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Origin, affinities and diversity hot spots of the Paraguayan dendrofloras

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ABSTRACT

SPICHIGER, R., R. PALESE, A. CHAUTEMS & L. RAMELLA (1995). Origin, affinities and diversity hot spots of the Paraguayan dendrofloras. *Candollea* 50: 515-537. In English, English and French abstracts.

On the basis of chorological studies, compared with palaeoclimatological, hydrographic, sedimentological and palynological works, an hypothesis about the Late Pleistocene and Holocene history of the Paraguayan vegetation is proposed. Due to its present environmental conditions, the Paraguayan territory is nowadays a region where several dendrofloras are in close contact and thus compete with each other: the Residual Pleistocenic Dry Seasonal, Paranean, Meridional Planalto, Dry Chaco, Wet Chaco, Cerrado, Dwarf Geoxylic, Atlantic Pluvial, and Widely Neotropical Wet/Dry Floras. The occurence of several flora types in the same area allows the circumscription of hot spots of specific tree diversity. A correlation between the distribution patterns of the present Paraguayan dendrofloras and specific ecological conditions and trends is discussed.

RÉSUMÉ

SPICHIGER, R., R. PALESE, A. CHAUTEMS & L. RAMELLA (1995). Origine, affinités et zones à haute diversité de la dendroflore paraguayenne. *Candollea* 50: 515-537. En anglais, résumés anglais et français.

Sur la base d'études chorologiques, comparées à des travaux en paléoclimatologie, hydrographie, sédimentologie et palynologie, une hypothèse sur l'histoire de la végétation paraguayenne durant le Pléistocène tardif et l'Holocène est proposée. Compte tenu des conditions environnementales actuelles, le territoire paraguayen est aujourd'hui une zone de contact et de compétition entre plusieurs types de dendroflores: flores sèche décidue résiduelle du Pléistocène, paranéenne, du Plateau méridional, du Chaco sec, du Chaco humide, du Cerrado, naine géoxylique, pluviale atlantique et flore à large distribution néotropicale. La rencontre de différents types de flores permet une délimitation de secteurs à haute diversité en espèces arborées. Une relation entre la distribution des dendroflores paraguayennes actuelles et les conditions écologiques du milieu est discutée.

KEY-WORDS: Paraguay — Palaeoenvironment — Dendrofloras — Diversity hot spots — Boundary zones

1. Introduction

According to PRADO (1993b), "[...] the whole of the Paraguay basin is an immense transition area with very complicated intermingled patterns". The Paraguayan territory is a region where several floras are in close contact and thus compete with each other. Although Man intervenes

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dramatically in the present vegetation pattern, the original vegetation can still be observed in various areas. In response to the global climatic changes, competition between the different floras takes place at their natural boundaries. BERNARDI (1984) rightly observed that Paraguay presents neither the topography nor the biogeographical position which could facilitate isolation, and in consequence speciation. On the contrary, the great rivers like the Paraná, Paraguay or Pilcomayo serve as access roads. Consequently, the Paraguayan territory would have to be considered as a region where various floras reach their extreme limits. BERNARDI (1984) considers that the great majority of the Paraguayan dendroflora is "pan-brasileña" to which a few Andean and Southern elements are added. He pinpoints the biogeographical signification of the separation between the Amazon basin and the Paraná drainage system, as well as the close relationships between the dendrofloras extending from E Paraguay up to the Río San Francisco.

One of the aims of this paper is to point out the affinities of the Paraguayan dendrofloras with those of neighbouring countries, in order to clarify their origin and the period of their settlement in the Paraguayan territory. Furthermore, we wish to define hot spots regarding the tree diversity in Paraguay. Finally, this paper opens new working hypothesis, which have to be corroborated in future field studies.

2. Material and methods

Taking some frequent tree species of the Paraguayan flora as indicators, we wish to put forward the following floristic elements as characteristic for the Paraguayan territory. However, as almost all species show a certain ecological amplitude, a particular taxon is frequently reported for several flora types. On deciding to which flora we have to attribute a species, we chose as basis for our judgement the habitat where the tree species reaches its optimum development in terms of growth and frequence.

The information has been extracted from recently published articles on the vegetation of the area in question (ORTEGA STUTZ, 1989; RAMELLA & SPICHIGER, 1989; SPICHIGER & al., 1991, 1992; PRADO, 1993a, 1993b; PRADO & GIBBS, 1993; LEWIS & al., 1994; etc.), as well as from papers of the "classical" Argentinian and Brazilian authors. Furthermore, the progress of floristic works, such as "Flora Neotropica", "Flora del Paraguay" and "Contribution to the study of the flora and vegetation of the Chaco" contributes to our understanding of the natural environment by providing new informations on the relationships between the Paraguayan floras. We also have added unpublished field-observations made by our colleagues and ourselves.

The word "Chaco" is used here in its Paraguayan political and geographical sense, i.e. the Paraguayan territory extending westwards from the right bank of the Río Paraguay (= "Paraguay Occidental" or "Chaco"). The "Paraguay Oriental" is the Paraguayan territory extending eastwards from the left bank of the Río Paraguay. It is synonymous with "Paraguayan Mesopotamy".

3. Hypothesis about the Late Pleistocene and Holocene history of the Paraguayan vegetation

The palaeoenvironment of the Paraguayan region can be drawn up on the basis of palynological, hydrographic, sedimentological, chorological and palaeoclimatological studies.

The periods of aridification in the Neotropics are more or less synchronous with the coldest phases of the European Late Glacial. The arid periods are deduced from the forest regression phases observed in the SE Amazon basin (Carajas: 50°25'W / 6°20'S) dated ca. 60'000 yr BP, 40'000 yr BP, and between 23'000 and 13'000 yr BP, respectively (ABSY & al., 1991; VAN DER HAMMEN & ABSY, 1994). The Cerrado vegetation probably settled in the Amazon basin during the Würm-Wisconsin glacial maximum (ca. 20'000-15'000 yr BP), on substrates unfavourable to the so-called "Residual Pleistocenic Dry Seasonal Flora" (PRADO & GIBBS, 1993). During the late Pleistocene,

i.e. as early as 50'000 yr BP, regression and expansion phases of the forests have also been noted in Salitre (46°46'W / 19°00'S), ca. 800 km NE from Paraguayan boundary (LEDRU, 1993).

One of the most ancient floras in Paraguay is probably the "Chamaedendrée" described by CHODAT & VISCHER (1916). These dwarf geoxylic formations of E Paraguay should be considered as remnants of a Pleistocenic or even Tertiary extremely dry flora due to their highly specialized features.

The *Araucaria* forests or woodlands were covering a wide range, extending from the Patagonian region up to SE Brazil and Paraguay, as long ago as up to the Oligocene. The disruption of these forests took place with the uplift of the Andes during the Oligocene (BIGARELLA & ANDRADE-LIMA, 1982). Also, if the climatic conditions had been moister and cooler than today, these *Araucaria* formations (forests, woodlands, grasslands), mixed with Andean and lowland taxa, would have covered a great part of the Paraguayan territory during the Pleistocene.

The Andean uplift during the Oligocene provoked the formation of a synclinal which was first occupied by the sea, leaving, after its withdrawing, marine sediments on which Andean deposits accumulated (PUTZER, 1962). This most particular substratum is now colonized by a xeromorphic flora, the alkaline soils favouring its extension from NW Argentina to NW Paraguay and SE Bolivia. Thus the Paraguayan xeromorphic forests with "quebrachos" (*Aspidosperma quebracho-blanco* Schldl., *Schinopsis quebracho-colorado* (Schldl.) F. Barkley & T. Meyer) have to be considered as edaphoclimacical extrazonal formations (SPICHIGER & al., 1991). ROMERO (1993) also suggests that the differenciation of the type of vegetation, that should later give rise to the xeromorphic formations of the present Chaco domain, began during the Oligocene. Indeed, before the settlement of the loamy salty and alkaline substratum in W Paraguay, i.e. before the Andean surrection, the Chaquenian vegetation should have been a cerrado-like formation or a forest built up by a mesophilous flora.

According to VAN DER HAMMEN (1974, 1982) and VAN DER HAMMEN & ABSY (1994) the driest Pleistocene periods correspond with the second part of the N Hemisphere glaciation (23'000-13'000 yr BP). The accentuation of the latter during the Upper Würm-Wisconsin led to regression of the forests and expansion of the intertropical and subtropical open formations. The global drop of temperature reached 4-6°C, and in some areas, rainfall was reduced by as much as 50%. Consequently tropical regions ranged from humid to semi-arid, providing ecological conditions suitable for caatingas, savannas, cerrados (AB'SABER, 1982; SERVANT & al., 1993).

According to LEDRU (1993), Brazilian regions neighbouring the Paraguayan territory (Salitre) should have been covered with a forest-grassland mosaic with clear predominance of open formations. In the palynological spectra of Salitre, several montane taxa *(Podocarpus, Drimys, Symplocos,* etc.) appear mixed with mesophilous lowland species, which indicates a then cooler climate than today. IRIONDO & GARCIA (1993) point out that, during the late Glacial, climatic isolines were located some 750 km NE of their present positions in the Argentine plains, thus favouring the Patagonian fauna. In NE Argentina (Misiones Province) the subtropical rain forest was replaced by grassland. The aeolian sub-activity deflated and redeposited large masses of silt and fine sand. These formed a broad loessic and sandy belt over the Chaco region, in which longitudinal dunes were built up. Nevertheless, in the Chaco-Pampa regions, these climatic conditions were probably established several thousand years prior to the last Glacial maximum.

On the basis of palaeoecological data and studies of regional patterns of evolution in neotropical forest butterflies, BROWN (1982) indicates areas where the probability for the permanence of forest systems (palaeoecological forest refuges) was high during the cold, dry period prevailing at the end of the latest Glacial maximum age. The Iguaçu area is one of those in which the stability of the tropical forest over the last 20'000 years is highly probable. According to KLEIN (1975) the then Paranean forest was a mixture of lowland semi-deciduous taxa *(Lauraceae, Meliaceae, Rutaceae, Sapindaceae, Myrtaceae), Araucaria* and other related species *(Drimys).*

Consequently, according to BROWN (1982) on one hand and to IRIONDO & GARCIA (1993) on the other, the tall semi-deciduous forests of the Paraná Valley and the dry deciduous forests of the Chaco should have been in place during the Würm-Wisconsin even if mixed with cooler elements than today. The Paraguayan Mesopotamy, i.e. the interfluvial area between the Ríos Paraná

and Paraguay, would have been an *Araucaria* woodland, or a mosaic of Patagonian grasslands and patches of *Araucaria* woodlands with some gallery and riverine forests.

During the end of Pleistocene and early Holocene (ca. 15'000-9'000 yr BP) the climate became wetter and warmer (MARKGRAF, 1989; MARKGRAF & BRADBURY, 1982) although BEHLING (1993) reports a still cool and relatively dry climate between 14'000 and 10'800 yr BP for highlands of E Santa Catarina State. The consequence in the Paraguayan territory was the expansion of forests to the detriment of open formations. The mesophilous taxa should still have been strongly mixed with conifers and montane ones (LEDRU, 1993).

The question of an eventual existence of a cooler and drier "Younger Dryas" period between 11'000 and 10'000 yr BP is discussed by the authors, but the presence of such an interval is generally challenged (MARKGRAF, 1991). Nervertheless, such a period is observed by BEHLING (1993) in highlands of E Santa Catarina between 10'500 and 10'000 yr BP.

The pollen record from Salitre (19°S) shows a maximum of expansion of the *Araucaria* forest at 9'500 yr BP which was interpreted as reflecting a cool and moist climate (LEDRU, 1993; LEDRU & al., 1994). On the contrary, during the same period, a Campos vegetation with very few *Araucaria* is reported for Boa Vista (27°42'S) (BEHLING, 1993). LEDRU & al. (1994) explain this difference by the fact that polar advections must then have reached the Salitre area, provoking moister and cooler climate and thus favouring *Araucaria* and other related taxa. On the contrary, the Boa Vista area, lying behind the polar front, was covered by a Campos vegetation related to a drier climate. In the Paraná riverine region, the presence of S Planalto taxa and of a patch of "Pinhais" can be a proof that the E Paraguayan territory was covered by *Araucaria* woodlands or by a mixture of *Araucaria* and lowland species. This vegetation type should have been established under a cooler and wetter climate than today's (SPICHIGER & al., 1992). According to BEHLING (1993) the *Araucaria* forests of the Meridional Planalto would have reached their present maximum distribution only since ca. 3'000 yr BP. The Meridional Planalto taxa *(Araucaria, Drimys)* recorded for the Paraguayan territory would rather be remnants of early holocene or even late pleistocene cold and moist climatic events linked with stronger polar advections than today's.

The Paranean Flora sensu stricto (= *Lauriflora)* would have colonized the Mesopotamy afterwards, i.e. during early and middle Holocene, arriving probably from the E (Iguaçu refuge), NE and NW, being favoured by the rise of temperature, and being repulsed from the Amazon basin by the reexpanding Hylaea (SPICHIGER & al., 1992). Such an expansion of wet tropical formations is recorded for Salitre and Boa Vista between 8'000 and 6'000 yr BP (LEDRU & al., 1994). IRIONDO & GARCIA (1993) observed that climatic limits migrated 50-150 km SW of the present position, and provoked a shift of tropical conditions towards the SW in NE Argentina. This shift would be due to a climatic optimum during the Middle Holocene in N Argentina (8'500-3'500 yr BP). Such a phenomenon would explain the expansion of wet-preferring taxa (Paranean and Atlantic Pluvial Floras, see below).

Drier phases have been observed between 7'000 and 5'000 yr BP in several Neotropical sites (MARKGRAF & BRADBURY, 1982; MARKGRAF, 1989). The presence of cerrado patches in NE Paraguay could be explained as a relict of a very dry Pleistocenic phase during the glacial maximum, or of the mid-Holocene central-Brazilian aridification (6'000-4'500 yr BP), reported by different authors. The aridification got more severe during the Middle Holocene (6'000-5'000 yr BP) (SERVANT & al., 1993). According to LEDRU (1993) and SERVANT & al. (1981, 1993), a strong regression of the then existing forest was observed in Salitre with the disappearing of *Araucaria* and the expansion of campos.

The flora of the "Residual Pleistocenic Dry Seasonal Formation Arc" according to PRADO & GIBBS (1993) would be the remnant of a drier flora once widely spread more towards the N (probably during the glacial maximum 20'000-15'000 yr BP and before) and surviving presently on the edges, and especially the S ones, of the Amazon basin. This flora would have reached the E Paraguay territory after the "Laurisilva", of which it is a drier facies, also repulsed southwards by the reexpansion of the Hylaean Flora upon the Amazon Basin. The rising temperature and xericity of the middle Holocene probably facilitated its settlement.

WIRRMANN & al. (1988) observed a gradual rise in the water level of Lake Titicaca between 4'500 and 2'200 yr BP, which indicates a rainfall increase. Anyway, from 4'000 yr BP, modern

climatic conditions were established at Salitre (19°S) and Boa Vista (27°42'S) (LEDRU & al., 1994). Since then, the pattern of natural domains in Paraguay should have been more or less the same as today's. During the whole span from the Mid-Holocene until today, we observe an expansion of the forest in SE Brazil, in spite of short regression phases of the forest after 3'600 yr BP. These short regression phases are deduced from the datation of aeolian dunes, which can have grown only in a non-forested landscape (SERVANT & al., 1993).

During the Late Holocene the general climatic trend is an increase of humidity and temperature, due to a shift of Inter Tropical Convergence Zone (ITCZ) towards the S of S America. According to MARTIN & al. (1992) several "El Niño" periods before 3'900 yr BP and between 2'800 yr BP and today should have created a palaeoenvironmental instability in the Paraguayan region. The "El Niño" phenomenon could have caused enhancement of rainfalls in an area extending from S Bolivia to S Brazil through Paraguay. Humid phases would have alternated with arid ones due to the absence of "El Niño". The drier Holocene periods, observed by SERVANT & al. (1981) between 3'400 and 1'400 yr BP, correspond partly with the absence of "El Niño". However, the aeolian dunes in the Paraguayan W Chaco could also have been built up during the short drier episodes of the Late Holocene. The latter seem to be synchronous with periods of failing "El Niño". IRIONDO & GARCIA (1993) also point out the presence of a dry subtropical phase in the Late Holocene with aeolian dynamics. According to these authors this arid episode is due to a prevailing anticyclonic centre situated over N Argentina and Paraguay. During this period they observe an absence of wetland in Corrientes Province and S Paraguay, a decrease in the discharge of the Río Paraná, as well as a deposit of a thin silt and sand layer, including dune fields, covering the entire region. Turning to historical sources they also record a "Little Ice Age" in Buenos Aires during the 18th and 19th centuries A.D. In spite of these short aridity episodes during the last four thousand years, the present pattern of vegetation was already drawn up in Paraguay, i.e. expansion of semi-deciduous forests to the detriment of savannas and *Araucaria* forests.

4. Dendrofloras occurring in the Paraguayan territory

According to BERNARDI (1984), as cited above, "las afinidades de la flora dendrologica paraguaya son masivamente pan-brasileñas". This opinion is globally true for the vegetation of Oriental Paraguay, i.e. E of Río Paraguay, but is not suitable for the vegetation in Occidental Paraguay — or the Paraguayan Chaco — which is rather to be considered as part of an Argentino-Paraguayan phytogeographic province ("Chacoan province" sensu TAKHTAJAN, 1986). If the Chaquenian vegetation has to be looked upon as a particular edaphoclimacic formation, the E Paraguayan dendroflora is basically built up of flora elements belonging to the "Residual Pleistocenic Dry Seasonal Formation Arc" sensu PRADO & GIBBS (1993). This mesophilous flora forms an arc starting from the NE Brazilian caatinga (= "Caatinga nucleus") and reaching the sub-Andean Tucumano-Bolivian forests (= "Piedmont nucleus") passing through the Paraguay-Paraná-Uruguay basins (= "Misiones nucleus") which are situated in the centre of this arc. The Chaco forests and Palm-savannas create a gap where hills and cordilleras act as relays between the "Piedmont-nucleus" and the "Misiones nucleus". According to PRADO & GIBBS (1993), this arc of mesophilous forest may be a relict of a formerly more extended Pleistocenic drier vegetation (see chap. 3). Beside these mesophilous elements, others play a prominent role, viz., widely Neotropical elements, strict Paranean species, Atlantic taxa, Cerrado elements, etc. The Paraguayan territory is thus a boundary zone where floras and vegetation types are intermingled and compete with each others.

It is worth including in this discussion the physionomic-ecological classification of Neotropical vegetation established for Brazil by VELOSO & GÓES-FILHO (1982). For each type of dendroflora described below, the corresponding Brazilian terminology is added.

4.1. South-east and South Brazilian Floras

The three following floras belong to a biogeographical area which includes the forests of SE and S Brazil, the Mata Atlantica being excluded.

This biogeographical notion corresponds more or less to the "Paraná Province" sensu TAKHTAJAN (1986), the "Provincia Paranense" sensu CABRERA & WILLINK (1973), and to PRANCE's "Southern Brazil Phytochorium" (1989). It includes the "Region der Ost- und Südbrasilianischen Wälder" and the "Region der Südbrasilianischen Araukarienwälder" sensu HUECK (1966).

The following floras share many elements and are closely related together, which makes it difficult to refer a species to one particular flora.

4.1.1. The Residual Pleistocenic Dry Seasonal Flora (Austro-Brazilian Flora) [= Floresta Estacional Decidual (VELOSO & GÓES-FILHO, 1982)]

According to PRADO & GIBBS (1993), the Residual Pleistocenic Dry Seasonal Flora (RPDS Flora) forms an arc S of the Amazon basin and the Brazilian Campo Cerrado. Three centres of distribution have been pointed out: the "Piedmont nucleus", the "Misiones nucleus" and the "Caatinga nucleus". Outside these centres, some species are distributed according to a more or less continuous peri-Amazonian pattern, coinciding with the drier areas. On the contrary, other species are restricted to only one or two nuclei, in which case a vicariant species might occur in the other centre(s).

Various predominant legumes species have a distribution pattern which coincides with the RPDS Formation Arc: *Anadenanthera colubrina* var. *cebil* (Griseb.) Altschul is the striking main element in the mesophilous forests of the "Cerro León" and "Cerro Cabrera" within the W Chaco ("*Bosque mesofilo de colina de Anadenanthera colubrina*" sensu SPICHIGER & al., 1991). This mesophilous species is closely connected with the Tucumano-Bolivian forest elements sensu PARODI (1945). According to MERELES (pers. com.), the variety *cebil* also occurs in xeromesophilous forests together with *Schinopsis balansae* Engl. and *Astronium* spp. in the Paraguayan E Chaco (= "Chaco Humedo"). This Chaquenian occurrence is confirmed by various Argentinian authors. Furthermore, *A. colubrina* var. *cebil* (Griseb.) Altschul has been frequently recorded in E Paraguay. Its commonness of occurrence on the Cerro León and Cerro Cabrera allows us to think that it has a Tucumano-Bolivian origin. Its calciphilous preferences make it colonize the Río Apa region. DUBS (1994) reports this species as preponderant in the semi-deciduous forest islands of the Pantanal in the Mato Grosso. Another calciphilous tree, *Amburana cearaënsis* (Allemão) A. C. Smith, has the same general distribution pattern, but with a rarer occurrence in Paraguay. It grows in the mesophilous forests of the Cerro León, on the hills of the E Chaco, on calcars of the Río Apa, and in the Sierra de Amambay. *A. cearaënsis* (Allemão) A. C. Smith is also recorded in the "Piedmont nucleus" (PRADO & GIBBS, 1993). *Pterogyne nitens* Tul. and *Enterolobium contortisiliquum* (Vell. Conc.) Morong have a frequent occurrence in the Paraguayan Mesopotamy and along the Ríos Paraguay and Paraná, as well as in the Chaquenian gallery forests. They have spread into the Chaco by colonizing the sand dunes (MERELES, pers. com.). Furthermore, *E. contortisiliquum* (Vell. Conc.) Morong is one of the leading species of the South Andean Piedmont forests. *Peltophorum dubium* (Sprengel) Taubert, a big psammophilous tree of the Paraguayan Mesopotamy, is particularly frequent in the "Misiones nucleus", but has an atypical occurrence on the Venezuelian coast, which may point to an ancient circum-Amazonian distribution. According to MERELES (pers. com.) the species also occurs in the xeromesophilous forests of the E Chaco, which means that it has a rather xerophilous habit (see also SPICHIGER & al., 1992). *Copaifera langsdorffii* Desf. occurs in W and, more frequently, in E Paraguay where it grows inside the forests and on their edges, as well as in forest islands inside the savannas. Nevertheless, it is more frequent in NE Brazil where it seems to have its origin. It even reaches the estuary of the Amazon (HUECK, 1978).

Cnicothamnus azafran (Cabrera) Cabrera and *Cochlospermum tetraporum* H. Hallier were so far only known from the "Piedmont nucleus". Their recent collection on Cerro Cabrera extends

their distribution more eastwards. These two species could be considered as relicts of an ancient link between the Andes and the hills and cordilleras of W Paraguay, which was disrupted by the instalment of the present Chaquenian substratum and vegetation.

The RPDS Flora, a tropophilous flora, which supports warmer and drier conditions than the below mentioned strict Paranean elements, is the basic element of vegetation in the E and central parts of the Paraguayan territory. It is more or less intermingled with species belonging to other floras. For example, the forest growing on the banks of the Río Paraná is a mixture of RPDS Flora and strict Paranean Flora representatives. In the Mesopotamy, along the banks of the Río Paraguay, in NE Paraguay, i.e. on sandy or calcareous or sandstone substrate, this flora is dominant. It is also present in the "Chaco Humedo" where it competes with the strict Chaquenian flora. There, it builds up the gallery forests, the hills (cerros and cordilleras) and, together with true Chaquenian species, it thrives on neutral or acid soils (sand dunes, savannas). For instance, *Patagonula americana* L. is widespread in the E part of the country where it grows on sandy soils or on clayey ill-drained substrates, as well as in rocky habitats. It is a forest tree, which can also be found as a pioneer or an element of the various succession stages. Besides, it has been frequently recorded in the wettest vegetation types of the Chaco: gallery forests, hill forests of the Cerro León and other "Cordilleras". Thus, this species has a great ecological plasticity. *Calycophyllum multiflorum* Griseb. has a typically "Piedmont-Misiones" distribution pattern. The species is a leading tree of the Piedmont, or Tucumano-Bolivian forests ("Palo blanco" forests). In Paraguay it occurs in the calcareous region of the Río Apa, in the mesophilous forest of the Cerro León (W Chaco), and especially in the semi-evergreen gallery forests of the Chaco ("Bosques higrófilos de galeria de *Calycophyllum multiflorum*" sensu SPICHIGER & al., 1991). This species can grow under most xeric climatical conditions, such as those of the central and W Chaco, provided that it finds a relatively wet substrate. Thus, together with *Phyllostylon rhamnoides* Taubert this species is a good indicator of local edaphic humidity and probably low salinity.

Where the Paranean Flora (see chap. 4.1.2) is dominant, i.e. in the "Misiones nucleus", the RPDS Flora is rather found on the unfavorable substrates, such as ill-drained or xeric, sandy soils, e.g.: the ill-drained facies with *Luehea divaricata* C. Martius & Zucc. of the tall semi-evergreen *Lauraceae* forests (SPICHIGER & al., 1992). *Luehea divaricata* C. Martius & Zucc. is a predominant *Tiliaceae* tree in the Paraguayan Alto Paraná where it is an important element of the tall semi-evergreen forests on ill-drained soils. It is a heliophilous, hygrophilous and anemochorous species found very frequently on forest edges or in clearings, disturbed forests and succession stages. In the Paranean region *Luehea divaricata* C. Martius & Zucc. is rather confined to unfavorable substrates (waterlogged soils). It has been recorded as very frequent in an *Araucaria* forest patch on ill-drained soil. The species has a wide extra-Amazonian S tropical distribution, extending from W-central Brazil to NE Brazil through Paraguay, Uruguay and N Argentina (CUNHA, 1985). *Luehea divaricata* C. Martius & Zucc. appears to be ecologically very tolerant and is able to grow under harsh conditions.

The RPDS Flora elements grow in a more xeric and more stressful environment than the Paranean ones.

The following trees are characteristic:

Anacardiaceae	*Astronium urundeuva* (Allemão) Engl., *Schinopsis brasiliensis* Engl., *Schinus molle* L., *S. terebinthifolia* Raddi, *S. weinmanniifolia* Engl.
Apocynaceae	*Aspidosperma australe* Müll. Arg., *A. cuspa* (Kunth) S. F. Blake, *A. pyrifolium* C. Martius, *A. riedelii* Müll. Arg., *Rauvolfia mollis* S. Moore, *Tabernaemontana catharinensis* A. DC.
Aquifoliaceae	*Ilex affinis* Gardner, *I. brasiliensis* (Sprengel) Loes.
Bombacaceae	*Ceiba pubiflora* Schumann, *Chorisia speciosa* A. St. Hil.
Boraginaceae	*Patagonula americana* L.
Burseraceae	*Protium heptaphyllum* (Aublet) Marchand.
Caricaceae	*Carica quercifolia* (A. St. Hil.) Hieron.

Cochlospermaceae	*Cochlospermum tetraporum* H. Hallier.
Compositae	*Cnicothamnus azafran* (Cabrera) Cabrera, *Gochnatia polymorpha* (Less.) Cabrera.
Combretaceae	*Terminalia triflora* Lillo.
Euphorbiaceae	*Sebastiana brasiliensis* Sprengel.
Leguminosae	*Acacia albocorticata* Burkart, *A. bonariensis* Hook. & Arn., *Amburana cearaënsis* (Allemão) A. C. Smith, *Anadenanthera colubrina* var. *cebil* (Griseb.) Altschul, *Copaifera langsdorffii* Desf., *Enterolobium contortisiliquum* (Vell. Conc.) Morong, *Geoffroea striata* (Willd.) Morong, *Gleditsia amorphoides* (Griseb.) Taubert, *Machaerium acutifolium* J. Vogel, *Microlobius foetidus* subsp. *paraguensis* (Benth.) M. Sousa & G. Andrade, *Mimosa balansae* M. Micheli, *M. polycarpa* var. *subandina* Barneby, *Parkinsonia aculeata* L., *Peltophorum dubium* (Sprengel) Taubert, *Pterogyne nitens* Tul., *Tipuana tipu* (Benth.) Kuntze.
Myrtaceae	*Eugenia ilhensis* O. Berg, *E. moraviana* O. Berg, *E. uniflora* L., *Myrcia ramulosa* DC.
Phytolaccaceae	*Phytolacca dioica* L.
Proteaceae	*Roupala meisneri* Sleumer.
Rhamnaceae	*Ziziphus joazeiro* C. Martius.
Rubiaceae	*Calycophyllum multiflorum* Griseb.
Rutaceae	*Fagara chiloperone* Chodat & Hassler, *F. hyemalis* (A. St. Hil.) Engl., *F. naranjillo* (Griseb.) Engl., *Pilocarpus pennatifolius* Lemaire.
Sapindaceae	*Allophylus pauciflorus* Radlk., *Dilodendron bipinnatum* Radlk., *Diplokeleba floribunda* N. E. Br., *Magonia pubescens* A. St. Hil., *Melicoccus lepidopetalus* Radlk., *Talisia esculenta* (A. St. Hil. & al.) Radlk.
Sapotaceae	*Sideroxylon obtusifolium* (Roemer & Schultes) Penn., *Pouteria gardneriana* Radlk.
Simaroubaceae	*Castela tweedii* Planchon.
Solanaceae	*Solanum granulo-leprosum* Dunal.
Theophrastaceae	*Clavija nutans* (Vell. Conc.) B. Ståhl.
Tiliaceae	*Luehea candicans* C. Martius, *L. divaricata* C. Martius & Zucc., *L. grandiflora* C. Martius.
Ulmaceae	*Celtis pubescens* Kunth, *Phyllostylon rhamnoides* Taubert.

4.1.2. The Paranean Flora (Lauriflora)
[Floresta Ombrófila Mista (VELOSO & GÓES-FILHO, 1982)]

This flora is centred in the "Misiones nucleus" sensu PRADO & GIBBS (1993), i.e. in the Paraguayan-Upper Paranean-Upper Uruguayan basins. It extends to SE Brazil and to the S Planalto where it is closely intermingled, up to 800 m altitude, with *Araucaria* and other taxa native of the latter region. It more seldomly reaches the centre of the Amazon Basin and the Mata Atlantica. For instance, *Tabebuia heptaphylla* (Vell. Conc.) Toledo — a paradigm of Paranean element — is a tall tree of E Paraguay. Its area of distribution ranges from the Mata Atlantica to N Argentina with concentration in E Paraguay (GENTRY, 1992). In Paraguay it seems to prefer clayey soils and to avoid temporarily flooded or ill-drained substrates. According to ESKUCHE (1982) it builds up, together with *Astronium balansae* Engl. and *Brunfelsia australis* Benth., the tall forests of the Argentinian Paraná riverine region. We have also observed numerous patches of such forests in the Paraguay-Paraná delta (Ñeembucú, Itapua, Misiones departments). It seems to be a sensitive species which cannot regenerate in too disturbed environments (foresters' pers. com.). *Ilex paraguariensis* A. St. Hil. and *I. brevicuspis* Reissek are also native of the PRADO's "Misiones nucleus",

and extend to S and SE Brazil. They migrate from the semi-evergreen forests into the understory of the *Araucaria* forests. The *Ilex* species grow frequently along rivers and sometimes on rocky substrate.

The Paranean species require a warm and wet environment, as well as well-drained, rather clayey and nutrient-rich soils. The forests that grow on the best substrates of the Paranean riverine regions are good representatives of this type of vegetation: the tall semi-evergreen *Lauraceae* forests, facies with *Balfourodendron riedelianum* (Engl.) Engl. sensu SPICHIGER & al. (1992). *B. riedelianum* (Engl.) Engl. (see PRADO's map, 1991), another paradigm of the Paranean Flora, is a 25-35 m high emergent tree overhanging the canopy of the tall *Lauraceae-Cedrela fissilis-Chrysophyllum gonocarpum* well-drained forests. It characterizes the typical vegetation facies of clayey or sandy-clayey soils. It is also present in disturbed vegetation and secondary stages. In the first secondary stages (10 yrs old or less) the species has been frequently recorded as a treelet. *B. riedelianum* is a leading species of the Upper Paraná-Upper Uruguay basins, more rarely found in the Meridional Planalto and the Mata Atlantica. Its S limit seems to be the State of Rio Grande do Sul (COWAN & SMITH, 1973).

The Paranean Flora is more or less synonymous with Paraguayan Flora sensu SMITH (1962). The Paraguayan tall semi-deciduous forests with *Lauraceae* ("Monte Alto de Laurel" sensu SPICHIGER, 1992) are also called *Parapiptadenia rigida-Nectandra saligna* forests in NE Argentina (ESKUCHE, 1983, 1984). Due to the high frequency of *Lauraceae* species, this flora could be called *Lauriflora.* The centre of distribution for the most frequent *Lauraceae* of the riverine Paraná forest (*Nectandra lanceolata* Nees, *N. megapotamica* (Sprengel) Mez, *Ocotea spectabilis* (Meissn.) Mez and *O. puberula* (Rich.) Nees) seems to lie in the Upper Paraná-Upper Uruguay basins, with a N extension into favourable, locally wet environments. The distribution pattern of these species may fit in with that of the *"Laurisilva"* or "Monte Alto de Laurel" extending into E Paraguay, S Brazil and NE Argentina, with the Paraná river as the pivot. By occupying the understories of *Araucaria* forests up to 1000 m, such species as *N. lanceolata* Nees, *N. megapotamica* (Sprengel) Mez and *O. spectabilis* (Meissn.) Mez allow the *"Laurisilva"* forest to compete successfully with the montane coniferous forests of S Brazil. It should also be pointed out that *N. megapotamica* (Sprengel) Mez, *O. puberula* (Rich.) Nees and *O. pulchella* (Nees) Mez are recorded for the Mata Atlantica, at least in the State of Santa Catarina (PEDRALLI, 1987; VATTIMO-GIL, 1980).

The forests growing on the well-drained substrates (upland or plateau forests) of the Paraguayan Alto Paraná could be legitimately called *"Meliaceae-forests"* due to the preponderance of trees belonging to this family (*Lauraceae-Cedrela fissilis-Chrysophyllum gonocarpum* forests sensu SPICHIGER & al., 1992), which is represented by a dozen species in Paraguay. *Cedrela fissilis* Vell. Conc., the "cedro", one of the principal components of the upper forest layer, generally grows on well-drained soils, but also occurs in ill-drained tall forests (*Lauraceae-Luehea divaricata-Myrciaria rivularis* forests sensu SPICHIGER, 1992). This species is widespread in the Neotropics, but is most frequent in the area ranging from S Brazil through to E Paraguay and N Argentina (PENNINGTON, 1981). According to KLEIN (1984), *Cedrela fissilis* Vell. Conc. grows in all the different types of forests in SE Brazil, viz. "Floresta Decidual do Alto Uruguai, Floresta Ombrófila Mista (zona dos pinhais)" and "Floresta Ombrófila Densa da Costa Atlântica". It is most commonly found in the "floresta decidual e semidecidual", which corresponds to the Paraguayan *Lauraceae* tall semi-deciduous forests. In the Paranean riverine forests, the species also grows as a treelet in secondary stages which are 10 and 30 yr old (ORTEGA STUTZ, 1989). In the Paraguayan Alto Paraná, *Cedrela fissilis* Vell. Conc. is a leading species with an important ecological plasticity. This could mean that the local environment is for the most part suitable for this species. Its present almost peri-Amazonian area of distribution could be explained by a Holocene rise in both temperature and humidity which made the semi-deciduous species move to the edges of the Amazonian Hylaea. According to KLEIN (1975), *Cedrela fissilis* Vell. Conc. is common in the understory of *Araucaria* forests on the Precambrian and Paleozoic plateau of Paraná State. This could mean that there is a present eastwards expansion of this species due to a change towards a warmer climate. *Cabralea canjerana* (Vell. Conc.) C. Martius presents more or less the same distribution pattern as the former species, but it extends along the gallery forests into areas with a drier climate (Goias, Minas Gerais).

This tree is common in the coastal forests of S Brazil and also reaches the drainage regions of the Ríos Paraná and Uruguay (PENNINGTON, 1981).

The following trees or treelets are to be considered as Paranean elements:

Anacardiaceae	*Astronium balansae* Engl., *Schinus longifolia* (Lindley) Speg.
Annonaceae	*Annona amambayensis* R. E. Fries.
Apocynaceae	*Aspidosperma polyneuron* Müll. Arg., *A. subincanum* A. DC., *Rauvolfia sellowii* Müll. Arg.
Aquifoliaceae	*Ilex brevicuspis* Reissek, *I. dumosa* Reissek, *I. paraguariensis* A. St. Hil.
Araliaceae	*Dendropanax cuneatus* Decne. & Planchon, *Pentapanax warmingianus* Harms.
Bignoniaceae	*Tabebuia heptaphylla* (Vell. Conc.) Toledo.
Boraginaceae	*Cordia ecalyculata* Vell. Conc., *Cordia trichotoma* Steudel.
Celastraceae	*Maytenus ilicifolia* Reissek.
Euphorbiaceae	*Sebastiana klotzchiana* Müll. Arg.
Lauraceae	*Nectandra angustifolia* Nees, *N. lanceolata* Nees, *N. megapotamica* (Sprengel) Mez, *Ocotea puberula* (Rich.) Nees, *O. spectabilis* (Meissn.) Mez.
Leguminosae	*Acacia monacantha* Willd., *Apuleia leiocarpa* (J. Vogel) Macbr., *Holocalyx balansae* Mich., *Lonchocarpus leucanthus* Burkart, *L. muehlbergianus* Hassler, *Machaerium paraguariense* Hassler, *M. stipitatum* (DC.) J. Vogel, *Mimosa oligophylla* M. Micheli, *M. paraguariae* M. Micheli, *M. tenuipendula* Burkart, *Myrocarpus frondosus* Allemão, *Parapiptadenia rigida* (Benth.) Brenan.
Meliaceae	*Cabralea canjerana* (Vell. Conc.) C. Martius, *Cedrela fissilis* Vell. Conc., *Guarea macrophylla* subsp. *spicaeflora* (A. L. Juss.) Penn., *Trichilia catigua* A. L. Juss., *Trichilia clausenii* C. DC., *Trichilia elegans* A. L. Juss.
Monimiaceae	*Hennecartia omphalandra* Poisson, *Mollinedia clavigera* Tul.
Moraceae	*Sorocea bonplandii* (Baillon) W. Burger.
Myrtaceae	*Hexachlamys edulis* (O. Berg) Kausel & D. Legrand.
Polygonaceae	*Ruprechtia laxiflora* Meissner.
Rutaceae	*Balfourodendron riedelianum* (Engl.) Engl., *Esenbeckia densiflora* (Chodat & Hassler) Hassler, *E. febrifuga* (A. St. Hil.) C. Martius, *Helietta apiculata* Benth.
Sapindaceae	*Allophylus guaraniticus* (A. St. Hil.) Radlk., *Averrhoidium paraguaiense* Radlk., *Cupania vernalis* Cambess., *Diatenopteryx sorbifolia* Radlk., *Matayba elaeagnoides* Radlk.
Sapotaceae	*Chrysophyllum gonocarpum* Engl., *C. marginatum* (Hook. & Arn.) Radlk., *Pouteria salicifolia* Radlk.
Simaroubaceae	*Picrasma crenata* (Vell. Conc.) Engl., *Picramnia parvifolia* Engl.
Solanaceae	*Brunfelsia australis* Benth.

4.1.3. The Meridional Planalto Flora (= "Pinhais Flora", Southern Plateau Flora)
[Floresta Ombrófila Mista Montana (VELOSO & GÓES-FILHO, 1982)]

It is worthwhile drawing attention to the occurrence of a small patch of *Araucaria* wood inside the semi-deciduous forest of the Alto Paraná department, as did LOPEZ & al. (1987). VELOSO & GÓES-FILHO (1982) noted the frequent occurence of *Araucaria* in circular patches along affluents of the Rio Grande (N part of the Río Paraná basin); they explained this fact with the down river dispersal of the diaspores and the consecutive formation of these patches around a few

mother-plants. Although we are not absolutely sure of its natural or anthropogenic origin, the proximity of the original *Araucaria* forests on the other side of the Río Paraná makes their natural occurrence in E Paraguay quite possible (LOPEZ & al., 1987).

The presence of Southern Plateau elements in the Alto Paraná department could be relevant for tracing the history of the vegetation, as they could be relicts of a formerly wetter and cooler climate. The Meridional Planalto elements reach their westernmost limit in the Paraná riverine area, where their chances for the future seem to be bad under the present climatic conditions.

Hereunder are listed the species present in Paraguay which could belong to the Meridional Planalto Flora:

Aquifoliaceae	*Ilex theezans* Reissek.
Araucariaceae	*Araucaria angustifolia* (Bertol.) Kuntze.
Lauraceae	*Ocotea porosa* (Mez) Barroso, *O. pulchella* (Nees) Mez.
Myrtaceae	*Calyptranthes concinna* DC., *Campomanesia xanthocarpa* O. Berg, *Eugenia involucrata* DC., *Myrcianthes pungens* (O. Berg) D. Legrand.
Winteraceae	*Drimys brasiliensis* Miers.

4.2. Chaquenian Floras

The following floras are to be referred to a biogeographical province corresponding to the "Chacoan Province" sensu TAKHTAJAN (1986), the "Provincia Chaqueña" sensu CABRERA & WILLINK (1973), the "Pantanal" and "Chaco phytochorium" according to PRANCE (1989), and to the "Regionen des Chaco und seiner Randgebiete" according to HUECK (1966). In the whole Chaco, anthropic communities have been described (SPICHIGER & al., 1991), especially the most frequent ones, those with *Prosopis ruscifolia* Griseb. ("Viñalares").

4.2.1. The Dry Chaco Flora

[Savana Estépica Arbórea Densa (VELOSO & GÓES-FILHO, 1982)]

The Paraguayan xeromorphic forests belong to the true Chaquenian communities of the Gran Chaco (PRADO, 1993b). They are a N extension of the "Quebrachales" with two and three "quebrachos" sensu Argentinian authors, and of the "Quebrachales" with white "quebracho" sensu LEWIS & PIRE (1981), this latter unit being an impoverished facies of the former. This flora has been described by various authors, and in particular by Argentinian authorities. PRADO (1993a, 1993b) and SPICHIGER & al. (1991) have given other recent accounts. In Paraguay, the occurrence of Chaquenian vegetation and flora is closely linked with the alkalinity and texture of the soils. Thus, the Chaquenian flora has to be considered as an edaphoclimacic one. It is characterized by the high frequency of "quebrachos": *Aspidosperma quebracho-blanco* Schldl., *Schinopsis balansae* Engl., *Schinopsis quebracho-colorado* (Schldl.) F. Barkley & T. Meyer.

Aspidosperma quebracho-blanco Schldl. is one of the leading species of the Chaquenian forests and of their succession stages ("Bosques xeromorfico de *Aspidosperma quebracho-blanco* y *Chorisia insignis*" = "quebrachales de quebracho blanco" sensu SPICHIGER & al., 1991). Its centre of distribution is the Argentinian and Paraguayan Chaco with an extension to the E drainage system of the Río Paraguay and to SE Bolivia. Its occurrence is connected with deep loamy substrates. *Aspidosperma quebracho-blanco* Schldl., like other true Chaquenian trees, grows where semideciduous or other salt sensitive deciduous species cannot survive due to the edaphic conditions. The anacardiaceous *Schinopsis quebracho-colorado* (Schldl.) F. Barkley & T. Meyer, a xerophilous species, has more or less the same origin and distribution as the apocynaceous *Aspidosperma quebracho-blanco* Schldl. It is a leading species of the "quebrachales de quebracho-blanco" that grows on xeric, deep loamy-sandy soils, i.e. the xerophilous forests in their psammophilous facies (SPICHIGER & al., 1991). In the whole Chaquenian region *Schinopsis quebracho-colorado*

(Schldl.) F. Barkley & T. Meyer is characteristic of the most xeric forests (MUÑOZ, 1990). Its origin is NW Argentina, SE Bolivia and W Paraguay, and it is also called "quebracho boli", i.e. quebracho of Bolivia (MUÑOZ, 1990).

The Dry Chaco Flora is spread over NW Argentina, W Paraguay and SE Bolivia. On its E limit it is in contact with the Palm-savannas and the RPDS Floras. Elements of the latter invade the Chaquenian Flora as soon as the substrate is suitable, i.e. rather well-drained and saltless. Under such conditions, even in the driest parts of the W and central Paraguayan Chaco, the RPDS and Cerrado Floras are found on hills and serranias (Cerro León, Cerro Cabrera), in gallery forests, taking advantage of the ground-levees and on sand dunes ("Vegetation der Sandflächen", according to ESSER, 1982). The Chaquenian Flora is associated with loamy or loamy-clayey, alkaline and salty soils which can suffer either from temporary aridity or temporary waterlogging.

The following species are typical Chaquenian species:

Achatocarpaceae	*Achatocarpus praecox* Griseb.
Anacardiaceae	*Schinopsis cornuta* Loes., *S. heterophylla* Ragon. & J. Castigl., *Schinopsis quebracho-colorado* (Schldl.) F. Barkley & T. Meyer, *Schinus fasciculata* (Griseb.) I. M. Johnston.
Apocynaceae	*Aspidosperma quebracho-blanco* Schldl.
Bombacaceae	*Chorisia insignis* Kunth.
Capparaceae	*Capparis retusa* Griseb., *C. salicifolia* Griseb., *C. speciosa* Eichler, *C. tweediana* Eichler.
Caricaceae	*Jacaratia corumbensis* Kuntze.
Cactaceae	*Cereus stenogosus* Schumann, *Pereskia saccharosa* Griseb., *Quiabentia chacoënsis* Backeb., *Stetsonia coryne* Britton & Rose.
Celastraceae	*Maytenus scutioides* (Griseb.) Lourt. & O'Don., *M. vitis-idaea* Griseb.
Leguminosae	*Acacia curvifructa* Burkart, *A. furcatispina* Burkart, *A. praecox* Griseb., *A. tucumanensis* Griseb., *Caesalpinia paraguariensis* (Parodi) Burkart, *Mimosa castanoclada* Barneby & Fortunato, *M. chacoënsis* Barneby & Fortunato, *M. detinens* Benth., *Mimozyganthus carinatus* Burkart, *Prosopis kuntzei* Harms.
Nyctaginaceae	*Bougainvillea praecox* Griseb.
Palmae	*Trithrinax schizophylla* Drude.
Polygonaceae	*Ruprechtia triflora* Griseb.
Rhamnaceae	*Ziziphus mistol* Griseb.
Sapindaceae	*Athyana weinmanniifolia* (Griseb.) Radlk.
Simaroubaceae	*Castela coccinea* Griseb.
Zygophyllaceae	*Bulnesia bonariensis* Griseb., *B. sarmientoi* Griseb.

4.2.2. The Wet Chaco Flora (Palm-savannas Flora)
[Savana Estépica Parque (VELOSO & GÓES-FILHO, 1982)]

This flora grows in the temporarily waterlogged soils of the so-called "Chaco humedo", i.e. the flooded plains of the Ríos Paraguay and Paraná. In Paraguay, the Palm-savannas Flora thrives mainly on the W side of the Río Paraguay, especially in the Río Pilcomayo region, and subsidiarily in the Paraná-Paraguay delta (Ñeembucú, Misiones, Itapua departments). *Copernicia alba* Morong builds up the extensive Palm-savannas of the E Chaco and of the Pantanal. In the "Chaco Humedo" these are in close contact with the xeromesophilous forests with *Schinopsis balansae* Engl. and *Astronium* spp., with the xerohygrophilous forests with *Prosopis* spp., and with the semi-evergreen gallery-forests. *Schinopsis balansae* Engl. is a leading species of the xeromesophilous forests of the E Chaco (= "Chaco Humedo") (SPICHIGER & al., 1991). Though frequent in the wet Chaco it also occurs in the E Paraguay where it enters into the semi-evergreen forests. The xeromesophilous

forests and the Palm-savannas form a forest-savanna mosaic landscape. According to FIEBRIG & ROJAS (1933), the limits of the Palm-savannas correspond precisely to contour-lines. The Palm-savannas occupy the parts of the land which are flooded during 3 to 4 months. The extension of this type of vegetation depends on the degree of flooding.

The "Chaco Humedo" region is a boundary zone where many elements are intermingled, viz. Chaco and RPDS species, not to mention anthropogenous pan-American or cosmopolitan species. For instance *Sebastiana virgata* Müll. Arg., a neotropical shrub, grows gregariously on the temporarily flooded banks.

The euphorbiaceous *Aporosella chacoënsis* (Morong) Speg. is a typical gregarious tree of the wet Paraguayan Chaco. It occurs strictly along the Chaquenian rivers and marshes, where it builds up monospecific populations on the temporarily flooded banks. We have observed this species around marshes in the foothills of the Cerro León.

The most significative Paraguayan representatives of the genus *Prosopis,* e.g. *P. alba* Griseb., *P. nigra* (Griseb.) Hieron., *P. kuntzei* Harms, and *P. vinalillo* Stuckert, rather belong to the wetter areas of the Paraguayan Chaco ("Chaco Humedo", and especially the Río Pilcomayo system) where they build up xerohygrophilous forests ("Bosques de algarobos"). Nevertheless, they can also be found, like other Chaquenian elements, in the E part of the Paraguay river drainage (Ñeembucú, Concepcion, San Pedro departments).

The following species can be related to the Wet Chaco Flora:

Anacardiaceae	*Schinopsis balansae* Engl.
Apocynaceae	*Aspidosperma triternatum* N. Rojas, *Thevetia bicornuta* Müll. Arg.
Bignoniaceae	*Tabebuia nodosa* (Griseb.) Griseb.
Compositae	*Tessaria dodoneaefolia* (Hook. & Arn.) Cabrera, *T. integrifolia* Ruíz Lopez & Pavón.
Euphorbiaceae	*Aporosella chacoënsis* (Morong) Speg., *Sapium haematospermum* Müll. Arg.
Leguminosae	*Acacia aroma* Hook. & Arn., *A. caven* (Molina) Molina, *Cathormion polyanthum* (A. Sprengel) Burkart, *Geoffroea decorticans* (Hook. & Arn.) Burkart, *Mimosa glutinosa* Malme, *Prosopis affinis* Sprengel, *P. alba* Griseb., *P. fiebrigii* Harms, *P. nigra* (Griseb.) Hieron., *P. nuda* Schinini, *P. rojasiana* Burkart, *P. ruscifolia* Griseb., *P. sericantha* Hook. & Arn., *Sesbania virgata* (Cav.) Poiret.
Palmae	*Copernica alba* Morong.
Santalaceae	*Acanthosyris falcata* Griseb.

4.3. Floras related to the Province of Uplands of Central Brazil (TAKHTAJAN, 1986)

[= Regionen der zentralbrasilianischen Campos Cerrados (HUECK, 1966); Planalto phytochorium (PRANCE, 1989)]

4.3.1. The Cerrado Flora

[Savana Arbórea Densa/Aberta (VELOSO & GÓES-FILHO, 1982)]

This xeric flora reaches the Paraguayan territory from the Central Brazilian Campo Cerrado and Cerradão. It occupies open formations of NE Paraguay (Amambay, Canendiyu, Concepcion departments) and the tops of the fossil sand dunes, serranias and Cerros of the "Paraguay Occidental" (presently Alto Paraguay, Boquerón departments).

Most *Annonaceae* are to be considered as savanna-shrubs native to central Brazil but also protruding southwards into the campos of E Paraguay. The most species cited by SPICHIGER & MASCHERPA (1983) are savanna species, or at least, species of open vegetation, viz. *Annona campestris* R. E. Fries, *A. dioica* A. St. Hil., *A. nutans* R. E. Fries, *Duguetia furfuracea* (A. St. Hil.) Benth.

& Hook. f. Often occurring together with dwarf *Myrtaceae*, they are leading species of the campos in the N and NE "Paraguay Oriental". *Annona campestris* R. E. Fries has even been collected by Spichiger and Ramella on the foothills of the Cerro León (W Chaco).

Vochysiaceae, with about 7 woody species in Paraguay, is also to be considered as a typical family native of the Campo Cerrado of Central Brazil. They spread into the "Paraguay Oriental" via the savannas. *Qualea cordata* Sprengel and *Vochysia tucanorum* C. Martius, the most frequent species recorded by SPICHIGER & LOIZEAU (1985), thrive in the savannas as well as in the open forests or galleries of NE Paraguay. They often present a gregarious habit, and grow frequently on rocky substrates. *Callisthene hassleri* Briq. seems to be an endemic species of the "Sierra de Amambay". *Qualea multiflora* C. Martius, *Q. parviflora* C. Martius and *Vochysia cinnamomea* Pohl are other species entering into the N of E Paraguay, whereas *Qualea grandiflora* C. Martius seems to extend more towards the N, reaching the Amazonian "campinas".

Typical species are:

Anacardiaceae	*Astronium fraxinifolium* Schott, *Schinus ferox* Hassler.
Annonaceae	*Annona calophylla* R. E. Fries, *A. campestris* R. E. Fries, *A. coriacea* C. Martius, *A. crassiflora* C. Martius, *A. crotonifolia* C. Martius, *A. dioica* A. St. Hil., *A. glaucophylla* R. E. Fries, *A. nutans* R. E. Fries, *A. paraguayensis* R. E. Fries, *A. phaeoclados* C. Martius, *Duguetia furfuracea* (A. St. Hil.) Benth. & Hook. f.
Apocynaceae	*Aspidosperma tomentosum* C. Martius, *Hancornia speciosa* Gomes, *Rauvolfia weddelliana* Müll. Arg.
Bignoniaceae	*Jacaranda cuspidifolia* C. Martius, *Tabebuia aurea* (Manso) Benth. & Hook. f.
Bombacaceae	*Eriotheca gracilipes* (Schumann) Robyns, *Pseudobombax argentinum* (R. E. Fries) Robyns, *P. longiflorum* (C. Martius & Zucc.) Robyns, *P. marginatum* (A. St. Hil. & al.) Robyns, *P. tomentosum* (C. Martius & Zucc.) Robyns.
Caryocaraceae	*Caryocar brasiliense* A. St. Hil.
Cochlospermaceae:	*Cochlospermum regium* Pilger.
Lauraceae	*Ocotea minarum* Nees.
Leguminosae	*Mimosa nuda* var. *glaberrima* (Chodat & Hassler) Barneby, *M. nuda* var. *gracilipes* (Harms) Barneby, *M. sensibilis* var. *urucumensis* Barneby.
Meliaceae	*Trichilia stellato-tomentosa* Kuntze.
Palmae	*Butia paraguariensis* (Barb. Rodr.) L. Bailey.
Rutaceae	*Helietta mollis* (Miq.) Kaastra[1], *Fagara hassleriana* Chodat.
Sapindaceae	*Toulicia tomentosa* Radlk.
Sapotaceae	*Pouteria ramiflora* Radlk., *P. torta* Radlk.
Simaroubaceae	*Simaba glabra* Engl., *S. trichilioides* A. St. Hil.
Tiliaceae	*Luehea paniculata* C. Martius.
Vochysiaceae	*Callisthene hassleri* Briq., *Qualea cordata* Sprengel, *Q. grandiflora* C. Martius, *Q. multiflora* C. Martius, *Q. parviflora* C. Martius, *Vochysia tucanorum* C. Martius.

4.3.2. The Dwarf Geoxylic Flora
[Savana Gramíneo Lenhosa (VELOSO & GÓES-FILHO, 1982)]

The Dwarf Geoxylic Flora builds up patches of a most peculiar vegetation called "chamaedendrée" by CHODAT & VISCHER (1916). The latter vegetation type is a very peculiar campo, built

[1]*Helietta mollis* sensu SPICHIGER & STUTZ DE ORTEGA (1987) = *H. puberula* Fries in the recent generic revision of PIRANI (1995).

up of dwarf trees or geoxylic subshrubs sensu PENNINGTON (1990). It is scattered throughout S and W-central Brazil, and E Paraguay. It is probably a relict of an ancient drier formation which has been maintained till now due to special local edaphic conditions associated with periodic fire ("fireclimax") (KLEIN, 1975).

Some characteristic species are:

Anacardiaceae	*Anacardium humile* A. St. Hil.
Erythroxylaceae	*Erythroxylum suberosum* A. St. Hil.
Caryocaraceae	*Caryocar brasiliense* Cambess.
Leguminosae	*Andira laurifolia* Benth.
Malpighiaceae	*Byrsonima crassa* Niedenzu, *B. intermedia* A. Juss.
Palmeae	*Cocos campicola* Barb. Rodr.
Sapindaceae	*Talisia pygmaea* Radlk.
Sapotaceae	*Pradosia brevipes* (Pierre) Penn.
Simaroubaceae	*Simaba praecox* Hassler.
Theophrastaceae	*Clavija hassleri* Mez.

4.4. The Atlantic Pluvial Flora (Mata Atlantica Flora)

[Region der brasilianischen Küstenregenwälder (HUECK, 1966); Provincia Atlantica (CABRERA & WILLINK, 1973); Floresta Ombrófila Densa (VELOSO & GÓES-FILHO, 1982); Atlantic Province (TAKHTAJAN, 1986); Atlantic Coastal Phytochorium (PRANCE, 1989)].

According to KLEIN (1975), several of the trees recorded for the Alto Paraná forests are also present in, and perhaps native of, the Atlantic Pluvial Forest. Having reached the Paraguayan territory via the Southern Plateau, Atlantic shrubs and treelets now build up the underlayer of some ill-drained, semi-deciduous *Lauraceae* tall forests of the Paraná-Uruguay basins. For instance, *Myrciaria rivularis* var. *baporeti* (D. Legrand) D. Legrand is a striking, preponderant element in most of the ill-drained forests, but also occurs frequently in rocky cerros and hill forests. Its great ecological plasticity is associated with a wide S tropical area of distribution, centred in the Mata Atlantica-Meridional Planalto region.

Other *Myrtaceae* constitute, together with RPDS Flora elements, the low vegetation covering and surrounding the sandstone cerros of the Mesopotamy. Low deciduous *Myrtaceae* forests are frequently reported as forming an ecoclinal belt on xeric, often hardened soils, or on a temporarily waterlogged substrate. Anyway this flora occurs in a stressfull environment. According to KLEIN (1975), the *Myrtaceae* flora, which reaches E Paraguay, is an important component of the Mata Atlantica.

Two Palms are also important Atlantic elements of the Paraguayan vegetation:

— *Syagrus romanzoffiana* (Cham.) Glassmann is wide-spread in all the tall semi-evergreen forests, especially in the Paranean region. It occurs most frequently in the swampy *Lauraceae-Luehea divaricata-Myrciaria rivularis* tall forest as observed by REITZ (1974) and HAHN (1990). It is also reported as being preponderant in the psammophilous *Helietta apiculata-Syagrus romanzoffiana* tall forests of the Hernandarias region (Alto Paraná department) (SPICHIGER & al., 1992). The species has a wide distribution in the S tropics through to Uruguay. It is found both in the Meridional Planalto and in the Mata Atlantica; it is rather to be considered as an element of the Mata Atlantica with a westwards extension in E Paraguay;

— *Euterpe edulis* C. Martius is a differential element of the Paraná riparian forests (riparian facies of the Paraná river with *Guarea kunthiana* A. L. Juss. and *Euterpe edulis* C. Martius sensu SPICHIGER & al., 1992). Here it probably reaches its westernmost limit. In the Mata Atlantica area it grows on red lateritic clayey soils (REITZ, 1974; HAHN, 1990).

Characteristic species are:

Anacardiaceae	*Astronium gracile* Engl.
Annonaceae	*Xylopia brasiliensis* Sprengel.
Guttiferae	*Rheedia gardneriana* Planchon & Triana.
Lecythidaceae	*Cariniana estrellensis* Kuntze.
Leguminosae	*Myrocarpus frondosus* Fr. Allem.
Myrtaceae	*Blepharocalyx salicifolius* (Kunth) O. Berg, *Calyptranthes concinna* DC., *Eugenia uniflora* L., *Myrcia multiflora* (Lam.) DC., *Myrciaria ciliolata* O. Berg, *Myrciaria rivularis* O. Berg.
Palmae	*Euterpe edulis* C. Martius, *Syagrus romanzoffianus* (Cham.) Glassmann.

4.5. The Widely Neotropical Wet Flora reaching its southernmost limit in Paraguay [Floresta Ombrófila Densa Aluvial (VELOSO & GÓES-FILHO, 1982)]

Tapirira guianensis Aublet, a forest tree with a wide neotropical distribution, reaches its southernmost limit in NE Paraguay and S Brazil. According to SMITH (1962) its origin could be Amazonian. We have also recorded it from the Peruvian Amazon (SPICHIGER & al., 1990). The abundance of *Guarea kunthiana* A. L. Juss. characterizes the riparian facies of the Paraná river (SPICHIGER & al., 1992). This species belongs to the Amazonian Flora where it normally grows in non-flooded lowland forests (PENNINGTON, 1981). But in Paraguay, under drier and less uniform climatic conditions, it is confined to gallery and riverine forests. It is a pioneer, or a relict, of a wetter and warmer vegetation type which reaches its southernmost limit in Paraguay. *Guarea guidonia* (L.) Sleumer is another Amazonian species reaching its southernmost outpost in the Río Apa region and in the Paraná riverine forest.

Following species are native of the Amazon basin and have reached Paraguay via the dry central Brazil by colonizing the gallery forests or other favourable relays (hills, cordilleras). The wettest forests of Paraguay (Paraná, Amambay department) constitute their southernmost border:

Anacardiaceae	*Tapirira guianensis* Aublet.
Lauraceae	*Nectandra cuspidata* Nees, *N. hihua* (Ruíz Lopez & Pavón) Rohwer.
Meliaceae	*Guarea guidonia* (L.) Sleumer, *G. kunthiana* A. L. Juss., *Trichilia pallida* Sw.
Monimiaceae	*Siparuna guianensis* Aublet.
Sapotaceae	*Pouteria glomerata* Radlk.
Rutaceae	*Fagara riedeliana* (Engl.) Engl.

Other species seem to be generalists belonging to a rather wet flora without being strictly Amazonian trees. For instance, *Actinostemon concolor* (Sprengel) Müll. Arg., a neotropical shrub, grows gregariously in the forests skirting the cerros of the Mesopotamy, often in association with *Myrtaceae* species and *Rollinia emarginata* Schldl. *Alchornea triplinervia* (Sprengel) Müll. Arg. is a heliophilous tree which grows on river banks; it is characteristic of the Paraná riverine forest. It is widely distributed in wet tropical America. We have also recorded it from the Peruvian Amazon.

The following species occur often in secondary stages and in natural or artificial gaps. Some of them even reach the tropical regions of N America:

Anacardiaceae	*Anacardium occidentale* L.
Annonaceae	*Rollinia emarginata* Schldl.
Araliaceae	*Schefflera morototoni* (Aublet) Maguire & al.
Bignoniaceae	*Tabebuia impetiginosa* (C. Martius) Standley.
Bixaceae	*Bixa orellana* L.
Caricaceae	*Jacaratia spinosa* (Aublet) A. DC.

Capparaceae	*Crataeva tapia* L.
Euphorbiaceae	*Actinostemon concolor* Müll. Arg., *Alchornea triplinervia* Müll. Arg.
Flacourtiaceae	*Casearia sylvestris* Sw.
Guttiferae	*Calophyllum brasiliense* Cambess.
Leguminosae	*Acacia polyphylla* DC., *Albizzia polyantha* (A. Sprengel) G. P. Lewis.
Moraceae	*Chlorophora tinctoria* Gaudich.
Olacaceae	*Ximenia americana* L.
Rutaceae	*Esenbeckia grandiflora* C. Martius, *Fagara rhoifolia* (Lam.) Engl.
Sapindaceae	*Allophylus edulis* (A. St. Hil. & al.) Radlk., *Sapindus saponaria* L.
Tiliaceae	*Heliocarpus americanus* L.
Verbenaceae	*Vitex cymosa* Sprengel.

4.6. The Widely Neotropical Dry Flora

Some species belong to a widely distributed dry flora. For instance, the palm *Acrocomia aculeata* C. Martius is widespread throughout the drier areas of the Neotropics, from Mexico to Argentina (HAHN, 1990). In Paraguay it is very frequent in the grasslands of central "Paraguay Oriental". BORDAS (pers. com.) attributes this wide distribution to the fruit dispersal by cattle.

In Paraguay some of the following species occur either in the Chaco, or in the NE and mesopotamian campos:

Annonaceae	*Xylopia aromatica* (Lam.) C. Martius.
Apocynaceae	*Vallesia glabra* (Cav.) Link.
Leguminosae	*Acacia farnesiana* (L.) Willd., *A. macracantha* Willd., *Cercidium praecox* (Ruíz Lopez & Pavón) Harms, *Mimosa hexandra* M. Micheli, *M. pellita* Willd., *M. pigra* L., *M. strigillosa* Torrey & A. Gray, *M. xanthocentra* C. Martius.
Meliaceae	*Trichilia hirta* L.
Palmae	*Acrocomia aculeata* C. Martius.
Rutaceae	*Fagara pterota* L.

5. Contact between floras and hot spots of specific tree diversity

The limits of and the relationships between the above-mentioned floras are not easy to draw. Furthermore, the species can occur in several different floras where they may have a different habitat as a result of the local environmental conditions. To summarize (Fig. 1): E of the Río Paraguay, the Paraguayan territory has a core of RPDS Flora; superposed on this, there is a wetter flora, the Paranean Flora or *Lauriflora,* mixed with elements of the Mata Atlantica. W of the Río Paraguay, the so-called "Paraguay Occidental", two edaphoclimacic floras are found, viz. the Chaquenian and the Palm-savannas Floras respectively, the former constituting the "Chaco Seco" and the latter the "Chaco Humedo". The open formations of NE Paraguay are covered with an allochtonous savanna or cerrado-type vegetation. The particular *Araucaria* patch mentioned could be a relict of the more E "Pinhais" flora. The Dwarf Geoxylic Campos Vegetation is a remnant of most ancient arid palaeoenvironment.

In various regions of the Paraguayan territory, different floras coexist or compete with each other. The occurrence of several flora types in the same area is the result of past climatic variations, or eventually of geomorphological transformations. Thus the following hot spots of specific tree diversity deserve mentioning:

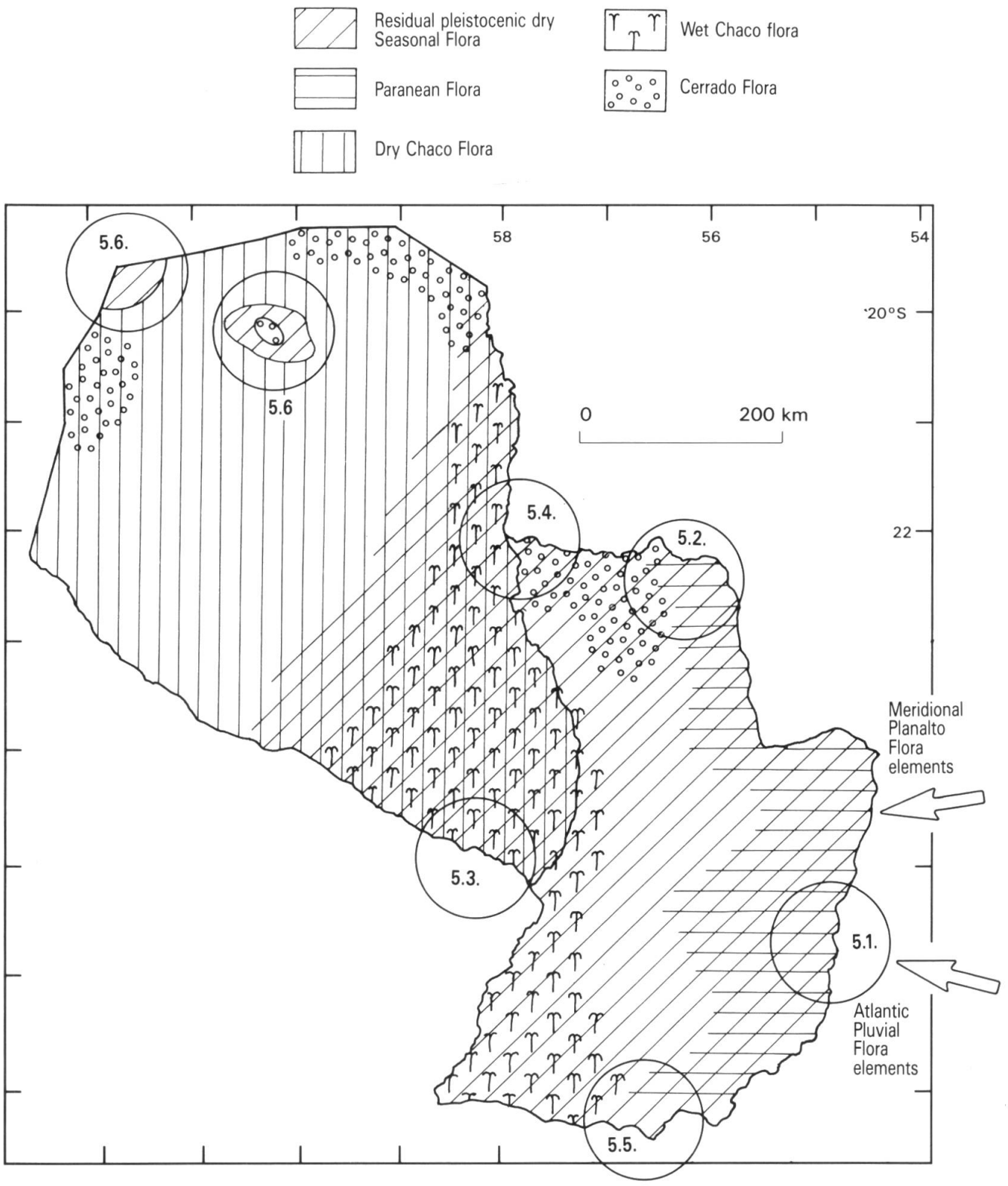

Fig. 1. — Distribution of the various dendrofloras occuring in the Paraguayan territory and hot spots of specific tree diversity.

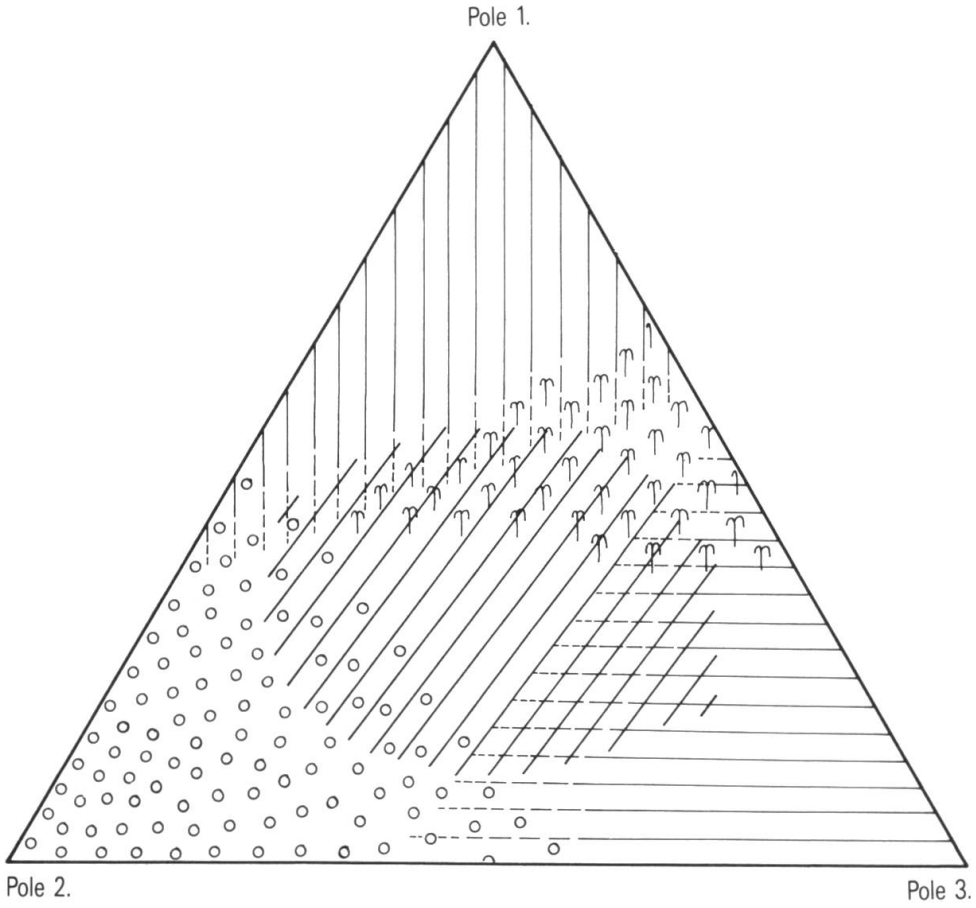

Fig. 2. — Main ecological trends affecting the present Paraguayan dendrofloras.
Pole 1: alkaline soil, loamy texture, low rainfall. **Pole 2:** acid soil, sandy texture, low rainfall. **Pole 3:** acid soil, clayey texture, high rain fall.

5.1. *The Paraná region* is the meeting point between the Paranean Flora *(Lauriflora)* and the RPDS Flora, the Atlantic Flora and some elements from the Amazon basin and from the Meridional Planalto. The result of this mixture is a high level of tree species diversity.

5.2. *The Amambay region* is a meeting point between the Cerrado and the South-east and South Brazilian Floras. Very interesting are the patches of savanna (Cerrado Flora) and *Chamaedendrées* (Dwarf Geoxylic Flora) enclosed in the Paranean forest mass.

5.3. Another most interesting boundary zone is the *Wet Chaco ("Chaco humedo")*, in the lower Pilcomayo region, where Palm-savannas, xeromesophilous forests with *Schinopsis balansae* Engl. and semi-evergreen forests meet. Thus the RPDS Flora (with some Paranean elements), the Palm-savannas and the Chaquenian Floras are closely intermingled in accordance with local topography, edaphic humidity and alkalinity (SPICHIGER & al., 1991).

5.4. *The Río Apa — Río Paraguay region* is particularily interesting because of the geomorphological and pedological diversity (calcareous soils, sandy meadows, etc.), as well as the confluence of RPDS, Cerrado and Chaco Floras.

5.5. *The Ñeembucú, Misiones, Itapua departments* also deserve mentioning because they form a most interesting boundary zone between the Chaquenian, the Palm-savannas, the RPDS and the Paranean Floras [island forests of *Tabebuia heptaphylla* (Vell. Conc.) Toledo and *Astronium balansae* Engl.].

5.6. *The Cerro vegetation situated within the Chaquenian region* is also quite diversified. For instance, in the Cerro León serrania three floras succeed each other in accordance with the local geomorphology: the Chaco Flora skirts the serranias; on the slopes there is a mesophilous vegetation made up of RPDS species; at last, on the tops a Cerrado Flora is present.

From a conservationist point of view, these regions should deserve top priority of protection and study due to the high specific diversity level (alpha-diversity) which is a result of the juxtaposition of several floras and vegetations (beta-diversity).

6. Discussion

The distribution patterns of the present Paraguayan floras are correlated with specific ecological conditions and trends, which can be summarized in the following manner (Fig. 2). Three poles determine these trends. One is related to alkaline, salty, loamy soils and low rainfall; the second to acid, sandy soils and also low rainfall; the third to clayey or sandy-clayey, acid soils and high rainfall. The central position of the RPDS Flora reflects its opportunist behavior due to its wide ecological plasticity in the Paraguayan territory.

The flora types, which can be identified along these trends, are the responses to present and past climatic conditions and to extrem edaphic constraints.

The Palm-savannas should expand as a consequence of the decreasing slope gradient of the Río Paraguay drainage system and of the filling up of the river beds. The strongly arid periods of the Pleistocene Glacial Maximum (and before) and of the middle Holocene led to the building up of aeolian dunes in W Chaco. These dunes were consolidated and colonized by a Cerrado or a RPDS Flora. Presently, the competition between the Chaquenian and the RPDS Floras seems to be at the advantage of the latter due to the present edapho-climatic conditions (PRADO, 1993). The RPDS Flora also occurs on the Cerros and Cordilleras of the Chaquenian region, often intermingled with patches of Cerrado vegetation. These two floras are anterior to the surrounding Chaco Flora which is bound to the youngest substrate. Where the peculiar Chaquenian substratum leaves place for sand dunes, ground-levees along the rivers or rocky hills, the edaphoclimacic xeromorphic Chaquenian formations disappear at the advantage of the Cerrado Flora (on dry sandy soils) or the RPDS Flora (on moister sandy-clayey soils or calcareous ones).

The Paranean Flora elements are fragmentary remnants of the once extensive ones, which very likely reached the Amazonian region during the dry climatic maxima of the Pleistocene (SPICHIGER & al., 1992) and which penetrated into the Andean region via the "Marañon Gap", thus establishing a further link with the Carribean-Guajira province through NW Peru and Ecuador (PRADO & GIBBS, 1993). Anyway, according to BROWN (1982), it seems that the Yguazú area and the Upper Paraná basin would have served as forest refuges since at least 20'000 yr BP. This is corroborated by the co-habitation of the different floras we have observed in the Paraguayan Alto Paraná: Pinhais, strict Paranean, RPDS and Atlantic Floras. This accumulation of different flora elements indicates that this region has long functioned as a refuge. It is typically a Quarternary region — refuge sensu the former author with regard to the high number of species and the low number of endemics.

On the contrary, the Cerrado and Dwarf Geoxylic Floras are reverse-refuges (according to GENTRY, 1982) to a Tertiary or early Pleistocene xeric flora.

The E Paraguayan territory is an ecoclinal region where endemism is low. This low rate can be explained by the recentness of the Paraná refuge (probably late Pleistocene), and/or by the

allochtonous origin of the other floras which reach the Paraguayan territory only on their edges (Atlantic, Cerrado, and Meridional Planalto Floras).

Considering the "Pinhais", we note that *Araucaria angustifolia* (Bertol.) Kuntze has very specific requirements: it does not regenerate inside a dark forest but, under the present-day climatic conditions, it could be considered as a pionneer species in open areas for the forest regeneration (BEHLING, 1993). This means that the climacical S Brazilian *Araucaria* formations are open woodlands rather than closed forests. Consequently the present S Brazilian *Araucaria* stands have to be considered as *Araucaria* woodlands which are presently invaded by (sub-)tropical semi-evergreen species, especially Paranean ones. Assuming a present-day rise of temperature, an extension in all directions of the Paranean Flora might be expected. This perspective is strongly darkened by the high level of destructive human activities and the depleting of the vegetation in the E Paraguay and S Brazil regions.

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