cotton, sorghum), logging, and the building of roads and gas and oil pipelines (Stotz et al. 1996, Parker et al. 1993).

There is a growing body of knowledge concerning the forests of the Chaco in general, and of the northern Chaco in Bolivia and Paraguay in particular (López 1984, Ramella & Spichiger 1989, Spichiger et al. 1991, Prado 1993a, 1993b, Navarro 1997, Mereles & Degen 1998, Navarro & Fuentes 1999, Fuentes & Navarro 2000, Navarro & Maldonado 2002, Josse et al. 2003). However there are no detailed studies of the forests of the Paraguayan Chaco using phytosociological methodology. The objectives of this work were the following: 1) to investigate the floristic composition and the general structure of the forests of the northern Paraguayan Chaco; 2) to identify the types of forest and the environmental factors that characterize it; 3) to propose a floristic-ecological classification which would integrate all existing information on the forests of northern Paraguay.

2. Methods

Several geobotanical transections were carried out in May 2003 in the northern Paraguayan Chaco. The variability of the forests was then analyzed, based on the variations in bioclimate, geomorphological features and soil in each territory. The sites in the study are considered representative of the diversity of forests existing in the northern Paraguayan Chaco.

The sampling of the vegetation was carried out according to phytosociological methodology (Braun Blanquet 1964, Westhoff & van der Maarel 1978, Géhu & Rivas-Martínez 1982). At each plot the flora composition was inventoried at each stratum of vegetation within a band of generally some 10 m wide and between 100 and 300 m long, until a repetitive representation of the species was obtained. Moreover for each relevé two important structural characteristics were measured: average height of the forest canopy and the presence and average height of emergents. A total of 65 relevés was obtained. Every site was geo-referenced. The degree of soil drainage was also documented in the field based on texture and on the presence/absence of signs of flooding. The type of drainage was estimated in the field and defined according to the following FAO-UNESCO (1995) classes: very poorly drained; poorly drained; imperfectly drained; moderately well drained; well drained; rather excessively drained; excessively drained.

The relevés were initially classified in forest type-communities according to the Braun-Blanquet method, based on characteristic and differential species and floristic combinations which are repeated in geographical areas with similar geophysical (bioclimatic and geo-edaphic) conditions. However, these type-communities have not been ascribed to associations here (Weber et al. 2000) as further studies in the surrounding territories are required. A numerical classification was subsequently carried out as a means of contrasting the initial phytosociological classification and to detect and corroborate the relations between the plant communities and the

environment. In order to do this, we used a matrix comprising 65 relevés and 368 species. The characteristic or differential taxa with presence in a single column and with values of + or r were discarded, which reduced the matrix to 231 variables (species). Then the scale of cover-abundance values was converted into an ordinal scale of values from 0 to 9 (van der Maarel 1979). These data were processed with the SYNTAX program (Podani 2001). The agglomerative hierarchization procedure was carried out using the options of Complete Linkage and Similarity Ratio as a measure of similarity. The complete linkage strategy is very useful when aiming to identify or define different groups (McGarigal et al. 2000); the similarity ratio is an index which is sensitive to the dominant species (Tongeren 1995).

Taking into account the results obtained in the numerical analyses, the forest type-communities were regrouped based on their floristic and eco-geographical affinities in detailed tables. When possible, the type-communities or groups of type-communities (ecological systems in the sense of Josse et al. 2003) were related with landscape units used previously in the Chaco (Navarro & Fuentes 1999).

For the interpretation of the results, the climatic data from the weather stations of the Paraguayan Chaco and the adjacent area in Bolivia were also analyzed in order to relate different bioclimatic indices (Rivas-Martínez et al. 1999) with the large geomorphologic units in the territory and with the variability of the vegetation (see study area). The bioclimatic indices used are briefly defined here. The thermicity index (It) is the sum of the annual mean temperature (T), mean daily maximum temperature of the coldest month (M) and mean daily minimum temperature of the coldest month (m), multiplied by ten; i.e., It = (T + M + m) 10. The Ombrothermic Index (Io) is calculated as 10 (Pp/Tp), where Tp is the above-zero temperature index (the sum of all monthly mean temperatures greater than 0 °C, multiplied by ten) and Pp is the above-zero precipitation index (the sum of mean monthly precipitation for those months in which mean temperature is greater than 0 °C). A variant of this index is the ombrothermic index of the driest bimonth within the driest quarter of the year, i.e., Iod2 = Ppd2/Tpd2.

We use the concept of "climatophilous" applied to potential forests on well-drained soils, and thus in balance with the moisture from precipitation only in the form of rain (zonal forests); these types of forest are called "climacical formations" by Ramella & Spichiger (1989), and also "zonal formations" by Spichiger et al. (1991). Hygrophytic or edapho-hygrophilous forests depend on the accumulated moisture or water in the soil, above all for reasons of topography (azonal hygrophytic forests) and are called "edapho-climacical formations" by Ramella & Spichiger (1989) or "azonal formations" by Spichiger et al. (1991). This first division in the classification of the forests of the Chaco is essential for a causal understanding of their distribution and composition.

The biogeographic units that appear in the text are based on Cabrera & Willink (1980), Rivas-Martínez et al. (1999) and Navarro & Maldonado (2003). Most of the territory in the study falls within the Gran Chaco

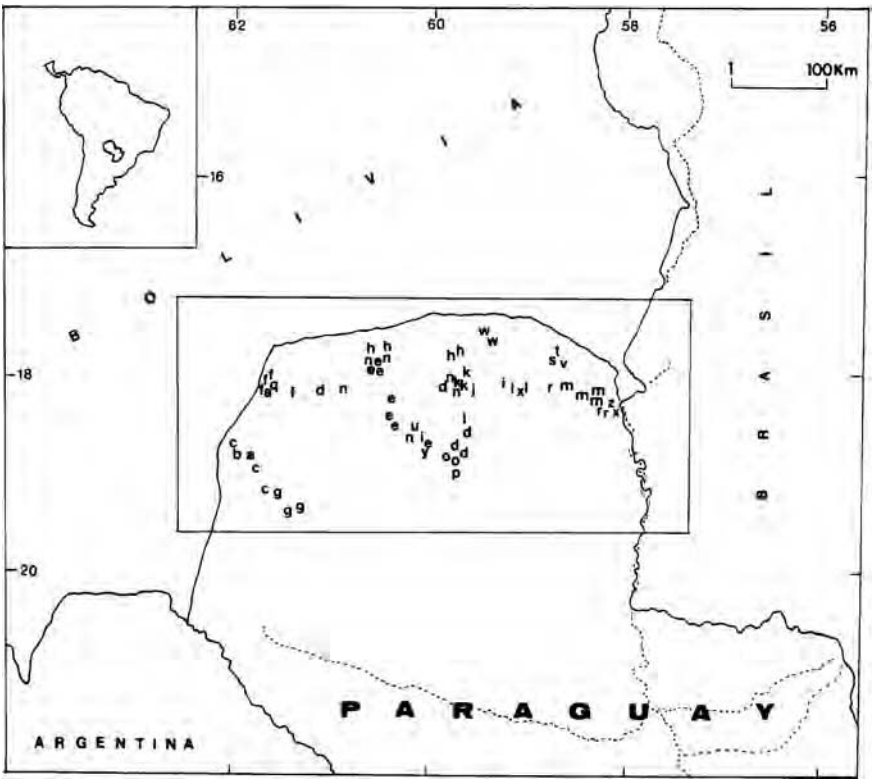


Fig. 1. Distribution of the sampled relevés in the study area. (a) *Agonandra excelsa-Schinopsis cornuta*; (b) *Piptadeniopsis lomentifera-Schinopsis cornuta*; (c) *Piptadeniopsis lomentifera-Schinopsis heterophylla*; (d) *Bulnesia sarmientoi-Aspidosperma quebracho-blanco*; (e) *Acacia emilioana-Schinopsis heterophylla*; (f) *Tabebuia nodosa-Schinopsis quebracho-colorado*; (g) *Piptadeniopsis lomentifera-Schinopsis quebracho-colorado*; (h) *Lonchocarpus nudiflorens-Schinopsis cornuta*; (i) *Pseudobombax heteromorphum-Astronium urundeuva*; (j) *Amburana cearensis-Athyana weinmannifolia*; (k) *Diplokeleba floribunda-Phyllostylon rhamnoides*; (l) *Diplokeleba floribunda-Schinopsis quebracho-colorado*; (m) *Lonchocarpus nudiflorens-Schinopsis balansae*; (n) *Prosopis elata-Tabebuia nodosa*; (o) *Prosopis rojasiana-Bulnesia sarmientoi*; (p) *Prosopis rojasiana-Tabebuia nodosa*; (q) *Cordia bordasii-Tabebuia nodosa*; (r) *Schinopsis balansae-Tabebuia nodosa*; (s) *Lonchocarpus lilloi-Acosmium cardenasii*; (t) *Calycophyllum multiflorum-Acosmium cardenasii*; (u) *Caesalpinia marginata-Anadenathera colubrina*; (v) *Sphingiphila tetramera-Terminalia argentea*; (w) *Pseudobombax tomentosum-Tabebuia selachidentata*; (x) *Coccoloba guaranitica-Geoffroea spinosa*; 3 (y): *Lonchocarpus pluvialis-Ruprechtia exploratricis*; 4 (z): *Triplaris gardneriana-Copernicia alba*.

biogeographical province; only the far northeast of the Paraguayan Chaco is in the el Cerrado biogeographical province, and represents the continuation to the south of the Bolivian Chiquitanía region (Ibisch & Mérida

2003), which is the westernmost portion of the whole Cerrado province in South America.

The taxa names are based on the on-line Missouri Botanical Garden's VAST (Vascular Tropicos) nomenclatural database (http://mobot.mobot.org/W3T/search/vast.html).

3. Study area

The study area is in northern Paraguay, with latitude 21° 30′ as the southern limit (Fig. 1). It has an extension of about 4,700,000 hectares, and is located in the Departments of Alto Paraguay and Boquerón. It includes the Paraguayan Chaco Biosphere Reserve which itself contains various Protected Wild Areas: the Río Negro National Park, the Cabrera-Timané National Monument, the Médanos del Chaco, Cerro Chovoreca, Defensores del Chaco and Teniente Agripino Enciso National Parks.

Based on the geomorphologic units proposed by Iriondo (1995) and on the ecological landscape systems proposed for areas bordering the Bolivian Chaco (Navarro & Fuentes 1999), the territory is divided into 5 large units: 1) Parapetí river old alluvial plain; 2) Pilcomayo river old western alluvial plain; 3) Alto Paraguay Eastern Chaco; 4) Chiquitanía peripheral mountain ranges transitional to the Chaco; 5) Chaco riverine landscape. The thermoclimate is lower thermotropical (It > 610) throughout the whole territory. The average annual temperature varies between 25 and 26.5 °C according to the areas. The average total annual rainfall values vary, in an increasing gradient from west to east, from 300–350 mm (in the west of the Parapetí alluvial plains and in the Chaco-Chiquitanía transitional mountain region) to 1000–1200 mm (in the east of the Chaco-Chiquitanía transitional mountain region and in the Alto Paraguay Eastern Chaco). According to these data, the bioclimate is xeric, and the ombroclimate changes from semi-arid (Io = 1.0–2.0) in the west of the area to upper dry (Io = 3.0–3.6) in the east of the Chaco-Chiquitanía transitional mountain region and in the Alto Paraguay Eastern Chaco (Table 1). Climate diagrams for four selected and representative localities of the territory are shown in Fig. 2.

4. Results

4.1. Numerical classification

The dendrogram generated in the classification analysis reveals three large types of forests constituted by a number of disparate elements according to their representation in the study area (Fig. 3). The first group (group I) contains 56 relevés, the second (group II) 6 and the third (group III) 3. Group I includes the whole set of forests in the centre-western-eastern areas (Médanos, old alluvial plains and Chaco-Chiquitanía transitional mountain region) on well- to poorly-drained soils (a–r). Group II basically comprises forests and shrublands of the far north of the Paraguayan Chaco

Table 1. Climatic and bioclimatic data from 14 selected weather stations in the northern Paraguayan Chaco and neighbouring countries. The same significance of P, T, M, m, It, Io and Iod2, as in the text.

Stations	Years of observation (P/T)	Position (Lat.S/Long.W)	T	M	m	P	It	Io	Iod2	Bioclimatic diagnosis
Fortín Nueva Asunción (Paraguay)	20/25	20°42′/61°57′	24.2	24.6	13.3	564	621	1.9	0.26	Xeric, lower thermotropical, upper semiarid
Bahía Negra (Paraguay)	51/21	20°15′/58°10′	25.9	26.5	15.7	965	681	3.1	0.99	Xeric, lower thermotropical, upper dry
Mariscal Estigarribia (Paraguay)	38/20	22°01′/60°34′	24.8	24.7	13.4	771	629	2.6	0.62	Xeric, lower thermotropical, dry
Base Adrián Jara (Paraguay)	6/4	19°32′/59°20′	24.2	27.5	14.4	1103	661	3.8	0.68	Pluviseasonal, lower thermotropical, lower subhumid
Pozo Colorado (Paraguay)	4/8	23°27′/58°52′	23.1	26.3	12.2	1140	616	4.1	1.7	Pluviseasonal, thermotropical, lower subhumid
Prats Gill (Paraguay)	7/8	22°33′/61°35′	23.6	24.3	11.5	573	594	2.0	0.3	Xeric, thermotropical, lower dry
Loma Plata (Paraguay)	52/6	22°22′/59°47′	25.0	25.7	14.4	826	651	2.7	0.8	Xeric, lower thermotropical, dry
Puerto Casado (Paraguay)	59/53	21°04′/57°53′	25.0	26.1	14.6	1143	657	3.8	1.7	Pluviseasonal, lower thermotropical, lower subhumid
Pedro P. Peña (Paraguay)	8/8	22°24′/62°20′	24.5	24.7	11.8	567	602	1.9	0.2	Xeric, thermotropical, upper semiarid
Ing. Juárez (Argentina)	9/9	23°53′/61°53′	23.2	23.5	11.0	671	577	2.4	0.48	Xeric, upper thermotropical, lower dry
Puerto Suárez (Bolivia)	33/36	19°01′/57°44′	25.6	27.4	14.6	1047	675	3.4	1.0	Xeric, lower thermotropical, upper dry
San Jose de Chiquitos (Bolivia)	36/29	17°40′/60°44′	25.2	27.7	14.3	1156	672	3.8	0.81	Pluviseasonal, lower thermotropical, lower subhumid
Robore (Bolivia)	36/29	18°19′/59°45′	26.3	28.5	15.6	1156	703	3.7	1.06	Pluviseasonal, lower thermotropical, lower subhumid
Huarirenda (Bolivia)	7/8	19°14′/62°30′	24.6	27.3	16.1	513	680	1.7	0.31	Xeric, lower thermotropical, upper semiarid

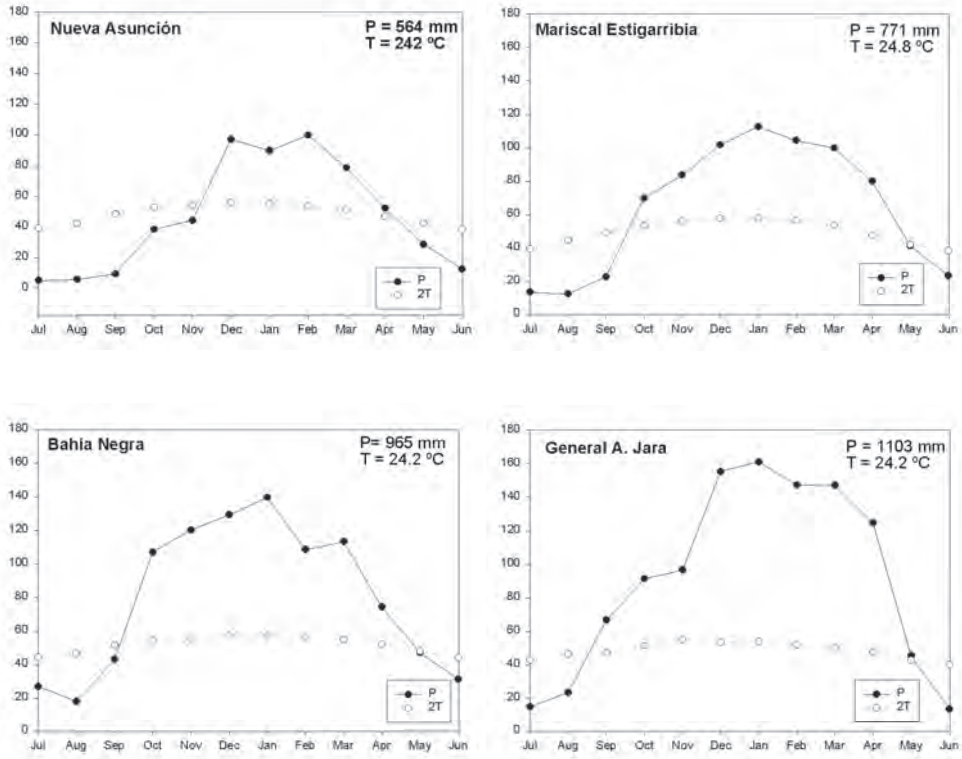


Fig. 2. Climate diagrams for 4 selected stations. P = mean monthly precipitation. T = mean monthly temperature.

in the Chaco-Cerrado transitional region (s, t, u, v, w). Finally, group III includes the hygrophytic forests and floodable palm forests of the northern Chaco (x, y, z). The divisions shown by these groups are related with floristic groups, of which the most divergent is the one characterized by the hygrophilous element (group III). Of the remainder, in one there is a predominance of the Chacoan element (group I) and the other is characterized by a significant representation of the Chiquitanian element (group II).

Within group I, which is the nucleus of the arboreal vegetation of the northern Chaco, four main subgroups can in turn be distinguished. Subgroup I_A corresponds to the xeromorphic Quebracho forests of the Médanos (a, b, c). Subgroup I_B includes mostly the quebracho forests of the alluvial paleo-plains on somewhat poorly-drained (d, f) to fairly well-drained soils (e, g). Subgroup I_C basically includes Quebracho, Quebrachillo, and Palolanza forests in the transitional areas of the Chaco to the Chiquitanía (h, i, j, k, l) and of the upper Paraguay River (m) on well- to fairly poorly-drained soils. Subgroup I_D includes Labon, Palosanto and

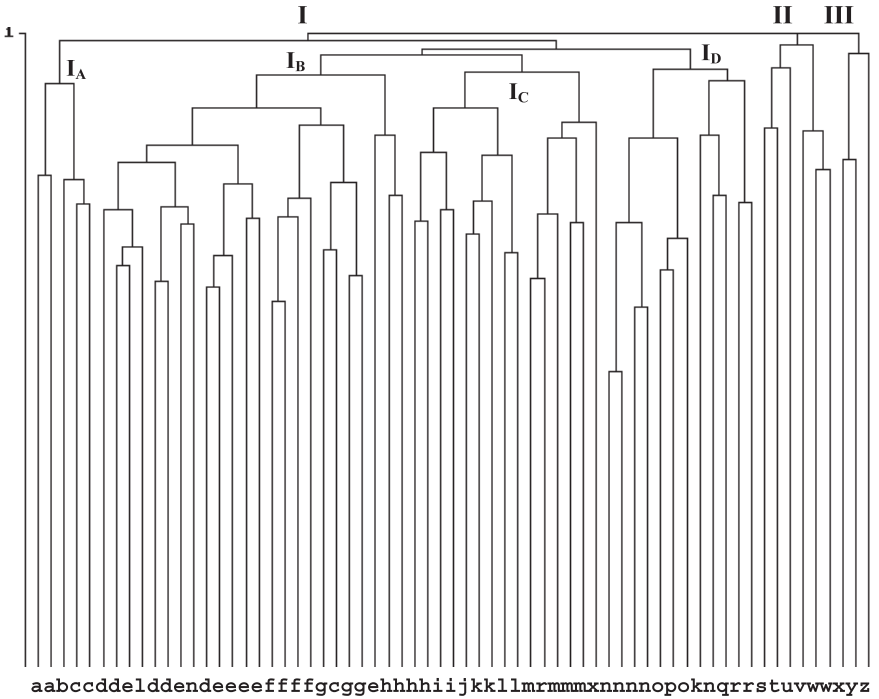


Fig. 3. Cluster analysis using Complete Linkage and Similarity Ratio for the forest relevés of the northern Paraguayan Chaco.

Quebracho forests of the poorly (o, p) to very poorly-drained (q, r) old alluvial plains.

Some dendrogram clusters show floristical similarities between different plant communities, often with ecological or catenal implications. For example within the first clusters of Subgroup I_B which comprise (the clusters) mainly Quebracho blanco forest releves (d) one relevé of Quebracho colorado coronillo forest (l) and another of dry Labon forest and can be seen (n). The relevé of the Quebracho colorado coronillo forest corresponds to one relevé in which there is a moderate high abundace of *Acacia emilioana* and there is a presence of *Celtis pallida*. Besides the relevé of the dry Labon forest contain a moderate abundance of *Tabebuia nodosa* and a presence of *Ptilochaeta nudipes*. Likewise the last clusters of I_C comprising the Quebracho forest of the eastern Chaco (m) includes also relevés of the Labón forest (r) and hygrophytic forest of the northern Chaco. The first case corresponds to the only relevé of the Quebracho forest of the eastern Chaco aported here with moderate abundance of *Bulnesia sarmentoi* and *Astronium urundeuva*. The second one corresponds to one relevé with presence of *Aspidosperma triternatum*, *Aechmea distichantha*, etc. It is notheworthy the splitting of the Quebracho forest of the transitional Chaco

(h) relevés into subgroup I_B the relevés with *Schinopsis* aff. *heterophylla* and I_C with *Helietta mollis*. Catenal relationships can be seen, for example, in one of the subclusters of I_C which includes not only the four relevés of the *Lonchocarpus nudiflorens-Schinopsis balansae* community (m) but also one relevé of the *Schinopsis balansae-Tabebuia nodosa* community (r) and another of the *Coccoloba guaranitica-Geoffroea spinosa* community (x) with which this community comes into contact in the eastern Chaco and in the transition zone between the eastern and western Chaco respectively. Similarly, one relevé of *Diplokeleba floribunda-Phyllostylon rhamnoides* community is close to two relevés of *Prosopis elata-Tabebuia nodosa* community (n) and *Prosopis rojasiana-Bulnesia sarmientoi* community (o) with which it comes into contact catenally to the north and south respectively.

5. Description of the vegetation

Tables 2–5 show the composition and floristic variation of the type-communities identified. Fig. 1 indicates the location of the relevés.

(a) Quebracho forest on sandy ridges and crests of the Médanos
Agonandra excelsa-Schinopsis cornuta community: Tab. 2, relevés 1–2; Fig. 4A

Forest growing on deep sandy soils in the high areas of the Médanos or sand dunes. This forest has suffered a great deal of human intervention, including fire in an attempt to convert it into savannah, so it is now difficult to find anything more than more or less degraded fragments. For this reason its physiognomy in the study areas corresponds to that of a forest with a variable semi-open and discontinuous tree canopy of 12–14 m in height, dominated by the "Soto" or "Quebracho de arenales" (*Schinopsis cornuta*). Next to it are characteristic forest species: *Jacaranda cuspidifolia*, *Hexachlamys edulis*, *Caesalpinia stuckertii*, *Bauhinia argentinensis*, *Annona nutans*, *Gymnocalycium marsoneri*, *Agonandra excelsa*, *Celtis spinosa* and *Aristida mendocina*.

(b) Quebracho forest on sandy slopes of the Médanos
Piptadeniopsis lomentifera-Schinopsis cornuta community: Tab. 2, relevé 3

Forest on soils with a sandy covering, generally less deep than in the previous case (a), growing on the slopes of the Médanos or sand dunes. This Quebracho forest is also characterized by *Schinopsis cornuta*, in this case associated to a group of differential species which are local indicators of less sandy soils, and which occur with frequency, such as: *Piptadeniopsis lomentifera*, *Aspidosperma quebracho-blanco* and *Ruprechtia triflora*.

(c) Quebracho colorado mestizo forest of the interdune valleys of the Médanos and of the peripheral alluvial-eolic plains
Piptadeniopsis lomentifera-Schinopsis aff. *heterophylla* community: Tab. 2, relevés 4–6

Forest growing on soils with a thin sandy cover in the interdune valley of the Médanos region, and on peripheral undulating alluvial-eolic plains

Table 2. Xerophytic and mesophytic forests of the north western Chaco (a–g) and of the transtitional Chaco to the Chiquitanía-Cerrado (h–l). 1–2 (a) *Agonandra excelsa-Schinopsis cornuta*; 3 (b) *Piptadeniopsis lomentifera-Schinopsis cornuta*; 4–6 (c) *Piptadeniopsis lomentifera-Schinopsis heterophylla*; 7–11 (d) *Bulnesia sarmientoi-Aspidosperma quebracho-blanco*; 12–18 (e) *Acacia emilioana-Schinopsis heterophylla*; 19–22 (f) *Tabebuia nodosa-Schinopsis quebracho-colorado*; 23–25 (g) *Piptadeniopsis lomentifera-Schinopsis quebracho-colorado*; 26–29 (h) *Lonchocarpus nudiflorens-Schinopsis cornuta*; 30–31 (i) *Pseudobombax heteromorphum-Astronium urundeuva*; 32 (j) *Amburana cearensis-Athyana weinmannifolia*; 33–35 (k) *Diplokeleba floribunda-Phyllostylon rhamnoides*; 36–38 (l) *Diplokeleba floribunda-Schinopsis quebracho-colorado*.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38
	a	a	b	c	c	c	d	d	d	d	d	e	e	e	e	e	e	e	f	f	f	f	g	g	g	h	h	h	h	i	i	j	k	k	k	l	l	l
Characteristic floristical combination of the different associations																																						
Agonandra excelsa	r	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Schinopsis cornuta	3	3	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	.	.	.	3	2	2	2	+	.	.	r	.	.	.	.	.
Piptadeniopsis lomentifera	.	.	2	4	3	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	3	2	3	.	.	.	.	.	.	.	.	.	.	.	.	.
Schinopsis aff. *heterophylla*	.	+	r	2	2	1	.	.	.	.	.	1	2	r	+	2	2	2	.	.	1	1	.	.	.	r	2	.	.	.	.	.	.	.	.	.	.	.	.
Bulnesia sarmientoi	.	.	.	.	.	.	.	.	.	+	r	.	.	+	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	+	+	.	r	.	.	+
Aspidosperma quebracho-blanco	r	r	2	2	2	2	2	1	2	3	2	2	2	2	1	1	2	2	2	.	2	.	1	.	.	1	1	1	r	1	.	1	1	1	2	2	1	1
Acacia emilioana	.	.	.	.	.	3	3	3	r	+	3	1	1	1	2	3	3	1	.	.	.	.	2	3	2	r	+	.	.	.	.	.	r	r	.	3	.	.
Tabebuia nodosa	.	.	.	.	+	.	1	.	+	1	r	+	+	.	.	r	.	.	r	2	1	r	.	.	.	.	.	.	.	.	+	+	.	.	1	.	.	.
Schinopsis quebracho-colorado	.	.	.	.	.	2	.	.	.	.	.	.	.	.	.	.	.	.	2	2	2	2	2	2	1	.	.	.	.	.	.	.	.	.	.	2	2	2
Lonchocarpus nudiflorens	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	2	.	.	.	.	.	.	.	2	2	1	2	1	.	r	r	.	.	.	.	.
Pseudobombax heteromorphum	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	+
Astronium urundeuva	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	1	2	3	.	.	.	.	.	+	.
Amburana cearensis	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	1	1	.	.	.	.	r	.	.
Athyana weinmannifolia	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	2	.	.	.	.	.	.	.	3	2	3	1	.	.	2	1	+	.	1	.	.
Diplokeleba floribunda	.	.	.	.	.	.	.	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	1	r	r	1	2	1	2	1	1	3
Phyllostylon rhamnoides	.	.	.	.	.	.	1	r	1	1	2	2	1	1	1	1	1	r	.	.	.	r	.	.	.	1	2	2	1	3	2	3	3	3	3	3	3	2
Ptilochaeta nudipes	.	.	.	.	.	3	1	1	.	.	2	2	1	2	2	1	.	.	.	.	1	r	1	2	2	1	2	1	1	1	.	+	1	2	r	2	r	r
Anisacanthus boliviensis	.	.	.	.	.	.	1	1	.	.	1	3	.	1	3	2	.	.	.	.	.	2	.	.	.	1	.	3	2	4	3	2	2	1	r	2	r	2
Mimosa castanoclada	.	.	.	.	1	2	1	1	.	.	2	1	2	2	2	2	.	1	.	.	1	.	2	2	1	r	r	+	.	.	.	.	r	.	.	.	.	.
Prosopis elata	+	r	+	.	+	r	r	.	+	+	+	.	.	.	.	.	+	.	.	.	.	1	r	r	.	.	+	.	.	.	.	.	.	.	r	.	.	.
Browningia caineana	.	.	.	.	.	.	+	r	.	.	+	+	r	r	.	1	.	+	.	.	.	.	.	.	+	r	+	.	.	.	.	.	+	.	.	.	.	.
Coccoloba aff. *argentinensis*	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	1	1	r	.	.	r	.	.	.	.	+	1	+	1	1	1	.	r	.	.	.	.	.
Helietta mollis	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	2	3	3	3	2	3	.	.	3	3
Pisonia zapallo var. *guaranitica*	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	1	1	2	1	1	1	.	.	.	1	1
Calycophyllum multiflorum	.	.	.	.	.	.	.	+	.	.	.	r	.	r	.	.	.	.	r	.	.	.	.	.	.	.	.	.	.	2	2	.	.	.	.	r	1	.
Schaefferia argentinensis	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	1	r	.	.	.	.	.	.	.	.	r	r	+	.	.	.	.	.	.	.	r	r
Reichenbachia paraguariensis	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	.	2	3	1	3	1	1	r	.	.	.	.
Bougainvillea infestans	3	.	.	.	1	2	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	1	1	.	.	.	.	.	.	.	.	.	.	.	.	.
Celtis pallida	.	.	.	.	.	.	2	r	1	1	.	+	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.
Coutarea hexandra	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	1	1	3	r	.	.	.	+	.	.
Acanthosyris falcata	.	.	.	.	.	.	.	.	+	+	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	r	1
Anadenanthera colubrina	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	.	2	2	3	3	3	.	.	.	.	.	.
Caesalpinia stuckertii	+	1	r	.	1	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Hexachlamys edulis	r	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	1	.	.	r	.	.	.	.	.	.
Maclura tinctorea subsp. *mora*	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	r	r	.	.	r	.	.	.	+	.	.
Opuntia quimilo	r	.	.	+	r	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Sebastiania brasiliensis	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	2	.	.	.	.	.	.	.	2	2
Allophylus pauciflorus	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	1	r	.	.	.	.	.	.	1	.
Aechmea distichantha	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	2	.	.	.	.	2	5
Bougainvillea modesta	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	+	.	.	.	.	+	1
Jacaranda cuspidifolia	2	1	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.

Philodendron undulatum	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	r	1
Annona nutans	1	.	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Patagonula americana	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1
Acacia furcatispina	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Cordia bordasii	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Justicia xylosteoides	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	2	.	.	.	.	.	.	.	.	.	.	.	.	.
Trithrinax schizophylla	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	1	.
Companions																																						
Ruprechtia triflora	.	.	1	2	2	3	3	3	4	4	3	3	3	3	3	3	3	.	4	4	4	3	1	3	2	2	2	1	1	2	3	2	2	3	3	3	2	2
Capparis retusa	r	1	.	.	.	+	2	.	1	2	2	1	2	1	1	2	2	2	2	1	1	1	2	2	2	2	1	2	1	.	1	2	2	1	1	r	1	1
Ceiba insignis	.	r	.	+	r	+	1	1	+	1	1	r	r	1	1	1	r	r	1	+	1	1	+	1	1	1	1	.	.	1	1	.	1	r	.	+	+	r
Castela coccinea	2	1	1	2	1	.	1	r	1	1	1	.	.	r	1	.	.	1	1	.	r	1	1	1	r	+	.	1	r	+	.	r	+	r	.	1	.	+
Capparis speciosa	1	.	1	+	1	1	2	1	1	1	1	1	.	1	1	1	.	1	1	1	1	1	1	1	.	1	.	r	r	r	.	1	1	1	.	+	.	1
Capparis salicifolia	r	+	1	1	1	1	1	1	+	1	1	1	.	1	.	1	1	.	+	1	1	1	1	2	1	1	1	.	.	.	.	1	1	.	1	r	.	2
Zizyphus mistol	1	+	2	2	+	r	1	2	1	2	1	.	1	.	1	r	1	.	1	.	.	1	1	1	.	+	1	.	1	r	.	.	1	r	2	r	r	1
Stetsonia coryne	.	r	.	+	r	1	r	r	.	+	1	1	.	1	.	1	1	r	r	1	1	1	.	1	1	r	1	.	.	+	.	r	1	r	1	1	+	r
Acacia praecox	.	.	.	.	.	.	3	2	3	3	2	2	3	2	2	3	2	1	2	3	2	3	1	2	.	1	1	1	1	1	.	1	1	.	3	3	2	r
Chloroleucon chacoense	.	2	.	r	.	1	r	1	r	r	r	r	.	.	1	1	1	2	.	.	1	1	1	1	1	.	1	.	1	r	.	1	1	+	.	r	r	1
Bromelia hieronymi	.	.	.	.	3	3	2	1	1	2	2	1	1	1	1	.	1	.	3	3	.	2	2	4	3	1	.	.	.	.	1	.	1	1	3	1	1	+
Arrabidaea corallina	2	.	2	2	.	2	1	1	1	1	.	1	.	2	.	.	1	2	.	.	.	2	.	.	1	2	2	1	r	.	2	2	2	2	2	1	.	1
Cereus validus	1	1	+	+	+	+	.	.	.	.	r	.	+	r	r	+	.	+	r	r	r	1	+	r	.	.	1	+	.	.	.	.	+	+	r	1	.	.
Arrabidaea truncata	.	.	.	1	2	1	2	2	1	r	.	2	1	1	.	1	1	.	.	1	.	.	2	2	.	r	r	r	1	.	.	2	2	r	2	1	.	.
Ximenia americana var. *argentinensis*	1	1	2	.	+	1	.	r	r	r	1	+	1	r	.	r	.	.	.	.	2	1	.	r	+	.	r	.	r	.	.	.	+	r	+	.	.	r
Bougainvillea praecox	r	.	.	2	r	2	1	1	2	2	2	2	1	1	2	.	1	.	2	2	2	2	.	2	1	1	.	.	.	.	.	.	.	.	.	1	.	.
Aspidosperma pyrifolium	2	.	.	.	+	.	.	1	.	.	2	1	.	r	1	.	.	1	r	.	1	+	.	.	.	2	2	1	1	.	2	2	1	1	.	r	1	r
Sideroxylon obtusifolium	1	.	.	.	.	r	.	1	.	2	1	1	1	1	.	2	1	1	r	.	1	.	.	.	.	1	1	.	2	1	.	1	2	2	.	1	1	.
Caesalpinia paraguariensis	+	.	.	.	.	.	.	r	.	.	.	r	.	r	.	1	1	1	+	+	r	1	.	+	+	1	1	r	r	1	.	1	.	1	.	1	.	1
Cleistocactus baumannii	.	.	+	1	1	1	.	1	+	.	1	r	1	.	r	1	.	r	2	1	1	1	r	r	.	.	1	+	.	.	.	.	r	.	.	1	.	.
Erythroxylum cuneifolium	.	.	.	.	.	.	.	1	r	2	1	2	3	1	1	.	.	.	r	r	.	+	.	.	.	1	r	.	1	1	2	1	1	2	.	2	r	+
Opuntia retrorsa	.	1	+	2	2	1	.	r	.	r	.	1	1	1	r	+	.	r	2	.	.	.	.	1	r	.	.	1	.	.	.	.	+	2	.	1	.	+
Harrisia guelichii	.	.	.	.	.	.	2	+	r	+	+	1	r	1	1	r	r	+	1	r	.	.	.	1	.	+	r	.	.	.	.	1	.	+	.	+	.	+
Herreria montevidensis	.	.	.	.	.	.	2	1	1	1	1	2	1	1	2	1	.	.	1	.	.	.	.	.	.	.	2	.	r	1	1	2	.	.	.	2	r	2
Setaria sp.	.	.	.	2	.	.	.	.	2	1	1	1	.	.	.	1	.	1	2	2	1	1	1	1	.	.	r	r	r	.	1	r	.	.	.	r	.	.
Quiabentia verticillata	.	.	.	.	.	+	.	.	.	.	.	.	+	+	.	+	+	1	+	r	.	r	+	r	r	r	r	.	.	+	.	r	+	.	.	.	.	.
Tillandsia loliacea	.	.	.	1	.	.	.	.	1	1	.	1	1	.	1	.	.	1	.	.	.	1	1	1	r	.	1	r	.	.	.	1	.	1	.	.	1	.
Monvillea cavendishi	.	.	.	.	.	.	1	2	.	.	1	2	.	.	2	.	2	.	1	.	.	.	.	.	1	.	1	.	.	1	.	2	2	1	.	2	1	1
Ruellia erythropus	.	.	.	.	.	.	.	1	1	1	1	1	2	3	3	1	.	.	.	.	.	1	.	.	.	2	.	.	.	.	.	1	.	3	.	2	1	1
Mandevilla angustifolia	.	.	.	.	.	.	.	.	1	.	.	1	1	1	1	1	.	r	1	1	r	1	.	.	1	.	.	1	.	.	1	r	.	1	.	.	.	.
Tillandsia streptocarpa	.	.	r	2	1		.	.	.	.	.	1	1	.	.	.	.	.	2	2	2	2	1	1	1	.	.	.	.	r	.	.	.	1	.	.	.	r
Pereskia sacharosa	.	.	.	.	r	.	.	+	.	.	.	+	.	.	1	r	r	r	.	.	.	+	.	.	+	+	r	r	.	+	+	1	.	.	.	.	.	.
Erythroxylum patentissimum	.	.	.	.	.	.	.	r	1	r	1	.	1	1	.	2	1	1	.	.	.	1	.	.	.	.	r	.	r	.	.	.	1	r	r	.	.	.
Argythamnia brevirramea	.	.	.	.	.	.	.	2	1	.	2	2	3	2	2	2	.	.	.	.	.	1	.	2	2	.	2	.	.	.	.	.	1	2	.	2	.	.
Serjania marginata	.	.	.	.	.	.	.	1	.	+	.	1	1	.	.	.	1	1	r	.	r	.	.	.	.	.	1	1	1	.	.	1	2	2	.	1	.	.
Bromelia serra	.	.	2	.	2	.	.	.	1	.	2	.	.	3	4	.	2	3	.	.	.	.	.	.	.	3	4	1	.	.	4	1	.	.	2	.	.	.
Jacaratia corumbensis	.	.	.	.	.	r	2	r	r	.	.	.	r	.	1	.	.	.	.	.	.	+	.	.	.	.	.	1	.	r	r	1	1	.	.	r	.	+
Senna chloroclada	r	.	2	1	r	r	.	.	.	.	.	.	.	.	.	.	+	r	.	.	.	.	.	r	r	+	r	r	r	.	.	.	.	.	.	.	.	.
Bougainvillea campanulata	.	1	1	.	.	.	.	.	.	.	.	.	.	1	1	1	1	1	.	.	1	.	.	.	.	1	.	.	2	.	.	2	.	r	.	r	.	.
Cereus aff. *dayamii*	.	+	.	+	+	.	.	.	.	.	r	+	r	.	r	+	+	+	1	+	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Capparis tweeddiana	.	.	.	.	.	.	.	+	.	.	.	.	1	r	.	.	.	.	.	.	r	.	.	.	.	r	.	.	.	1	.	1	1	r	+	r	1	1
Deinacanthion urbanianum	.	.	.	.	.	.	.	1	2	3	1	1	2	.	.	.	.	r	1	.	.	.	.	1	3	.	.	.	.	.	.	1	.	r	.	1	.	.
Mimozyganthus carinatus	.	.	.	.	.	.	.	.	.	.	r	1	+	1	2	2	2	.	1	1	1	.	.	1	.	r	+	.	.	.	.	.	.	.	.	.	.	.
Celtis chichape	r	1	2	3	+	1	.	.	.	.	.	.	.	.	+	.	1	+	.	.	.	.	1	1	1	.	.	.	.	.	.	.	.	.	.	.	.	.
Cnidoscolus vitifolius	.	.	.	1	1	+	.	r	+	+	+	.	.	+	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	+	.	.	+	.

Table 2. (cont.)

Commelina aff. *erecta*	.	.	.	2	r	.	.	.	.	r	.	1	.	.	1	.	1	1	r	1	.	.	.	.	.	.	1	r	.	.	.	1	.	.	.	.	.	.
Marsdenia castillonii	.	.	.	.	.	1	.	.	r	r	1	.	.	.	r	+	r	.	1	1	.	r	1	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.
Croton cf. *argyroglossum*	.	.	.	.	.	.	.	1	.	r	.	.	.	.	1	.	r	1	.	.	.	.	.	.	.	.	1	1	.	.	.	r	1	1	.	+	.	r
Opuntia discolor	1	.	1	r	.	1	.	.	.	.	+	.	.	.	.	.	.	.	1	1	r	r	.	1	.	.	.	.	.	.	.	.	.	.	r	.	.	.
Oxalis frutescens	.	.	r	.	+	.	.	.	.	+	.	r	r	.	.	.	r	r	.	r	.	r	r	.	.	.	.	r	.	.	.	.	.	.	.	.	.	r
Maytenus scutioides	.	.	.	.	.	.	.	.	r	1	+	.	2	.	.	1	1	.	.	.	.	1	.	.	.	+	+	.	+	.	.	.	r	.	.	.	.	.
Harrisia pomanensis	r	1	.	1	.	1	.	.	.	.	.	.	.	.	1	.	.	1	+	.	1	.	1	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Selaginella sellowii	.	.	.	.	.	.	2	1	.	r	.	.	1	.	.	.	.	.	2	2	1	2	.	1	2	.	.	.	.	.	.	.	.	.	.	.	.	.
Maytenus spinosus	+	+	.	.	1	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	1	1	2	1	.	.	.	.	.	.	.	.	.	.	.	.	.
Jatropha macrocarpa	.	.	.	.	r	1	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	r	+	.	+	r	+	r	.	.	.	.	.	.	.	.	.
Notholaena obducta	.	.	.	.	.	.	.	.	.	r	r	1	1	r	.	.	.	r	.	1	.	2	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Hybanthus sp.	.	.	.	.	.	.	.	.	.	3	.	r	.	r	.	r	r	.	.	.	.	1	.	.	.	1	r	.	.	.	.	.	.	.	.	r	.	.
Ipomoea bonariensis var. *chacoensis*	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	r	.	.	.	.	.	.	.	.	r	.	.	r	r	r	.	1	.	1	.	.	.	+
Serjania perulacea	.	.	1	.	.	.	.	1	.	.	.	.	.	.	.	2	.	.	.	.	.	.	.	.	.	2	.	.	.	1	1	1	.	2	.	.	.	.
Ruellia cf. *ciliatiflora*	.	.	.	.	.	1	.	.	.	.	.	.	.	.	r	.	.	2	1	1	.	.	1	1	r	.	.	.	.	.	.	.	.	.	.	.	.	.
Dyckia ferox	.	.	.	.	.	.	1	r	.	.	1	.	.	1	.	.	.	.	r	2	.	2	.	.	.	.	.	.	.	.	.	.	.	.	.	2	.	.
Ipomoea amnicola	.	.	.	.	.	.	.	r	r	r	.	r	.	.	r	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	+	r	.	.	.	.	.
Wissadula densiflora	.	.	.	.	.	.	.	+	1	r	.	.	.	.	.	.	.	.	1	1	1	.	.	r	r	.	.	.	.	.	.	.	.	.	.	.	.	.
Monvillea kroenleinii	.	.	.	.	.	.	.	+	.	.	1	3	.	3	.	.	.	.	r	.	.	.	.	2	1	r	.	.	.	.	.	.	.	.	.	.	.	.
Tillandsia vernicosa	.	.	.	.	.	.	.	.	1	.	.	.	r	1	.	.	.	.	.	.	.	r	.	.	.	1	1	.	.	.	.	.	.	.	.	r	1	.
Tillandsia duratii	.	.	.	.	.	.	.	.	2	.	.	.	.	r	.	r	r	.	r	.	.	1	r	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.
Cereus aff. *stenogonus*	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	r	r	.	.	.	+	.	+	.	+	.	r
Opuntia elata	.	.	.	.	.	.	.	.	.	.	1	+	.	1	1	1	1	2	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.
Janusia guaranitica	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	2	1	2	1	.	.	.	.	1	.	.	.	.	.	.	.	.	1	.	r
Acacia aroma	3	1	2	r	+	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Pithecocthenium cynanchoides	.	.	2	1	2	.	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.	1	2	1	.	.	.	.	.	.	.	.	.	.	.	.	.
Monvillea ebenacantha	.	.	.	.	.	+	.	.	.	r	.	r	.	.	.	.	.	.	.	.	.	.	r	r	r	.	.	.	.	.	.	.	.	.	.	1	.	.
Ruellia hygrophila	.	.	.	.	.	.	.	.	3	1	.	.	2	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	r	r	.
Trixis aff. *antimenorhaea*	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	.	.	.	+	r	.	.	.	r	r	1	.	.	.	1	.	.	.	.	.
Achatocarpus praecox	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	3	.	.	1	1	.	2	1	.	.	.	2	1
Pterogyne nitens	1	2	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	1	.	.	+	.	.	.	.	.	.
Tournefortia rubicunda	.	r	2	r	2	.	.	.	.	.	.	.	.	.	.	.	r	4	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Croton cf. *lachnostachys*	.	.	r	.	r	.	.	.	.	.	+	.	.	.	.	.	+	1	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.	.	.	.	.
Tillandsia meridionalis	.	.	.	r	.	.	.	.	+	1	.	.	.	.	.	.	.	.	.	.	.	+	.	.	1	.	.	.	.	.	.	.	r	.	.	.	.	.
Urvillea chacoensis	.	.	.	.	2	2	r	.	.	.	.	.	.	.	.	.	.	+	.	.	.	1	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Cercidium praecox	.	.	.	.	1	r	.	+	.	.	.	.	.	.	.	.	.	.	.	+	.	.	1	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Mimosa detinens	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	1	2	.	.	+	.	1	.	.	.	.	.	.	.	.	.
Tripogandra aff. *glandulosa*	.	.	.	.	.	.	.	r	2	1	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	2	.	.	.	.
Deuterocohnia meziana	.	.	.	.	.	.	.	1	2	.	4	.	2	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	.	.
Jatropha grossidentata	.	.	.	.	.	.	.	.	+	.	.	.	+	.	.	.	.	.	1	r	.	.	.	.	r	.	.	.	.	.	.	.	.	.	.	+	.	.
Cissus verticillata	.	.	.	.	.	.	.	.	.	r	.	.	1	r	.	1	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	r	.	.
Parthenium cinereum	.	.	.	.	.	.	.	.	.	.	1	.	.	.	+	.	+	1	.	.	.	.	.	.	.	+	r	.	.	.	.	.	.	.	.	.	.	.
Macfadyena unguis-cati	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	.	.	2	.	1	.	.	.	1	1	2
Celtis spinosa	2	1	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	r	.	.
Lasiacis sorghoidea	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	1	1	.	.	.	.	.	.	1	r
Tragia sp.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	r	2	.	.	1	.	1
Abutilon herzogianum	.	.	.	2	1	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Prosopis kuntzei	.	.	.	.	.	.	+	.	+	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.
Rivina humilis	.	.	.	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.	r	.	.	.	.	.	.	2	.	.	.	.	.	2	.	.	.	.	.	.
Croton cf. *hieronymi*	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	1	.	1	1	.	.	.	.	.	.	.	.	.	.	.	.	.
Aristida mendocina	2	3	3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Aloyisia virgata	+	.	.	.	r	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Morrenia cf. *odorata*	.	.	.	.	+	.	+	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Bulnesia bonariensis	.	.	.	.	.	r	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.

Ayenia o'donnellii	.	.	.	.	.	.	r	.	.	.	.	.	.	.	.	1	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Morrenia cf. *herzogii*	.	.	.	.	.	.	.	.	r	+	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Manihot guaranitica	.	.	.	.	.	.	.	.	+	r	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Gochnatia palosanto	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	+	.	.	.	.	.	.	.	+	.	.
Pseudoananas sagenarius	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	.	.	.	2	1	.	.	.	.	.
Schubertia grandiflora	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	r	1	.	.	.	.	.
Capsicum chacoense	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.
Croton andinus	.	1	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Bauhinia sp.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	.	.	.	.	.	.	.	.	.
Lantana fiebrigii	.	.	.	.	2	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Ruellia cf. *macrosolen*	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	4	.	.	.	.	.	.	.	.	r	.	.	.	.	.	.	.	.	.	.	.
Pseudobombax argentinum	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.
Cereus aff. tacuaralensis	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	r	.	.	.	.	.	.	.
Serjania cf. *neei*	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.	r	.	.	.	.	.	.	.
Serjania confertiflora	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	1
Acacia aff. *tucumanensis*	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	1	.	.	.	.	.	.	.
Tournefortia salzmannii	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	.	.	.	1	.	.	.	.	.
Sphingiphila tetramera	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	1	.	.	.	.
Petiveria alliacea	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	3	.	.	.	.	.	.	.	1
Odontocarya tamoides	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	r	.
Galactia sp.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	2	.	.	.
Manihot sp.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.	+	.
Dorstenia sp.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	.	.	.	r	.

Other characteristics: *Bauhinia argentinensis* 1 and *Gymnocalycium marsoneri* + in 1; *Echinopsis rhodotricha* + in 20; *Pseudobombax tomentosum* 1 and *Celtis iguanea* r in 30; *Tabebuia impetiginosa* 1 in 31. **Other companions:** *Alternanthera albida* 1 and *Sebastiana* cf. *hispida* 1 in 2; *Lantana* sp. 3, *Borreria densiflora* var. *perennis* 2, *Pappophorum krapovickasii* 2, *Turnera krapovickasii* 1, *Rhynchosia burkartii* 1, *Heliotropium campestre* 1 and *Turnera krapovickasii* 1 in 3; *Cardiospermum halicacabum* 1 in 4; *Clematis montevidensis* + in 9; *Selaginella convoluta* r and *Tragia volubilis* r in 10; *Cochlospermum tetraporum* r in 19; *Gymnocalycium friedrichii* r in 21; *Prosopis nigra* + and *Aloysia scorodonioides* + in 23; *Tragia* cf. *hieronymi* 1 in 25; *Plumbago scandens* r, *Prockia crucis* r and *Celtis pubescens* r in 26; *Dyckia* sp. 1 and *Passiflora* sp. + in 27; *Arrabidea cf. florida* 1 and *Croton* sp. r in 28; *Serjania caracasana* 2, *Vernonia* sp. 1, *Wissadula wissadifolia* 1, *Caesalpinia marginata* 1, *Aristolochia gibertii* +, *Forsteronia pubescens* r, *Fagara* aff. *rhoifolia* r and *Cardiospermum grandiflorum* r in 29; *Arrabidea* cf. *florida* 1 and *Randia armata* r in 30; *Selenicereus setaceus* 1, *Microgramma vaccinifolia* 1 and *Tillandsia tricholepis* r in 37; *Ptilochaeta* cf. *bahiensis* r in 38.

Localities (positions in degrees, minutes and seconds): **1:** Garay to Nueva Asunción, km 26, 204019S/615824W, 341 m; **2:** Gabino Mendoza to Garay, km 6.5, 200552S/615358W, 366 m; **3:** Garay to Nueva Asunción, km 5.4, 203305S/620629W, 368 m; **4:** Garay to Nueva Asunción, km 1, 203114S/620833W, 368 m; **5:** Nueva Asunción to Enciso, km 8.5, 204657S/615444W, 330 m; **6:** Nueva Asunción to Enciso, km 38, 210026S/614648W, 307 m; **7:** Madrejón, 203748S/595248W, 135 m; **8:** Line 1, 21 km west of Agua Dulce, 195902S/595635W, 164 m; **9:** Agua Dulce to Madrejón, km 54.5, 202711S/594713W; **10:** Madrejón to Cerro León, km 0.5, 203750S/595259W, 128 m; **11**: Lagerenza-í to Gabino Mendoza, km 20, 200415S/611519W, 280 m. **12:** Madrejón to Cuatro de Mayo, km 73.3, 202326S/603018W, 180 m; **13:** Madrejón to Cerro León, km 23.4, 203500S/600520W; **14:** Madrejón to Los Laureles, km 86, 201805S/603202W, 186 m; **15:** Los Laureles to Lagerenza, km 3, 195720S/604444W, 215 m; **16:** Madrejón to Los Laureles, km 104, 200839S/603154W, 169 m; **17:** around Los Laureles, 195855S/604336W, 215 m; **18:** Lagerenza to Palmar de las Islas, km 12.5, 195103S/604208W, 236 m; **19:** 1 km from Gabino Mendoza towards the Bolivian border; **20:** 2 km to the south of Gabino Mendoza, 200432S/615322W; **21:** 3 km to the south of Gabino Mendoza, interdune valley; **22:** Lagerenza-í to Gabino Mendoza, km 52, 200429S/613246W, 328 m; **23:** Nueva Asunción to La Patria, km 45.5, Parque Nacional Tte. Enciso, 210354S/614443W, 304 m; **24:** Parque Nacional Tte. Enciso, 211224S/613746W, 260 m; **25:** Parque Nacional Tte. Enciso, 210840S/613046W, 255 m; **26:** east of Colonia Sierra León, 194115S/604427W, 217 m; **27:** Lagerenza to Palmar de las Islas, km 45, 193815S/603551W; **28:** Agua Dulce to Adrián Jara, km 28, 194503S/594533W, 132 m; **29:** Agua Dulce to Adrián Jara, km 36, 194122S/594450W, 136 m; **30**: Line 1, km 136 from Bahía Negra to Agua Dulce, 195902S/592151W; **31**: Southern foothills of the Cerro León, 202626S/601915W, 155 m. **32**: Agua Dulce, area around the park-keeper's post; **33**: Agua Dulce to Adrian Jara, km 15, 195113S/594530W; **34**: Line 1, 1.5 km west of Agua Dulce, 195902S/594623W, 137 m; **35**: in contact with the relevé Nº 32; **36**: Agua Dulce to Madrejón, km 35, 201725S/594532W, 138 m; **37**: Line 1, Bahía Negra to Agua Dulce, km 115, 195903S/591017W, 101 m; **38**: Line 1, Bahía Negra to Agua Dulce km 128, 195903S/591406W, 114 m.

in the same region. Characteristic of areas where there is a thin sand cover deposition by wind that overlays the lime-clay sediments of the former alluvial plain of the Parapetí. The dominant and main characteristic species in the emergents layer (16–18 m height) of the forest is the "Quebracho colorado mestizo" (*Schinopsis* aff. *heterophylla*), associated in the forest tree canopy (here between 4 and 6 m in height) with *Piptadeniopsis lomentifera* and *Ruprechtia triflora*.

(d) Quebracho blanco forest of the Parapetí old alluvial fan on rather poorly drained soils
Bulnesia sarmientoi-Aspidosperma quebracho-blanco community: Tab. 2, relevés 7–11; Fig. 4B

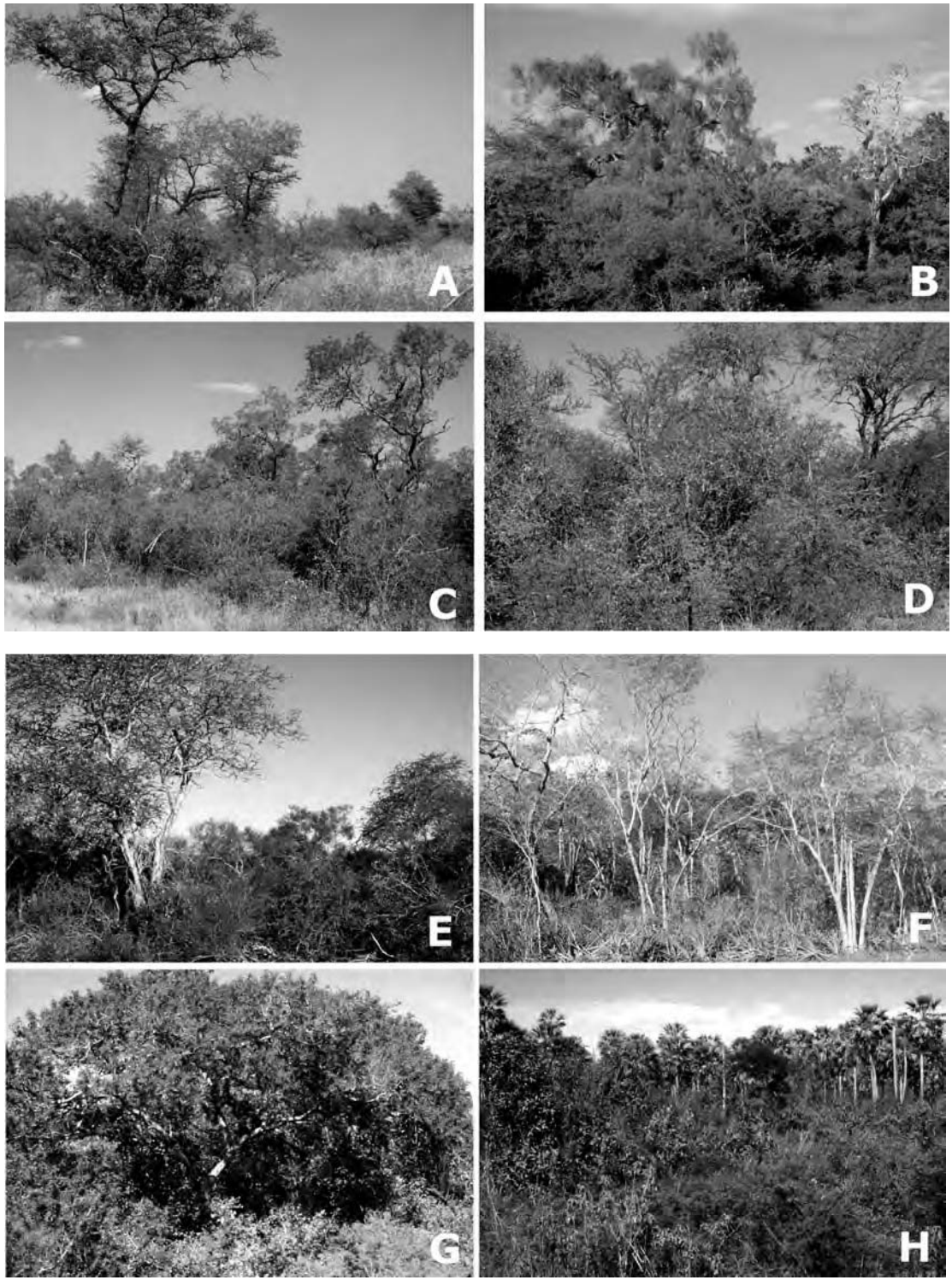
Xerophytic forest of the Parapetí old alluvial plain on fairly well-drained to seasonally rather poorly-drained soils in the lower soil horizons. The emergents stratum is dominated by the "Quebracho blanco" (*Aspidosperma quebracho-blanco*), associated in the forest canopy (5–6 m in height) with frequent and characteristic elements in this forest such as: *Acacia emilioana* and *Celtis pallida*. The relative seasonal deficiency in drainage is shown by the presence of *Bulnesia sarmientoi*, which is characteristic of the community, and sometimes also by that of *Prosopis elata* or *Tabebuia nodosa*.

(e) Quebracho colorado mestizo forest of the Parapetí old alluvial fan
Acacia emilioana-Schinopsis aff. *heterophylla* community: Tab. 2, relevés 12–18

Xerophytic forest on fairly well-drained soils with slight to moderate sandy eolic influence, growing in the south of the alluvial paleo-plain of the Parapetí. The emergents layer (15–18 m high) is characterized by *Schinopsis* aff. *heterophylla* and *Aspidosperma quebracho-blanco* distributed spatially with a grouping tendency. The forest canopy is dense, 5–8 m high, and is characterized by *Acacia emilioana*, *Ptilochaeta nudipes, Erythroxylum patentissimum, Mimosa castanoclada, Schaefferia argentinensis, Mimozyganthus carinatus* and *Browningia caineana*. The forest-type *Acacia emilioana-Schinopsis* aff. *heterophylla* is exclusive to the Paraguayan Chaco, according to the existing data.

(f) Quebracho colorado coronillo forest of the south of the Parapetí old alluvial fan on rather poorly-drained soils
Tabebuia nodosa-Schinopsis quebracho-colorado community: Tab. 2, relevés 19–22; Fig. 4C

Fig. 4. A. *Agonandra excelsa-Schinopsis cornuta*, between Fortín Garay and Fortín Nueva Asunción; B. *Bulnesia sarmentoi-Aspidosperma quebracho-blanco*, between Lagerenza and García Mendoza; C. *Tabebuia nodosa-Schinopsis quebracho-colorado*, Fortín Teniente García Mendoza; D. *Piptadeniopsis lomentifera-Schinopsis quebracho-colorado*, between Teniente Enciso and La Patria; E. *Prosopis rojasiana-Bulnesia sarmentoi*, to the south of Fortín Madrejón; F. *Lonchocarpus lilloi-Acosmium cardenasii*, between Agua Dulce and Adrián Jara; G. *Coccoloba guaranitica-Geoffroea spinosa*, to the east of Agua Dulce; H. *Triplaris gardneriana-Copernicia alba*, to the west of Bahía Negra.


A
B
C
D
E
F
G
H

Xerophytic forest on vertic soils with dominant clay and lime textures, poorly drained in the lower horizons. This quebracho forest is characterized by emergents of up to 10–15 m in height, constituted mainly by *Schinopsis quebracho-colorado* and *Aspidosperma quebracho-blanco*. Moreover, it is also worth noting the scattered presence among the emergents of *Cochlospermum tetraporum*, a frequent xerophytic element in the sub-Andean mountain ranges in southern Bolivia and in the Bolivian Chaco, which only reaches Paraguay in this area of the Chaco. The forest tree canopy (4–5 m in height) is dominated by *Ruprechtia triflora* and characterized by the moderately abundant presence of *Acacia furcatispina*. The poor seasonal soil drainage is shown by the presence of *Tabebuia nodosa* and *Cordia bordasii*. The association *Tabebuia nodosa-Schinopsis quebracho-colorado* is distributed in the far northwest of the Paraguayan Chaco and in adjacent areas of the Bolivian Chaco (Navarro & Fuentes 1999, Navarro & Maldonado 2002).

(g) Quebracho colorado coronillo forest of the Pilcomayo old alluvial fan *Piptadeniopsis lomentifera-Schinopsis quebracho-colorado* community: Tab. 2, relevés 23–25; Fig. 4D

Xerophytic forest on fairly well-drained soils. This forest is distributed in the north of the Pilcomayo old alluvial plain, and occupies a considerable area of the centre-west of the Paraguayan Chaco. The emergents layer (12–18 m average height) is constituted above all by *Schinopsis quebracho-colorado* and *Aspidosperma quebracho-blanco*. The forest canopy is fairly dense and continuous with an average height of 5–6 m and is characterized by the following species, among others: *Piptadeniopsis lomentifera*, *Acacia emilioana*, *Mimosa castanoclada*, *Maytenus spinosus*, *Mimozyganthus carinatus*, *Bougainvillea praecox* and *Ruprechtia triflora*. They include, *Piptadeniopsis lomentifera*, an element whose centre of distribution is in the Paraguayan Chaco and which only overflows slightly to adjacent areas in Bolivia; the association of this species with *Schinopsis quebracho-colorado* is unique in the Gran Chaco.

(h) Quebracho forest on sands of the transitional Chaco to the Chiquitanía *Lonchocarpus nudiflorens-Schinopsis cornuta* community: Tab. 2, relevés 26–29

Forest on sands of the northern transitional Chaco to the Chiquitanía. This forest appears with different physiognomies; either with a discontinuous tree canopy of 16–18 m and almost without emergents in the south and west of its area; or with a discontinuous tree canopy of 8–10 m and emergents of 15–16 m in the north of its area. It is characterized by the floristic combination of Chacoan sand elements such as *Schinopsis cornuta* and *Hexachlamys edulis*, together with elements of the less dry Chaco and of the semi-deciduous forests of the Bolivian Chiquitanía, such as: *Anadenanthera colubrina*, *Maclura tinctorea* subsp. *mora*, *Lonchocarpus nudiflorens*, *Diplokeleba floribunda*, *Pisonia zapallo* var. *guaranitica*, *Sebastiania brasiliensis*, *Allophyllus pauciflorus*, *Helietta mollis*, *Coutarea hexandra*, *Reichenbachia paraguariensis* and *Astronium urundeuva*. The association

Lonchocarpus nudiflorens-Schinopsis cornuta is distributed in the far north of the Paraguayan Chaco and in adjacent areas of the southeastern Bolivian Chaco (Navarro & Fuentes 1999, Navarro & Maldonado 2002).

(i) Hill forest of the transitional Chaco to the Chiquitanía
Pseudobombax heteromorphum-Astronium urundeuva community: Tab. 2, relevés 30–31

Forest growing on the slopes of hills and low mountain areas with moderately stony and relatively deep soils in the transitional region between the northern Chaco and the Chiquitanía. This forest has an irregular and discontinuous tree canopy, 15–18 m high, dominated by *Anadenanthera colubrina, Astronium urundeuva, Calycophyllum multiflorum* and *Aspidosperma pyrifolium*, where *Amburana cearensis, Tabebuia impetiginosa, Pisonia zapallo, Chorisia insignis, Athyana weinmannifolia* and *Phyllostylon rhamnoides* are fairly frequent. The frequent presence of *Pseudobombax heteromorphum* is also characteristic, and this is an endemic element of the contact area between the biogeographical provinces of the Chaco and the Cerrado in southeast Bolivia and the far north of Paraguay, where the association has its distribution.

(j) Quebrachillo forest on the alluvial plain of the transitional Chaco to the Chiquitanía
Amburana cearensis-Athyana weinmannifolia community: Tab. 2, relevé 32

Forest on well-drained more or less sandy soils, occupying small fringes of the landscape, geomorphologically corresponding to the paleo-albardones (levées) of the south of the former alluvial plain of the Parapetí, in its area of contact towards the Chiquitanía in the far north of the Paraguayan Chaco. This forest has a discontinuous tree canopy of 15–18 m and disperse emergents of up to 20–22 m height. Floristically, the forest is characterized by the high frequency of the "Quebrachillo" or "Sotillo" (*Athyana weinmannifolia*), an element of the xero-mesophytic Chaco with a preference for fairly sandy soils, as well as by the abundance of more mesophytic Chaco elements, also present in Chiquitanian forests, such as *Anadenanthera colubrina*, *Amburana cearensis*, *Lonchocarpus nudiflorens*, *Calycophyllum multiflorum*, *Pisonia zapallo*, *Maclura tinctorea* subsp. *mora*, *Bougainvillea modesta*, *Phyllostylon rhamnoides*, *Reichenbachia paraguariensis*, *Helietta mollis*, *Coutarea hexandra*, *Allophyllus pauciflorus* and *Pseudoananas sagenarius*.

(k) Palolanza forest on the alluvial plain of the transitional Chaco to the Chiquitanía
Diplokeleba floribunda-Phyllostylon rhamnoides community: Tab. 2, relevés 33–35

Transitional forest growing on fairly well-drained or rather poorly-drained alluvial soils. The tree canopy is characterized and frequently dominated by "Palopiedra" (*Diplokeleba floribunda*) and "Palolanza" (*Phyllostylon rhamnoides*), both of which are Chacoan elements of a mesophytic tendency, which also penetrate into the Chiquitanian forests in contact with

the Chaco. The following are companion species in the forest canopy as well as in the emergents layer: *Aspidosperma quebracho-blanco*, *Chorisia insignis*, *Zizyphus mistol*, *Sideroxylon obtusifolium*, *Caesalpinia paraguensis*, *Stetsonia coryne* and *Aspidosperma pyrifolium*. The *Diplokeleba floribunda-Phyllostylon rhamnoides* community is known in the far north of the alluvial plains of the Paraguayan Chaco (the Cerro León region) and in the east of the Bolivian Chaco (Santa Cruz) where it has its greatest representation (Navarro & Fuentes 1999, Navarro & Maldonado 2002).

(l) Quebracho colorado coronillo forest on the alluvial plain of the transitional Chaco to the Chiquitanía
Diplokeleba floribunda-Schinopsis quebracho-colorado community: Tab. 2, relevés 36–38

Transitional forest on fairly well-drained alluvial soils. Structurally, its appearance is that of a forest with an irregular tree canopy of 15–18 m and few emergents, or also a forest with a dense tree canopy of 6–8 m in height and emergents of 15–20 m. This community is fairly close floristically to the previous one (k), with which it is interspersed in the landscape in slightly higher topographic locations where the soils have a loose texture in the upper horizons and better internal drainage. It is characterized and differentiated from the previous community by the frequent presence in the emergents stratum of *Schinopsis quebracho-colorado*, which is probably an indicator of a relatively better drainage of the sub-surface soil horizons. The *Diplokeleba floribunda-Schinopsis quebracho-colorado* community has its distribution in the northern Paraguayan Chaco and in the north-eastern Bolivian Chaco (El Tinto to San José de Chiquitos area in eastern Santa Cruz Department).

(m) Quebracho forest of the eastern Chaco of the Alto Río Paraguay
Lonchocarpus nudiflorens-Schinopsis balansae community: Tab. 3, relevés 1–4

Forest growing on vertisoles and vertic soils (moderately to extremely poorly-drained soils). It is distributed in areas of the north-eastern Chaco transitional to the Pantanal, approximately to the east of the 59 W meridian, with an upper dry in transition to a lower subhumid ombroclimate. This Quebracho forest is comparatively high, with an irregular or discontinuous tree canopy of 15–18 m in height and disperse emergents of up to 22 m. It is characterized by the following floristic arboreal combination: *Lonchocarpus nudiflorens*, *Schinopsis balansae*, *Astronium urundeuva*, *Diplokeleba floribunda*, *Trithrinax schizophylla*, *Patagonula americana*, *Pisonia zapallo*, *Aspidosperma pyrifolium*, *Aspidosperma quebracho-blanco*, *Phyllostylon rhamnoides* and *Calycophyllum multiflorum*. There are abundant woody vines and climbers, and among the epiphytes, it is worth noting *Campylocentron neglectum*, *Microgramma vaccinifolia*, *Rhipsalis baccifera*, *Selenicereus setaceus*, *Tillandsia vernicosa* and *Tillandsia loliacea*. The *Lonchocarpus nudiflorens-Schinopsis balansae* community is distributed in the northeast of the Paraguayan Chaco (Bahía Negra region) and in the southeast of the Bolivian Chaco (southern Otuquis, in Santa Cruz Department). This

represents the southernmost aspect of the large extension of Chacoan mesophytic forests, dominated by *Schinopsis balansae*, which characterize the eastern Chaco in Paraguay and Argentina (Cabrera & Willink 1980, Morello & Adamoli 1974). In the far southeast of Matogrosso (the area near Porto Murtinho), the *Schinopsis balansae* forests have been interpreted (Prado et al. 1992) as an area of biogeographical transition between the Chaco, Pantanal and Cerrado.

(n) Dry Labón forest of the Parapetí old alluvial fan
Prosopis elata-Tabebuia nodosa community: Tab. 3, relevés 5–10

Forest on clay or clay-silty soils (vertics soils and vertisoles), poorly drained, liable to flooding and compact when dry, of the alluvial paleoplain of the Parapetí (approximately to the north of latitude 20° 20′ S and to the west of longitude 59° 30′ W). The forest, which is dominated by the "Labón" (*Tabebuia nodosa*), has a semi-closed to semi-open tree canopy of 4–6 m in height, with emergents of 8–10 m. This Labón forest has a high constancy of *Prosopis elata* and *Zizyphus joazeiro*, and is characterized by the association of *Prosopis elata* with *Tabebuia nodosa*, both elements of the poorly-drained soils in the Chaco; other species with the same ecological significance, such as *Bulnesia sarmientoi* and *Aspidosperma triternatum*, are scarce or do not occur in this community. The *Prosopis elata-Tabebuia nodosa* forest is distributed in the north of Paraguay as well as in the south of the Bolivian Chaco.

(o) Palosanto forest of the Pilcomayo old alluvial fan
Prosopis rojasiana-Bulnesia sarmientoi community: Tab. 3, relevés 11–12; Fig. 4E

Forest on poorly-drained clay vertisoles and vertic soils, and somewhat saline on the sub-surface horizons, of the northern half of the Pilcomayo old alluvial plain. The emergents layer (12–18 m) is dominated by the "Palosanto" (*Bulnesia sarmientoi*) sometimes jointly with *Tabebuia nodosa*. The tree canopy is dense and with a height of 6–8 m, and is constituted mainly by *Prosopis rojasiana, Tabebuia nodosa, Ruprechtia triflora, Capparis retusa, Zizyphus mistol, Prosopis sericantha* and *Mimozyganthus carinatus*. The "Algarrobo" (*Prosopis rojasiana*), an endemism restricted to the Paraguayan Chaco (Burkart 1976), is the main characteristic of the community. The *Prosopis rojasiana-Bulnesia sarmientoi* community is distributed exclusively in the central area of the Paraguayan Chaco where it still covers a considerable extension.

(p) Labón forest of the Pilcomayo old alluvial fan
Prosopis rojasiana-Tabebuia nodosa community: Tab. 3, relevé 13

Forests growing on poorly-drained clay vertics soils and vertisoles which are liable to flooding, scarcely or not at all saline, of the northern alluvial paleo-plain of the Pilcomayo. This community is exclusive to the central Paraguayan Chaco. The forest is dominated by *Tabebuia nodosa* both in the tree canopy (4–6 m) and in the emergents layer (8–10 m). Co-dominant with the Labón in the tree canopy are mainly *Tabebuia nodosa*, *Prosopis*

Table 3. Forests on poorly-drained soils of the north eastern Chaco (m, r) and of the north western Chaco (n, o, p, q). 1–4 (m) *Lonchocarpus nudiflorens-Schinopsis balansae*; 5–9 (n) *Prosopis elata-Tabebuia nodosa*; 11–12 (o) *Prosopis rojasiana-Bulnesia sarmientoi*; 13 (p) *Prosopis rojasiana-Tabebuia nodosa*; 14 (q) *Cordia bordasii-Tabebuia nodosa*; 15–17 (r): *Schinopsis balansae-Tabebuia nodosa*.

	1 m	2 m	3 m	4 m	5 n	6 n	7 n	8 n	9 n	10 n	11 o	12 o	13 p	14 q	15 r	16 r	17 r
Characteristic floristical combination of the different associations																	
Bulnesia sarmientoi	r	.	.	.	1	r	1	1	r	+	3	2	r	.	2	.	.
Aspidosperma quebracho-blanco	+	.	2	1	2	1	1	1	2	.	.	.	.	.	+	.	.
Tabebuia nodosa	r	1	r	.	2	4	4	3	3	4	3	2	4	4	3	3	3
Lonchocarpus nudiflorens	3	2	1	1	.	.	.	.	.	.	.	.	.	.	2	.	1
Astronium urundeuva	2	r	3	2	.	.	.	.	.	.	.	.	.	.	2	.	.
Diplokeleba floribunda	2	.	1	1	.	.	.	.	.	.	.	.	.	.	1	.	1
Phyllostylon rhamnoides	1	1	2	1	r	1	1	3	2	1	1	r	.	+	.	r	2
Schinopsis balansae	2	2	1	2	.	.	.	.	.	.	.	.	.	.	r	1	r
Prosopis elata	.	.	.	.	1	2	3	+	2	1	.	.	.	.	.	.	.
Prosopis rojasiana	.	.	.	.	.	.	.	.	.	.	3	3	3	.	.	.	.
Cordia bordasii	.	.	.	.	.	1	.	.	.	2	r	.	.	3	.	.	.
Coccoloba aff. *paraguariensis*	r	1	.	.	.	.	.	1	.	r	.	.	.	+	1	2	1
Pisonia zapallo var. *zapallo*	r	1	r	r	.	.	.	.	.	.	.	.	.	.	r	+	+
Geoffroea spinosa	r	r	+	.	.	.	.	.	.	1	.	.	.	.	r	.	1
Maytenus vitis-idaea	r	1	.	.	.	.	.	.	.	.	+	3	2	.	.	1	.
Aechmea distichantha	4	3	4	4	.	.	.	.	.	.	.	.	.	.	4	.	.
Trithrinax schizophylla	2	3	2	2	.	.	.	.	.	.	.	.	.	.	2	.	.
Philodendron undulatum	1	r	r	r	.	.	.	.	.	.	.	.	.	.	r	.	.
Adelia spinosa	1	r	4	3	.	.	.	.	.	.	.	.	.	.	.	.	1
Fagara pterota	1	1	1	2	.	.	.	.	.	.	.	.	.	.	.	.	1
Allophylus pauciflorus	2	.	r	1	.	.	.	.	.	.	.	.	.	.	2	.	1
Calycophyllum multiflorum	r	.	1	.	.	.	.	.	.	1	.	.	.	r	1	.	.
Aspidosperma triternatum	.	r	.	+	.	.	.	.	.	1	.	.	r	.	r	.	.
Echinopsis rhodotricha	.	.	.	.	.	.	.	r	r	.	r	r	r	.	.	.	.
Sebastiania brasiliensis	3	1	r	.	.	.	.	.	.	.	.	.	.	.	1	.	.
Patagonula americana	1	.	1	r	.	.	.	.	.	.	.	.	.	.	1	.	.
Acanthosyris falcata	+	.	.	+	.	r	.	.	.	.	.	.	.	.	.	.	+
Machaonia brasiliensis	.	r	.	.	.	.	.	.	.	2	.	.	.	.	.	2	2
Coccoloba guaranitica	.	.	r	.	.	.	.	.	.	r	.	.	.	.	r	.	1
Mimosa castanoclada	.	.	.	.	1	.	.	1	1	2	.	.	.	.	.	.	.
Ceiba sp.	1	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	r
Celtis pallida	.	.	.	.	.	.	.	+	1	.	r	.	.	.	.	.	.
Ruellia coerulea	.	.	.	.	.	.	.	.	.	1	1	1	.	.	.	.	.
Lycium cf. *cuneatum*	.	.	.	.	.	.	.	.	.	.	2	1	1	.	.	.	.
Anadenanthera colubrina	.	.	2	1	.	.	.	.	.	.	.	.	.	.	.	.	.
Celtis iguanea	.	.	r	.	.	.	.	.	.	.	.	.	.	.	.	2	.
Lycium cf. *nodosum*	.	.	.	.	.	.	.	.	.	r	.	.	1	.	.	.	.
Prosopis sericantha	.	.	.	.	.	.	.	.	.	.	1	r	.	.	.	.	.
Prosopis ruscifolia	.	.	.	.	.	.	.	.	.	.	r	.	r	.	.	.	.
Coutarea hexandra	.	.	.	.	.	.	.	.	.	.	+	.	.	.	r	.	.
Companions																	
Ruprechtia triflora	2	1	1	1	3	3	3	3	3	3	2	2	3	3	3	1	2
Capparis retusa	2	3	.	2	2	3	2	2	2	2	3	.	2	2	3	2	2
Zizyphus mistol	r	1	.	1	1	1	2	2	3	.	2	3	1	.	1	r	r
Capparis tweeddiana	1	1	1	1	+	.	r	.	r	r	r	r	r	.	1	.	r
Ruellia hygrophila	1	3	.	2	2	3	3	3	2	.	1	2	2	.	2	.	.
Acacia praecox	2	.	2	2	3	2	2	2	3	2	.	.	.	1	2	.	.
Harrisia guelichii	r	.	1	1	.	.	.	1	1	+	1	1	1	1	.	+	.
Commelina aff. *erecta*	.	1	r	1	1	+	.	1	.	1	1	.	.	1	r	.	r
Arrabidaea corallina	1	2	2	2	.	.	.	1	2	1	.	.	.	.	1	1	2
Tillandsia loliacea	.	1	1	.	1	2	1	1	1	.	.	1	1	.	r	.	.
Ipomoea bonariensis var. *chacoensis*	.	.	r	.	.	2	1	+	.	.	.	.	.	.	.	.	.
Sideroxylon obtusifolium	r	1	1	1	r	.	.	.	1	r	.	.	.	.	.	1	1
Monvillea cavendishi	1	1	2	1	1	.	.	.	2	.	2	.	1	.	1	.	.
Serjania marginata	r	1	r	1	r	.	.	.	.	+	.	.	.	.	1	1	1
Capparis speciosa	.	+	r	.	r	2	.	1	1	.	.	1	.	r	r	.	.
Capparis salicifolia	.	.	+	.	1	1	2	.	1	.	1	1	1	1	.	.	.
Stetsonia coryne	.	.	.	+	1	1	.	1	1	.	r	r	2	+	.	.	.
Bougainvillea praecox	.	.	.	.	1	1	1	1	1	.	1	2	2	1	.	.	.
Bromelia hieronymi	r	.	2	.	.	.	.	1	.	.	.	2	1	3	1	.	r
Mandevilla angustifolia	.	1	.	+	1	.	.	1	.	.	r	1	1	1	.	.	.
Setaria sp.	.	.	1	.	r	.	.	1	1	.	r	1	1	.	r	.	.
Opuntia discolor	.	.	.	.	1	1	1	1	1	.	+	.	r	r	.	.	.
Erythroxylum cuneifolium	1	r	1	1	.	.	.	.	.	.	r	.	.	.	1	.	+
Herreria montevidensis	1	.	1	2	1	.	.	1	.	.	.	.	1	.	2	.	.
Opuntia retrorsa	.	r	+	.	+	.	.	.	.	.	1	+	+	.	.	.	+
Tillandsia vernicosa	.	1	1	.	.	.	r	.	1	1	.	.	.	.	1	.	1

Deinacanthion urbanianum	.	.	.	.	1	3	3	2	.	.	3	3	4	.	.	.	.
Tillandsia meridionalis	.	.	.	.	1	1	r	1	.	.	.	1	r	.	r	.	.
Galactia sp.	.	.	.	.	2	3	3	.	3	.	2	4	3	.	.	.	.
Campylocentron neglectum	1	2	2	1	.	.	.	.	.	.	.	.	.	.	2	.	r
Microgramma vaccinifolia	1	2	1	1	.	.	.	.	.	.	.	.	.	.	1	.	1
Caesalpinia paraguariensis	+	.	1	1	.	1	.	.	+	.	.	.	.	.	+	.	.
Ceiba insignis	.	+	.	.	r	+	.	r	.	.	.	.	+	+	.	.	.
Erythroxylum patentissimum	.	1	.	.	.	.	.	2	1	1	.	.	.	.	.	2	r
Castela coccinea	.	.	.	1	r	1	1	1	.	.	.	.	r	.	.	.	.
Ayenia o'donnellii	.	.	.	1	1	1	.	2	2	.	.	.	1	.	.	.	.
Dyckia ferox	.	.	.	3	2	.	.	2	3	.	1	.	1	.	.	.	.
Tillandsia streptocarpa	.	.	.	.	1	r	.	3	2	.	.	1	.	2	.	.	.
Randia armata	r	+	.	1	.	.	.	.	.	.	.	.	.	.	r	r	.
Lasiacis sorghoidea	1	1	.	.	.	.	.	.	.	.	.	.	.	.	1	2	1
Tripogandra aff. *glandulosa*	.	.	1	1	.	1	.	.	.	.	.	.	r	r	.	.	.
Ximenia americana var. *argentinensis*	.	.	.	r	r	.	.	r	r	.	.	.	r	.	.	.	.
Marsdenia castillonii	.	.	.	.	1	.	1	.	.	.	+	1	2	.	.	.	.
Cleistocactus baummannii	.	.	.	.	1	.	.	2	r	.	.	r	+	.	.	.	.
Wissadula densiflora	.	.	.	.	r	.	.	1	.	.	+	1	r	.	.	.	.
Cereus validus	.	.	.	.	+	.	.	.	r	.	+	+	+	.	.	.	.
Deuterocohnia meziana	.	.	.	.	.	3	3	3	3	.	.	4	.	.	.	.	.
Aspidosperma pyrifolium	1	.	1	1	.	.	.	.	.	.	.	.	.	.	1	.	.
Achatocarpus praecox	.	2	r	2	.	.	.	.	.	.	.	.	.	.	2	.	.
Rhipsalis baccifera	.	1	2	1	.	.	.	.	.	.	.	.	.	.	r	.	.
Selenicereus setaceus	.	1	r	1	.	.	.	.	.	.	.	.	.	.	1	.	.
Macfadyena unguis-cati	.	2	.	1	.	.	.	.	.	.	.	.	.	.	2	.	1
Bromelia serra	.	r	.	.	1	.	.	.	.	.	.	.	+	.	r	.	.
Morrenia cf. *odorata*	.	.	.	r	.	+	.	r	.	.	+	.	.	.	.	.	.
Bougainvillea campanulata	.	.	.	1	.	.	.	1	r	.	.	1	.	.	.	.	.
Arrabidaea truncata	.	.	.	1	.	.	.	1	.	.	.	.	.	1	r	.	.
Monvillea ebenacantha	.	.	.	.	r	.	r	.	.	.	+	.	1	.	.	.	.
Morrenia cf. *herzogii*	.	.	.	.	1	.	.	1	2	.	.	.	.	1	.	.	.
Tillandsia duratii	.	.	.	.	.	.	1	.	1	.	r	.	1	.	.	.	.
Mimozyganthus carinatus	.	.	.	.	.	.	.	.	r	.	1	r	.	1	.	.	.
Anthurium paraguensis	r	1	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.
Ipomoea amnicola	.	r	.	.	.	.	.	.	.	1	r	.	.	.	.	.	.
Jacaratia corumbensis	.	.	1	.	.	1	.	.	.	.	.	.	+	.	.	.	.
Prosopis kuntzei	.	.	.	+	+	+	.	.	.	.	.	.	.	.	.	.	.
Selaginella sellowii	.	.	.	.	1	.	.	.	2	.	.	.	2	.	.	.	.
Argythamnia brevirramea	.	.	.	.	2	.	.	.	1	.	+	.	.	.	.	.	.
Ruellia sp.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	1	r
Grabowskia cf. *duplicata*	.	.	.	.	.	.	.	.	.	r	.	.	.	.	+	.	+
Oncidium cf. *cebolleta*	+	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.
Mikania sp.	.	r	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Eupatorium christieanum	.	r	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.
Euglypha rojasiana	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	r	.
Ruellia erythropus	.	.	.	2	2	.	.	.	.	.	.	.	.	.	.	.	.
Oxalis frutescens	.	.	.	r	.	.	.	.	.	r	.	.	.	.	.	.	.
Pereskia sacharosa	.	.	.	r	.	.	.	.	.	.	.	.	.	.	+	.	.
Forsteronia pubescens	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	r	.
Selaginella convoluta	.	.	.	.	1	.	.	.	.	.	.	.	r	.	.	.	.
Chloroleucon chacoense	.	.	.	.	+	.	.	r	.	.	.	.	.	.	.	.	.
Gymnocalycium aff. *pflanzii*	.	.	.	.	.	.	.	1	r	.	.	.	.	.	.	.	.
Jatropha grossidentata	.	.	.	.	.	.	.	+	+	.	.	.	.	.	.	.	.
Monvillea kroenleinii	.	.	.	.	.	.	.	+	r	.	.	.	.	.	.	.	.
Gymnocalycium friedrichii	.	.	.	.	.	.	.	.	r	.	.	1	.	.	.	.	.
Bulnesia bonariensis	.	.	.	.	.	.	.	.	.	.	.	.	1	1	.	.	.
Tillandsia tricholepis	.	.	.	.	.	.	.	.	.	.	.	.	.	r	r	.	.
Paspalum sp.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	1	.
Byttneria filipes	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	+	.
Sorocea saxicola	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	1

Other characteristics: *Maclura tinctorea* subsp. *mora* r in 1; *Anisacanthus boliviensis* 2 in 3; *Coccoloba* aff. *argentinensis* 1 and *Schaefferia argentinensis* 1 in 4; *Bauhinia argentinensis* +, *Schinopsis cornuta* + and *Ptilochaeta nudipes* + in 5; *Browningia caineana* r in 9; *Pisonia zapallo* var. *guaranitica* + in 10; *Acacia furcatispina* r in 14. **Other companions:** *Serjania glutinosa* 2 and *Cereus* aff. *stenogonus* + in 1; *Justicia* sp. 1 in 2; *Hippocratea volubilis* 2, *Petiveria alliacea* 1, *Tragia volubilis* + and *Ptilochaeta* cf. *bahiensis* r in 3; *Urvillea ulmacea* 1, *Cardiospermum* sp. 1, *Polygala albicans* + and *Frailea* sp. r in 4; *Notholaena obducta* 1, *Quiabentia verticillata* + and *Tragia* cf. *hieronymi* r in 5; *Prosopis* aff. *algarrobillo* r in 8; *Cissus verticillata* + and *Turnera krapovickasii* r in 10; *Janusia guaranitica* r in 12; *Zexmenia* sp. 1 and *Harrisia pomanensis* r in 14; *Oncidium* cf. *jonesianum* 1, *Oncidium macropetalum* r, *Cyperus* sp. r, *Opuntia elata* r *Turnera weddelliana* r in 15; *Neea* sp. 3, *Oryza latifolia* 2, *Smilax* sp. 1 *Rivina humilis* 1, *Copernicia alba* +, *Triplaris gardneriana* +, *Ayenia magna* r and *Caperonia palustris* r in 16; *Marsdenia* sp. r in 17.

Localities: **1**: Line 1, Bahía Negra to Agua Dulce, km 36.8; **2**: Line 1, Bahía Negra to Agua Dulce, km 68, 195903S/584502W, 106 m; **3**: 3.5 km from the north of Line 1 towards Fortín Patria, 200443S/582543W, 97 m; **4**: Line 1, 47 km from Bahía Negra to Agua Dulce, 200237S/583404W; **5**: Colonia San Alfredo to Lagerenza-í, km 23, 200225S/610027W, 236 m; **6**: Line 1, 2 km to the west of Agua Dulce, 195902S/594641W; **7**: Line 1, 17.5 km to the west Agua Dulce, 195902S/595442W; **8**: Madrejón to Lagerenza, km 59, 202642S/602309W, 173 m; **9**: Lagerenza to Palmar de las Islas, km 27, 194801S/603534W, 209 m; **10**: Lagerenza to Colonia S. Alfredo km 8.5, 195231S/604924W, 212 m; **11**: km 4.5 al sur de Madrejón, 204009S/595303W, 127 m; **12**: Madrejón to Cerro León, km 4.4, 203757S/595514W; **13**: 22 km to the south of Madrejón, 204857S/595216W, 123 m; **14**: 5 km to the west of Gabino Mendoza, 200257S/615046W, 364 m. **15**: Line 1, Bahía Negra to Agua Dulce, km 88, 195903S/585555W, 107 m. **16**: Line 1, Bahía Negra to Agua Dulce, km 5; **17**: Line 1, Bahía Negra to Agua Dulce, km 20.

rojasiana, Bougainvillea praecox, Zizyphus mistol and *Ruprechtia triflora.* This community is differentiated from the previous (o) fundamentally by the absence or scarcity of *Bulnesia sarmientoi*, which may be related with the absence of perceivable salinity in the subsoil.

(q) Semi-arid Labón forest of the Parapetí old alluvial fan
Cordia bordasii-Tabebuia nodosa community: Tab. 3, relevé 14

Forest-type growing on very heavy, poorly-drained red clay vertisoles of the alluvial paleo-plain of the Parapetí. Structurally it corresponds to a semi-dense to semi-open shrub layer, with a tree canopy of 3–4 m in height dominated by *Tabebuia nodosa, Cordia bordasii, Ruprechtia triflora* and *Capparis retusa*. The emergents layer (6–8 m), is constituted basically by *Tabebuia nodosa*, the only species which, together with *Cordia bordasii*, is indicative of the poorly-drained soils of the Chaco in this community. This Labón forest has been identified in the far northeast of the Paraguayan Chaco (in the Gabino Mendoza area) and in adjacent areas of the Bolivian Chaco (Navarro & Fuentes 1999, Navarro & Maldonado 2002).

(r) Labón forest of the eastern Chaco of the Alto Río Paraguay
Schinopsis balansae-Tabebuia nodosa community: Tab. 3, relevés 15–17

Forest growing in the north-eastern Paraguayan Chaco and in adjacent areas of southeast Bolivia (Otuquis), where it grows on poorly-drained clay soils (eutric vertisols) with a very developed gilgai microrelief. The tree canopy of this Labón forest is fairly dense, 8–10 m in height, and is dominated by *Tabebuia nodosa*, to which the following characteristic floristic combination is associated: *Cordia bordasii*, *Coccoloba guaranitica*, *Machaonia brasiliensis*, *Sorocea saxicola*, *Ruprechtia triflora*, *Erythroxylum patentissimum*, *Bulnesia sarmientoi*, *Geoffroea spinosa*, *Aspidosperma triternatum* and *Calycophyllum multiflorum*. In the emergents layer, the "Quebracho colorado oriental" (*Schinopsis balansae*) is disperse to more frequently present. In the areas which have been greatly affected by human intervention (deforestation, cultivation, cattle grazing), these Labón forests have been replaced by secondary forests ("Vinalares") which are floristically very poor and dominated by the "Vinal" (*Prosopis ruscifolia*). Forest communities similar to the one described have been identified in nearby areas in the Pantanal (Prance et al. 1982, Adamoli 1982) and in the far southeast of the Matogrosso: Corumbá and Porto Murtinho regions (Ratter et al. 1988, Prado et al. 1992).

(s) Tasaá forest of the transitional Chiquitanía to the Chaco
Lonchocarpus lilloi-Acosmium cardenasii community: Tab. 4, relevé 1; Fig. 4F

Semi-deciduous forest growing on deep reddish sandy soils which are well drained, on the slopes and ridges of undulating peneplainized mountain areas with eolic cover, existing in the Cerro Chovoreca region. It has a fairly dense tree canopy of 15–16 m in height and has practically no emergents. It is dominated by the "Tasaá" (*Acosmium cardenasii*), an endemic species of the Chiquitanian forests in southeast Bolivia and adjacent

Table 4. Forests and shrublands of the transitional Chiquitanía-Cerrado to the Chaco. 1 (s) *Lonchocarpus lilloi-Acosmium cardenasii*; 2 (t) *Calycophyllum multiflorum-Acosmium cardenasii*; 3 (u) *Caesalpinia marginata-Anadenathera colubrina*; 4 (v) *Sphingiphila tetramera-Terminalia argentea*; 5–6 (w) *Pseudobombax tomentosum-Tabebuia selachidentata*.

	1	2	3	4	5	6
	s	t	u	v	w	w
Characteristic floristical combination of the different associations						
Lonchocarpus lilloi	2	.	.	.	.	.
Acosmium cardenasii	4	2	.	.	.	.
Calycophyllum multiflorum	.	2	.	.	+	.
Caesalpinia marginata	.	.	3	2	2	2
Anadenanthera colubrina	2	3	4	2	.	+
Sphingiphila tetramera	.	.	.	1	.	.
Terminalia argentea	.	.	.	4	r	.
Pseudobombax tomentosum	+	+	.	.	1	2
Tabebuia selachidentata	.	.	.	3	r	4
Luehea sp.	1	r	.	2	1	2
Astronium urundeuva	1	1	.	.	r	2
Jacaranda cuspidifolia	.	+	.	1	r	1
Schinopsis cornuta	.	r	.	r	1	2
Acacia aff. *tucumanensis*	1	1	.	.	.	r
Ananas ananassoides	1	r	.	.	.	2
Tabebuia aurea	.	+	.	1	r	.
Astronium fraxinifolium	.	+	.	1	.	1
Combretum leprosum	.	.	.	1	2	1
Allophyllus pauciflorus	2	1	.	.	.	.
Aspidosperma pyrifolium	3	1	.	.	.	.
Cassearia gossypiosperma	r	2	.	.	.	.
Helietta mollis	r	3	.	.	.	.
Tabebuia impetiginosa	2	r	.	.	.	.
Pseudoananas sagenarius	r	1	.	.	.	.
Pterogyne nitens	+	+	.	.	.	.
Aspidosperma tomentosum	1	.	.	r	.	.
Serjania glutinosa	2	.	.	1	.	.
Machaerium aff. *hirtum*	r	.	.	.	.	r
Phyllostylon rhamnoides	.	2	r	.	.	.
Sterculia striata	.	+	.	+	.	.
Maclura tinctorea subsp. *mora*	.	r	.	.	+	.
Sebastiania brasiliensis	.	1	.	r	.	.
Magonia pubescens	.	.	.	+	.	1
Tocoyena formosa	.	.	.	1	1	.
Companions						
Monvillea kroenleinii	1	+	2	.	.	.
Acrocomia aculeata	.	r	.	+	+	.
Anemia tomentosa var. *anthriscifolia*	.	.	1	2	.	2
Gochnatia sp.	.	.	.	3	3	3
Ximenia americana var. *argentinensis*	.	.	.	r	1	1
Lasiacis sorghoidea	2	1	.	.	.	.
Lygodium sp.	+	r	.	.	.	.
Herreria montevidensis	2	.	1	.	.	.
Monvillea cavendishi	1	.	1	.	.	.
Capparis speciosa	+	.	r	.	.	.
Gouania mollis	1	.	.	r	.	.
Mimosa aff. *bimucronata*	.	.	.	1	r	.
Annona nutans	.	.	.	r	1	.
Cordia glabrata	.	.	.	r	1	.

Other characteristics: *Simira* aff. *sampaioana* 3, *Trigonia boliviana* 2, *Amburana cearensis* 1, *Capparis* aff. *cynophallophora* 1, *Coutarea hexandra* 1, *Strychnos parvifolia* 1 and *Commiphora leptophloeos* + in 1; *Prockia crucis* 2, *Siolmatra brasiliensis* 2, *Philodendron undulatum* 1, *Fagara pterota* 1, *Celtis iguanea* 1, *Cereus* aff. *tacuaralensis* + and *Patagonula americana* + in 2; *Deuterocohnia* cf. *longipetala* 3, *Gymnocalycium paediophilum* 3 and *Gymnocalycium stenopleurum* 1 in 3; *Bredemeyera floribunda* 1, *Platypodium elegans* +, *Cochlospermum regium* r and *Hymenaea courbail* var. *stilbocarpa* r in 4. **Other companions:** *Nissolia fruticosa* 1, *Capparis retusa* + and *Chorisia insignis* r in 1; *Ruellia hygrophila* 1, *Sideroxylon obtusifolium* +, *Jacaratia corumbensis* +, *Smilax* sp. + and *Tabebuia* aff. *ochracea*

+ in 2; *Croton* cf. *argyroglossum* 3, *Mandevilla angustifolia* 2, *Opuntia retrorsa* 1, *Ipomoea wrightii* 1, *Croton* sp.1, *Quiabentia verticillata* +, *Harrisia guelichii* +, *Marsdenia castillonii* r, *Ipomoea bonariensis* var. *chacoensis* r, *Cissus verticillata* r, *Cleistocactus baumannii* r, *Commelina* aff. *erecta* r, *Serjania marginata* r, *Tillandsia duratii* r and *Ipomoea nil* r in 3; *Mimosa polycarpa* 2, *Pappophorum krapovickasii* 1, *Celtis pubescens* 1, *Rhynchosia burkartii* 1, *Croton andinus* 1, *Mimosa* sp. 1, *Serjania glutinosa* 1, *Machaerium dubia* +, *Sterculia striata* +, *Rhamnidium elaeocarpum* +, *Helicters ihotzkyana* + and *Aspidosperma cuspa* r in 4; *Arrabidaea corallina* 1, *Bromelia serra* 1, *Cereus* aff. *stenogonus* r, *Randia armata* r and *Acacia aroma* + in 5; *Aristida mendocina* 3 in 6.

Localities: **1:** 28.1 km from Line 1 to the north of Estancia Campo Grande, 194422S/584807W, 151 m; **2:** Estancia Campo Grande -Estancia Chovoreca, 32 km to the north of Line 1, 194231S/584807W, 162 m; **3:** Upper slopes and crest of the south of Cerro León, 202544S/601842W, 260 m; **4:** 27 km to the north of Line 1, Estancia Campo Grande, 194648S/584654, 132 m; **5:** 3.6 km from Adrian Jara to Agua Dulce, 193330S/592933W, 128 m; **6:** 8 km from the north of Adrian Jara to Estancia Karenina, 193224S/593127W, 147 m.

areas of Brazil and Paraguay. There are also other species which are frequent and characteristic in the forest such as: *Lonchocarpus lilloi*, *Anadenanthera colubrina*, *Tabebuia impetiginosa*, *Amburana cearensis*, *Aspidosperma tomentosum*, *Casearia gossypiosperma*, *Luehea* sp., *Astronium urundeuva* and *Commiphora leptophloeos*. This forest represents the contact between the southwest Cerrado Biogeographical Province (Chiquitanía) and the far north of the Paraguayan Chaco. Forests have been described in Bolivia which are very floristically related with this community, and which grow in adjacent areas to the north of the Cerro Chovoreca (Navarro & Maldonado 2002).

(t) Hygrophytic forest of the transitional Chiquitanía to the Chaco *Calycophyllum multiflorum-Acosmium cardenasii* community: Tab. 4, relevé 2

Semi-deciduous forest with a fairly dense tree canopy (15–18 m), growing on poorly-drained soils, or which are seasonally somewhat prone to flooding. They are located at the bottom of river beds with seasonal drainage which dissect the low undulating mountain ranges in areas in the far north of Paraguay which are a transition between the Chiquitanía to the Chaco (eastern Cerro Chovoreca). The forest tree canopy is characterized by *Calycophyllum multiflorum* associated to *Maclura tinctorea* subsp. *mora* and *Patagonula americana*, species with a mesophytic-hygrophytic tendency which are not present in the forests with well-drained soils of the previous community (s), which are topographically in contact. *Acosmium cardenasii* is co-dominant in these small poorly-drained valleys, together with *Calycophyllum multiflorum, Anadenanthera colubrina, Phyllostylon rhamnoides* and *Casearia gossypiosperma*, basically. In the understorey the abundance of *Prockia crucis*, *Helietta mollis*, *Fagara pterota*, *Celtis iguanea* and *Lasiacis sorghoidea* is characteristic: these are typical elements of the whole transitional zone between the Chaco and the Chiquitanía (Fuentes & Navarro 2000).

(u) Saxicolous shrubland of Cerro León
Caesalpinia marginata-Anadenanthera colubrina community: Tab. 4, relevé 3

Very low forest or more frequently shrubland ("chaparral"), on stony slopes and hill tops. It has a dense tree canopy of 3–5 m in height, dominated and characterized by the combination of *Anadenanthera colubrina*, *Phyllostylon rhamnoides*, *Astronium urundeuva* and *Caesalpinia marginata* (this last species is an endemic element of the transitional Cerrado to Chaco hill areas in Bolivia and Paraguay). Other characteristic species are endemic to these mountains such as the shrub *Mimosa bimucronata* var. *adenocarpa* (not present in the table) and the *Cactaceae*, abundant in the understorey, *Gymnocalycium paediophilum* and *G. stenopleurum*. The *Caesalpinia marginata-Anadenanthera colubrina* community is restricted to the isolated mountain systems in the north of the Paraguayan Chaco (Serranía de Cerro León) where they cover considerable extensions.

(v) Chaparral of the transitional Chiquitanía to the Chaco on calcareous substrates
Sphingiphila tetramera-Terminalia argentea community: Tab. 4, relevé 4

Low forest or sclerophyllous and xeromorphic shrubland, with notably diverse flora predominantly made up of elements of the Cerrado, growing on stony or sandy calcareous soils on the plateaus and undulating peneplainized mountains with eolic cover of the Cerro Chovoreca region. It has a semi-closed to semi-open tree canopy of 4–6 m in height dominated by *Terminalia argentea*. The characteristic species of the sandy soils of the Chaco, *Schinopsis cornuta*, is generally the only emergent (10–12 m). In the sub-canopy or shrubby undergrowth, *Tabebuia selachidentata* and *Caesalpinia marginata* are abundant; these elements are almost restricted to the Chaco-Cerrado transition in Bolivia and Paraguay; together with numerous elements of the Cerrado with a wide distribution. The common or frequent presence of *Sphingiphila tetramera*, a regional endemic species, characterizes this chaparral on calcareous soils. The *Sphingiphila tetramera-Terminalia argentea* community is known both in the far north of Paraguay and in the southeast of Bolivia (Navarro & Maldonado 2003). In most of its area, this community has been seriously affected by forest fires set for farming motives.

(w) Chaparral of the transitional Chiquitanía to the Chaco on non-calcareous soils
Pseudobombax tomentosum-Tabebuia selachidentata community: Tab. 4, relevés 5–6

Low forest or shrubland growing on soils formed on siliceous sandstone which share the landscape of this region with the previous community. Floristically it is characterized and differentiated from the previous community by the frequency of *Pseudobombax tomentosum* and the absence of *Sphingiphila tetramera*; these occurrences appear to be correlated with the change in the lithological substrate. However, additional studies are needed to rule out the possibility that it may be simply another aspect of the previ-

Table 5. Hygrophytic and floodable forests. 1–2 (x): *Coccoloba guaranitica-Geoffroea spinosa*; 3 (y): *Lonchocarpus pluvialis-Ruprechtia exploratricis*; 4 (z): *Triplaris gardneriana-Copernicia alba*.

	1	2	3	4
	x	x	y	z
Characteristic floristical combination of the different associations				
Geoffroea spinosa	3	4	3	+
Coccoloba guaranitica	2	3	3	.
Lonchocarpus pluvialis	.	.	2	.
Ruprechtia exploratricis	.	.	2	.
Triplaris gardneriana	.	.	.	4
Copernicia alba	.	+	.	3
Machaonia brasiliensis	2	1	2	.
Tabebuia nodosa	1	3	r	.
Cordia bordasii	+	.	+	.
Parkinsonia aculeata	.	+	.	1
Companions				
Oryza latifolia	.	1	1	2
Capparis retusa	2	r	.	.
Serjania marginata	1	1	.	.
Capparis tweeddiana	+	+	.	.
Caperonia palustris	.	.	+	1

Other characteristics: *Aspidosperma triternatum* r and *Trithrinax schizophylla* r in 1; *Coccoloba* aff. *paraguariensis* 3 and *Chomelia obtusa* var. *pubescens* 2 in 2; *Celtis iguanea* 1 in 3; *Albizia inundata* 2 and *Mimosa hexandra* 1 in 4. **Other companions:** *Aechmea distichantha* 3, *Arrabidaea corallina* 2, *Ruprechtia triflora* 2, *Ruellia hygrophila* 2, *Diplokeleba floribunda* 1, *Achatocarpus praecox* 1, *Bromelia hieronymi* 1, *Erythroxylum patentissimum* 1, *Harrisia guelichii* 1, *Herreria montevidensis* 1, *Phyllostylon rhamnoides* 1, *Pisonia zapallo* var. *guaranitica* 1, *Rhipsalis baccifera* 1, *Tillandsia loliacea* 1, *Opuntia discolor* +, *Cayaponia apodantha* +, *Stetsonia coryne* +, *Janusia guaranitica* r, *Arrabidaea truncata* r, *Astronium urundeuva* r, *Tillandsia vernicosa* r, *Tillandsia meridionalis* r, *Tillandsia tricholepis* r, *Oncidium macropetalum* r, *Zizyphus mistol* r and *Ruellia* sp. r in 1; *Sideroxylon obtusifolium* 1, *Euglypha rojasiana* 1, *Macfadyena unguis-cati* 1, *Selenereiceus setaceus* 1, *Prosopis ruscifolia* +, *Aporosella chacoensis* + and *Randia armata* r in 2; *Hymenachne amplexicaulis* 1, *Caesalpinia paraguariensis* +, *Calycophyllum multiflorum* +, *Coccoloba spinescens* + and *Cordia glabrata* + in 3; *Pavonia vitifolia* 4, *Ipomoea amnicola* 3, *Coccoloba cujabensis* 2, *Byttneria filipes* 1, *Thevetia bicornuta* 1 and *Panicum mertensii* 1 in 4;

Localities: **1:** Bahía Negra to Agua Dulce, km 117, 195904S/591122W; **2:** Bahía Negra to Agua Dulce, km 3, 201415S/581029W, 80 m; **3:** Madrejón to Cerro León, km 43.4, 203020S/601519W, 158 m; **4:** Line 1, Bahia Negra to Agua Dulce, km 12.1.

ous community (v) which has suffered more degradation by human intervention.

(x) Hygrophytic forest of the northern Chaco

Coccoloba guaranitica-Geoffroea spinosa community: Tab. 5, relevés 1–2; Fig. 4G

Forest occupying the intermittent fluvial beds, marshlands and banks of temporary lakes in the western xerophytic Chaco and areas which are relatively less liable to flooding of the recently-flooded plain of the upper Paraguay River and of the north-eastern distant paleo-alluvial fan of the Pilcomayo in the north-eastern Paraguayan Chaco. It grows on clay gleyic soils temporarily flooded by rainwater and river overflow. From the physiogno-

mic point of view, its forests range from those with a tree canopy of between 5–6 m and emergents of some 10 m in height in areas which are more liable to flooding, to forests with an irregular tree canopy of 10 m in height and almost without emergents in areas which are less liable to flooding. Both the tree canopy and the emergents layer are dominated and characterized by *Geoffroea spinosa* associated to *Tabebuia nodosa*. The understorey is dominated and characterized by *Coccoloba guaranitica*, associated to other abundant species and very characteristic of these environments, such as, for example, *Machaonia brasiliensis*. The *Coccoloba guaranitica-Geoffroea spinosa* community is widely distributed in southeast Bolivia (Navarro & Fuentes 1999, Fuentes & Navarro 2000, Navarro & Maldonado 2003) and in the north of Paraguay.

(y) Hygrophytic forest of the transitional Chaco to the Chiquitanía
Lonchocarpus pluvialis-Ruprechtia exploratricis community: Tab. 5. relevé 3

Forest occupying the banks of the seasonal river beds in the biogeographical transition zone between the Chaco and the Chiquitanía (Cerrado). This forest is characterized by the dominance or abundance of the species *Ruprechtia exploratricis*. *Lonchocarpus pluvialis* is associated with notable constancy and generally more sparsely *Seguieria paraguariensis* (not present in the table) and *Geoffroea spinosa*. The shrubby undergrowth is basically dominated and characterized by *Coccoloba guaranitica, Chomelia obtusa* and *Machaonia brasiliensis*. The *Lonchocarpus pluvialis-Ruprechtia exploratricis* community extends throughout southeast Bolivia (Navarro & Fuentes 1999, Navarro & Maldonado 2002) and the far north of Paraguay (in the area round Cerro León, N. Lagerenza, Colonia Sierra León, E. Cerro Chovoreca).

(z) Floodable palm forest of the north-eastern Chaco
Triplaris gardneriana-Copernicia alba community: Tab. 5, relevé 4; Fig. 4H

Palm forest, seasonally and regularly flooded (six months a year or more) by river overflow waters and/or rain water, which may reach a depth of more than 1 meter. It grows on very heavy blackish or grey clay gleyic soils, in the transition of the eastern Chaco with the Gran Pantanal. The shrub or small tree *Triplaris gardneriana*, endemic in the upper basin of the Paraguay River, is the main characteristic species of the community. Other characteristic species are: *Copernicia alba*, *Albizia inundata* and *Parkinsonia aculeata*. Due to intensive cattle grazing in the area, this palm forest undergoes periodic burning in the dry period in order to encourage the production of herbaceous and subfruticous plants. The *Triplaris gardneriana-Copernicia alba* community is known both in north-eastern Paraguay (Bahía Negra region), and in south-eastern Bolivia and adjacent areas of Brazil (Navarro & Maldonado 2003).

6. Discussion

The predominant biogeographical element in the north of the Paraguayan Chaco is the Chacoan element, which constitutes the floristical matrix of

Table 6. Biogeographical distribution of identified forest type-communities in north Paraguayan Chaco.

Type-communities	Chaco (at least Bolivia and Paraguay)	Paraguayan Chaco endemics (*) or quasi-endemics (**) (slightly overlapping into adjacent Bolivian Chaco)	Chaco transitional to Chiquitanía (Cerrado) in Paraguay and Bolivia	Chiquitanía (Cerrado) transitional to Chaco in Paraguay and Bolivia	Chaco transitional to Pantanal in Paraguay and Bolivia
a	X				
b		X (**)			
c		X (**)			
d	X				
e					
f	X				
g		X (*)			
h			X		
i			X		
j			X		
k			X		
l			X		
m					X
r					X
n	X				
o		X (*)			
p		X (*)			
q	X				
s				X	
t				X	
u				X	
v				X	
w				X	
x	X				
y				X	
z					X

the forests with the largest extensions in the territory (Table 6). These genuinely Chacoan forests belong to the following groups (Table 7): sand Médanos forests (group 1); xerophytic forests of the old alluvial plains of the north western Chaco (group 2); forests on poorly drained soils of the north western Chaco (group 3); and partially, hygrophytic forests of the northern Chaco (group 12: x).

The second most important biogeographical component in spatial extension is represented by several types of transitional forests which show in their composition the presence of various elements of the Chiquitanía (Cerrado) on a still predominantly Chacoan floristic base (Table 6). These forests of the transitional Chaco to the Chiquitanía belong to the following groups (Table 7): forest on sands of the transitional Chaco to the Chiquitanía (group 5); hill forest of the transitional Chaco to the Chiquitanía (group 6); forests on the alluvial plain of the transitional Chaco to the Chiquitanía (group 8); and, partially, hygrophytic forests of the northern Chaco (group 12: y).

The third biogeographical component, present above all in the far north of the Paraguayan Chaco and in a partially disjunctive form in the mountain ranges of Cerro León, comprises forests and chaparrals whose dominant floristic composition is made up of elements of the Chiquitanian forest, including *Acosmium cardenasii*, the endemism of this formation in Bolivia, Paraguay and Brazil. On this Chiquitanian floristic base some wider Chacoan elements are superimposed. These formations of the transitional Chiquitanía (Cerrado) to the Chaco are represented by the following groups (Tables 6 and 7): forest of the transitional Chiquitanía to the Chaco on well-drained soils (group 9); hygrophytic forest of the transitional Chiquitanía to the Chaco (group 10); saxicolous shrubland of Cerro León Serranía (group 7); and chaparrales of the transitional Cerrado to the Chaco (group 11).

Finally a biogeographical component of the transitional Chaco to the Pantanal is identified, present only in the far northeast of the territory in the study, and comprising the following groups (Tables 6 and 7): forests on poorly drained soils of the north-eastern Chaco (group 4), and floodable palm forests of the north-eastern Chaco (group 13).

Thus, from a biogeographical point of view, the 26 types of forest identified and described in this work are divided in the following manner: 11 (42.3 %) are biogeographically Chacoan, 6 (23 %) are Chiquitanian (Cerrado) transitional to the Chaco, 5 (19.2 %) are transitional between the Chaco and the Chiquitanía (Cerrado) and 3 (11.5 %) are transitional to the Pantanal. Among the Chacoan forests we must highlight the fact that 3 (11.5 %) are endemic to the Paraguayan Chaco, and 2 (7.6 %) almost endemic, that is, they are shared to a small degree with the neighbouring Bolivian Chaco.

It is worth noting the clear floristic influence of the Cerrado in the northeast of the Paraguayan Chaco (Ramella & Spichiger 1989). Many of the floristic elements appearing in our relevés (for example *Anadenanthera colubrina* and *Astronium urundeuva*, among others), whose optimum bio-

Table 7. Classification of the forests of the northern Paraguayan Chaco based on both their floristical composition and a multi-scale of environmental factors. The names of the groups of vegetation and the community include former names considered here as synonyms at least pro parte.

CLIMATOPHILOUS XEROPHYTIC AND MESOPHYTIC FORESTS	**1. Sand Médanos Forests (north western Chaco)** Matorral de médanos y mantos arenosos, López (1984); Matorral de médanos (UNA-FIA-CIF-GTZ (1991); Matorral xerófito sobre dunas, MAG-DOA.BGR (1998); Matorral sobre dunas, Mereles & Degen (1998)	**a**: *Agonandra excelsa-Schinopsis cornuta* Matorral de crestas de dunas, MAG-DOA-BGR (1998) **b**: *Piptadeniopsis lomentifera-Schinopsis cornuta* **c**: *Piptadeniopsis lomentifera-Schinopsis* aff. *heterophylla* Bosque xerófito en transición, MAG-DOA-BGR (1998)
	2. Xerophytic forests of the old alluvial plains of the north western Chaco Monte xerófilo bajo y monte xerófilo alto, Fiebrig & Rojas (1933); Bosque xerofítico, López (1984); Bosque mesoxerofítico claro, López (1984); Quebrachal de Quebracho Blanco y Samu'u, UNA-FIA-CIF-GTZ (1991); Quebrachal de Quebracho Blanco, UNA-FIA-CIF-GTZ (1991); Bosque Xeromórfico de *Aspidosperma quebracho-blanco* y *Chorisia insignis*, Spichiger et al. (1991); Matorral xerófito denso, Mereles & Degen (1998); Bosque xerófito denso, MAG-DOA-BGR (1998); Bosque xeromórfico abierto semidecíduo, DPNVS-DeSdelChaco-TNC (1999); Bosque xerofítico denso semideciduo subhúmedo, DPNVS-DeSdelChaco-TNC (1999); Bosque xerofítico abierto semideciduo subhúmedo, DPNVS-DeSdelChaco-TNC (1999)	**d**: *Bulnesia sarmentoi-Aspidosperma quebracho-blanco* **e**: *Acacia emilioana-Schinopsis* aff. *heterophylla* **f**: *Tabebuia nodosa-Schinopsis quebracho-colorado* **g**: *Piptadeniopsis lomentifera-Schinopsis quebracho-colorado*
	5. Forest on sands of the transitional Chaco to the Chiquitanía	**h**: *Lonchocarpus nudiflorens Schinopsis cornuta* Bosque xerofítico sobre arenas hídricas, MAG-DOA-BGR (1998)
	6. Hill forest of the transitional Chaco to the Chiquitanía	**i**: *Pseudobombax heteromorphum-Astronium urundeuva* Bosque mesófilo de colina de Anadenanthera colubrina, Spichiger et al. (1991)
	8. Forests on the alluvial plain of the transitional Chaco to the Chiquitanía Bosque mesoxerofítico denso, López (1984); Bosque mesoxerofítico claro, López (1984)	**j**: *Amburana cearensis-Athyana weinmannifolia* **k**: *Diplokeleba floribunda-Phyllosthylon rhamnoides* **l**: *Diplokeleba floribunda-Schinopsis quebracho-colorado*
	4. Forests on poorly-drained soils of the north eastern Chaco Bosque mesofítico, López (1984); Campo con islas de bosque, López (1984); Bosque Xeromesófilo con *Schinopsis balansae* y *Astronium*, Spichiger et al. (1991); Quebrachal de Quebracho Colorado, UNA-FIA-CIF-GTZ (1991); Quebrachal de Quebracho Colorado en isletas, UNA-FIA-CIF-GTZ (1991); Unidad mesoxeromófica: Bosque de *Schinopsis balansae*, MAG-DOA.BGR (1998); Bosques mesoxeromorfos, Mereles & Degen (1998)	**m**: *Lonchocarpus nudiflorens-Schinopsis balansae* **r**: *Schinopsis balansae-Tabebuia nodosa*

CLIMATOPHILOUS XEROPHYTIC AND MESOPHYTIC FORESTS (cont.)	**3. Forests on poorly-drained soils of the north western Chaco** Palosantales, López (1984); Palocruzales, López (1984); Matorral xerohigrófito de *Bulnesia sarmientoi* y *Tabebuia nodosa*, Spichiger et al. (1991); Peladares, Spichiger et al. (1991); Palosantal y Labonal, UNA-FIA.CIF-GTZ (1991); Matorral con Labón (Labonales), MAG-DOA-BGR (1998); Matorral sobre paleocauces recientes del río Pilcomayo, MAG-DOA-BGR (1998); Labonales, Mereles & Degen (1998); Bosque denso semideciduo estacionalmente saturado, DPNVS-DeSdelChaco-TNC (1999)	**n**: *Prosopis elata-Tabebuia nodosa* **o**: *Prosopis rojasiana-Bulnesia sarmientoi* **p**: *Prosopis rojasiana-Tabebuia nodosa* **q**: *Cordia bordasii-Tabebuia nodosa*
	9. Forest of the transitional Chiquitanía to the Chaco on well-drained soils	**s**: *Lonchocarpus lilloi-Acosmium cardenasii*
	10. Hygrophytic forest of the transitional Chiquitanía to the Chaco	**t**: *Calycophyllum multiflorum-Acosmium cardenasii*
	7. Saxicolous shrubland of Cerro León Serrania	**u**: *Caesalpinia marginata-Anadenanthera colubrina* Matorral xeromesófilo de colina, Spichiger et al. (1991)
	11. Chaparrales of the transitional Chaco to the Chiquitanía Campos cerrados, Spichiger et al. (1991)	**v**: *Sphingiphila tetramera-Terminalia argentea* **w**: *Pseudobombax tomentosum-Tabebuia selachidentata*
HYGROPHYTIC AND FLOODABLE FORESTS	**12. Hygrophytic forests of the northern Chaco** Paloblancal, López (1984); Bosques claros higrófilos de *Geoffroea* o *Aporosella chacoensis*, Spichiger et al. (1991); Bosques higrófilos de galería de *Calycophyllum multiflorum*, Spichiger et al. (1991); Bosques higrófilos con Palo Blanco ("Paloblancales") y Bosques higrófilos con Timbo'y (*Cathormion polyanthum*), MAG-DOA-BGR (1998); Sabana de *Cathormion polyanthum* , DPNVS-DeSdelChaco-TNC (1999)	**x**: *Coccoloba guaranitica-Geoffroea striata* **y**: *Lonchocarpus fluvialis-Ruprechtia exploratricis*
	13. Floodable palm forest of the north-eastern Chaco Campo-palmares, Fiebrig & Rojas (1933); Palmares de *Copernicia alba* y Campo palmar, López (1984); Sabanas palmares de *Copernicia alba*, Spichiger et al. (1991); Palmares de Caranda'y, UNA-FIA.CIF-GTZ (1991); Sabana hidromórfica, Mereles & Degen (1998); Sabana hidromórfica de *Copernicia alba*, MAG-DOA-BGR (1998); Sabana de *Copernicia alba*, DPNVS-DeSdelChaco-TNC (1999)	**z**: *Triplaris gardneriana-Copernicia alba*

geography is found in the Chiquitanía, are characteristic of the Pleistocene Arc along which the seasonal forests are distributed in South America (Prado & Gibbs 1993). This paleodistribution, on which Prado's (2000) Tropical Seasonal Forest Region of South America is based, would explain the floristic connections between: a) the sub-Andean Piedmont, b) the northern Paraguayan Chaco (Cerro León), c) south-eastern Bolivia (Chiquitanía), d) Caatinga and e) the Paraná province in eastern Paraguay and central-southern Brazil. Moreover, except for the Andean Piedmont, this region largely coincides with the Brazilian-Paranean biogeographical region described by Rivas-Martínez et al. (1990) and Navarro (2000). Our results confirm the important floristic affinity of the north-eastern Para-

guayan Chaco with the Chiquitanía region in southeast Bolivia (Cerrado province) and thus with the flora of the forests and 'Campos Cerrados' of central-southern Brazil. However, the floristic connections with the forests of the sub-Andean Piedmont in southern Bolivia and northern Argentina are almost solely through more widely-distributed and thus more euryecious elements of the Pleistocene Arc (for example, *Anadenanthera colubrina* and *Astronium urundeuva*, among others).

Our results also indicate that the far northeast of the Paraguayan Chaco (Bahía Negra region) is an area of floristic transition to the Pantanal province, as shown by the existence of forests such as *Triplaris gardneriana-Copernicia alba* community, *Schinopsis balansae-Tabebuia nodosa* community and *Lonchocarpus nudiflorens-Schinopsis balansae* community. This fact was also highlighted for south-eastern Mato Grosso (Brazil) by Adamoli (1982), Ratter et al. (1988) and Prado et al. (1992).

Table 7 shows the classification of the forests of the northern Paraguayan Chaco proposed in this work, based on several discriminating factors depending on the scale used. On the regional scale (north Paraguayan Chaco) the forests are separated at a primary level into two units: climatophilous (zonal) forests on soils ranging from well- to poorly-drained, and hygrophytic (azonal) forests which are subject to flooding. Within the first group, the second division segregates the forests according to their origins and floristic composition: whether from the Chaco or from the Chiquitanía (Cerrado). In the third place, and as a more discriminating factor in the local biogeographic sphere, soil features, and in particular the degree of internal drainage in relation to structure and geomorphology, conform the main ecological factors affecting the composition of the forests, their structure and geographic distribution.

The equivalences between our units and those postulated by other authors can only be drawn in most cases at the general level of groups of communities or formations. The vegetation units of the aforementioned authors are largely based almost exclusively on sets of dominant species and on the physiognomy they confer on the formation (for example: López 1984, UNA-FIA-CIF-GTZ 1991, MAG-DOA-BGR 1998, DPNVS-DeSdelChaco-TNC 1999). These large units or formations are in general related with major discontinuities in the physical environment (for example, Ramella & Spichiger 1989, Spichiger et al. 1991, MAG-DOA-BGR 1998). The classification given here introduces detail into the geo-edaphic variations of the Chacoan environment.

This is, in sum, a floristic-ecological and biogeographical classification. This means that the different plant communities identified and their respective differential and characteristic floristic combinations are related in the landscape with a determining and particular set of geo-edaphic and bioclimatic characteristics. Moreover, their floristic composition is ultimately controlled by the geographic situation of each community, in relation with the regional biogeographical centres of paleo-historic origin and diversification of floras (the Chaco, Cerrado-Chiquitanía and Pantanal). For all these reasons, and according to our results, although in many cases most of the

flora is shared by groups of several like communities with a similar structure (for example, groups 1, 2, 3 and 8 in Table 6), these communities differ among themselves in the presence or absence of significant and indicative floristic elements associated with different geo-hydro-edaphic, bioclimatic or biogeographic conditions.

7. Conclusions

1. Although the northern Paraguayan Chaco has a low relief and is an area with no significant geographical boundaries, it has a great richness of potential forests. In addition, several of these forests are characterized by species whose timber is of considerable value, such as *Schinopsis quebracho-colorado, Schinopsis balansae, Astronium urundeuva* and *Amburana cearensis* (Cozzo 1967).

2. The most extensive forests in the territory are the different types of Quebracho forests [Quebracho blanco (*Aspidosperma quebracho-blanco*) forests, Quebracho colorado coronillo (*Schinopsis quebracho-colorado*) forests, Quebracho colorado oriental (*Schinopsis balansae*) forests, Quebracho mestizo (*Schinopsis* aff. *heterophylla*) forests] and, in hygrophytic environments, the forests of the *Coccoloba guaranitica-Geoffroea spinosa* community. The Palolanza with the Quebracho colorado coronillo forest (*Diplokeleba floribunda-Schinopsis quebracho-colorado* community) and the Quebrachillo forest (*Amburana cearensis-Athyana weinmannifolia* community) have the most limited area of distribution.

3. The northern forests of the Paraguayan Chaco are constituted by a particular flora in which the most characteristic phytogeographical element is that of the Chaco. This element decreases in importance in favour of the Chiquitanía (Cerrado) element over a gradual clinal gradient from west to east and from south to north. The most north-easterly forests in the area, in which both elements are juxtaposed, are interpreted as transitional forests either of the Chaco to the Cerrado (*Lonchocarpus nudiflorens-Schinopsis cornuta* community, *Pseudobombax heteromorphum-Astronium urundeuva* community, *Caesalpinia marginata-Anadenanthera colubrina* community, etc.), or of the Cerrado to the Chaco (*Lonchocarpus lilloi-Acosmium cardenasii* community, *Sphingiphila tetramera-Terminalia argentea* community, *Pseudobombax tomentosum-Tabebuia selachidentata* community) depending on the predominance in floristic composition of one or other phytogeographical component. The endemic element may even characterize some communities such as *Prosopis rojasiana* in the central zone of the Paraguayan Chaco (*Prosopis rojasiana-Bulnesia sarmientoi* community, *Prosopis rojasiana-Tabebuia nodosa* community).

4. The flora found in the forests of the northern Paraguayan Chaco shows little relation with that of the dry inter-Andean valleys of Bolivia where limited floristic elements of the Gran Chaco appear, in a matrix dominated by the distinctive xerophytic inter-Andean flora of central-southern Bolivia and north-eastern Argentina (Navarro 2000). This also agrees with the results of Linares-Palomino et al. (2003) who propose

both groups, the Chaco and the dry inter-Andean valleys of Bolivia, as different biogeographical entities within the group of South America's dry forests.

5. At a regional level, the forest vegetation follows the statements by Mitlöhner (1990) for the vegetation of the northern Paraguayan Chaco: a higher rainfall increases species richness, the volumes and heights of the individuals and the basal area of the arboreal community.

6. At a local level the soil features are revealed to be the main determining ecological factor. Specifically, edapho-ecological factors such as the texture and internal drainage of the soils in relation to the local geomorphology are the main variables explaining the changes both in structure and in the floristic diversity of the vegetation. These soil features mentioned above are important in the classification presented here, but their quantitative influence still needs to be investigated.

7. The use of a forest classification method based on the identification of differential floristic combinations associated with edaphic, bioclimatic and biogeographical discontinuities allows a more minute and accurate separation of the forest plant communities. This represents an advance in regard to other approaches which are fundamentally based on the dominant species and on the physiognomy of the formation, and permits a more detailed classification which can be more precisely applied as a basis for a the fine detection of priority areas for conservation and sustainable land use.

References

Adámoli, J. (1982): O Pantanal e suas relações fitogeográficas com os Cerrados. Discussão sobre o conceito de "Complexo do Pantanal". – XXXII Congresso Nacional de Botânica, Teresina, PI: 109–119.

Braun-Blanquet, J. (1964): Pflanzensoziologie. – 3rd ed. Grundzüge der Vegetationskunde. Springer-Verlag. Vienna, New York.

Burkart, A. (1976): A monograph of the genus Prosopis (Leguminosae Subfam. Mimosoideae). – J. Arnold Arboretum **57**: 450–525.

Cabrera, A. L. & Willink, A. (1980): Biogeografía de América Latina. – Monografía No. 13. Organización de los Estados Americanos (OEA), Washington, DC. 120 pp.

Cozzo, D. (1967): La Argentina Forestal. – Editorial Universitaria de Buenos Aires.

DPNVS-DeSdelChaco-TNC (1999): 1065 Motivos iniciales para proteger el Parque Nacional Defensores del Chaco. – Evaluación ecológica rápida. San Lorenzo.

FAO/UNESCO (1995): Soil Map of the World. – Roma.

Fiebrig, C. & Rojas, T. (1933): Ensayo Fitogeográfico sobre el Chaco boreal. – Revista Jard. Bot. Mus. Hist. Nat. Paraguay **3**: 3–87.

Fuentes, A. & Navarro, G. (2000): Estudio fitosociológico de la vegetación de una zona de contacto Chaco-Cerrado en Santa Cruz (Bolivia). – Lazaroa **21**: 73–109.

Géhu, J. M. & Rivas-Martínez, S. (1982): Notions fondamentals de phytosociologie. – Ber. Internat. Symp. IVVS, Syntaxonomie: 1–33. J. Cramer ed.

Gentry, A. (1977): Endangered plant species and habitats in Ecuador and Amazonian Peru. – In: Prance, G.T. & Elias, T.S. (eds.): Extintion is forever: 136–149. New York Botanical Garden.

Ibisch, P. L. & Mérida, G. (eds.) (2003): Biodiversidad, la riqueza de Bolivia. Estado de conocimiento y conservación. – Ministerio de Desarrollo Sostenible. Editorial FAN, Santa Cruz de la Sierra, Bolivia. 638 pp.

Iriondo, M. (1995): El cuaternario del Chaco. – In: Argollo, J. & Mourguiart, P. (eds.): Climas cuaternarios en América del Sur: 263–282. ORSTOM, La Paz.

Janzen, D. H. (1988): Tropical dry forests: the most endangered major tropical ecosystem. – In: Wilson E.O. (ed.): Biodiversity: 130–137. National Academy Press, Washington, D.C.

Josse, C., Navarro, G., Comer, P., Evans, R., Faber-Lagendoen, D., Fellows, M., Kittel, G., Menard, S., Pyne, M., Reid, M., Schulz, K., Snow, K. & Teague, J. (2003): Ecological Systems of Latin America and the Caribbean: A Working Classification of Terrestrial Systems. – NatureServe, Arlington, VA.

Linares-Palomino, R., Pennington, R. T. & Bridgewater, S. (2003): The phytogeography of the seasonally dry tropical forests in Equatorial Pacific South America. – Candollea **58**: 473–499.

López, O. (1984): Formaciones Vegetales del Chaco Paraguayo. – Comisión Nacional de Desarrollo del Chaco. Organización de Estados Americanos (OEA). Serie de Información Básica n° 2. Asunción. 34 pp.

MAG/DOA-BGR (1998): Sistema Ambiental de la República del Paraguay. Potencial de los espacios naturales de la Región Occidental. Mapa de Vegetación.

McGarigal, K., Cushman, S. & Stafford, S. (2000): Multivariate Statistics for Wildlife and Ecology Research. – Springer. 283 pp.

Mereles, F. & Degen, R. (1998): Formaciones Vegetales del Chaco Boreal Paraguayo. – In: Proyecto Sistema Ambiental del Chaco. Tomo II: Investigaciones especiales: 76–87.

Mitlöhner, R. (1990): Die Konkurrenz der Holzgewächse im regengrünen Trockenwald des Chaco Boreal, Paraguay. – Göttinger Beitr. zur Land- und Forstwirtschaft in den Tropen und Subtropen **54**, 177 pp. Göttingen.

Morello, J. & Adámoli, J. (1974): Las grandes unidades de vegetación y ambiente del Chaco argentino. Segunda parte: Vegetación y ambiente de la Provincia del Chaco. – Instituto Nacional de Tecnología Agropecuaria, Serie Fitogeográfica, 13. Buenos Aires.

NatureServe (2003): International Ecological Classification Standard: Terrestrial Ecological Systems of Latin America and the Caribbean. – Natural Heritage Central Databases. NatureServe, Arlington, VA.

Navarro, G. (1997): Contribución a la clasificación ecológica y florística de los bosques de Bolivia. – Rev. Bol. Ecol. **2**: 3–37.

Navarro, G. & Fuentes, A. (1999): Geobotánica y sistemas ecológicos de paisaje en el Gran Chaco de Bolivia. – Rev. Bol. Ecol. **5**: 25–50.

Navarro, G. & Maldonado, M. (2002): Geografía Ecológica de Bolivia. Vegetación y Ambientes Acuáticos. – Fundación Simón I. Patiño, Cochabamba. 620 pp.

Parker, T. A. III, Gentry, A., Foster, R. B., Emmons, L. H. & Remsen, J. V. Jr. (1993): The lowland dry forests of Santa Cruz, Bolivia: a global conservation priority. – Conservation International, RAP working paper n° 4.

Podani, J. (2001): Syn-Tax 2000. Computer Program for Data Analysis in Ecology and Systematics. User's Manual.

Prado, D. E. (1993a): What is the Gran Chaco vegetation in South America?. I. A review. Contribution to the study of flora and vegetation of the Chaco. V. – Candollea **48**: 145–172.

– (1993b): What is the Gran Chaco vegetation in South America?. II. A redefinition.

Contribution to the study of flora and vegetation of the Chaco. VII. – Candollea **48**: 615–629.
– (2000): Seasonally dry forests of tropical South America: From forgotten ecosystems to a new phytogeographical unit. – Edinb. J. Bot. **57**: 437–461.
Prado, D. E. & Gibbs, P. E. (1993): Patterns of species distributions in the dry seasonal forests of South America. – Ann. Missouri Bot. Gard. **80**: 902–927.
Prado, D. E., Gibbs, P. E., Pott, A. & Pott, V. J. (1992): The Chaco-Pantanal transition in southern Mato Grosso, Brazil. – In: Furley, P. A., Proctor, J. & Ratter, J. A. (eds.): Nature and Dynamics of Forest-Savanna Boundaries: 451–470. – Chapman & Hall, London.
Prance, C. T. & Schaller, G. B. (1982): Preliminary study of some vegetation types of the Pantanal, Mato Grosso, Brazil. – Brittonia **34**: 228–251.
Ramella, L. & Spichiger, R. (1989): Interpretación preliminar del medio físico y de la vegetación del Chaco Boreal. Contribución al estudio de la flora y de la vegetación del Chaco I. – Candollea **44**: 639–680.
Ratter, J. A., Pott, A. & Pott, V. J. (1988): Observations on woody vegetation types in the Pantanal and at Corumbá, Brazil. – Notes Roy. Bot. Garden, Edinburgh **45**: 503–525.
Rivas-Martínez, S., Sánchez-Mata, D. & Costa, M. (1999): North American boreal and western temperate forest vegetation. – Itinera Geobot. **12**: 5–316.
Scarpa, G. F. & Arenas, P. (2004): Vegetation units of the Argentine semi-arid Chaco: The Toba-Pilagá perception. – Phytocoenologia **34**: 133–161.
Spichiger, R., Ramella, L., Palese, R. & Mereles, F. (1991): Proposicion de leyenda para la cartografía de las formaciones vegetales del Chaco paraguayo. Contribución al estudio de la flora y de la vegetación del Chaco III. – Candollea **46**: 541–564.
Stotz, D. F., Fitzpatrick, F. W., Parker, T. A. III, & Moskovits, D. K. (1996): Neotropical birds: ecology and conservation. – University of Chicago Press, Chicago.
UNA-FIA-CIF-GTZ (1991): Vegetación y Uso de la Tierra de la Región Occidental de Paraguay (Chaco). – San Lorenzo, Asunción. 22 p.
van der Maarel, E. (1979): Transformation of cover-abundance values in phytosociology and its effects on community similarity. – Vegetatio **39**: 97–114.
van Tongeren, O. F. R. (1995): Cluster Analysis. – In: Jongman, R. H. G., Ter Braak, C. J. F. & van Tongeren, O. F. R. (eds.): Data Analysis in community and landscape ecology: 174–212. Cambridge University Press.
Weber, H. E., Moravec, J. & Theurillat, J. P. (2000). International. code of phytosociological nomenclature. 3rd. ed. – J. Veg. Sci. **11**: 739–768.
Westhoff, V. & van der Maarel, E. (1978): The Braun-Blanquet approach. – In: Whittaker, R. H. (ed.): Classification of plant communities: 287–399. Junk, Den Haag.

Addresses of the authors:
Dr. Gonzalo Navarro, Cochabamba (Bolivia). E-mail: gnavarro@entelnet.bo
Dr. José Antonio Molina, Departamento de Biología Vegetal II, Facultad de Farmacia, Universidad Complutense de Madrid, 28040-Madrid (Spain). E-mail: jmabril@farm.ucm.es
Dra. Lidia Pérez de Molás, Dirección General de Postgraduación Académica, Universidad Nacional de Asunción, Asunción (Paraguay). E-mail: bibagr@agr.una.py