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What is the Gran Chaco vegetation in South America? I. A review. Contribution to the study of flora and vegetation of the Chaco. V

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ABSTRACT

PRADO, D. E. (1993). 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. In English, English and Spanish abstracts.

A review of the available knowledge on the Gran Chaco vegetation and the modelling environmental factors is presented. The latter are the best studied, and the plant taxonomy is well established. While thorough and shallow phytogeographical surveys and inventories abound, very little is known on the phytosociology, ecology and plant physiology of the Chaco. Woody climaxic communities analyzed are, in E-W direction (following the environmental gradients): Gallery Forest, "Selva de Ribera", Austro-Brazilian Transitional Forest, "Quebrachal" of *Schinopsis balansae.* "Quebrachales" of three, of white and of two "quebrachos", "Palosantales" of *Bulnesia sarmientoi,* Arid Chaco Woodland, Pampean and Subandean Sierra Chaco, and the Subandean Piedmont Forests. The azonal communities are "Algarrobales" of *Prosopis* spp., "Cardonales" of *Stetsonia coryne,* "Palmares" of *Copernicia alba,* and "Vinalares" of *Prosopis ruscifolia.* The Bolivian, Paraguayan and Brazilian Chaco problems are briefly discussed. The vegetation analysis shows that a number of communities of widely different floristic lineages, still regarded as "chaquenian" in the literature, need further objective studies. Most authors have simply equated the Chaco Geographical Region with the Chaco Phytogeographical Province, which therefore requires an adequate redefinition.

RESUMEN

PRADO, D. E. (1993). ¿Qué es la vegetación del Gran Chaco de Sudamérica? I. Una revisión. Contribución al estudio de la flora y de la vegetación del Chaco. V. *Candollea* 48: 145-172. En inglés, resúmenes en inglés y en español.

Se presenta una revisión del conocimiento disponible sobre la vegetación del Gran Chaco y de los factores ambientales que la modelan. Estos últimos son los mejor estudiados, y la taxonomía de las especies es bien conocida. Pese a que abundan las prospecciones fitogeográficas e inventarios florísticos, profundas o superficiales, se sabe muy poco sobre la fitosociología, ecología y fisiología vegetal del Chaco. Las comunidades leñosas climáxicas analizadas son, en dirección E-W (siguiendo los gradientes ambientales): Bosque en Galería, Selva de Ribera, Bosque Transicional Austro-Brasileño, Quebrachales de *Schinopsis balansae,* de tres y de dos quebrachos, y de quebracho blanco, Palosantales de *Bulnesia sarmientoi,* formaciones leñosas del Chaco Árido, el Chaco Serrano Pampeano y Subandino, y los Bosques Pedemontanos Subandinos. Las comunidades azonales son: Algarrobales de *Prosopis* spp., Cardonales de *Stetsonia coryne.* Palmares de *Copernicia alba,* y Vinalares de *Prosopis ruscifolia.* Los problemas del Chaco boliviano, paraguayo y brasileño son discutidos brevemente. El análisis de la vegetación muestra que varias comunidades de linajes muy diferentes, hasta hoy tomadas como "chaqueñas" en la literatura, necesitan estudios objetivos adicionales. La mayoría de los autores han simplemente equiparado la Región Geográfica Chaqueña con la Provincia Fitogeográfica Chaqueña, la cual por ende requiere una redefinición adecuada.

KEY-WORDS: Chaco — Climate — Geology — South American phytogeography — Vegetation — Woody communities.

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Introduction

Within the framework of Southamerican phytogeography the term Chaco or Gran Chaco is applied to the vegetation covering the vast plains of N-central Argentina, W Paraguay and SE Bolivia, and entering into Brazil as a narrow strip parallel to the river Paraguay in Mato Grosso do Sul (Fig. 1). Covering about 800 000 km^2 (HUECK, 1972) or 1 000 000 km^2 (BUCHER, 1982), it is one of the few areas in the world where the transition between the tropics and the temperate belt does not occur in the form of a desert but rather as semiarid forests and woodlands (MORELLO, 1967; MORELLO & ADÁMOLI, 1968). In Fig. 2a & 2b the main political divisions, geographical features, and some critical localities of the Gran Chaco area are shown.

The present-day most widely accepted concept of the Chaco province is that of CABRERA (1976), that is to say from the forests close to the river Paraná in the east (but excluding the gallery forest and "Selva de ribera" units), to the Sierra Chaco in the west (but excluding the "Palo blanco", i.e. the so-called Transitional forests). There are other relevant but not widely accepted ideas of what the Chaco is, such as that of HUECK (1972) which simply adds the "Palo blanco" unit. The map of the Chaco region in MORELLO & ADÁMOLI (1968) provides the most useful phytogeographical subdivisions of the Chaco to date, which were later slightly modified by MARLANGE (1972). Their subdivisions will be followed and frequently referred to throughout this work, though with more simplified nomenclature. Thus, their "Chaco de esteros, cañadas y selvas de ribera" along with the "Chaco de pastizales y sabanas" equals what here is called Eastern Chaco; their "Chaco de parques y sabanas secas" will be referred to as Central Chaco; their "Chaco leñosa" as Western Chaco; and the "Chaco serrana" is equivalent to the Sierra Chaco. These equivalents are only used as convenient subdivisional names, but the vegetation or phytogeographical territories ascribed to them by these authors are not necessarily accepted.

In this contribution an exhaustive review of the environmental factors modelling the vegetation of the Gran Chaco, and the floristics and structure of the vegetation itself is provided. The analysis follows an E-W direction, which coincides with the main ecological gradients of the Chaco: topography, soil types, rainfall, continentality of the climate (MORELLO, 1967). The actual geographical area encompassed by this analysis corresponds to the broadest one, i.e.: from the gallery forest on the islands of the river Paraguay and Paraná in the east to the western mountainous ranges, and from the Santiago and Chiquitos ranges in Bolivia to the Periestepic Thorn Woodlands (Espinal Periestépico, sensu LEWIS & COLLANTES, 1973, and CABRERA, 1976) in the south, which is actually an enormous ecotone Chaco-Pampa. The rational of choosing the broadest possible concept as starting point for this analysis arises from the need to take into account every vegetation unit susceptible to being regarded as chaquenian, and then, in a future contribution, test the validity of its inclusion within the province vis-à-vis both the core area of the Chaco itself and neighbouring formations. Meanwhile, the questions posed here are: what and how much is it known of the Chaco vegetation today?; can one get an homogeneous picture out of it?; is it necessary to redefine the Chaco province as it is known so far?

Usage of the word Chaco

In all likelihood the word "Chaco" is from quechua origin. When the first Spanish Conquistadores arrived to present-day Peru, the quechua-speaking Inca civilization used the term "chacu" or "chaku" to designate the method of hunting by surrounding a piece of land with a large number of natives, shouting and producing noises so as to frighten the game and progressively closing the circle. COBO (1964, p. 269) described a "chacu" involving some 10 000 Indians and spreading over leagues of land in honour of Pizarro by mandate of Manco Inca. This meaning has been widely accepted by most scholars (LIRA, sine die; MIDDENDORF, 1890; CASTELLANOS & PÉREZ-MOREAU, 1944; MÉTRAUX, 1946; MORÍNIGO, 1966) and by the Dictionary of the Royal Academy of Spanish, and usually accepted in a shortened version as "hunting land".

However, it seems that the Inca dominium never spread into the geographical Chaco or if it did it was very sporadically and in short-lived settlements, since archaeological evidence is very scarce and of arguable origin (MÉTRAUX, 1946; FOCK, 1961). By contrast, the plains of the Chaco were roamed by war-like semi-nomadic hunter-gatherer aborigines, whose fierceness prevented

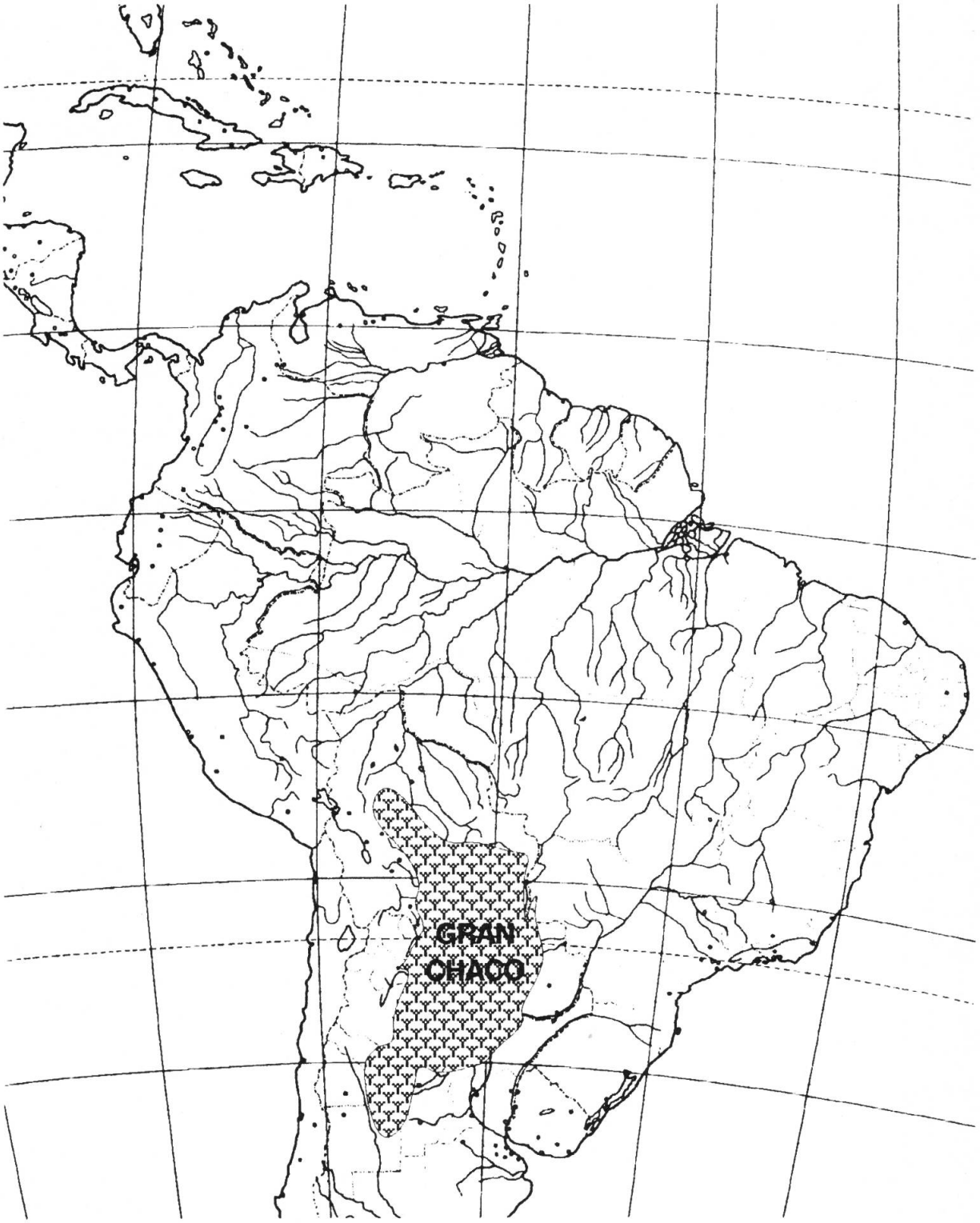

Fig. 1. — Position of the Gran Chaco in South America.

Fig. 2a. — Political divisions and main geographical features of the Gran Chaco area.

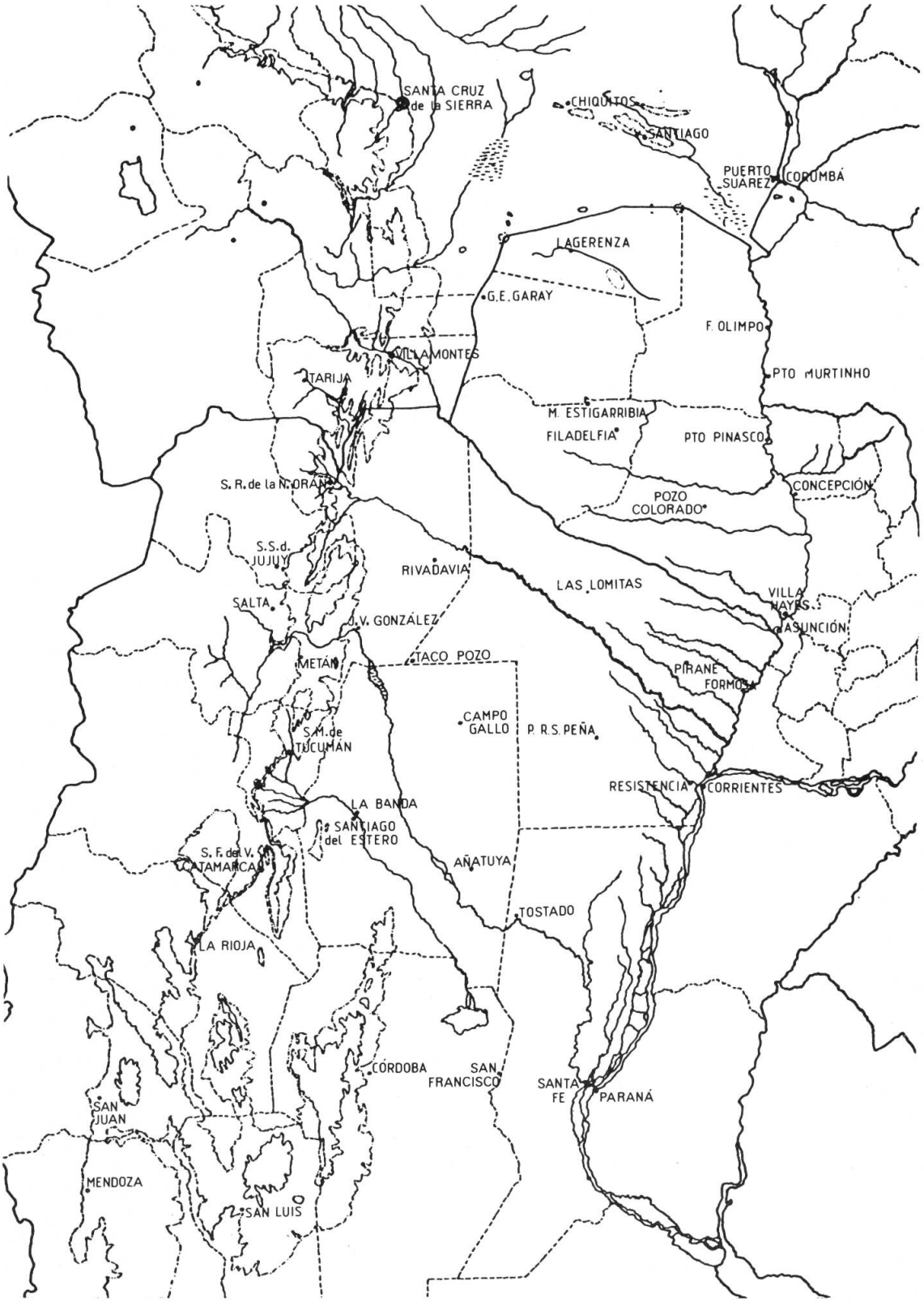

Fig. 2b. — Some critical localities of the Gran Chaco area.

white-man settlements until late XIX century in certain parts of the Argentine Chaco and the first third of this century in Paraguay and Bolivia. Their languages pertained mainly to the Zamucoan, Matacoan, Guaicuruan, Mascoian and Lule-Vilelan language families, rather than Quechua (MÉTRAUX, 1946). How is it then that the name "Chaco" was so widely used for this area since early colonial times in South America? The jesuit CAMAÑO (1955) provided the most likely and logical explanation: the quechua-speaking Indians of Humahuaca (in NW Argentina) used to go hunting in the plains east of their mountainous country; the Spaniards, who came from Peru to NW Argentina to found the oldest cities of that country, must have enquired what lay further to the east, and the answer "chacu" — and subsequently by mispronunciation: "chaco" — was believed to be the name of those lands. When finally the first Spanish colonies were established on the margins of the Paraguay and Paraná rivers, which are the actual eastern borders of the geographical Chaco, the name had already spread throughout the River Plate Dependencies.

The limit set by the rivers Paraná and Paraguay proved most difficult to colonize and it was not until nearly 1880 that the first contingents of immigrants founded Resistencia and Formosa cities on the W margin of the Paraná and Paraguay rivers respectively. This protracted stage of *terra incognita* must have helped cement the concept of the Gran Chaco Geographical Region as a unit, which is a very useful abstraction from the anthropological, economic and administrative point of view (see MORELLO, 1985), but not necessarily so as regards the phytogeography of the continent.

Geology and geomorphology

The topography of the Chaco shows an amazing monotony all over the region, with some low-height elevations towards the western limit in Argentina and Bolivia, and also in a sector of the Paraguayan-Bolivian border (RAMELLA & SPICHIGER, 1989); the terrain is nearly horizontal, thus provoking the only three rivers crossing the Chaco (all of them alochthonous) to meander, and at the same time to have laterally fluctuating courses[1] (SENNHAUSER, 1991) within an up to 100 km wide flat valley covered with abandoned oxbows (called "madrejones" in Argentina; "cauces", "raleras" or "aguadas" in Paraguay).

Perhaps the most characteristic feature of the geomorphology of the Chaco-Pampean plains is that they consist of a massive accumulation of Quaternary sediments over the deeply sunk Pre-Cambrian Brazilian Shield. These sediments are the result of the erosion of the at that time recently risen Andes, which were transported aeolically to the southern half of the Chaco geosinclinal (therefore called Chaco-Pampean loess or loessic sediments), or aeolically but mainly hydrologically to the northern half of the Chaco trough, to form the scarcely known Paraguayan "Chaco sediments" (PUTZER, 1962). These plains must have originated as a vast sedimentary basin in the Palaeozoic, extending further east than today over the Pre-Cambrian Shield (Fig. 3a). From the beginning it had a tendency to subside (POPOLIZIO & al., 1980a), and the pressure of the successive layers of sediments provoke the crystalline base to fracture in smaller blocks with a general NE-SW direction (Fig. 3b). During the Tertiary these blocks moved differentially; the Argentinian Mesopotamia and E Paraguay, where the loess is missing, started to rise (TERUGGI, 1970), thus putting an abrupt eastern border to the Chaco, while in the W the Subandean Sierras were formed as an even more straightforward limit. In the middle of the plains, a line of blocks rose forming what today is known as the Charata-Eastern Córdoba Arc or Dorse (PADULA & MINGRAMM, 1963) (Fig. 3c), which divides the area in two geomorphological basins. During the Quaternary the modern features of the Chaco were settled with the deposition of massive loessic sedimentary layers, obliterating most of the previous relief caused by the movements of the crystalline blocks (Fig. 3d).

The differential block movements in the same NE-SW direction (Brazilian alignment) spread also to the Paraguayan Chaco, as shown in PUTZER's geological map (1962). In NW Paraguay the Brazilian alignment of fractures meets a Caribbean one (NW-SE direction), this allowing for a much deeper fault movement of over 1000 m (PUTZER, 1962) which created the tectonic *horst*

[1]For example, geomorphologists have detected at least five changes of course of the Salado river (CASTELLANOS, 1968), and its bed fluctuated of position once in this century.

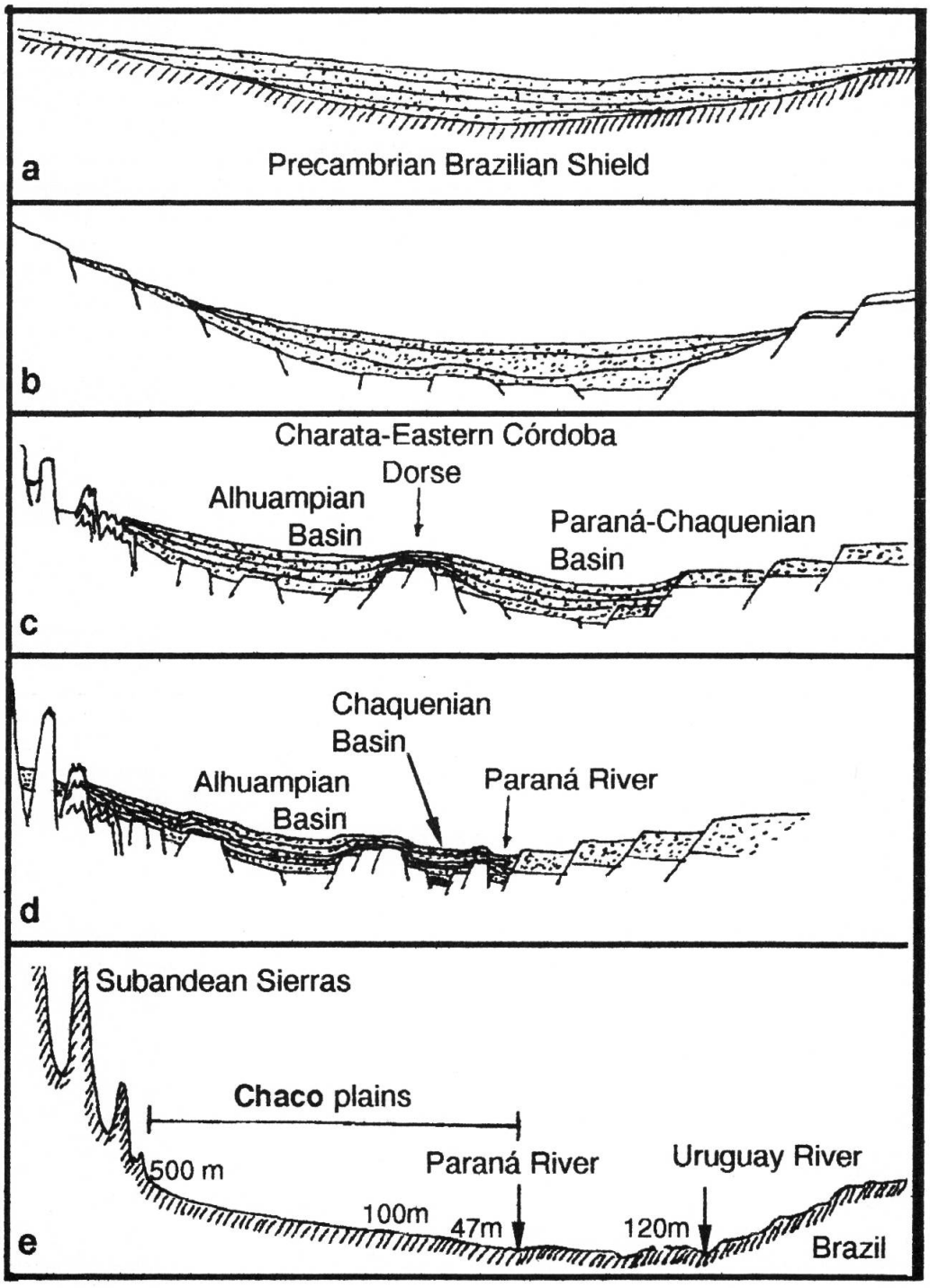

Fig. 3. — Geological origin of the Gran Chaco plains (see explanation in text). Modified from POPOLIZIO & al., 1980a.

of the Cerro León area. This block, basically formed by Lower Devonian and Silurian outcroppings, has risen up to 720 m above sea level (L. RAMELLA, in litt.). There are some other isolated hills near the Cerro León area which generally share a common tectonic horst genesis, such as the Cristián, Cabrera, Caimán and San Miguel tableland hills, of which the latter is the highest point within the expanse of the Chaco (RAMELLA & SPICHIGER, 1989). Thus, it is clear that the sparse relief basically originated from an underlying *horst* and *graben* structure covered by a thick sedimentary layer, and that the Chaco comprises true plains caused by accumulation. These plains cannot be regarded as peneplains as claimed by RAMELLA & SPICHIGER (1989), i.e. extensive piedmonts caused by erosion and removal of massive amounts of material; there is absolutely no evidence of such a process in the Chaco, where no glacis or inselbergs can be found. The origin of the localized palaeodunes fields in W Paraguay and E Bolivia is also debatable; this author believes they can hardly have originated from fluvial transport and accumulation (cf. RAMELLA & SPICHIGER, 1989), but rather they must be the remnants of a much drier period probably caused by Pleistocenic climatic fluctuations such as those which formed the palaeodunes fields of the middle São Francisco river valley in the Caatingas (TRICART, 1985). Such fluctuations did occur in N Chaco where the draining system of a more humid period is recognizable from the air (PUTZER, 1962), leaving behind the youngest sedimentation to be found.

POPOLIZIO & al. (1980a) divided the Chaco region in four major morphogenetical units, from west to east:

a) *piedmont chaco,* in transition with the western mountainous ranges and in the shape of a narrow fringe along them;

b) *bajada chaco,* over a huge alluvial apron of extinct rivers and which is under the influence of a semiarid subtropical modelling system;

c) *western chaco plains,* coinciding with the slightly elevated Charata dorse;

d) *eastern chaco plains,* under a humid, with no dry season, subtropical modelling system on mainly recent alluvial deposits from the Paraguay-Paraná axis.

This latter unit is the only one with autochthonous rivers, which are still modelling the surface in a dendritic net unique in the Chaco region, and this fact together with the scarce energy of the relief, soils with impeded drainage and higher rainfalls, provoke the unit to undergo the effects of waterlogging, floodings and marsh formation.

Climate

The highest absolute temperatures in South America have been registered in the Chaco. PROHASKA (1959) referred to the area encompassed by the 47°C isotherm of absolute maxima as the "South American Pole of Heat" (Fig. 4). Nevertheless, this very hot summer with maxima up to 48.9°C (GALMARINI & R. DEL CAMPO, 1964) is associated with frosts in winter. In fact, apart, from a narrow fringe in the east and parallel to the major rivers, no point within the Chaco geographical region is free from frosts, their average frequency ranging from nearly 0 in the east to 11.3 days or more in the west (MARLANGE, 1972). Consequently, there is also an E-W gradient with regard to the lowest absolute temperatures, from −1.1°C in Corrientes to −7.2°C in Santiago del Estero. In contrast, the mean annual temperature varies in a N-S latitudinal effect from about 26°C in N Paraguay (FARIÑA SÁNCHEZ, 1973) to 17°C or less in the Sierra Chaco (RAGONESE & CASTIGLIONI, 1970).

The map of Fig. 5 shows the rainfall isolines extracted from GALMARINI & R. DEL CAMPO (1964). Again there is an outstanding E-W gradient from 1267 mm in Formosa city to 514 mm in Rivadavia, and down to about 350 mm in Catamarca or La Rioja in SW Chaco. There is a manifest yearly variation in rainfall, with a strong, marked dry season in winter-spring, and a rainy season from October to April; the length of the dry season increases markedly from E to W, with no dry month in Formosa (PAPADAKIS, 1973) to 6 months with negligible rainfall in Rivadavia in the Salta province. In the western limit of the area there is a sudden inversion of the rainfall gradient as a result of the cooling of the warm air masses (which cross the plains and lose most of their humidity in the eastern third), as they encounter the first heights in the western border of the Chaco

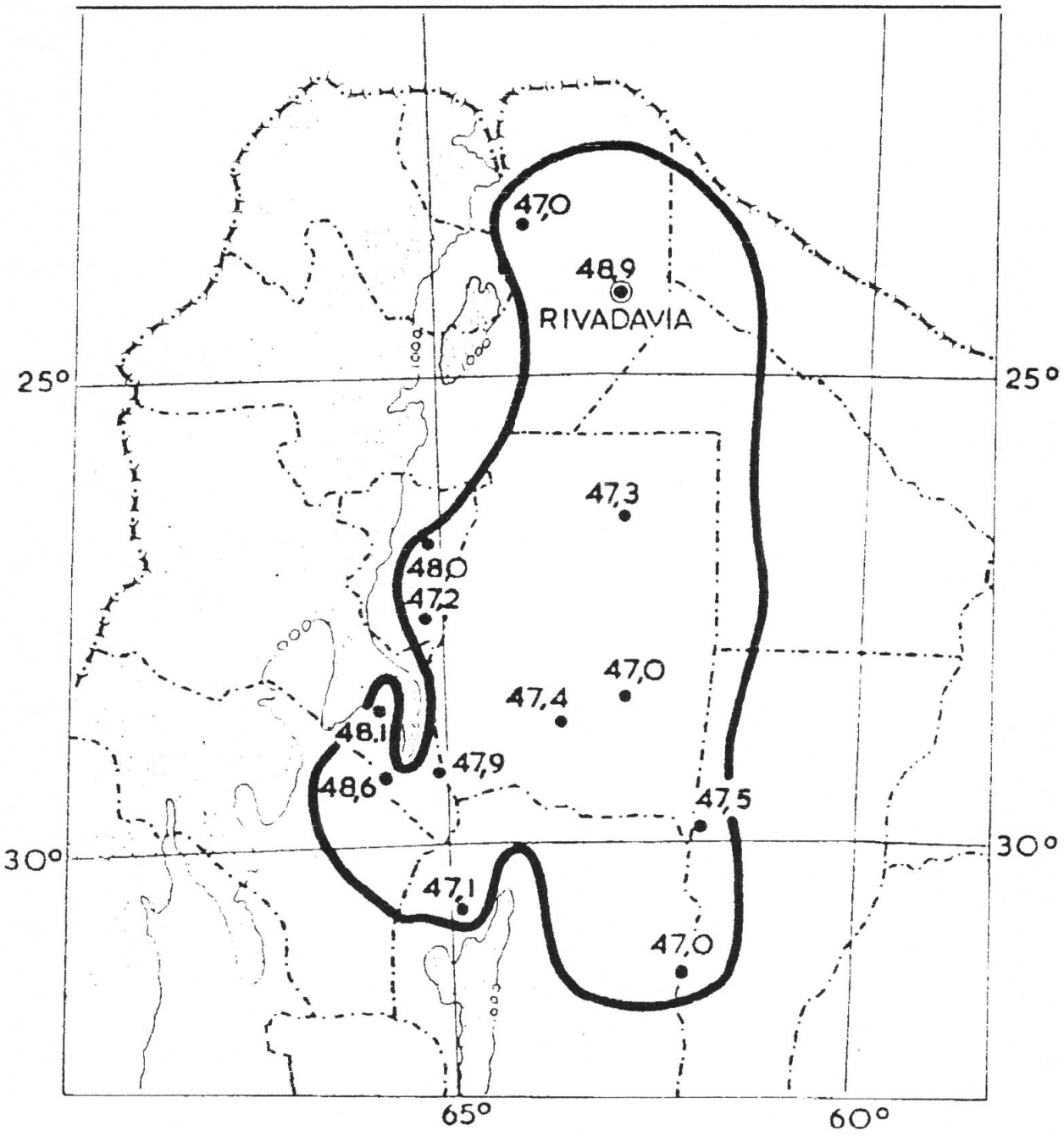

Fig. 4. — The "South American Pole of Heat", according to PROHASKA (1959). Modified from GALMARINI & R. DEL CAMPO, 1964.

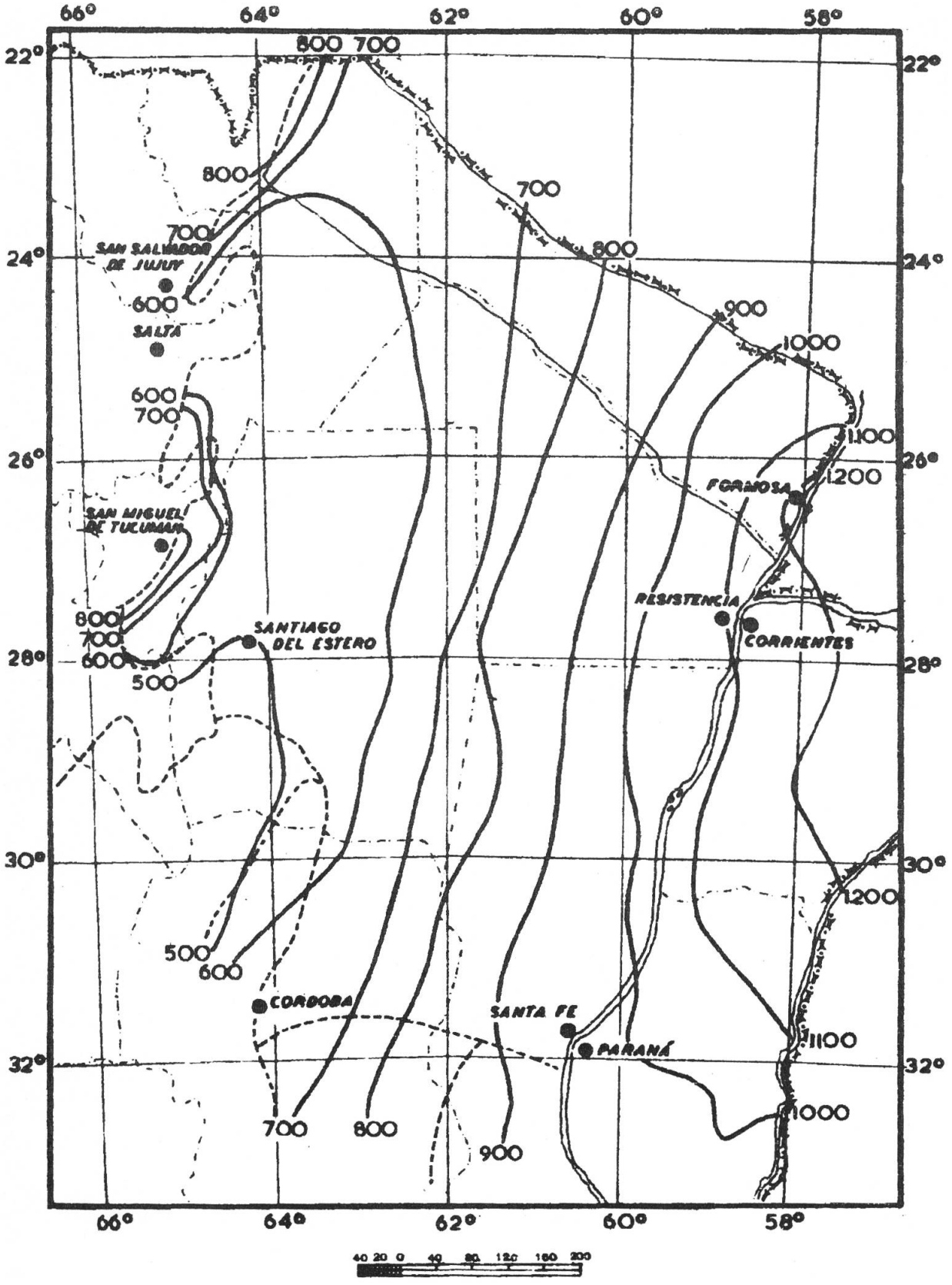

Fig. 5. — Rainfall isolines for the Argentine Chaco. Modified from GALMARINI & R. DEL CAMPO, 1964.

(Pampean Sierras in the S, Subandean Sierras in the N). Thus, there is a moderate increase of rainfall in the Pampean Sierras (owing to their relatively low altitude) from about 500 mm in the nearby plains to over 700 mm, and a more dramatic one along the eastern slope of the Subandean Sierras from the province of Tucumán to the north. In this latter case the first low hills, although not high enough to generate orographic rains, benefit from the effect of the mountains to the west and receive up to 800 or 900 mm/year (SARMIENTO, 1972). Further away from the plains height has increased from about 500 m to 2000 m or more, and with it rainfall rises from 900 mm up to 1500 or even 2000 mm (GROEBER, 1958). Again there is a marked drop in rainfall in the rain-shadow slopes of the subsequent ranges of mountains, resulting in dry west-facing slopes (700 mm down to 300 mm) as opposed to humid east-facing slopes in the same valleys (up to 1500 mm) (HUECK, 1954; SARMIENTO, 1972).

Although the general E-W rainfall gradient of the Gran Chaco is a well-known fact, it is not a gradual and steady decrease. In Table 1 two E-W rainfall transects are shown, with data from GALMARINI & R. DEL CAMPO (1964) and BOLETTA (1988). In the first case, since the localities are nearly at the same latitude, distances shown are measured on a straight line uniting each pair of localities; in the second case an imaginary line uniting Corrientes with Santiago del Estero was drawn, and distances measured where it intersects with the meridian corresponding to each locality. In both cases the decreasing rainfall rate shows a dramatic fall in the first 100 km of over 2 mm/year for every km to the west, but once deeply within the Chaco, the rate decreases only gradually to reach virtually zero values in the far west of the region.

Potential evapotranspiration decreases southwards from 1150 mm to 900 mm, but increases westwards up to 1200 mm in the centre of W Chaco, to decrease again near the mountainous ranges with very close isolines. A sharp fall in Moisture Index values (sensu BOX, 1986) from E to W would be expected as a consequence, and this is confirmed by his figures and also by PAPADAKIS' Hydric

a)	WEST					EAST
Locality	*J. V. González*	*Rivadavia*	*Ing. Juárez*	*Pozo del Tigre*	*Pirané*	*Formosa*
Rainfall (mm year)	539	514	672	858	1027	1267
Appr. distance (km)	165.00	107.50	178.75	157.00	100.00	
Decreasing rainfall rate (mm/km)	0.15	−1.47	−1.04	−1.08	−2.40	
b)	WEST					EAST
Locality	*Cruz del Eje*	*Santiago del Estero*	*Campo Gallo*	*Corzuela*	*Pres. de la Plaza*	*Corrientes*
Rainfall (mm year)	481	554	580	799	985	1186
Appr. distance (km)	322.50	142.50	180.00	110.00	100.00	
Decreasing rainfall rate (mm/km)	−0.23	−0.18	−1.21	−1.69	−2.01	

Table 1. – Rate of decreasing rainfall (mm/km) in two W-E transects across the Gran Chaco (data from GALMARINI & DEL CAMPO, 1964, and BOLETTA, 1988).

Index (1973) values across the area. It should be pointed out that the critical MI = 1 isoline, the hypothetical boundary between humid and dry climates, when using the Thornthwaite potential evapotranspiration estimate, runs parallel to the meridians and puts most of Eastern Chaco on the humid side (BOX, 1986).

Soils

The parent materials of the Gran Chaco soils are fine sediments brought in by a aeolian or fluvial transportation, or depositions of lacustrine or even Devonic marine ingressions sediments. In this context stones and pebbles are of extremely rare occurrence, and rock outcroppings are non-existent. Only a few exceptions occur and always in marginal areas close to the borders and linked to mountain ranges. One of the constant features of the soils across the area is their texture, since particles never go beyond 2 mm (MARLANGE, 1972); this characteristic is not only important because of its mechanical and physical implications, but also because whilst several pedogenetical elements vary from E to W (climate, vegetation), texture remains fairly constant. Thus, the kind of soil present is a direct result of the influence of the prevailing environmental factors, particularly climate.

As a consequence, there is an E-W gradient of climatogenic soil types; according to BONFILS (1970) well developed Brunizem soils are present in a narrow strip parallel to the river Paraná on high topographic position. ESPINO & al. (1983) in their description of the soils of N Santa Fe, and that of LEDESMA (1973) for another province, coincide in assigning the most important soils of the eastern area to Brunizem with a clay textural B horizon through illuviation. Further inland, Grumosols and Reddish Chestnuts dominate the landscape, usually with an argillic B horizon, and associated to Planosols and Solonetz together with others of the saline cycle. Towards the centre of the Gran Chaco, Regosolic Chestnuts are common, while in the western third of the region some aridic soils prevail, such as Cinnamon Chestnuts and finally Reddish Browns (BONFILS, 1970), associated with extended Alluvial soils in the NW and massive saline areas in the extreme SW. The Sierra Chaco is generally established on Lithosols in the Pampean Sierras, while in the northern Subandean mountains there are Alluvial soils in the bottom of dry valleys, Lithosols on dry slopes and Forest Brown on the humid windward slopes (BONFILS, 1970). VARGAS GIL & VORANO (1988) classified the Gran Chaco soils according to the 7th Appr., but this does not alter the E-W gradient; they found typical Hapludols and Argiudols in the extreme east, Argiustols and Haplustols in the central area, and typical Haplustol, aridic Haplustol and aridic Haplustalfs in the west.

Some non-climatogenic soils also occur in the Gran Chaco. The overflowing of rivers, now extinct or severely diminished in their caudal, provided extensive layers of alluvial Quaternary sediments (PUTZER, 1962) to form a series of young soils such as those in the Alluvial Chaco in E Salta (ADÁMOLI & al., 1972); alluvial soils also occur in E Formosa. Planosols with a perched water table can be found in depressions all across the Gran Chaco, although hardly perceptible by topographic difference. There are extensive areas with soils of the saline cycle, and due to the semi-arid climate soluble salts are abundant. Thus, Saline, Solonetz and Soloth soils are a common feature in low areas with poor drainage. The abundance of salts provokes an easy dispersion of clay, and the consequent heavy-textured sub-soils are prone to flooding in the rainy season (BEEK & BRAMAO, 1968).

The Gran Chaco soils are poor in organic matter, and the humic horizon is relatively shallow; in the east it can extend up to 20 or 25 cm depth (ESPINO & al., 1973), but it nearly disappears in the west. Daily maxima temperatures are high even in winter, and this together with environmental dryness and scarcity of protective Graminae facilitates a very quick mineralization of organic residues (PAPADAKIS, 1973). Parent materials and the mainly semiarid climate make mineral deficiencies very improbable, and Chaco soils are generally regarded as highly fertile (ADÁMOLI & al., 1990), although ant mounds generate very localized sterile spots (BUCHER, 1982). There is usually a calcium carbonate-rich horizon, and nearly all soils give an increasing effervescent reaction to HCl from W to E (PAPADAKIS, 1973). Hardpans of calcium carbonate and silica are

frequent in E Chaco. In Papadakis' view, the main set-backs of the Gran Chaco soils are poor drainage, salinity and alkalinity, flooding under occasional excessive rainfalls, and the presence of clay textured horizons or even hardpans in places.

Vegetation

The plant cover of the plains of the Gran Chaco, considering its extension and the several environmental gradients described, inevitable shows a certain degree of variability, although some general features might remain constant. The analysis will be mainly focused on the Argentine Gran Chaco, for which there is abundant information coupled with field experience of this author. For the Bolivian and Paraguayan Chaco, and also for the Brazilian sector with allegedly Chaco vegetation, information is scanty and sometimes imprecise, but nevertheless some tentative conclusions can be reached.

In general terms the most peculiar feature of the vegetation of the Chaco consists of the dominance by species of the arboreal genus *Schinopsis.* In the humid, frequently waterlogged eastern plains the predominant species is the simple-leaved *S. balansae;* in the dry and flat plains of Central and Western Chaco the most important tree is *S. quebracho-colorado,* with imparipinnate, linear-lanceolate, numerous leaflets. In the lower belt of the western Sierras the dominant species is *S. haenkeana,* which closely resembles the former but with ovate leaflets. Their vernacular names — "quebracho" (from "quiebra-hacha" or axe-breaker) — reflects the hard quality of their tannin-rich wood. Also characteristic are the forests of *Bulnesia sarmientoi* ("palo santo") in W Formosa and E Salta, and those dominated by *Aspidosperma quebracho-blancho* ("quebracho blanco") in the plains of E Catamarca, La Rioja and San Juan, NW San Luis and W of Córdoba in Argentina (RAGONESE & CASTIGLIONI, 1970).

However, forests and woodlands are not the only feature of the Gran Chaco, since savannas are also a very important component of the landscape: *Elionurus muticus* savannas with scattered *Prosopis* spp. trees are common throughout the region (MORELLO & ADÁMOLI, 1973); *Spartina argentinensis* savannas, with or without trees, have been extensively studied by LEWIS & al. (1990a & b). Palm savannas and palm-tree woodlands of *Copernicia alba* are very important and sometimes dominant in the landscape from the Brazilian Pantanal to NE Santa Fe in Argentina, always on alluvial, seasonally flooded ground under the influence of river systems in the east of the region. The savannas are not evenly distributed across the Gran Chaco and there is an evident decreasing frequency of savanna physiognomy towards the west, as the subregional names by MORELLO & ADÁMOLI (1968) clearly show. This is why, as already stated by MORELLO & ADÁMOLI (1974), it is certainly improper to denominate this region as Chaquenian Park ("Parque Chaqueño"), as employed by PARODI (1945), CABRERA (1953) and RAGONESE & CASTIGLIONI (1970), since although this physiognomy is frequent and in areas dominant, it is not the case for the whole of the Gran Chaco.

A number of woody communities can be found in each sector, some of which are exclusive to it and some others, with minor variants, are roughly the same throughout the three main sectors of the Chaco. In dealing with every sector only the exclusive communities will be described, while the more generalized ones will be dealt with under the heading "Azonal woody formations". In Table 2 an attempt has been made to fit the main chaquenian woody communities into BEARD's (1955) system of vegetation physiognomy, and this is compared with SARMIENTO's (1972) nomenclature when available. Since Beard's system was designed for tropical vegetation, the term "subtropical" should be added before his classes in this table.

Gallery Forest

The islands in the river Paraná, together with the banks of the river Paraguay and their western tributaries, present a peripheral levee ("albardón") above the level of waters except for the flooding season, which is formed by the deposition of coarse materials brought in by the river floods. The vegetation is usually a forest up to 20 m high, which is floristically rich although it is in effect an impoverished version of the Subtropical Rain Forests of Misiones (Argentina), S Brazil and

	BEARD (1955)	SARMIENTO (1972)
Gallery forest	Semideciduous seasonal forest	Deciduous rain forest
Selva de ribera	Semideciduous seasonal forest	–
Austro-Brazilian transitional forest	Deciduous seasonal forest	Subtropical deciduous forest
Quebrachal of *Schinopsis balansae*	Thorn woodland	–
Quebrachal of 3 quebrachos	Deciduous seasonal forest – Thorn woodland	Dry subtropical forest
Quebrachal of white quebracho	Thorn woodland	–
Quebrachal of 2 quebrachos	Deciduous seasonal forest – Thorn woodland	Dry subtropical forest
Palosantales of *Bulnesia sarmientoi*	Deciduous seasonal forest – Thorn woodland	–
Arid Chaco woodland	Thorn woodland	Dry subtropical wood
South Sierra Chaco	Deciduous seasonal forest – Thorn woodland	Dry montane forest
North Sierra Chaco	Deciduous seasonal forest – Thorn woodland	Dry montane forest
Algarrobales of *Prosopis* spp.	Thorn woodland	–
Cardonales of *Stetsonia coryne*	Cactus scrub	–
Palmares of *Copernicia australis*	Seasonal-swamp thicket with palms	–
Vinalares of *Prosopis ruscifolia*	Thorn woodland	–
"Palo blanco" forest	Deciduous seasonal forest	Deciduous subtropical forest
"Tipa" and "pacará" forest	Deciduous seasonal forest	Deciduous subtropical forest

Table 2. – Physiognomy classes equivalences for the main woody communities of the Chaco and neighbouring formations.

E Paraguay (CABRERA, 1970 & 1976; SARMIENTO, 1972; KLEIN, 1972; SPICHIGER & al., 1992). It comprises up to three tree strata and is rich in lianas, ferns and vascular epiphytes (RAGONESE, 1941), and the species not rising above the middle storey are evergreen. This forest is subject to yearly floodings from the nearby rivers and this strongly determines the floristic composition, e.g. as the presence of Lauraceous trees *(Nectandra falcifolia)* and several other species found only in this kind of community demonstrates: *Albizia polyantha, Crateva tapia, Hexachlamis edulis, Peschiera australis, Inga uruguensis, Geoffroea striata, Croton urucurana, Arecastrum romanzoffianum, Banara arguta,* etc. Following the courses of the tributaries such forests may penetrate up to 100 to 150 km into the Gran Chaco plains. Good descriptions of this formation can be found in BURKART (1957), MORELLO & ADÁMOLI (1974, p. 108, sub "bosque alto o selva de inundación"), FRANCESCHI & LEWIS (1979), and a thorough phytosociological analysis in FRANCESCHI & al. (1985), ESKUCHE (1986) and SENNHAUSER (1991).

"Selva de ribera" (River margin forest), "Selva" or "Monte Alto"

This forest can be found side by side with the previous unit but on higher ground, which is never reached even by the extraordinary floods of the Paraná river (LEWIS & al., 1987). In the provinces of Chaco and Santa Fe there is a strong erosion scarp 3 m high (POPOLIZIO & al., 1980b) left by an ancient course of the river Paraguay (POPOLIZIO, 1970), and which extends in N-S direction from the cities of Resistencia to Santa Fe and is the effective western limit of the alluvial valley of the river Paraná (MORELLO & ADÁMOLI, 1973). It holds an up to 30 m tall forest, locally called "selva" for its abundance in lianas and epiphytes (SCHULZ, 1967) and its floristic richness. It is very closely related to the previous unit, with which it is often confused, and most available descriptions have mixed floristic lists (HAUMAN, 1931; RAGONESE, 1941; HUECK, 1972; SARMIENTO, 1972; CABRERA, 1976; REBORATTI & NEIFF, 1986). However, the unique topographical position above the highest possible peaks of floodings, on well developed soils (typical Argiudols, ESPINO & al., 1983), and the peculiar floristic composition — free from hygrophilous trees such as the Lauraceae, and from inland xerophytic Chaquenian trees — allow for a definitive detachment from the Gallery Forest. To date only SCHULZ (1967), MORELLO & ADÁMOLI (1967 & 1974), and PRADO & al. (in press, a) show this forest as a distinct unit. The latter also provide a quantitative assessment of this "bosque subtropical semideciduo" dominated by *Holocalyx balansae, Ficus luschnathiana* and *Patagonula americana,* and also *Pouteria gardneriana, Ruprechtia laxiflora, Enterolobium contortisiliquum, Phytolacca dioica, Sorocea sprucei, Trichilia elegans, Pisonia aculeata, Peltophorum dubium,* etc., with the addition of those species cited by MORELLO & ADÁMOLI (1974) which appear further north because of a latitudinal enrichment. Again this forest is an impoverished version of floristically much richer formations in Brazil (KLEIN, 1967 & 1972) and Paraguay (TORTORELLI, 1967; SPICHIGER & al., 1992).

Eastern Chaco Forests (sensu MORELLO & ADÁMOLI, 1968, see above)

In this area there are two major woody communities which have been repeatedly mistaken for a single one (e.g.: HAUMAN, 1931; RAGONESE, 1941; HUECK, 1959 & 1972; RAGONESE & CASTIGLIONI, 1970; CABRERA, 1971 & 1976; SARMIENTO, 1972; MARLANGE, 1972; CABRERA & WILLINK, 1980; BUCHER, 1982). Although MORELLO & ADÁMOLI (1974, p. 103) hint at these differences when they refer to the forestal types "monte alto" and "monte fuerte", it was not until LEWIS & PIRE (1981) pointed out their very distinct topographical position and soil substratum that the matter was settled. These two subunits are:

(a) Austro-Brazilian Transitional Forest (PRADO, 1991)

This forest corresponds to what LEWIS & PIRE (1981) denominated "bosque chaqueño", and the "monte alto" in MORELLO & ADÁMOLI (1974). It occupies the highest topographical position in NE Santa Fe, E Chaco administrative province and E Formosa (MORELLO & al., 1971),

in well developed and intermediate soils (LEDESMA, 1973; ESPINO & al., 1983). Usually two strata can be distinguished, the superior continuous but of variable density. Lianas and epiphytes are frequent but not abundant, and in dense stands shrubs are inconspicuous. The floristic composition suffers an evident N-S temperature gradient (LEWIS, 1991), and is much richer in Chaco and Formosa provinces. The dominant species of this kind of forest are what HAUMAN (1931) called "elements venus des forêts hygrophiles: *Tecoma ipe [= Tabebuia impetiginosa], Patagonula [= P. americana], Gleditschia [= Gleditsia amorphoides],* quelques Myrtacées...". The simple-leaved "quebracho" *Schinopsis balansae,* if at all present, is here a foreigner coming from the nearby communities of the next unit, and is usually scarce and in marginal position (E. F. PIRE, unpubl. data; LEWIS, 1991). The floristic list comprises as well *Ruprechtia laxiflora, Myrcianthes pungens, M. cisplatensis, Eugenia uniflora, Pisonia zapallo, Scutia buxifolia,* etc.; further north in Argentina several other very important species are added: *Astronium balansae, Diplokeleba floribunda, Ceiba speciosa* (MORELLO & al., 1971; MORELLO & ADÁMOLI, 1974), or even *Pithecellobium scalare* and others (CABRERA, 1976).

b) "Quebrachal" (quebracho woodland) of Schinopsis balansae

Also called "monte fuerte" in MORELLO & ADÁMOLI (1974), and "quebrachal" in LEWIS & PIRE (1981). This unit is always found at a lower topographical position than the previous one, on heavy-textured soils of the saline cycle, such as typical Natracualf with over 15% of Na^{++} in the exchangeable ion complex (ESPINO & al., 1983). Furthermore, the ground is usually waterlogged in the rainy season because of the strongly argilic subsoil, local microrelief and consequent impeded drainage. DURLAND (1924) pointed out the close relationship between the "Quebrachal" and underground water, since it had been consistently established that water originating from subterranean sources within a belt or patch of "quebracho"-forest is invariably brackish, while beyond the limits of this community it is invariably fresh (obviously out of the range of Na-rich soils). Thus the dominant hygrophilous tree species of the Austro-Brazilian Forest are excluded from this kind of substratum and the forest is dominated by *Schinopsis balansae* ("quebracho colorado chaqueño"), from which this community derives its name. Two arboreal strata can be distinguished, the higher generally composed of *S. balansae, Aspidosperma quebracho-blanco* and *Caesalpinia paraguariensis,* and the lower by Mimosoideae *(Prosopis nigra, Acacia praecox, A. aroma), Geoffroea decorticans, Sideroxylon obtusifolium, Ziziphus mistol,* etc. Often the lower stratum comprises only a dense population of young *S. balansae* treelets. The broken canopy allows a shrubby layer of *Achatocarpus praecox, Schinus fasciculatus, Capparis* spp. and *Celtis* spp., far more conspicuous than in the previous unit, and Cactaceae are a common feature. In slightly higher areas where the "quebracho" can generate a dense, continuous canopy, massive spiny Bromeliaceae populations predominate. Lianas and vines are extremely scarce, but the abundance of lichens and epiphytic *Tillandsia* is a typical feature of this formation.

Central Chaco Forests

Essentially this sector is transitional to both the Eastern and Western ones; it does not possess a floristic individuality that could characterize its vegetation. However, from an ecological point of view some of the communities to be found here are unique, or nearly so, to this sector, such as the case of the "quebrachal of three quebrachos" unit. It is in the Central Chaco where the *Elionurus muticus* savannas, established on ancient river beds (ADÁMOLI & al., 1990), are more conspicuous and have provided most of the agricultural land. These savannas are mainly determined here by heavy-textured soils with a perched water table (BEEK & BRAMAO, 1968; BUCHER, 1982), whereas in Eastern Chaco they are determined either by stronc salinity or by flooding tolerance.

a) "Quebrachal" of three "quebrachos"

This unit, treated in detail by LEWIS & PIRE (1981), is also called "Bosque Mixto" (Mixed Forest) in RAGONESE & CASTIGLIONI (1970). It has been brefly described in RAGONESE

(1941), SARMIENTO (1972), MORELLO & ADÁMOLI (1974) and BUCHER (1982). This unit is characterized by the shared dominance of *Schinopsis quebracho-colorado, Schinopsis balansae* and *Aspidosperma quebracho-blanco.* This is the only area within the Chaco in which the three species occur together in the same community. This forest, with its definitely more xerophilous character than those in the east, consists of two continuous and dense arboreal strata (LEWIS & PIRE, 1981), the higher comprising the three dominants plus generally *Ziziphus mistol, Caesalpinia paraguariensis* and sometimes *Sideroxylon obtusifolium,* and the lower comprising *Geoffroea decorticans, Prosopis* spp. and *Acacia* spp. There is a conspicuous shrub layer of *Maytenus vitisidaea, Capparis* spp., *Porlieria microphylla,* etc., while the herbaceous layer is very variable in importance or absent.

b) "Quebrachal" of white "quebracho"

Described in LEWIS & PIRE (1981), D'ANGELO & al. (1987) and in MORELLO & al. (1971). Mainly towards the S-E of the sector, but also in localized areas elsewhere within the Central Chaco, the *Schinopsis* spp. disappear and *Aspidosperma quebracho-blanco* takes over dominance. This unit is somewhat lower, with variable density of the arboreal layer and a scattered emergent stratum of *A. quebracho-blanco,* 5 to 8 m high in the south to 8 to 16 m high in the north. The bulk of the forest is in the second stratum, 4 to 5 m high in the south and up to 8 m in the north, with a very similar floristic composition to the previous unit. In Formosa this community can be found on slightly elevated areas above the position of the "vinalares" on less alkaline loamy soils (MORELLO & al., 1971).

Western Chaco Forests

In this part of the region environmental factors (e.g. rainfall) are more uniform (Table 1), and consequently the vegetation is more homogeneous. Western Chaco is the driest, most continental sector, with the highest maxima and lowest minima in both absolute and average temperature values, longest frost period, and its vegetation shows the most pronounced xeromorphy. Cactaceae are very abundant, and amongst them the arborescent habit is particularly conspicuous: *Stetsonia coryne, Opuntia quimilo, Cereus validus, Quiabentia pflanzii, Pereskia sacharosa;* lianas and epiphytes are generally extremely rare. There are a number of anthropogenic communities (MORELLO & SARAVIA TOLEDO, 1959a), because of the higher fragility of these semiarid ecosystems and older European colonization. A few endemic genera *(Lophocarpinia, Mimoziganthus, Stenodrepanum, Setiechinopsis)* are present as well as numerous endemic species (RAGONESE & CASTIGLIONI, 1970) and there is also an important intrusion of species coming from the Monte phytogeographical province (MORELLO, 1958).

a) "Quebrachal" of two "quebrachos"

This unit of ADÁMOLI & al. (1972) is also known as "quebrachal of quebracho-colorado" (RAGONESE & CASTIGLIONI, 1970), "quebrachal" by MORELLO & ADÁMOLI (1968), forests of "quebracho colorado" and "quebracho blanco" in CABRERA (1971, 1976), "quebrachaie" in MARLANGE (1972). Also described briefly in CASTELLANOS (1958), HUECK (1959, 1972), SARMIENTO (1972), BUCHER (1982), and extensively in MORELLO & SARAVIA TOLEDO (1959a & b) and MORELLO & ADÁMOLI (1974). The most widespread vegetation unit in the sector consists of a medium-tall forest, 16-18 m high, dominated by *Schinopsis quebracho-colorado* and *Aspidosperma quebracho-blanco.* The second arboreal stratum, 12 m high, comprises *Ziziphus mistol, Geoffroea decorticans, Prosopis alba, P. nigra, P. kuntzei, Cercidium praecox, Caesalpinia paraguariensis, Ceiba chodatii, Acacia* spp. and arboreal cacti, whereas the shrub layer consists of *Ruprechtia triflora, Celtis* spp., *Capparis* spp., *Bougainvillea* spp., *Maytenus spinosa, Ximenia americana,* etc. The area dominated by this forest coincides roughly with the "Woody Chaco" of MORELLO & ADÁMOLI (1968), and with RAGONESE & CASTIGLIONI's (1970) "Santiaguenian District" in their Western Chaco Park, excluding the subdistrict "Santiaguenian Park" which corresponds to the Central Chaco. Other minor communities

within the range of this forest, such as the "iscayantales" of *Mimoziganthus carinatus* and communities of *Tabebuia nodosa* in depressed localities, will not be dealt with here.

b) "Palosantales" of Bulnesia sarmientoi

Studied by MORELLO & ADÁMOLI (1968, 1974), RAGONESE & CASTIGLIONI (1970), HUECK (1972), ADÁMOLI & al. (1972), and as "forests of quebracho colorado and palo santo" in CABRERA (1971 & 1976). The dominant species, up to 20 m high, is often accompanied by *Aspidosperma triternatum, Tabebuia nodosa, Prosopis kuntzei, Ruprechtia triflora, Capparis* spp., *Cereus validus* and *Stetsonia coryne.* Moreover, *Schinopsis quebracho-colorado* may be present as a subdominant (CASTELLANOS, 1958) unless the community is on clayish, heavy-textured soils with very impeded drainage and temporary anaerobiosis (ADÁMOLI & al., 1972). The area covered by this unit, with or without the "quebracho colorado", is what Ragonese & Castiglioni called the "Matacoan District", to which some exclusive species pertain: *Jatropha matacensis, Lophocarpinia aculeatifolia.*

c) Arid Chaco Woodland (SARMIENTO, 1972)

Also called "Quebrachales" of *Aspidosperma quebracho-blanco* in RAGONESE & CASTIGLIONI (1970) and SAYAGO (1969). This community appears everywhere within Western Chaco, particularly as a result of overgrazing pressure and selective felling (MORELLO & SARAVIA TOLEDO, 1959a). In SW Chaco, which corresponds to the "Llanos District" of RAGONESE & CASTIGLIONI (1970), it is particularly dominant due to the disappearance here of *Schinopsis quebracho-colorado.* Some authors have proposed that this district should be referred to the Monte province on account of the high number of Monte intruders, but both RAGONESE (1951) and MORELLO (1958) have demonstrated the propriety of keeping it within the Chaco. This formation shows an open and scattered arboreal stratum comprising isolated individuals of *Aspidosperma quebracho-blanco,* accompanied by *Geoffroea decorticans, Prosopis nigra, Cercidium praecox, Capparis atamisquea, Stetsonia coryne, Cyclolepis genistoides,* but also some Monte species, as shown by SAYAGO (1969, p. 159) floristic list: *Prosopis torquata, P. pugionata, Larrea divaricata, L. cuneifolia, Bulnesia retama, Plectrocarpa tetracantha,* etc.

Sierra Chaco

a) South Sierra Chaco (Pampean Sierra Chaco)

In the western fringe of the region the vegetation covering the mountainous ranges of the Pampean Sierras has been considered to be of undoubted chaquenian lineage and physiognomy, despite a number of endemic species in the dominant and subsidiary taxa. The Pampean Sierra Chaco received detailed study by SAYAGO (1969) and LUTI & al. (1979), but further analysis or mapping can be found in MORELLO & ADÁMOLI (1968), RAGONESE & CASTIGLIONI (1970), CABRERA (1971, 1976[1]), MARLANGE (1972), SARMIENTO (1972), BUCHER (1982) and VARGAS GIL & VORANO (1988). However, it was inexplicably overlooked by HUECK (1959, 1972) and HUECK & SEIBERT (1981) although these authors do recognize a very similar formation further north in the Subandean Sierras. LEWIS, J. P. (unpub. data) distinguishes three basically different kinds of woody associations within the Pampean Sierra Chaco:

a) piedmont Sierra forest, mainly comprising *Prosopis* spp.;

b) "quebrachal" of *Schinopsis haenkeana* in middle slope;

[1]However, the *Polylepis australis* woodlands occurring in the Córdoba Sierras should not be regarded as chaquenian, as in CABRERA (1976). These communities comprise basically an Andean flora with little contact with the Chaco itself (VUILLEUMIER, 1986; M. CABIDO, in litt.), and their restriction to N Argentina appear to be attributable to range retraction of the progenitor of *P. australis* during Pleistocene wet-dry events (SIMPSON, 1986).

c) "mollar" of *Lythraea ternifolia* on the slopes above the quebrachal and below the shrublands of *Flourensia* or *Heterothalamus* spp., and also in the south of this sector where *S. haenkeana* disappears (LEWIS & PIRE, 1981).

The floristic list of what SAYAGO (1969, p. 224) qualified as the most typical Sierra Chaco forest includes *Schinopsis haenkeana, Fagara coco, Lythraea ternifolia, Ruprechtia apetala, Aspidosperma quebracho-blanco, Bougainvillea stipitata, Kageneckia lanceolata, Prosopis chilensis, P. alba, P. nigra, P. torquata, Celtis* spp., *Geoffroea decorticans, Acacia* spp., etc.

b) North Sierra Chaco (Subandean Sierra Chaco)

A rather more contentious issue is raised by the entity referred to as the Subandean Sierra Chaco. Some authors have apparently merged this unit with the so-called Transitional Forest (MORELLO & ADÁMOLI, 1968; RAGONESE & CASTIGLIONI, 1970), whereas others (HUECK, 1959 & 1972; CABRERA, 1971 & 1976; MARLANGE, 1972; ADÁMOLI & al., 1972; SARMIENTO, 1972) have separated them, a treatment favoured here since floristic composition clearly links the Subandean to the Pampean Sierra Chaco (cf. MARLANGE, 1972, list for the Lomas de Olmedo area, with most species common to the Pampean Sierra Chaco). Because it only occupies a small area and interdigitates with the several neighbouring phytogeographical provinces, this forest has been generally omitted from vegetation maps with the exception of VERVOORST's detailed regional map in HAWKES & HJERTING (1969, p. 38).

Azonal woody formations of the Chaco

a) "Algarrobales"-Prosopis spp. communities

These thorn woodlands, also called "raleras" (MORELLO & ADÁMOLI, 1974), are found throughout the Chaco proper in low lying areas. In Eastern Chaco, if the topographic gradient is followed down from the *Schinopsis balansae* "quebrachales" towards a high water table, the first species to disappear is *S. balansae,* followed by *Caesalpinia paraguariensis* and most of the accompanying species of the "quebrachal", until the arboreal stratum is reduced to mainly *Prosopis nigra* or *P. alba* dominated stands. These "algarrobales" are common around seasonal swamps or small, somewhat undefined streams; the soil is regularly flooded in the rainy season mostly by overflow from the adjacent water courses. When the flooding recedes, the salinization process of soils is resumed, resulting generally in typical Natracualf or Natracuol (ESPINO & al., 1983). The arboreal stratum may be very simple: *P. nigra, Geoffroea decorticans, Aspidosperma quebracho-blanco* and *Acacia caven,* and is continuous and often dense and just over 3 m high (LEWIS & PIRE, 1981). There is no well defined shrub layer, and during the dry season the herbaceous layer has very low coverage or is absent altogether. Further north in Formosa (MORELLO & al., 1971, p. 78) the "algarrobales" show a much richer composition.

b) "Cardonales" of Stetsonia coryne

This kind of low-height formation is rare in Eastern Chaco (LEWIS & PIRE, 1981), but very frequent in Western Chaco (SAYAGO, 1969). It is dominated by candelabra-like individuals of the monotypic Cactaceous genus *Stetsonia,* endemic to the Chaco, and usually 60% or more of the strongly saline soil is bare ground or covered only by mosses and *Selaginella sellowii.* The stands are very poor in the east, but a much richer western one is listed in SAYAGO (1969, p. 157). Similar communities are described by ADÁMOLI & al. (1972), and sub "peladares" by RAMELLA & SPICHIGER (1989) for Paraguay.

c) "Palmares" of Copernicia alba

These palm groves and savannas usually comprise a nearly monospecific open arboreal layer of very variable density, 8 to 10 m high, of this fan-leaved palm-tree. They are always found in low lying position close to or within marshes, on seasonally flooded alkaline soils (RAGONESE, 1941; RAGONESE & CASTIGLIONI, 1970). The herbaceous layer is dominated by *Spartina argentinensis,* though sometimes *Paspalum* spp. might replace it (LEWIS & PIRE, 1981). Additional informa-

tion can be found in MARKLEY (1955), HUECK (1959, 1972) and DAHLGREN & GLASSMAN (1961); references for Paraguay in FIEBRIG (1933), ROJAS & CARABIA (1945), TORTORELLI (1967), ESSER (1982), SPICHIGER & RAMELLA (1989) and RAMELLA & SPICHIGER (1989). Citations of this community in the Bolivian Chaco in WERDING (1976), and for Brazil in VELOSO (1947), PRANCE & SCHALLER (1982) and RATTER & al. (1988). The more complete floristic lists of these "palmares" available to date refer to the Argentine Eastern Chaco, comprising *Copernicia alba, Tabebuia nodosa, Geoffroea decorticans, Prosopis alba, Acacia caven, Sapium haematospermum, Schinus fasciculatus,* etc. The "palmares" in Western Chaco show a somewhat different composition (MORELLO & SARAVIA TOLEDO, 1959a; CABRERA, 1971, 1976; ADÁMOLI & al., 1972).

d) "Vinalares" of Prosopis ruscifolia

In Central and Western Chaco the areas under the influence of the only three rivers running across the Gran Chaco are ecologically very unstable; the lack of energy of these flat plains generates a wide divagation of the water courses, and subsequently creates new open spaces to be colonized, especially alkaline swamps in dessication (such as drying out abandoned ox-bows). *Prosopis ruscifolia* is particularly adapted to this kind of environment and successfully colonizes large expanses of land, even forming virtually monospecific communities with no herbaceous layer and where the shrub stratum is the only one to add some variability. There is a host of different facies for these woodlands according to relative degrees of flooding, salinity or anthropogenic influence, as studied proficiently and extensively by MORELLO & al. (1971).

Subandean Piedmont Forests (usually known as Transitional Forests)

These forests occupy a narrow strip between the dry forests of Western Chaco and the more humid Lower Montane Forest (SARMIENTO, 1972) or "Distrito de las Selvas Montanas" (CABRERA, 1976), extending in a meridional fashion from the area of Santa Cruz de la Sierra in Bolivia to slightly south of the limit Tucumán-Catamarca provinces in NW Argentina. Their very peculiar position as a wedge between two major phytogeographical units (the Chaco and Yungas provinces, sensu CABRERA, 1976), at an intermediate altitude (350 to 500 m in CABRERA, 1976, or 450 to 900 m in MEYER, 1963), and also with intermediate rainfall figures (from 700 to 1000 mm) of monsoonian character (VERVOORST, 1982), allows for a particular kind of forest to develop with its own floristic identity. According to SARMIENTO (1972) this formation has the highest proportion of deciduous species (79%) of all the subtropical seasonal forests. They are located in the piedmont area of the Subandean Mountains in SW Bolivia and NW Argentina (hence their name), but their southernmost extension is actually placed in the northern extreme of the Sierras Pampeanas in S Tucumán and E Catamarca.

Towards the east and down the topographic gradient these forests intermingle with Sierra or Western Chaco, whereas to the west and uphill they receive some elements from the Yungas forests. Some authors have regarded the Piedmont Forests as having more in common with the Chaco area than with the Yungas (HUEK, 1959 & 1972; MORELLO & ADÁMOLI, 1968; RAGONESE & CASTIGLIONI, 1970; MARLANGE, 1972; HUECK & SEIBERT, 1981; VARGAS GIL & VORANO, 1988). However, leaving aside the nigligible ecotonal areas with Chaco proper, their floristic composition clearly puts them within the Yungas or Tucumanian-Bolivian Forests province (HAUMAN, 1931; MEYER, 1963; CABRERA, 1971, 1976), whereas a sizeable number of its species can be found in the communities of the east of the Gran Chaco as well. CORREA LUNA (1955) describes a locality in which Piedmont Forest occurs side by side with Chaco scrubland, but their elements do not intermix at all: at this site there is a relatively dry valley, the lower plains of which are covered by *Acacia* spp., *Prosopis* spp., *Geoffroea decorticans, Celtis spinosa, Opuntia* sp. and *Cereus* sp., while small elevations within the range of this valley hold *Anadenanthera colubrina* var. *cebil, Pterogyne nitens, Ceiba chodatii,* all species which also appear in the tall humid forests on the nearby mountains bordering the valley. Species of the genera *Schinopsis, Caesalpinia, Cercidium* do not appear in the valley, since they belong to less elevated grounds (i.e. the Chaco plains).

There are two major types of forests within this unit, ordered in N-S direction by a temperature gradient, and separated by a gap dividing the mountainous ranges (VERVOORST, in HAWKES & HJERTING, 1969, p. 38) which allows the intrusion of Chaco communities into the inner dry valleys (e.g. the Lerma valley):

a) "Palo blanco" forest

This unit takes its name from its most conspicuous dominant, the elegant Rubiaceous tree *Calycophyllum multiflorum.* Also known as "Übergangswalder" in KANTER, 1936; "Forest with *Calycophyllum multiflorum*" in HUECK, 1954, 1959 & 1972; "High Mesophytic Forest" in Coro, 1956; "Palo blanco and Palo amarillo" forest in CABRERA, 1971 & 1976; "Paloblancal" in SARMIENTO, 1972; "Bosque Húmedo Templado" in UNZUETA, 1975 (p. 218). It was briefly studied by FRENGUELLI & CABRERA (1938), MEYER (1944), ADÁMOLI & al. (1972) and MARLANGE (1972), and mapped by HUECK (1954), VERVOORST (in HAWKES & HJERTING, op. cit.), UNZUETA (1975), HUECK & SEIBERT (1981), and VARGAS GIL & VORANO (1988). Unfortunately, and despite the apparent wealth of references, this forest is one of the least known vegetation units in Argentina, a fact also pointed out by UNZUETA (1975, p. 223) for Bolivia. Placed on good agricultural soils, and located along the corridor of the early Spanish colonization, it was cleared or well-logged before any settlement was established in, for example, neighbouring Chaco forests. The present day information on this forest is therefore extremely scanty and patchy, and although some relictual stands seem to remain in NW Argentina and in Bolivia, a thorough phytosociological study has never been carried out. In NW Argentina this unit reaches 30 m high, with white straight boles up to 1 m diameter mainly of "palo blanco" *(Calycophyllum multiflorum)* and "palo amarillo" *(Phyllostylon rhamnoides),* together with *Amburana cearensis, Pterogyne nitens, Ruprechtia laxiflora, Anadenanthera colubrina* var. *cebil, Astronium urundeuva, Tabebuia impetiginosa, Senna spectabilis* var. *spectabilis, Enterolobium contortisiliquum, Patagonula americana, Myroxylon balsamum, Cordia trichotoma,* etc. A shrub layer of about 2 m high makes transit very difficult, together with abundant lianas, vines and epiphytes (CABRERA, 1976), which are completely absent from the nearby dry Chaco forests.

b) "Tipa" and "Pacará" forest

This is a latitudinally impoverished version of the previous unit, deprived of the two major dominants ("palo blanco" and "palo amarillo"). It underwent a complete destruction by human activity, as pointed out by HAUMAN in 1931, and nowadays sugar cane fields and citrus orchards are found instead. Paradoxically the "tipa" *(Tipuana tipu)* and "pacará" *(Enterolobium contortisiliquum)* forest is somewhat better known than the previous unit, with brief descriptions to be found in HAUMAN (1931), HUECK (1954, 1959, 1972), MEYER (1963), DIGILIO & LEGNAME (1966) and CABRERA (1971, 1976). A complete phytosociological survey of a stand, itself transitional between these two subunits, was performed by BROWN & al. (1985) sub "selva de quina y cebil".

The Bolivian and Paraguayan Chaco

There are no comprehensive surveys or descriptions of the Bolivian Chaco. Only HERZOG's travel notes (1910, 1912), and brief comments in CÁRDENAS (1945), BRAUN (1956), CORO (1956), UNZUETA (1975), WERDING (1976), and VELÁSQUEZ & al. (1988) are available. HERZOG (op. cit.) found west of Puerto Suárez up to the Santiago Sierras communities resembling those of PRADO & al. (in press b) surveyed in Mato Grosso do Sul, and he correctly regarded them as related to the Pantanal vegetation and the Caatingas rather than the Chaco. No true Chaco vegetation is described in his notes until, when travelling from the Sierras of Chiquitos to the Río Grande, he found a low xerophilous formation, rich in spiny shrubs and cacti, known as "Monte" and comprising *Aspidosperma quebracho-blanco, Caesalpinia paraguariensis, Capparis* spp., *Maytenus vitis-idaea, Bulnesia sarmientoi,* etc. The description of Chaco vegetation in UNZUETA (1975, pp. 209-218, sub "Bosque Seco Templado") is very shallow, and the mixed floristic list indicates that no distinction was made between the true Chaco and the non-chaquenian neighbouring formations

(such as the "Palo blanco" forest), differences that have been pointed out by previous authors (HERZOG, 1910 & 1912; CORO, 1956) in their skilful, albeit brief, surveys.

However, to what extent the Chaco vegetation expands to the north of the line Chiquitos-Santa Cruz de la Sierra remains to be seen. HERZOG (1912) hypothesized that the "monte" would not go beyond 16°LS, whereas ELLENBERG's (1981) map of the Bolivian ecoregions presents the Chaco (sub "monte semiárido bajo") extending north through the Rio Grande plains only up to 17°LS. What is certain is that the Chaco does not reach the Llanos de Mojos in NE Bolivia (approx. 12°LS to 15°LS), as implied by CABRERA & WILLINK's (1980) map. The Llanos de Mojos have been studied in part by BECK (1984), HAASE & BECK (1989), and HAASE (1989 & 1990), and some communities show strong links with the savannas of N South America, while the "chaparral" resembles the Humaitá savannas and the Cerrados of central Brazil (HAASE & BECK, 1989). Although the vegetation of this area comprises some very few and isolated Chaco elements (BECK, 1984), it is far from being chaquenian in character.

Most of the works on the Paraguayan Chaco (HOCHREUTINER, 1923; FIEBRIG, 1933; ROJAS & CARABIA, 1945; TORTORELLI, 1967; CHODAT & VISCHER, 1977) have been very shallow. More recent works have improved the knowledge on the area. ESSER's contributions (1982 & 1984), focused mainly in cacti vegetation, have provided a very interesting classification of the Paraguayan Chaco and the most detailed vegetation map available (ESSER, 1982). The last author characterized the vegetation of E Paraguayan Chaco as transitional ("Übergangsgebiet") since in this area the hygrophilous elements find their westernmost limit (ESSER, 1982 & 1984), with which PRADO (1991) agrees.

More recently, a general survey of the Paraguayan Chaco was published by RAMELLA & SPICHIGER (1989; see also SPICHIGER & RAMELLA, 1989 and SPICHIGER & al., 1991), who give abundant information on the unquestionable Chaco vegetation from the region. However, their data on the gallery forests along the river Paraguay tributaries in SE Paraguayan Chaco and those along the Timane-Lagerenza river in the NW of the region, dominated by relatively hygrophilous species such as *Calycophyllum multiflorum, Pisonia zapallo, Maclura tinctoria, Albizia polyantha, Geoffroea striata* (SPICHIGER & RAMELLA, 1989; RAMELLA & SPICHIGER, 1989), unmistakably link these forests to the Subandean Piedmont Forest and other Gallery Forests in the Gran Chaco. The descriptions, diagrams and remarks of RAMELLA & SPICHIGER (1989) and SPICHIGER & al. (1991) on the vegetation of the scattered hills of NW Paraguayan Chaco are also of extreme interest. While surrounded by true Chaco vegetation on the plains, the slopes of the Cerro León and Cerro Cabrera are covered by a deciduous forest of *Anadenanthera colubrina* (very probably var. *cebil*), accompanied by *Pterogyne nitens, Astronium urundeuva, Amburana cearensis* and *Aspidosperma pyrifolium,* which not only show a very strong link with the "Palo blanco" forest in NW Argentina and the calcareous forests around Corumbá, but also an amazing resemblance of the arboreal caatinga vegetation of NE Brazil (PRADO, 1991). On top of these hills cerrado-like vegetation has been found, that is savannas of *Tabebuia caraiba, Jacaranda cuspidifolia* and *Pseudobombax campestre* (RAMELLA & SPICHIGER, 1989). This sequence of vegetation seems to be repeated in the Santiago and Chiquitos Sierras of Bolivia (HERZOG, 1910 & 1912).

The Brazilian Chaco problem

A number of phytogeographical accounts and vegetation maps of South America depict a narrow wedge of so-called Chaco vegetation, entering into Brazil in SW Mato Grosso do Sul state as a continuation of the main area in Argentina, Paraguay and Bolivia (Fig. 1). The alleged presence of Chaco forests in that area has been reported by diverse authors, e.g. HUECK (1955, 1959, 1972), MORELLO & ADÁMOLI (1968), RAGONESE & CASTIGLIONI (1970), CABRERA & WILLINK (1980), HUECK & SEIBERT (1981), BUCHER (1982), PRANCE & SCHALLER (1982), ADÁMOLI (1982), EITEN (1983), RATTER (1984), ALLEM & VALLS (1987), and RATTER & al. (1988). The first phytogeographer to report "bosques chaquenhos" within Brazil was HUECK (1955), and he included a map showing the extent of the Chaco intrusion in Mato Grosso, which has been followed by all subsequent workers. However, PRADO & al. (in press, b) carried out

a survey in the spur of Chaco in Brazil in 1989, on the basis of which they segregated the vegetation into five major woody communities:

a) *Diplokeleba-Tabebuia-Capparis* scrubland;
b) *Schinopsis balansae* parkland;
c) *Aspidosperma-Mimosa* scrubland;
d) Calcareous woodland;
e) Chaquenian forest at Porto Murtinho.

The latter community is the only one they accept as truly chaquenian, with about 70% of Chaco elements s.s. between both dominant and accompanying species. The first three communities are regarded as transitional, since they comprise only a minority of chaquenian elements together with cerrado and semideciduous forest species. Finally, the *Schinopsis brasiliensis*-dominated calcareous woodlands are absolutely non-chaquenian, both in physiognomy and floristic composition, and some of its elements can be found elsewhere in South America in formations such as the Caatingas in NE Brazil, the Subandean Piedmont Forest of Bolivia and Argentina, and the subtropical forests on both banks of the rivers Paraguay and Paraná (PRADO & al., in press, b). No trace was found in the studied area of *Schinopsis quebracho-colorado,* although this should be a very frequent and dominant tree according to HUECK (1955), and these authors conclude that a case of mistaken identity with *S. brasiliensis* misled Hueck. Thus, the extent of the Chaco ingression into Brazil, which is a meeting place for three different floristic stocks, is dramatically diminished, now restricted to a reduced area around Porto Murtinho, far less than previously thought and hardly mappable on a continental scale.

Preliminary conclusions

This contribution intends to be a general review of the available knowledge on the Gran Chaco vegetation, through an exhaustive revision of the literature on the region. Paradoxically, the environmental factors modelling the Chaco are seemingly better studied than the vegetation itself. So far, only general phytogeographic inventories and vegetation surveys of variable depth are published, whereas the few studies on the phytosociology (RAGONESE, 1951; SAYAGO, 1969; LEWIS & al., 1990a; PRADO & al., in press, b) and dynamics (ADÁMOLI & al., 1990; LEWIS & al., 1990b; LEWIS, 1991; SENNHAUSER, 1991) of the vegetation are just token samples of the formidable task ahead. The relatively stronger school of plant physiologists have done virtually nothing for the understanding of the mechanisms permitting the Chaco species to put up with such peculiar environmental conditions. On the contrary, taxonomists have long ago nearly settled the matter as regards the systematics of chaquenian taxa, leaving behind a much better basis for ecologists.

The preceding vegetation analysis has shown that there is number of floristic elements of widely different lineages involved in the woody communities nowadays still regarded as chaquenian. There are obvious similarities between the gallery forests, "Selva de ribera" and Austro-Brazilian Transitional forests, in the east of the Gran Chaco, vis-à-vis the Subandean Piedmont Forests in the west, whereas there is a conspicuous absence or little relevance here for those species or even genera *(Schinopsis, Prosopis)* that can be regarded as tipically chaquenian. On the other hand, the forests and woodlands in most of the intervening extensive plains show a prima facie clear-cut floristic and physiognomic homogeneity. These preliminary conclusions require further study by more objective techniques.

Most authors have simply equated the Chaco phytogeographical province with the Chaco Geographical Region, as shown in HAUMAN (1931), KANTER (1936), CABRERA (1953, 1971, 1976), MORELLO & ADÁMOLI (1968, 1974), RAGONESE & CASTIGLIONI (1970), HUECK (1972), HUECK & SEIBERT (1981), and ZELLWEGER & al. (1990), and no attempt has been made to date to critically evaluate the homogeneity of the resulting vegetation. The limits set by RAGONESE & CASTIGLIONI for the "Chaquenian Park" (1970) most closely equate with the Chaco Geographical Region as defined by KANTER (1936); the map of the Chaco region in MORELLO & ADÁMOLI (1968) is a similar case. For the present author the protracted cohabita-

tion of, say, gallery forests and "algarrobales", piedmont forests and "quebrachales" within the limits of dubious concepts of "Gran Chaco", "Chaco region" or "Chaco province" with no well-defined limits is no longer acceptable. Therefore, an adequate phytogeographical redefinition of the Chaco Province is still wanting.

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