The Forests of the Paraguayan Alto Parana

RODOLPHE SPICHIGER
BERNARDINO S. BERTONI
&
PIERRE-ANDRÉ LOIZEAU

ABSTRACT

SPICHIGER, R., B. S. BERTONI & P.-A. LOIZEAU (1992). The Forests of the Paraguayan Alto Parana. *Candollea* 47: 219-250. In English, English and French abstracts.

The frequent occurrence of *Lauraceae* characterizes most of the Paraguayan Alto Parana tall semi-evergreen forests. *Lauraceae-Cedrela fissilis-Chrysophyllum gonocarpum* tall forests grow on the well-drained soils and are to be considered as the climacical vegetation. Three facies are described: typical facies with *Balfourodendron riedelianum*, riparian facies with *Guarea kunthiana* and *Euterpe edulis*, xeric facies with *Helietta apiculata*. Other *Lauraceae* tall forests with *Luehea divaricata* and *Myrciaria rivularis* are confined to the swampy substrates. The number of trees by ha, the basal area and the tree biodiversity are lower than in other more northern neotropical tall forests. Other tall forests are allochtonous formations: *Araucaria angustifolia-Luehea divaricata* forests native to the south-eastern Brazilian Planalto, and *Helietta apiculata-Syagrus romanzoffiana* forests native to the basin of the Paraguay river. The *Myrtaceae* low forests are ecoclinal formations.

RÉSUMÉ

SPICHIGER, R., B. S. BERTONI & P.-A. LOIZEAU (1992). Les forêts de l'Alto Parana paraguayen. *Candollea* 47: 219-250. En anglais, résumés anglais et français.

L'abondance de *Lauraceae* caractérise les forêts semi-décidues du département paraguayen du Alto Parana. Les forêts hautes à *Lauraceae-Cedrela fissilis-Chrysophyllum gonocarpum* représentent la formation climacique et occupent les meilleurs sols. Les auteurs ont mis en évidence trois faciès: un faciès typique à *Balfourodendron riedelianum*, un faciès caractéristique de la forêt riveraine du Parana (faciès à *Guarea kunthiana* et *Euterpe edulis*), un faciès plus xérique à *Helietta apiculata*. D'autres forêts hautes à *Lauraceae-Luehea divaricata-Myrciaria rivularis* sont confinées aux substrats mal drainés. Le nombre d'arbres par hectare, l'aire basale et la biodiversité des arbres sont inférieurs à ce qui a été relevé dans les forêts néotropicales plus septentrionales. D'autres forêts hautes sont des formations allochtones: forêts à *Araucaria angustifolia* et *Luehea divaricata* originaires du Planalto sud-est brésilien, forêts à *Helietta apiculata* et *Syagrus romanzoffiana* provenant du bassin du rio Paraguay. Les forêts basses à *Myrtaceae* sont des formations écoclinales.

1. Introduction

The aims of this paper are:

— to describe the almost undisturbed and undamaged-looking forests of the Paraguayan department of Alto Parana (structure, biodiversity, floristic relationships, ecological trends);

— to propose a classification of these forests.
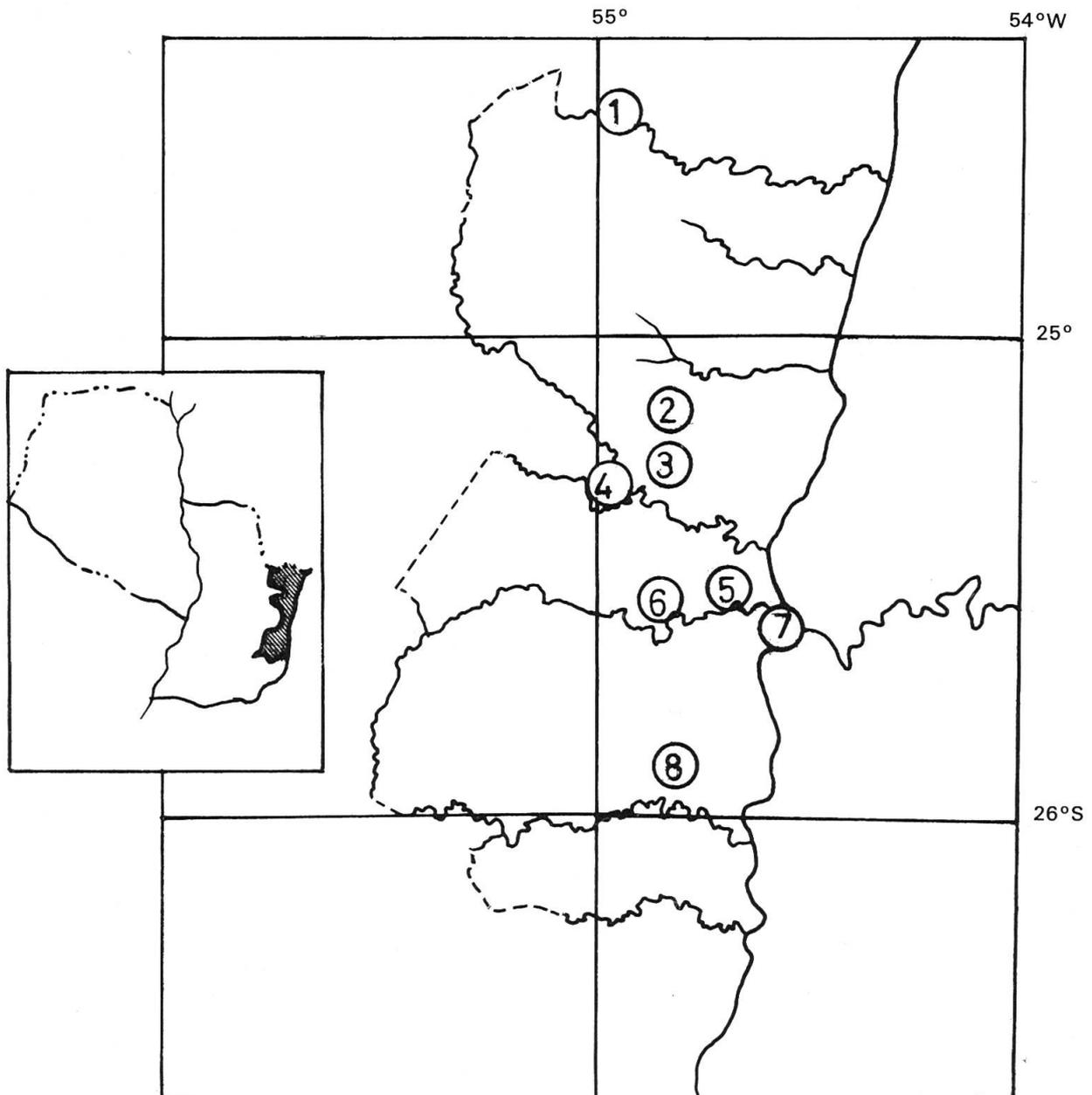
Fig. 1. — Department of Alto Parana with the situation of the study areas.

1, BS10, BS11, BS12   **5,** SP01, FU, LC, BS05, BS06
2, BS09   **6,** BS03
3, BS08   **7,** BS01, BS02
4, BS07   **8,** BS4

The Alto Parana department is situated between 54°30'W and 55°30'W, and between 24°30'S and 26°20'S, respectively (Fig. 1). According to GORHAM (1973), cited by STUTZ DE ORTEGA (1986), this department is located on the annual isotherm of 22°C and the annual isohyet of 1700 mm. January, February and March are the warmest and wettest months, July and August the coldest and dryest. During these winter months, absolute minima below 0°C are frequently recorded. According to different authors, the climate is considered continental-subtropical, continental-tropical, or rainy-subtropical (STUTZ DE ORTEGA, 1986, 1987). Applying the classification of Bagnouls & Gaussen, ESKUCHE (1984) describes the climate of the Iguaçu Valley as perhumid.

Several detailed studies on the secondary stages of the Alto Parana forests have been carried out by STUTZ DE ORTEGA (STUTZ, 1983; STUTZ DE ORTEGA, 1984, 1986; ORTEGA STUTZ, 1989). In these papers she provided many data referring to the structure, the dynamics and the floristic composition of the vegetation.

More recently BOLOS, CERVI & HATSCHBACH (1991) published an interesting paper on the vegetation of the neighbouring Brazilian state of Parana. In this contribution they describe some phytosociological communities of forests that are closely related to those figuring in our proposed typification.

2. Material and methods

According to our own field observations in Paraguay and our experience elsewhere in the intertropical zone, the occurrence of different lowland forest types in the same area may be related to the following interdependent factors: the catenary position of the vegetation (i.e. the topography), the soil texture, the proximity of savannas or streams, and the degree of disturbance of the vegetation. Consequently we took these environmental factors into consideration when chosing our forest plots.

Today, the high degree of human interference in the Paraguayan Alto Parana forests makes it difficult to find natural or even little disturbed formations. As a result it is not easy to describe the true original vegetation and flora. Nevertheless we chose forest plots that seemed to be as undamaged as possible and that proved not to have been disturbed for at least 25 years. In addition to these almost untouched-looking surfaces we also studied secondary stages and more disrupted patches of forest. Human interference is such a common phenomenon in the Paraguayan forests that it would be wrong not to include disturbed forests in our analysis.

16 surveys were carried out by Bertoni (BS-relevés) and by Spichiger and Loizeau (SP-relevés). Their surfaces vary from 0.2 to 1 ha, with the exception of four plots which are smaller and situated in ecoclinal situations. We completed our data by including others collected in the same area by STUTZ DE ORTEGA (STUTZ DE ORTEGA, 1987; ORTEGA STUTZ, 1989) (LC-relevés), and by FISCHER (1981) (FU-relevés).

Only the trees having a diameter at breast height (i.e. 1.3 m above ground level) of ⩾ 10 cm were considered.

The degree of preponderance of each species in a survey is obtained by calculating the Importance Value Index (I.V.I.) (CURTIS & McINTOCH, 1951). This value is the sum of the relative abundance, the relative frequency and the relative dominance. The I.V.I. allows us to weight each species in a sample and makes it easier to differentiate between plots having almost the same floristic composition.

The species lists, weighted by the I.V.I., were compared with each other by means of ordination procedures using an EDA programme at the University of Geneva. The ANACOR method (ANAlyse factorielle des CORrespondances) of BENZÉCRI (1973) seemed to be the most appropriate for our treatment of variable-area surveys. Furthermore, this method is currently applied in phytosociology. The plots and species are scattered along different axes whose ecological

significance has to be interpreted. The plots which are floristically similar are thus placed close together. The same applies to species which have the same ecological trends. The ANACOR method allows us to corroborate a classification that we had empirically established during our field-work!

3. Results

3.1. *Landscape, geomorphology and soils*

The Paranean landscape of Paraguay is made up of a succession of low topographic undulations separated by rivulets or wet depressions. Each topographic undulation consists of a crest (upland or alluvial zone), a slope (colluvial zone) and a depression (downslope or illuvial zone). In the region with almost untouched vegetation, the landscape is either covered with a continuous mantle of forest, or more rarely with a forest-savanna mosaic. In the latter case the forest occupies the uplands, the higher parts of the slopes and the riversides, whereas the savannas occupy the sandier lower parts of the slopes or the swampy downslopes. The banks of the Parana river are fringed by tall riverine forest which is in continuation with the lowland forests. Unfortunately these original landscapes are nowadays considerably affected by uncontrolled deforestation.

The soils (Table 1) are generally clayey, sandy-clayey or clayey-sandy. The soils which are poorer in clay are those of the Parana valley sensu-stricto and of the forest-savanna mosaic. In the forest-savanna mosaic area, the percentage of sand sometimes exceeds 80% on the slopes.

The upland soils are well-drained, clayey or sandy-clayey, dark-red or dark-chestnut coloured, and acid. The A-horizon is not deeper than 15 cm and is sandier than the B-horizon. On the slope, the soils are rather similar to the upland ones but with a deeper A-horizon.

The downslope soils are ill-drained and seasonnally swampy. Their texture is sandy in the A-horizon, while they are clayey, sandy-clayey or loamy-clayey underneath. They are dark in colour: dark-grey, dark-violet or dark-chestnut red. They are also acid. The A-horizon is deeper than that of the crests. Due to poor drainage, hydromorphic redox spots are present at a depth of 30 cm and more.

According to FAO/UNESCO (1971), cited by STUTZ DE ORTEGA (1987), the Alto Parana soils may belong to the orthic acrisols (a narrow western fringe), to the dystic nitosols (in the south and the center), and to the rhodic ferralsols (north-east). The texture is clayey, the colour dark-red or dark reddish-brown and the pH acid (about 5.0). In downslope locations, hydromorphic redox spots are present.

3.2. *Forest structure (Table 2)*

The virtually untouched forests of the Paraguayan Alto Parana area present two different aspects:

— tall forests with an average height of about 13 m, and with emergent trees exceeding 25 m in height (maximum observed 32 m). Following to BEARD (1944), STUTZ DE ORTEGA (1987) describes them as "semi-evergreen seasonal forests";

— low forests with an average height of 6 m.

The tall forests constitute the typical formations of this region, whereas the low forests are ecoclinal formations: transitional belts between tall forests and savannas, gallery-forest fringes inside savanna areas, invasive forest-islets surrounded by grasslands.

The basal areas measured for 1 ha of tall forest (SP01, FU01, FU02) fluctuate between 15.8 m^2 and 18.5 m^2. The extrapolated values from the smaller plots (0.2 and 0.25 ha) present a high

Plots	Localisation	A-horizon	B-horizon
SP01	Plateau, well-drained 54°47'W/25°30'S Tall forest: 1 ha	0-20 cm. pH 4.8 2.5 YR 2/4 Sand: 17.6%. Clay: 41.2%	> 20 cm. pH 5.2 2.5 YR 3/4 Sand: 6.4%. Clay: 77.6%
FU01	Plateau, well-drained 54°47'W/25°30'S Tall forest: 0.96 ha	0-20 cm. pH 4.8 2.5 YR 2/4 Sand: 17.6%. Clay: 41.2%	> 20 cm. pH 5.2 2.5 YR 3/4 Sand: 6.4%. Clay: 77.6%
BS07	Plateau, well-drained 54°57'W/25°22'S Tall forest: 0.2 ha	0-10 cm. pH 5.9 2.5 YR 2/4 Sand: 33.6%. Clay: 28.4%	> 10 cm. pH 4.6 2.5 YR 2/4 Sand: 13.6%. Clay: 69.2%
BS05	Plateau, well-drained 54°47'W/25°30'S Tall forest: 0.2 ha	0-20 cm. pH 4.8 2.5 YR 2/4 Sand: 17.6%. Clay: 77.6%	> 20 cm. pH 5.2 2.5 YR 3/4 Sand: 17.6%. Clay: 77.6%
BS02	Plateau, well-drained 54°40'W/25°38'S Tall forest: 0.2 ha	0-13 cm. pH 5.9 2.5 YR 3/4 Sand: 66.9%. Clay: 21.1%	> 13 cm. pH 5.3 2.5 YR 3/4 Sand: 66.4%. Clay: 25.6%
BS01	Slope, riverine forest 54°40'W/25°38'S Tall forest: 0.2 ha	0-45 cm. pH 7.1 7.5 YR 4/3 Sand: 84.0%. Clay: 6.8%	> 45 cm. pH 5.5 7.5 YR 4/3 Sand: 82.0%. Clay: 8.8%
BS10	Plateau, well-drained 54°57'W/24°33'S Tall forest: 0.2 ha	0-11 cm. pH 4.5 2.5 YR 3/6 Sand: 39.6%. Clay: 45.2%	> 11 cm. pH 4.6 2.5 YR 3/4 Sand: 39.6%. Clay: 47.2%
BS11	SLope, well-drained 54°57'W/24°33'S Ecoclinal tall forest: 0.2 ha	0-5 cm. pH 4.3 2.5 YR 3/4 Sand: 71.6%. Clay: 21.6%	> 5 cm. pH 4.4 2.5 YR 3/4 Sand: 64.9%. Clay: 27.1%
FU02	Downslope, ill-drained 54°47'W/25°30'S Tall forest: 0.96 ha	0-30 cm. pH 4.2 10 YR 7/1 Sand: 63.6%. Clay: 8.4%	> 30 cm. pH 4.6 2.5 YR 4/1 Sand: 17.6%. Clay: 69.2%
BS06	Depression, ill-drained 54°47'W/25°30'S Tall forest: 0.2 ha	0-30 cm. pH 4.2 10 YR 7/1 Sand: 63.6%. Clay: 8.4%	> 30 cm. pH 4.6 2.5 YR 4/1 Sand: 17.6%. Clay: 69.2%
BS03	Depression ill-drained 54°55'W/25°35'S Tall forest: 0.2 ha	0-30 cm. pH 3.9 5 YR 7/1 Sand: 47.6%. Clay: 9.2%	> 30 cm. pH 4.1 2.5 YR 2/4 Sand: 11.6%. Clay: 69.2%
BS08	Plateau, well-drained 54°52'W/25°20'S Tall forest: 0.2 ha	0-13 cm. pH 5.6 2.5 YR 3/3 Sand: 44.4%. Clay: 45.6%	> 13 cm. pH 4.4 5 YR 3/4 Sand: 52.9%. Clay: 31.1%
BS4C	Plateau, well-drained 54°52'W/25°52'S Tall forest: 0.03 ha	0-7 cm. pH 5.4 2.5 YR 2/4 Sand: 51.2%. Clay: 28.4%	> 7 cm. pH 4.7 2.5 YR 2/4 Sand: 23.6%. Clay: 58.4%
BS12	Slope, well-drained 54°57'W/24°33'S Ecoclinal low forest: 0.05 ha	0-10 cm. pH 3.6 10 R 3/4 Sand: 83.4%. Clay: 9.2%	> 10 cm. pH 3.9 2.5 YR 3/4 Sand: 70.0%. Clay: 26.0%
BS4B	Slope, ill-drained 54°52'W/25°52'S Ecoclinal low forest: 0.02 ha	0-5 cm. pH 4.0 2.5 YR 2/4 Sand: 23.6%. Clay: 57.2%	> 5 cm. pH 4.2 2.5 YR 3/4 Sand: 17.6%. Clay: 68.4%
BS09	Depression, ill-drained 54°52'W/25°08'S Invasive islet (low forest): 0.025 ha	0-50 cm. pH 3.6 7.5 YR 3/3 Sand: 29.6%. Clay: 37.2%	> 50 cm. pH 4.2 5 YR 3/4 Sand: 11.6%. Clay: 49.2%
BS4A	Riverside, seasonally strong contrasted edaphic humidity 54°52'W/25°52'S Gallery fringe (low forest): 0.03 ha	0-24 cm. pH 3.3 5 YR 3/1 Sand: 11.6%. Clay: 21.2%	> 24 cm. pH 4.2 7.5 YR 5/4 Sand: 7.6%. Clay: 53.2%

Table 1. – Soil characteristics (tall and low forests).

	Area (ha)	Height mean (m)	Height max (m)	Diam mean (cm)	Trees nb	Trees nb/ha	Basal area (m^2)	Basal area ha (m^2)
SP01	1.0	13	32	23.1	442	442	18.5	18.5
FU01	0.96	14	30	27.3	258	(270)	15.2	(15.8)
BS07	0.2	12	27	25.4	93	(465)	4.7	(23.5)
BS05	0.2	13	29	31.9	89	(445)	7.1	(35.5)
BS02	0.2	13	24	22.3	131	(655)	5.1	(25.5)
BS01	0.2	13	23	23.6	100	(500)	4.4	(22.0)
BS10	0.2	11	23	19.9	167	(835)	5.2	(26.0)
BS11	0.2	8	17	20.2	112	(560)	3.6	(18.0)
FU02	0.96	14	27	25.3	306	(320)	15.3	(15.9)
BS06	0.2	14	32	27.4	118	(590)	6.9	(34.8)
BS03	0.2	12	26	26.4	143	(715)	7.8	(39.0)
BS08	0.2	20	28	17.5	111	(555)	2.7	(13.5)
BS4C	0.03	13	24	*	44	*	*	*
BS12	0.05	6	11	10.7	43	(860)	0.4	(8.0)
BS4B	0.02	7	16	*	33	*	*	*
BS09	0.025	7	15	*	55	*	*	*
BS4A	0.03	5	8	*	80	*	*	*
Data according to STUTZ DE ORTEGA (1987: 222, 223)								
LC01	0.25				169	(676)	9.9	(39.6)
LC02	0.25				190	(769)	8.7	(34.8)
LC03	0.25				165	(669)	8.2	(32.8)
NB: ( ) = Figures extrapolated. * = Area not sufficient for an extrapolation.								
Table 2. – Forest structure.								

variability [from 19.5 m²/ha (BS08) to 39.6 m²/ha (LC01)] and give generally higher figures. The average basal areas for the tall forest plots are about 26.4 m²/ha, and the average diameter of the trees is approximatively 24 cm. Past disruption of the 1 ha-surveys SP01, FU01 and FU02 might explain the relatively low figures for their basal areas and number of trees. Nevertheless these slightly disrupted forests are nowadays the usual forest-type in Paraguay in places where the forests still exist!

Concerning the basal areas, STUTZ DE ORTEGA (1987) cites the following figures for other neotropical forests: 23,1 m² (French Guiana); 29.2 m² (Venezuela); 32.6 m² (Brazilian Amazonia); 27-32 m² (Surinam). BALSLEV & al. (1987) measured 33.7 and 35.5 m² in Ecuadorian Amazonia for average diameters of 24 and 33 cm respectively. BOOM (1986) states 21.5 m² for Beni (Bolivian Amazonia) and MORI & al. (1983a) 31.1 m² for the Brazilian state of Para. For the same region, CAMPBELL & al. (1986) give figures varying from 27.6 to 31.4 m². Consequently it appears that the calculated average basal area in the Paraguayan Alto Parana is generally lower than the one measured in Amazonian areas. Moreover, if we consider only the 1 ha area measured SP01 without taking into account the other extrapolated values, the 18.5 m² basal area is by far the lowest figure. This figure is close to the 21.5 m² measured by BOOM (1986) in Beni.

Our data for the low forests are not extensive enough to allow a quantitative comparison with tall forests. Nevertherless the basal area is evidently much lower (BS12: 8 m²/ha) and the average diameter smaller (ca. 10 cm).

The number of trees counted in one hectare of tall forest ranges from 270 (FU01) to 442 (SP01). The extrapolation of the 0.2 and 0.25 ha plot provides, (as for the basal areas) far higher values [from 445 (BS05) to 760 (LC02)]. The average number of trees for the tall forest plots is about 560, but we must attach more importance to the results based on a one-hectare survey, which are significantly lower (SP01: 442, FU01: 270, FU02: 320).

The 442 trees in the representative SP01-survey is close to the number counted by Balslev in an Ecuadorian floodplain forest (417), or by Gentry in Neblina base camp (493); it is also approximate to Campbell's figures for a Tierra firme forest in Brazilian Para (460) and a Varzea forest in the same state (440), and to Holdridge's value in Alajuela in Costa Rica (490). The SP01 figure is generally lower than the other values observed in neotropical moist forests.

The surveys made in low forest show that here the number of trees is considerably higher than in tall forests (860).

According to STUTZ DE ORTEGA (1987), there are up to 26-27% caducifolious trees in the Alto Parana tall forest. Thus the latter is to be considered as semi-caducifolious or semi-evergreen. Our surveys in low forests show a much higher simultaneous fall of the leaf ($\geqslant 80\%$).

In all our surveys of tall forests we have also observed the frequent occurrence of the climbing bamboo *Chusquea ramosissima*.

3.3. *Floristic composition and biodiversity (Tables 3, 4 and 5)*

According to Table 4, 12 families compose most of the Paranean forests: *Lauraceae, Sapotaceae, Meliaceae, Leguminosae, Palmae, Rutaceae, Myrtaceae, Sapindaceae, Tiliaceae, Euphorbiaceae, Moraceae* and *Boraginaceae.*

Palmae and *Lauraceae* are numerous in all the tall forest plots, whereas the trees belonging to *Meliaceae* and *Sapotaceae* are predominant only on the well-drained and more clayey soils (SP01, FU01, BS07, BS05, BS02). *Rutaceae* are well represented on the latter by *Balfourodendron* and *Fagara,* but are also abundant in the tall forests growing on sandier substrate (BS08) where *Helietta apiculata* makes up almost monospecific populations in the upper layer.

Tiliaceae and *Sapindaceae* are the most important components of the tall forests growing on ill-drained substrate (BS06, BS03, FU02). This has also been observed by STUTZ DE ORTEGA (1987).

The presence of *Leguminosae* is not as significant as the one of the precedent families. It often seems to be correlated with the secundarization processes of the forests. Genera like *Lonchocarpus* and *Machaerium* play an important role in the forest rehabilitation due to their heliophilous and anemochorous habits (ORTEGA STUTZ 1989).

Trees of *Myrtaceae* are most numerous in the low forests (BS12), in the invasive forest-islets (BS09) and in the ecoclinal formations (BS11). Some species of this family, such as *Myrciaria rivularis,* are also frequent in the ill-drained tall forests.

Other families are present in several plots but are generally of minor importance in the forest composition *(Euphorbiaceae, Boraginaceae, Moraceae).*

Thus, the Paraguayan Alto Parana tall forests are dominated by *Lauraceae*. The *Lauraceae* predominate together with *Meliaceae* and *Sapotaceae* on well drained soils, and with *Tiliaceae* and *Sapindaceae* on ill-drained substrate. These forests may be called *Lauraceae*-forests if we use a classification based on the preponderant families and by analogy with other neotropical forests. The Alto Parana *Lauraceae* tall forests should be added to other lowland neotropical forests dominated by families that are cited by CAMPBELL & al. (1986): *Myrtaceae*-forests near Bahia (Mori & al.); *Leguminosae*-forests in Amapa (Daly & al.); *Lecythidaceae*-forests near Manaus (Prance & al.); *Moraceae*-forests in Beni (Boom), *Myristicaceae-Euphorbiaceae*-forests in Acre (Campbell & al.), and so on.

Table 3. – Floristic composition, including I.V.I. of each tree species.

Species	LC01	BS07	BS02	BS01	BS10	LC02	BS06	BS03	BS08	LC03	BS05	LC30	LC10	BS4C	BS11	BS4B	BS09	BS12	BS4A	SP01	FU01	FU02	SP02
Cedrela fissilis	030.6	041.9	012.3	000.0	013.1	000.0	006.9	000.0	003.1	015.6	017.3	032.2	002.1	000.0	018.0	000.0	000.0	000.0	000.0	020.4	037.7	018.9	000.0
Arecastrum romanzoffianum	026.2	018.2	009.5	003.0	000.0	047.7	008.5	012.4	111.4	000.0	000.0	000.0	000.0	000.0	000.0	000.0	017.6	000.0	000.0	008.0	012.6	013.0	002.2
Allophylus edulis	021.2	000.0	002.1	000.0	000.0	007.2	000.0	003.5	003.2	002.5	003.5	002.1	000.0	000.0	000.0	000.0	000.0	000.0	000.0	001.9	004.1	010.1	000.0
Chrysophyllum gonocarpum	015.8	027.5	006.0	017.7	000.0	000.0	000.0	000.0	000.0	016.2	010.1	005.2	006.9	015.0	003.1	000.0	000.0	000.0	000.0	033.4	014.3	005.7	023.0
Jacaratia spinosa	016.3	000.0	000.0	007.2	000.0	000.0	000.0	000.0	000.0	010.3	033.1	000.0	022.5	000.0	000.0	000.0	000.0	000.0	000.0	011.6	001.7	000.0	000.0
Balfourodendron riedelianum	019.9	032.3	003.0	019.5	000.0	002.6	002.1	000.0	000.0	009.3	018.3	002.1	002.7	000.0	000.0	000.0	000.0	000.0	000.0	020.7	019.3	013.3	000.0
Sebastiana brasiliensis	008.7	000.0	000.0	000.0	000.0	008.7	000.0	016.4	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	013.6	000.0
Ocotea spectabilis	016.2	010.2	022.9	000.0	000.0	010.7	000.0	000.0	000.0	000.0	000.0	030.8	010.6	000.0	000.0	000.0	000.0	000.0	000.0	009.5	002.6	005.0	002.6
Cabralea canjerana	008.4	008.7	009.6	003.5	014.3	000.0	000.0	000.0	000.0	000.0	000.0	024.2	006.7	015.0	000.0	000.0	000.0	000.0	000.0	019.3	004.6	001.2	000.0
Diatenopteryxsorbifolia	008.8	007.4	000.0	000.0	000.0	022.2	002.1	017.5	006.3	008.3	005.7	002.8	000.0	015.0	000.0	000.0	000.0	000.0	000.0	001.3	000.0	008.1	000.0
Styrax leprosum	005.8	000.0	000.0	000.0	000.0	000.0	000.0	000.0	003.1	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	001.2	000.0
Cecropia pachystachya	004.2	000.0	000.0	009.7	000.0	002.1	000.0	000.0	056.6	000.0	020.6	067.8	000.0	000.0	000.0	000.0	000.0	000.0	000.0	006.6	002.2	000.0	002.5
Nectandra megapotamica	007.1	035.4	042.3	049.4	000.0	004.1	057.0	001.9	009.8	016.3	023.7	000.0	006.7	030.0	000.0	000.0	000.0	000.0	000.0	021.8	021.2	010.5	000.0
Urera caracasana	005.6	002.5	000.0	000.0	000.0	000.0	000.0	000.0	000.0	001.9	000.0	003.9	000.0	000.0	000.0	000.0	000.0	000.0	000.0	004.2	000.0	000.0	000.0
Nectandra lanceolata	007.6	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	001.9	000.0	058.8	009.5	000.0	000.0	000.0	000.0	000.0	000.0	000.7	000.0	017.4	000.0
Holocalyx balansae	012.3	007.1	000.0	011.3	000.0	000.0	000.0	000.0	000.0	002.1	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	004.8	007.4	002.7	017.4
Hexachlamys edulis	002.9	000.0	000.0	000.0	000.0	007.6	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0
Sorocea bonplandii	002.6	006.2	002.0	000.0	004.4	000.0	000.0	000.0	002.8	006.6	000.0	000.0	030.0	000.0	000.0	000.0	000.0	000.0	000.0	012.0	002.7	000.0	000.0
Patagonula americana	009.3	000.0	000.0	001.8	009.6	000.0	007.0	006.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	002.1	000.0	007.2	021.4
Bastardiopsis densiflora	005.0	003.7	024.8	017.2	000.0	003.7	000.0	000.0	000.0	000.0	003.5	002.3	013.2	000.0	000.0	000.0	000.0	000.0	000.0	006.0	010.5	000.0	000.0
Citronella paniculata	002.5	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.9	000.0	000.0	000.0
Helietta apiculata	004.4	000.0	000.0	000.0	015.5	008.2	017.9	010.0	105.5	000.0	000.0	000.0	000.0	030.0	042.9	000.0	035.0	025.0	000.0	000.0	000.0	000.0	000.0
Ocotea puberula	010.8	002.5	000.0	000.0	043.1	000.0	007.2	016.4	021.6	000.0	016.7	024.7	020.3	003.8	000.0	000.0	000.0	000.0	000.0	004.1	001.6	006.9	000.0
Cordia trichotoma	003.8	000.0	004.1	004.4	000.0	000.0	002.2	000.0	000.0	005.0	005.2	002.9	008.5	000.0	000.0	000.0	000.0	000.0	000.0	008.1	006.6	000.0	000.0
Banara tomentosa	003.9	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.7	000.0	002.5	000.0
Didimopax longepetiolata	003.8	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	002.1	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	001.6	000.0	000.0
Aegiphila sellowiana	002.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	002.0	000.0	000.0	000.0	000.0	000.0	000.0	002.4	000.0	000.0	000.0
Annona amambayensis	001.9	000.0	002.1	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	001.3	000.0	000.0	000.0
Bauhinia forficata	001.8	000.0	000.0	005.4	000.0	002.0	000.0	000.0	000.0	002.3	002.6	000.0	000.0	030.0	000.0	000.0	000.0	000.0	000.0	003.3	000.0	003.1	017.5
Trichila catigua	001.8	005.0	000.0	000.0	001.9	000.0	000.0	000.0	000.0	000.0	000.0	002.1	000.0	015.0	000.0	000.0	000.0	000.0	000.0	003.3	000.0	000.0	002.5
Guarea macrophylla	001.9	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	007.9	003.5	000.0	004.8	000.0	000.0	000.0	000.0	000.0	000.0	001.9	002.4	000.0	000.0
Chorisia speciosa	002.0	002.7	000.0	000.0	000.0	000.0	000.0	000.0	000.0	002.0	000.0	002.2	004.0	000.0	000.0	000.0	000.0	000.0	000.0	004.5	007.0	001.2	013.3
Cordia ecalyculata	001.8	005.9	000.0	003.3	000.0	000.0	000.0	000.0	000.0	000.0	007.9	000.0	000.0	004.8	000.0	000.0	000.0	000.0	000.0	001.7	000.0	000.0	000.0
Ficus citrifolia	002.1	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	005.3	002.6	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	003.5	002.0	006.9	015.1
Campomanesia xanthocarpa	001.9	008.0	000.0	000.0	000.0	000.0	000.0	004.1	000.0	005.9	002.6	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	003.5	002.0	006.9	015.1
Solanum citrifolium	002.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0
Matayba eleagnoides	002.0	000.0	000.0	009.2	047.4	016.6	027.6	003.2	002.0	000.0	000.0	000.0	000.0	036.0	000.0	017.6	000.0	025.0	000.0	000.0	000.0	009.4	000.0
Chrysophyllum marginatum	001.8	005.6	027.7	000.0	000.0	000.0	004.8	000.0	000.0	009.0	002.6	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	006.0	001.8	009.0	002.1
Sebastiana klotzschiana	001.9	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0

	LC01	BS07	BS02	BS01	BS10	LC02	BS06	BS03	BS08	LC03	BS05	LC30	LC10	BS4C	BS11	BS4B	BS09	BS12	BS4A	SP01	FU01	FU02	SP02
Fagara riedeliana	001.9	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	002.2	002.0	000.0	000.0	000.0	000.0	000.0	000.0	001.5	000.0	003.7	000.0
Machaerium stipitatum	002.7	012.3	017.4	002.6	001.9	002.0	002.4	002.0	010.8	000.0	014.6	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	004.5	003.7	001.7	000.0
Apuleia leiocarpa	006.8	004.4	000.0	003.0	000.0	006.0	002.1	000.0	000.0	000.0	000.0	000.0	000.0	030.0	000.0	000.0	000.0	000.0	000.0	000.0	008.6	009.0	000.0
Acacia polyphylla	000.0	002.5	003.0	007.4	000.0	000.0	000.0	000.0	003.3	000.0	005.9	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0
Albizia hasslerii	000.0	005.4	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	001.2	000.0
Calliandra foliolosa	000.0	002.5	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0
Gilibertia cuneata	000.0	006.0	000.0	015.0	003.8	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.8	000.0	000.0	000.0
Guarea kunthiana	000.0	005.0	016.9	055.2	000.0	000.0	000.0	000.0	001.9	000.0	002.9	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	001.2	000.0
Lonchocarpus leucanthus	000.0	008.7	007.1	014.4	000.0	008.6	000.0	000.0	012.4	000.0	004.3	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	006.0	012.3	019.0	000.0
Lonchocarpus muehlbergianus	000.0	002.5	000.0	000.0	000.0	000.0	000.0	000.0	007.1	005.7	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	005.5	016.7	008.4	000.0
Myrciaria rivuralis	000.0	010.4	000.0	000.0	001.8	000.0	038.3	000.0	002.3	008.5	000.0	000.0	030.0	000.0	000.0	000.0	000.0	000.0	000.0	001.5	000.0	021.2	045.6
Pilocarpus pennatifolius	000.0	001.2	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0
Pterogyne nitens	000.0	007.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	008.1
Tabebuia heptaphylla	000.0	002.5	000.0	000.0	000.0	000.0	007.9	000.0	003.3	002.0	003.9	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	008.2	000.0	002.9	003.5
Alchornea triplinervia	000.0	000.0	002.6	006.9	000.0	000.0	006.4	000.0	002.7	000.0	004.2	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	001.8	000.0	000.0	000.0
Aloysia virgata	000.0	000.0	002.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	005.2	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	001.6	000.0	000.0
Chlorophora tinctoria	000.0	000.0	009.3	000.0	000.0	000.0	000.0	000.0	008.1	000.0	005.9	006.1	000.0	000.0	000.0	000.0	000.0	000.0	000.0	001.8	000.0	000.0	002.5
Citrus aurantium	000.0	000.0	004.1	003.9	000.0	000.0	000.0	000.0	001.9	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0
Euterpe edulis	000.0	000.0	031.6	011.5	000.0	000.0	000.0	000.0	002.0	000.0	013.8	007.2	000.0	000.0	000.0	000.0	000.0	000.0	000.0	003.1	000.0	000.0	000.0
Machaerium aculeatum	000.0	000.0	000.0	002.6	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0
Hovenia dulcis	000.0	000.0	004.1	000.0	000.0	000.0	000.0	000.0	000.0	005.5	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0
Inga uraguensis	000.0	000.0	004.6	000.0	001.8	000.0	000.0	000.0	002.3	000.0	000.0	000.0	010.2	000.0	000.0	000.0	000.0	060.0	000.0	000.0	000.0	000.0	000.0
Machaerium paraguariense	000.0	000.0	002.1	000.0	000.0	009.2	000.0	000.0	000.0	000.0	000.0	000.0	002.0	000.0	000.0	000.0	000.0	000.0	000.0	001.5	000.0	001.9	000.0
Myrocarpus frondosus	000.0	000.0	004.3	002.8	000.0	000.0	002.6	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	002.2	000.0
Piptadenia rigida	000.0	000.0	015.5	003.8	000.0	010.9	000.0	000.0	013.4	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	002.2	004.6	000.0
Peltophorum dubium	000.0	000.0	000.0	010.5	000.0	000.0	000.0	000.0	007.2	002.0	034.6	000.0	030.0	004.9	000.0	000.0	000.0	000.0	000.0	002.9	002.4	004.8	000.0
Prunus subcoriacea	000.0	000.0	003.6	016.3	000.0	000.0	005.3	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.8	002.0	005.5	000.0
Rollinia emarginata	000.0	000.0	002.2	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.7	000.0	001.2	006.4
Elaeocarpus americanus	000.0	000.0	000.0	002.6	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0
Enterolobium contortisiliquum	000.0	000.0	000.0	008.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	003.0	000.0	000.0	000.0	000.0	000.0	000.0	001.4	000.0	000.0	011.1
Eugenia jambos	000.0	000.0	000.0	002.7	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0
Annona pyriformis	000.0	000.0	000.0	002.7	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	007.0	000.0	000.0
Annona squamosa	000.0	000.0	000.0	003.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	011.3	005.2	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0
Astronium fraxinifolium	000.0	000.0	000.0	010.2	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	002.8	000.0	000.0	000.0	000.0	000.0	000.0	002.0	002.2	000.0	000.0
Casearia decandra	000.0	000.0	000.0	003.6	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	017.6	000.0	000.0	000.0	000.0	001.3	004.1
Casearia sylvestris	000.0	000.0	000.0	015.9	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	005.9	000.0	000.0	000.0	000.0	000.0	000.0	000.0	002.0	000.0	005.0
Cupania vernalis	000.0	000.0	000.0	003.9	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.8	003.0	000.0
Ilex paraguariensis	000.0	000.0	000.0	002.6	000.0	000.0	004.4	018.2	000.0	000.0	000.0	017.7	000.0	000.0	006.1	000.0	017.6	000.0	000.0	000.7	000.0	001.3	000.0
Luehea candicans	000.0	000.0	000.0	068.6	000.0	000.0	000.0	000.0	007.1	000.0	000.0	000.0	009.5	000.0	009.5	000.0	017.6	000.0	000.0	001.4	000.0	000.0	011.1
Myrciaria ciliolata	000.0	000.0	000.0	003.9	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	062.1	000.0	035.2	050.0	000.0	000.0	000.0	000.0	000.0
Rapanea umbellata	000.0	000.0	000.0	010.4	000.0	000.0	002.1	000.0	000.0	000.0	002.7	006.4	002.0	000.0	046.2	000.0	000.0	000.0	000.0	006.3	001.8	000.0	002.6

Species	LC01	BS07	BS02	BS01	BS10	LC02	BS06	BS03	BS08	LC03	BS05	LC30	LC10	BS4C	BS11	BS4B	BS09	BS12	BS4A	SP01	FU01	FU02	SP02
Rudgea major	000.0	000.0	000.0	038.8	000.0	000.0	004.4	000.0	000.0	000.0	000.0	000.0	000.0	015.0	000.0	000.0	017.6	000.0	000.0	000.0	000.7	000.0	000.0
Luehea divaricata	000.0	000.0	000.0	000.0	000.0	041.7	058.1	074.8	000.0	001.9	000.0	000.0	004.2	000.0	000.0	000.0	000.0	000.0	000.0	000.0	004.6	012.7	021.1
Enneatypus tenuiflorus	000.0	000.0	000.0	000.0	000.0	008.4	010.8	010.0	002.1	002.1	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.9	002.1	001.9	002.1
Vitex cymosa	000.0	000.0	000.0	000.0	000.0	006.6	013.7	020.7	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	004.1	000.0
Fagara najanrillo	000.0	000.0	000.0	000.0	000.0	008.3	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	001.7	000.0	000.0	000.0
Strychnos brasiliensis	000.0	000.0	000.0	000.0	000.0	007.6	004.2	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	001.6	001.3	000.0
Erythroxylon deciduum	000.0	000.0	000.0	000.0	000.0	002.4	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	035.2	000.0	000.0	000.0	000.0	000.0	000.0
Xylosma ciliatifolium	000.0	000.0	000.0	000.0	000.0	002.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	001.2	000.0
Roupala meisneri	000.0	000.0	000.0	000.0	000.0	002.1	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0
Aspidoperma polyneuron	000.0	000.0	000.0	000.0	000.0	000.0	002.1	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0
Jacaranda micrantha	000.0	000.0	000.0	000.0	000.0	000.0	002.2	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	003.6	000.0	000.0
Myrcianthes pungens	000.0	000.0	000.0	000.0	000.0	000.0	006.7	004.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	001.8	000.0	021.0
Terminalia triflora	000.0	000.0	000.0	000.0	000.0	000.0	005.0	000.0	000.0	000.0	000.0	000.0	000.0	015.0	000.0	100.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0
Actinostemon concolor	000.0	000.0	000.0	000.0	000.0	000.0	000.0	015.7	000.0	000.0	000.0	000.0	000.0	000.0	000.0	100.0	000.0	000.0	000.0	000.0	000.0	000.0	022.1
Araucaria angustifolia	000.0	000.0	000.0	000.0	000.0	000.0	000.0	037.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0
Ilex brevicuspis	000.0	000.0	000.0	000.0	000.0	000.0	000.0	003.8	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	001.6	000.0	000.0
Trichilia clausseni	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	009.6	002.6	000.0	000.0	000.0	001.4	000.0	000.0	000.0	000.0	001.4	001.4	000.0	000.0
Cestrum intermedium	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	005.9	000.0	000.0	002.7	000.0	000.0	000.0	000.0	000.0	000.0	004.6	003.6	001.4	000.0
Peschiera australis	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	002.7	000.0	000.0	010.7	000.0	000.0	000.0	000.0	000.0	000.0	000.0	001.7	001.7	000.0
Fagara chiloperone	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	005.3	000.0	000.0	002.8	000.0	000.0	000.0	000.0	000.0	000.0	000.8	002.3	001.7	000.0
Alchornea iricurana	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	003.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0
Pentapanax warmingianus	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	001.9	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0
Solanum inaequale	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	001.9	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0
Tetrorchidium rubrinervium	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	002.3	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	037.4	006.6	000.0
Solanum granulo-leprosum	000.0	000.0	000.0	000.0	000.0	000.0	000.0	008.5	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0
Fagara rhoifolia	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	010.9	000.0	000.0	000.0	000.0	000.0	000.0	000.7	000.0	001.3	000.0
Pisonia ambigua	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	012.6	000.0	000.0	000.0	000.0	000.0	000.0	001.7	002.0	000.0	000.0
Fagara hyemalis	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	010.1	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0
Inga marginata	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	005.4	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0
Endlicheria paniculata	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	006.4	000.0	000.0	000.0	000.0	000.0	000.0	006.3	011.5	008.0	000.0
Trema micrantha	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	006.3	000.0	000.0	000.0	000.0	000.0	000.0	000.0	001.3	001.3	000.0
Aspidosperma australe	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	002.7	000.0	000.0	000.0	000.0	000.0	000.0	000.0	002.8	002.8	000.0
Eugenia uniflora	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	032.0	000.0	035.2	000.0	000.0	000.0	000.0	000.0	000.0
Ocotea pulchella	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	003.7	003.7	035.2	000.0	000.0	000.0	000.0	000.0	000.0
Moquinia polymorpha	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	010.0	000.0	000.0	050.0	000.0	000.0	000.0	000.0	000.0
Myrcia multiflora	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	100.0	000.0	025.0	120.0	000.0	000.0	000.0	000.0
Blepharocalyx salicifolius	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	017.6	025.0	000.0	006.3	011.5	008.0	000.0
Calyptranthes concinna	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	017.6	025.0	000.0	000.0	001.3	000.0	008.0
Copaifera langsdorffii	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	017.6	000.0	000.0	000.0	000.0	001.9	000.0
Gomidesia sellowiana	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	017.6	025.0	060.0	000.0	001.9	000.0	000.0
Lithrea molleoides	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	050.0	000.0	000.0	000.0	000.0	000.0

	LC01	BS07	BS02	BS01	BS10	LC02	BS06	BS03	BS08	LC03	BS05	LC30	LC10	BS4C	BS11	BS4B	BS09	BS12	BS4A	SP01	FU01	FU02	SP02
Schinus terebinthifolius	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	025.0	000.0	000.0	000.0	000.0	000.0
Cereus stegonosus	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	060.0	000.0	000.0	000.0	000.0
Picrasma sellowii	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	003.1	009.9	001.2	000.0
Erythrina falcata	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	004.0	000.0	000.0	000.0
Hennecartia omphalocarpa	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	001.4	000.0	000.0	000.0
Sapium klotzschianum	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.7	000.0	000.0	000.0
Casearia gossypiosperma	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	001.6	002.9	000.0
Inga affinis	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	001.7	000.0	000.0
Seguiera paraguariensis	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	001.2	000.0
Eugenia involucrata	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	002.9	000.0
Celtis pubescens	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	001.2	000.0
Pisonia aculeata	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	010.8
Garcinia brasiliensis	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	007.4
Guazuma ulmifolia	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	002.1
Gleditschia amorphoides	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	000.0	002.0

	SP01	FU01	BS07	BS05	LC01	LC03	BS02	BS01	BS10	BS11	FU02	BS06	LC02	BS03	SP02	BS08	BS4C	BS12	BS4B	BS09	BS4A	LC10	LC30
Lauraceae	42.4	36.9	48.1	40.4	41.7	18.2	65.2	49.4	43.1	7.5	30.4	64.2	14.8	18.3	2.6	31.4	30.0	–	–	35.2	–	53.5	114.3
Leguminosae	31.9	46.4	48.0	69.2	16.8	44.6	58.1	52.9	14.2	4.9	48.4	5.0	30.7	5.0	38.6	18.0	30.0	–	–	17.6	60.0	25.5	19.7
Meliaceae	44.4	42.3	60.6	42.4	42.7	49.4	38.8	64.1	29.3	18.0	24.4	6.9	2.0	–	20.0	3.1	60.0	–	–	–	–	8.8	62.8
Sapotaceae	39.4	16.1	33.1	12.7	17.6	25.2	33.7	23.6	–	3.1	14.7	4.8	–	10.0	25.1	–	15.0	–	–	–	–	6.9	5.2
Rutaceae	25.4	21.6	33.5	18.3	26.2	16.6	7.1	23.4	15.5	42.9	20.0	20.0	19.1	48.6	–	105.5	30.0	25.0	–	35.2	–	28.5	4.3
Sapindaceae	3.2	4.1	7.4	9.2	32.0	12.8	2.1	–	13.1	36.0	30.6	18.7	77.2	74.8	23.2	12.7	15.0	25.0	–	17.6	–	–	4.9
Tiliaceae	–	4.6	–	–	–	1.9	–	–	68.6	9.5	12.7	58.1	41.7	12.4	2.2	7.1	–	–	–	–	–	4.2	–
Palmae	11.1	12.6	18.2	13.8	26.2	2.0	41.1	14.5	3.9	–	13.0	8.5	47.7	8.1	44.1	111.4	–	125.0	–	17.6	–	–	7.2
Myrtaceae	3.5	3.8	8.0	2.6	4.8	6.0	–	5.4	4.4	94.1	9.8	6.7	7.6	32.1	22.1	–	–	–	0.2	88.0	180.0	–	–
Euphorbiaceae	2.5	–	–	–	10.6	8.0	2.6	9.6	1.8	–	13.6	6.4	8.7	7.0	5.0	–	–	–	0.2	–	–	–	6.3
Moraceae	20.4	4.9	6.2	6.6	6.8	67.5	11.3	9.7	–	–	–	2.2	2.1	–	34.7	–	30.0	–	–	–	–	73.9	26.5
Boraginaceae	14.7	13.6	5.9	5.2	14.9	7.0	4.1	7.7	19.5	–	8.4	2.2	9.6	–	–	6.0	–	–	–	–	–	12.5	5.1
Apocynaceae	–	1.7	–	–	–	2.7	–	–	3.8	5.9	4.5	2.1	–	–	4.1	–	–	–	–	–	–	13.4	–
Flacourtiaceae	2.7	1.6	–	–	3.9	1.9	–	15.0	–	4.2	7.9	–	2.0	–	–	–	–	–	–	17.6	–	–	–
Araliaceae	0.8	–	6.0	–	3.8	2.1	2.0	–	3.0	–	4.1	–	–	20.7	–	–	–	–	–	–	–	–	2.9
Verbenaceae	–	3.2	–	–	2.0	–	2.2	–	–	5.2	1.2	13.7	6.6	–	–	–	–	–	–	–	–	–	5.2
Annonaceae	10.1	–	–	–	1.9	16.3	–	–	–	–	8.0	–	–	–	6.4	–	–	–	–	–	–	4.0	11.3
Solanaceae	4.6	41.0	2.5	3.9	2.0	2.0	–	–	–	–	2.9	10.1	–	–	–	3.3	–	–	–	–	–	2.7	–
Bignoniaceae	8.2	3.6	–	–	–	–	–	–	3.6	–	1.3	–	–	–	3.5	–	–	75.0	–	7.6	–	–	–
Anacardiaceae	2.0	–	–	–	–	–	–	–	2.6	6.1	2.9	4.4	–	22.0	4.1	–	–	–	–	7.6	–	–	17.7
Aquifoliaceae	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Nyctaginaceae	1.7	2.0	–	–	–	–	–	–	–	–	2.5	–	–	–	10.8	–	–	–	–	–	–	12.6	–
Ulmaceae	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	6.3	–

Table 4. – Family value index (only the families present in more than one relevé are taken into account).

	SP01	FU01	BS07	BB05	BS02	BS01	BS10	BS11	FU02	BS06	BS03	BS08
Families nb. (1 ha)	28	26							25			
Families nb. (1/5 ha)	21		15	17	15	14	17	16		20	14	10
Species nb. (1 ha)	60	44							58			
Species nb. (1/5 ha)	35		32	31	31	31	25	18		28	20	14
Individual/species (1 ha)	7.37	6.13							5.52			
Individual/species (1/5 ha)	2.34		2.91	2.87	4.23	3.23	6.68	6.22		4.21	7.15	7.93
One tree/species (1 ha)	13	18							20			
One tree/species (1/5 ha)	18		11	14	12	15	8	7		10	4	6
Minimum area (ha)	0.36											
Species nb. (min. area)	45											
Individual/species (min. area)	3.8											
One tree/species (min. area)	16											

Table 5. – Biodiversity values for tall forests (indicating number of families and species as well as individual/species ratios and species represented by only one tree).

In three one-hectare plots, 60, 58 and 44 species, respectively, were counted, while the individual/species ratio for 1 ha varies from 5.52 to 7.37. The minimum area was calculated for the SP01 survey (Fig. 2). The first plateau of the curve is reached at 0.36 ha, with 45 species (individual/species ratio = 3.8), 16 species being represented by only one tree.
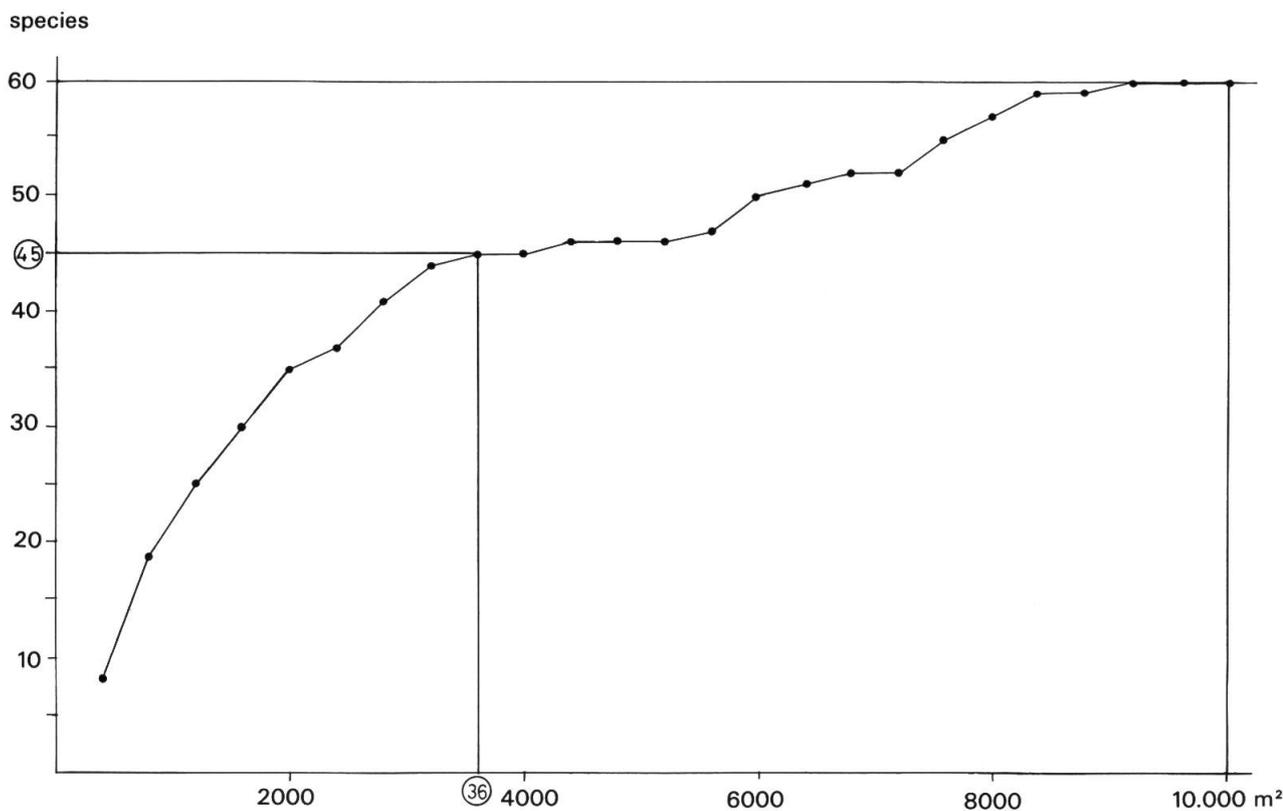
species

Fig. 2. — Area/species curve for relevé SP01 (1 ha): the first plateau is reached at 0.36 ha including 45 species of trees; the total number for 1 ha is 60.

In the 0.2 ha plots, the number of species varies between 14 and 32, and the individual/species ratio from 2.91 to 7.93. If we extrapolate the values of the 1 ha SP01 plot to a 0.2 ha plot, which allows us to compare it with the other surveys, we obtain 35 spp. and an individual/species ratio of 2.34.

The highest biodiversity is observed in the clayey upland surveys and plots disturbed in the past (SP01, BS07, BS05), i.e, for 1/5 ha: 31-35 spp. or a ratio of 2.34-2.91 individuals/species, 12-18 species being represented by only one tree. The sandier upland plots (BS08, BS10), the ill-drained depression surveys (BS03, BS06) and the ecoclinal survey (BS11) show lower figures: 14-28 spp., i.e, a ratio of 4.21-7.93 individuals/species, 6-10 species being represented by only one tree. The surveys in the Parana valley (BS01, BS02) give figures close to those of the upland-relevés.

The third step of the ANACOR method (see Chapter 3.4) separates the disturbed survey areas SP01, BS05 and LC03. It is interesting to note that the tree diversity is rather higher in these selectively exploited forests than the one calculated for the less disturbed plots. This is due to the invasion in the clearings of heliophilous species with a wide distribution area (*Chlorophora tinctoria, Chorisia speciosa, Jacaratia spinosa, Solanum* spp.).

For two 2500 m² surveys of tall forests, STUTZ DE ORTEGA (1987) gives the following data:

— upland (LC01): 42 species,

— depression (LC02): 27 species,

— disturbed forest (LC03): 45 species.

To be able to compare Stutz de Ortega's results with ours, we extrapolated the three former 1/4 ha values to 1/5 ha, using her area-species curve (STUTZ DE ORTEGA, 1987: 252). We obtained approximately 35 spp. (upland and disturbed) and 25 spp. (depression). These figures correspond to what we observed on the same type of soil and topographical location (see above).

Comparing these figures with other neotropical data, we observe that the biodiversity of the Alto Parana *Lauraceae* tall forests is much lower than that measured in other Amazonian surveys (from 118 to more than 300/ha) (see: BALSLEV & al., 1987; GENTRY, 1982, 1988; MORI & al., 1983a). These figures are a little lower than those observed near Belem (87) (GENTRY, 1982) and in Beni (94) (BOOM, 1986). They are more or less equivalent, if not higher than those of Costa Rica and São Paulo (GENTRY, 1982). It should be pointed out that the areas surveyed in Costa-Rica receive more or less the same rainfall as our survey areas. This circumstance could lend additional support to GENTRY's theory (1982) which suggests a positive correlation between rainfall and biodiversity.

As to species diversity, the richest families are *Leguminosae, Meliaceae, Lauraceae, Sapindaceae* and *Myrtaceae*.

3.4. Ecological trends

Results

From a step-by-step application of the ANACOR method, we obtained the following graphs and diagrams which show the ecological trends of the forest types and species.

A. First step: using all the species (Fig. 3a, b)

By using all the species, including those represented in a single survey, three axes can be drawn which are interpreted as follows:

— The first axis places the tall forests along a gradient varying from xerophily to mesophily. The segregated surveys are *BS10* and *BS11*. Both are located on the clayey-sandy and dry substrate of a plateau in the forest-savanna mosaic area, i.e. in a rather xeric environment. These two xeric surveys are opposed to mesophilous ones (LC03, BS01). The xerophily of the following species also emerges: *Eugenia uniflora, Myrciaria ciliolata, Casearia sylvestris, Moquinia polymorpha, Rapanea umbellata, Helietta apiculata, Matayba elaeagnoides, Ocotea pulchella, Astronium fraxinifolium, Luehea candicans, Rudgea major.* They are contrasted with the following mesophilous species: *Chrysophyllum gonocarpum, Balfourodendron riedelianum, Cordia trichotoma, Nectandra megapotamica, Bastardiopsis densiflora, Lonchocarpus leucanthus, Chorisia speciosa.*

— The second axis separates the forests that are in close contact with the campos (i.e the ecoclinal formations) from the others. The forests are also arranged according to their mean heights, BS4A being the lowest forest surveyed. Both these parameters are correlated since the ecoclinal vegetation consists of low trees. The segregated surveys are those incorporating low forests: *BS4A, BS4B, BS09, BS12*. The following species emerge as characteristic components of the ecoclinal formations: *Cereus stegonosus, Myrcia multiflora, Gomidesia sellowiana, Lithraea molleoides, Schinus terebinthifolius* and *Blepharocalyx salicifolia.*

Fig. 3a. — Anacor method, step 1: using all the species of trees recorded.
Axis 1 segregates the xeric (▲) from the mesophilous (■) surveys.
Axis 2 segregates the forests that are in close contact with the campos (*) from the others.
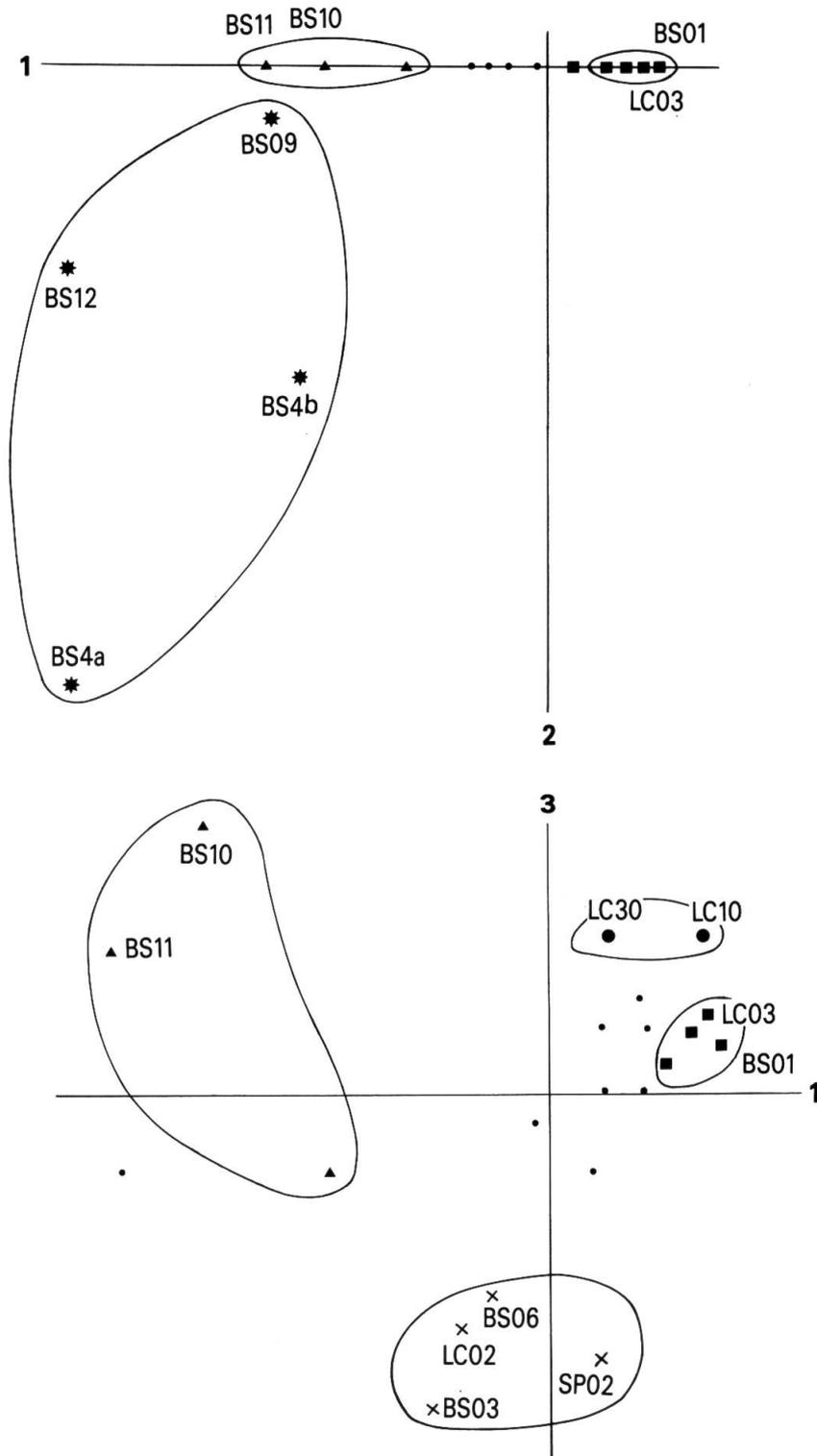
Fig. 3b. — Anacor method, step 1: using all the species of trees recorded.
Axis 1 segregates the xeric (▲) from the mesophilous (■) surveys.
Axis 3 segregates the survey areas that are located on ill-drained substrates (×) from the xeric ones (▲), and from the secondary stages (●).

Fig. 3c. — Anacor method: analysis of the survey areas whose ecological trends have not been clearly defined by the first steps of application.
Axis 1 segregates the xeric area BS08 (▲) from the others.
Axis 2 segregates the two surveys of the Parana riverine forest (×) from the other forest types.
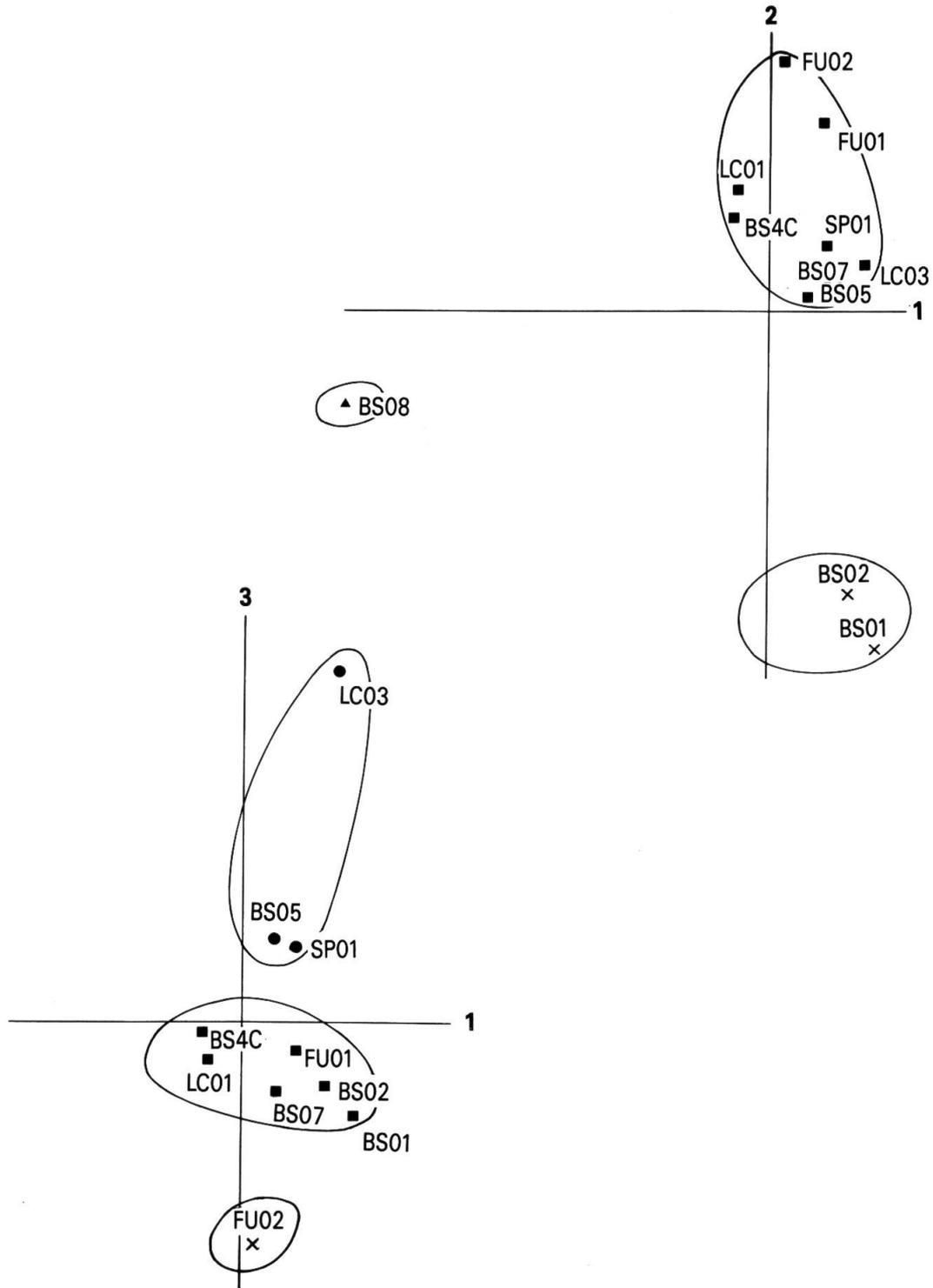
Fig. 3d. — Anacor method: analysis of the survey areas whose ecological trends have not been clearly defined by the first steps of application.
Axis 3 segregates the swampiest survey area (×) from the disturbed study plots (●). At the crossing of the two axes, the less disturbed forests occurring in a mesophilous environment (■) are grouped.

— The third axis draws up a gradient varying from strong hygrophily to xerophily. It separates the forests that are located on ill-drained and clayey substrates *(BS03, SP02, BS06, LC02)* from the xeric ones that have already been segregated by the first axis and from the secondary stages *(LC10 and LC30)*. This means that allochtonous species belonging to a dryer flora play a role in the secondarization processes of the tall forests.

The species indicating the wettest edaphic conditions are: *Actinostemon concolor, Araucaria angustifolia, Myrcianthes pungens, Vitex cymosa, Luehea divaricata, Roupala meissneri, Calyptranthes concinna, Enneatypus tenuifolius, Pisonia aculeata, Patagonula americana, Erythroxylum deciduum, Myrciaria rivularis, Sebastiana brasiliensis, Gleditschia amorphoides, Diatenopteryx sorbifolia, Rollinia emarginata, Ilex brevicuspis, Styrax brasiliensis, Terminalia triflora, Garcinia brasiliensis.* The species occurring in the secondary forests are: *Jacaratia spinosa, Cecropia pachystachya, Annona squamosa, Nectandra lanceolata, Pisonia ambigua, Fagara rhoifolia, Fagara hyemalis* and *Inga* spp.

To sum up, by the first step we distinguish:

— low deciduous forests (BS4A, BS4B, BS09, BS12) as ecoclinal formations;

— swampy tall forests (BS03, BS06, SP02, LC02);

— xeric tall forests (BS11, BS10);

— secondary stages (LC10, LC30), 10 and 30 years old.

B. Second step: using the species present in at least two surveys

In this step we eliminated the rarest species whose presence may be considered to be coincidental and which could complicate the interpretation. It does not significantly change the general complex interpretation of the axis or the distribution of the surveys and species along them.

The ecological trends are however emphasised, and a new piece of information emerges: the intermediate position of BS08 on axis 1 (xerophily-mesophily), between the xeric surveys BS10, BS11 and the mesophilous ones.

C. Third step: analysing the non-segregated surveys (Fig. 3c, d)

We continued by analysing only the surveys whose ecological trends have not yet been clearly pointed out because of their central position: BS01, BS02, BS4C, BS05, BS07, BS08, LC03, SP01, FU01, FU02.

The high contribution of survey BS08 to axis 1 puts forward a xeric-mesic gradient. BS08 stands out as more xeric than the others. The relative xerophily of *Helietta apiculata, Luehea candicans, Styrax leprosum* and *Ocotea puberula*, as well as the abundance of *Syagrus romanzoffiana* in survey BS08 also emerge from this. The former, which are relatively xerophilous species are contrasted on the axis with mesophilous ones: *Chrysophyllum gonocarpum, Balfourodendron riedelianum, Cabralea canjerana, Lonchocarpus leucanthus, Cordia trichotoma.*

Axis 2 separates the two surveys of the riverine forest of the Parana (BS01, BS02) from the others. The species segregated are: *Guarea kunthiana, Alchornea triplinervia, Inga uraguensis, Euterpe edulis, Gilibertia cuneata, Acacia polyphylla, Bastardiopsis densiflora.*

On the first extremity, axis 3 points out the swampiest survey area (FU02), with the following species: *Sebastiana brasiliensis, Ilex paraguariensis, Cupania vernalis, Vitex cymosa, Ilex brevicuspis, Myrciaria rivularis, Rollinia emarginata, Xylosma ciliatifolium, Aspidosperma australe, Seguiera paraguariensis, Celtis pubescens.*

This survey (FU02), like BS08, had already been distinguished by steps 1 and 2, but not as clearly.

Fig. 3e. — Anacor method, step 4, analysing the most frequent species of trees, i.e. those occurring in ≥ 33% of the relevés. The ecological trends of the survey areas are indicated as follows: xerophilous (▲), hygrophilous (×), mesophilous (■), secondary stages (●).
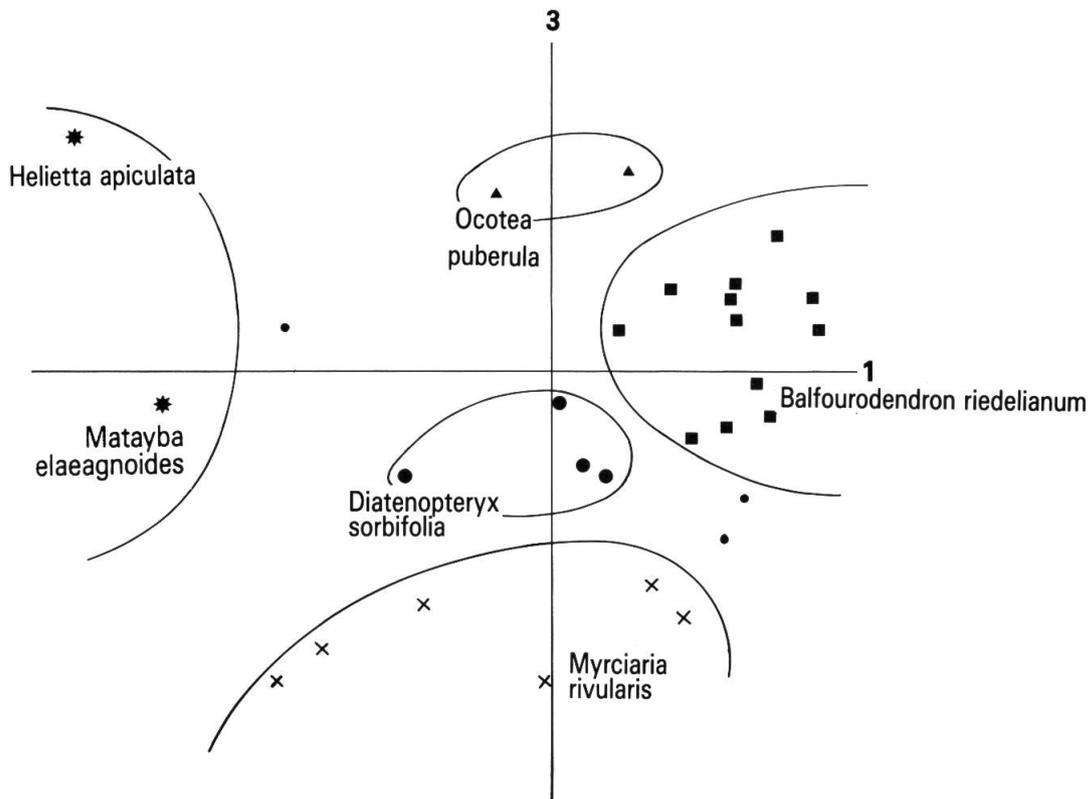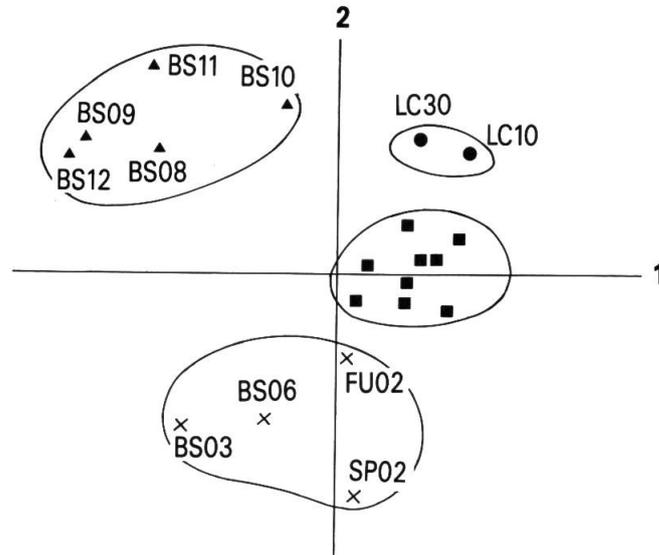

Fig. 3f. — Anacor method; ecological trends of the predominant species: xerophilous (▲), mesophilous (■) and hygrophilous (×) species; species having a trend towards hygrophily (●); stress-tolerant species (∗).

The other extremity features the more strongly disturbed forests, viz. LC03, BS05 and SP01, with the following species: *Cecropia pachystachya, Trichilia claussenii, Fagara* spp., *Aegiphylla sellowiana, Alchornea iricurana, Pentapanax warmingianus, Solanum* spp., *Jacaratia spinosa, Cestrum integrifolium, Chorisia speciosa, Chlorophora tinctoria, Rapanea umbellata, Tetrorchidium rubrinervium.*

Between these two extremities, at the crossing of the two axes, the less disturbed or almost untouched forests growing in a mesophilous environment are grouped: LC01, BS07, BS4C, BS01, BS02, FU01.

D. Fourth step: analysing the most frequent species (Fig. 3e, f)

In this fourth analysis we considered only those species that are present in more than 33% of the surveys, with the aim of showing the ecological trends of the predominant species in the Paraguayan Alto Parana forests. The first graph represents four groups of surveys which correspond to the ones that the former analyses distinguished: the xerophilous one, the hygrophilous, the mesophilous, and the secondary stages.

The second graph shows the ecological trends of the following predominant species:

—   Typically hygrophilous species: *Myrciaria rivularis, Luehea divaricata, Enneatypus tenuiflorus, Patagonula americana, Trichilia catigua, Campomanesia xanthocarpa.*

—   Other species show a trend towards hygrophily: *Diatenopteryx sorbifolia, Holocalyx balansae, Tabebuia heptaphylla, Allophylus edulis, Apuleia leiocarpa.*

—   *Ocotea puberula, Peltophorum dubium* can be considered as rather xerophilous.

It is interesting to note that *Helietta apiculata* and *Matayba elaeagnoides* (see Step 1) can grow as well on xeric as on swampy substrate, i.e. in a stressful environment.

The other predominant species were observed rather in mesic, environmental conditions, and on well-drained soils *(Cedrela fissilis, Cabralea canjerala, Ocotea spectabilis, Nectandra megapotamica, Cordia trichotoma, Fagara riedeliana, Balfourodendron riedelianum, Chrysophyllum gonocarpum, C. marginatum, Lonchocarpus leucanthus, Bastardiopsis densiflora). Sorocea bonplandii* was observed in well-drained as well as in swampy forests.

Finally, *Syagrus romanzoffiana* was observed in the three mesophilous, hygrophilous and xerophilous surveys, but neither in secondary surveys, nor in low forests.

E. Fifth step: analysing the predominant families (Fig. 3g)

The species and their I.V.I. were grouped by families and the nine predominant ones were analysed.

Tiliaceae and *Sapindaceae* are contrasted on axis 1 to *Meliaceae, Sapotaceae, Leguminosae* and *Lauraceae,* i.e. axis 1 clearly shows a gradient varying from hygrophily to mesophily. The forests growing on ill-drained substrate are effectively characterized by the frequency of *Sapindaceae* and *Tiliaceae* trees, while *Meliaceae* and *Sapotaceae* are predominant on the well-drained soils.

Axis 2 separates the tall from the low forests, the latter being characterized by the frequency of *Myrtaceae* and the absence of palm-trees.

Fig. 3g. — Anacor method, step 5: analysis of the nine predominant families.
Axis 1 shows a gradient ranging from hygrophily to mesophily.
Axis 2 separates tall forests from low forests.
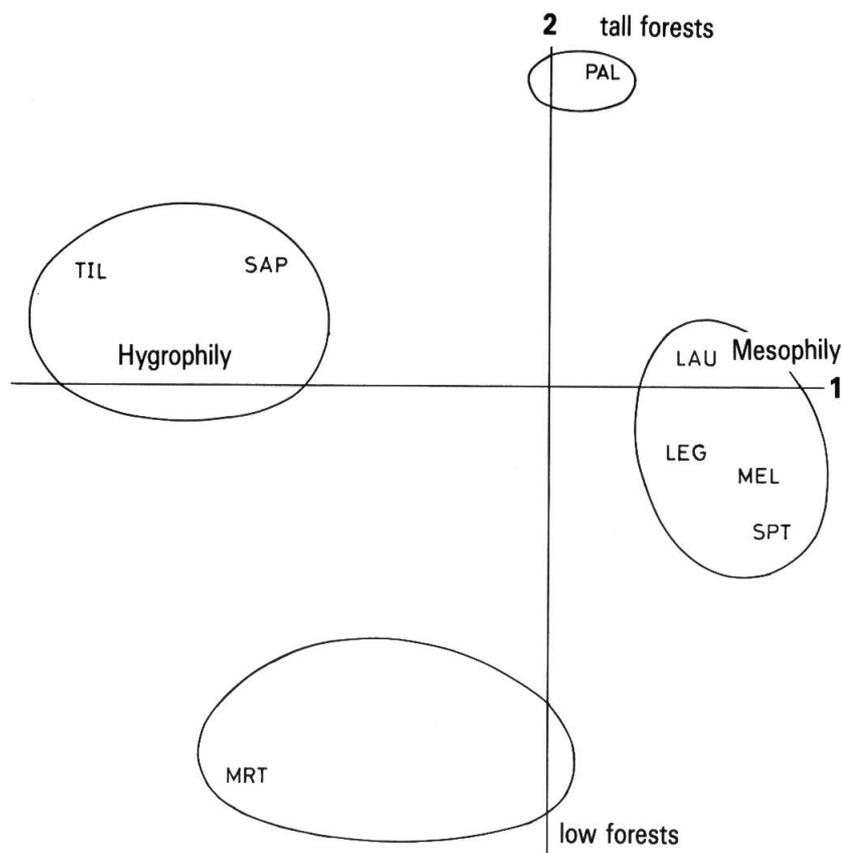
4. A proposed classification

According to the relevés of Spichiger & Loizeau (SP), Fischer (FU), Bertoni (BS) and Stutz de Ortega (LC), the following classification of the Paraguayan Alto Parana forests is proposed.

However, in using this classification we must keep in mind that the former human interference with, and exploitation of, the Alto Parana forests have more or less transformed the original flora. In fact timbers of economic value have been over-exploited. The rareness of genera like *Tabebuia* and *Aspidosperma* in our surveys is due more to a selective extraction than to natural distribution.

We must also point out the striking occurrence of the climbing bamboo *Chusquea ramosissima* which invades all the tall forests we surveyed, especially the more disturbed ones.

4.1. Tall semi-evergreen forests with Lauraceae (Monte Alto de Laurel)

Surveys: SP01, SP02, FU01, FU02, BS01, BS02, BS4C, BS05, BS06, BS07, BS10, BS11, LC01, LC02, LC03.

(Secondary stages: LC10, LC30.)

These forests correspond to the *Cedrelo fissilis-Ocotea puberulae* phytosociological concept of BOLOS & al. (1991). They also correspond to the *Parapiptadenia rigida-Nectandra saligna*-forests according to ESKUCHE (1983, 1984).

This is the climacical formation of the Paraguayan Parana-region. These forests grow on clayey, sandy-clayey or, more rarely, sandy soils. Their structure and floristic composition vary with soil texture and drainage.

The Legumes are generally the best represented with regard to the number of species, whereas *Lauraceae* represent the biggest tree population.

Lauraceae species are characteristic of our tall upland and depression forests, where they are preponderant. The family forms part of the central and south-eastern Brazilian flora (ROHWER, 1986; VATTIMO, 1979). The trees belonging to this family build up the highest intermediate layer (10-20 m) of the tall forests, and form an important part of the canopy, but giant trees are absent.

Ocotea puberula has a wide neotropical range, whereas the most characteristic species of our *Lauraceae* tall forests, *Nectandra megapotamica* (sensu lato) (ROHWER, 1986), has a wide extra-Amazonian south-tropical distribution which is limited in the north by the Hylaea. Most of the species occurring in the tall Paraguayan Alto Parana forests are rather considered to be gallery-, cerrado- or even wet savanna species in the Central Brazilian area. That could mean that the center of their distribution lies in the Upper Parana-Upper Uruguay basins, with a northern extension into a favourable, locally wet environment (though the opposite hypothesis would also be consistent...).

Ocotea pulchella reportedly occurs in the driest forests of Central Brazil (VATTIMO, 1979). This observation is cross-checked by its only presence in our more xeric surveys.

With regard to another preponderant species belonging to the palm-family, we observed that *Syagrus romanzoffiana* is widespread in all our tall forest surveys. It occurs most frequently in the swampy *Lauraceae-Luehea divaricata-Myrciaria rivularis* tall forests as was observed by REITZ (1974) and HAHN (1990). Due to its great ecological plasticity, this palm is not suitable for the characterization of the different *Lauraceae* tall forest facies. However we observed that *Syagrus romanzoffiana* is absent from the low deciduous *Myrtaceae* forests.

The first step of the ANACOR method (see Chapter 3.4) segregates the secondary stages. According to ORTEGA STUTZ (1989) these surveys correspond to a zoochorous secondary stage (ca. 10 years) with *Cecropia, Jacaratia, Ocotea* (survey LC10) and to a anemo-zoochorous secondary forest (ca. 30 years) with *Nectandra, Cedrela, Ocotea* (survey LC30).

Lastly, we must point out the strictly Upper Parana-Upper Uruguay distribution of the shrub *Hennecartia omphalocarpa (Monimiaceae)* (MARTINEZ-LABORDE, 1983). This characteristic component is widespread in the lowest underlayer of the Paraguayan Alto Parana *Lauraceae* tall forests.

According to topographical location, type of soil and geographical range we might list the following forest types.

A. Lauraceae-Cedrela fissilis-Chrysophyllum gonocarpum well-drained forests

Surveys: BS01, BS02, BS05, BS07, BS10, BS11, SP01, FU01, LC01, LC03.

These are located on the highest topographical levels of the landscape (plateau, higher part of the slope), on well-drained, dark-red and acid soils. From a phenological point of view, most of the trees keep their foliage during the dry season, especially in the lower layer.

The tall forests of the Paraguayan Alto Parana area growing on well-drained substrate (upland forests) could legitimately be called *"Meliaceae* forests", due to the preponderance of *Cedrela fissilis* in the upper layer and to the presence of other species in the intermediate and lower strata *(Cabralea canjerana, Trichilia* spp., *Guarea kunthiana).*

Plot LC01 (STUTZ DE ORTEGA, 1987: 212) was chosen by BOLOS & al. (1991) as type-survey of their *Piptadenia rigidae-Nectandretum megapotamicae* association.

In our surveys *Meliaceae* species were generally recorded in tall forests on well-drained soils (PENNINGTON, 1981). But *Cedrela fissilis,* one of the principal components of the upper forest layer, also grows in some of the ill-drained, tall forests *(Lauraceae-Luehea divaricata-Myrciaria rivularis-forest).*

Cedrela fissilis and *Cabralea canjerana* are widespread in the neotropics, but were mostly recorded in the area ranging from south-eastern Brazil through to eastern Paraguay and northern Argentina. *Trichilia catigua* and *T. clausseni* are limited to the southern tropics and subtropics. Thus most *Meliaceae* species seem to be centred around the Upper Parana-Upper Uruguay basins where they form part of the native flora.

Our surveys showed the preponderance of a species of *Sapotaceae*: *Chrysophyllum gonocarpum* has a wide range and a wide variety of habitats. It extends along the Atlantic coast from Bahia to the south Brazilian states and reaches the Andean foothills in their westernmost range (Bolivia, Argentina). Habitats vary from wet lowland to dryer deciduous and montane forests (PENNINGTON, 1990). However it is most frequently recorded in the Upper Parana-Upper Uruguay basins. Thus we can assume that the distribution center of *C. gonocarpum* is the Paranean forests. In the Paraguayan Alto Parana, *C. gonocarpum* occurs in tall upland *Lauraceae-Cedrela fissilis*-forests (A) where it is an important component of the intermediate strata. The species is also frequent in the disturbed forests and in the secondary successions of tall forests. *C. gonocarpum* may be considered an original species of the tall Paraguayan Alto Parana forests.

Sorocea bonplandii (Euphorbiaceae) has been observed in almost all our upland-surveys. This species must be considered a characteristic element of the underlayer of the tall *Lauraceae-Cedrela fissilis-Chrysophyllum gonocarpum* forests. Its distribution area extends from southern Brazil through to northern Argentina, eastern Paraguay and south-eastern Brazil. In southern Brazil this species is reported (SMITH & al., 1988) as characteristic of the underlayer of the "Floresta latifoliada do Alto Uruguay" (see below: low *Myrtaceae* forests with *Actinostemon concolor).*

With regard to soil texture and the proximity of the Parana valley, three facies are recognized.

A.1. *Typical facies with Balfourodendron riedelianum*

Surveys: SP01, FU01, BS4C, BS05, BS07, LC01, LC03.

These forests grow on clayey or sandy-clayey, well-drained soils. Before deforestation, they might have been the best represented among the Paranean formations.

The canopy reaches an average height of about 13 m, with tall trees exceeding 25 m (see Table 2). The giant trees exceeding 30 m have become rare because of former selective exploitation of the forest.

The basal area measured for one ha reaches 18.5 m², with an average trunk diameter of 23.1 cm. 60 species and 442 trees have been counted in the same plot (SP01). The values for 1 ha extrapolated from the 1/5 or 1/4 ha surveys give higher figures (see Chapter 3.2.). The minimum area measured in plot SP01 is about 0.36 ha, with 45 species, an individual/species ratio of 3.8, 16 species being represented by only one tree.

The biodiversity is highest among the Paranean forests, as indicated by the number of species (31-35 for 1/5 ha), the individual/species ratio (2.34-2.91 for 1/5 ha) and the number of species represented by only one specimen (11-18 for 1/5 ha).

In the Paraguayan Alto Parana area, *Balfourodendron riedelianum (Rutaceae)* plays an important role in the floristic composition and vegetation structure of the forests. It constitutes a distinct element of the tall upland forests on well-drained soils, together with *Cedrela fissilis* and *Chrysophyllum gonocarpum.* This 25-35m high emergent tree overhangs the canopy. It is also present in disturbed and secondary forests. This species is widespread, occurring from south-eastern Brazil through to north-eastern Argentina and eastern Paraguay.

Floristically, this facies is most closely related to the Parana riverine forest (A2).

Species particularly well represented are: *Cedrela fissilis, Balfourodendron riedelianum, Chrysophyllum gonocarpum, Cabralea canjerana, Nectandra megapotamica, Ocotea spectabilis, Syagrus romanzoffiana, Cordia trichotoma, Lonchocarpus leucanthus, Fagara riedeliana.*

A.2. Riparian facies of the Parana river with Guarea kunthiana and Euterpe edulis

Surveys: BS01, BS02.

The soil texture of these forests is much sandier than in the former facies. Nevertheless the proximity of the Parana river provides a constant hydric equilibrium which allows for a tall semi-evergreen forest.

Tree numbers, basal areas and biodiversity seem to correspond to what has been observed in the former typical facies. The particularity of this riparian facies lies in the abundance of *Guarea kunthiana, Euterpe edulis, Bastardiopsis densiflora* and *Alchornea triplinervia.* The latter two species are typical heliophilous trees taking advantage of the gap provided by the river.

This facies could possibly be related to the *Euterpe edulis-Alchorneetum triplinerviae* association described by BOLOS & al. (1991) for the littoral zone of the "Serra do Mar".

Guarea kunthiana belongs to the Amazonian flora; in its original environment it normally grows in non-flooded lowland forests (PENNINGTON, 1981). But in the southern part with a dryer and less uniform climate, like Paraguay, it is confined to gallery forests. In our area, *G. kunthiana* is a differential species of the Parana riparian forest. This northern element moves into the Paraguayan Alto Parana forests by taking advantage of the favourable environment of the Parana river.

Euterpe edulis is also a differential element of the Parana riparian forests. The species has a disjunct distribution with its center in the Mata Atlantica area.

Bastardiopsis densiflora is a tree which forms the upper-intermediate layer of the Parana riparian forest where it can be considered a characteristic species. Elsewere this heliophilous species occurs frequently in the succession stages and more rarely in the "climacical" but slightly disrupted *Lauraceae* tall forests.

A.3. Xeric facies with Helietta apiculata

Surveys: BS10, BS11.

This facies has been observed on the edge of the main Paranean forest, in a forest-savanna mosaic area and on sandy-clayey substrate.

The forest structure is more or less the same as that observed in the two former facies. Nevertheless its biodiversity seems to be the lowest among all the *Lauraceae-Cedrela fissilis* formations (see Table 5).

The most preponderant species in this survey, *Luehea candicans,* is reported to have a wide neotropical distribution (CUNHA, 1985) extending from northern Brazil through to Uruguay, northern Argentina and Bolivia. As its extensive occurrence in our survey seems to be due to a gregarian habit, we preferred to use another preponderant species for the general characterization of this xeric facies: *Helietta apiculata.* The former species will be presented below (see: tall forests with *Helietta apiculata* and *Syagrus romanzoffiana,* Chapter 4.2:D).

The particularity of the *Lauraceae-Cedrela fissilis-Helietta apiculata* tall forests is the mixture of species belonging to the typical well-drained facies A.1 *(Cedrela fissilis, Cabralea canjerana, Balfourodendron riedelianum),* to the ill-drained facies B *(Matayba elaeagnoides, Rapanea umbellata),* to the low deciduous *Myrtaceae* forests and, lastly, to the xerophilous flora of central Brazil and

the Chaco *(Astronium fraxinifolium)*. The influence of a xeric flora is especially pronounced in the BS11-relevé, which is situated in an ecoclinal position between tall- and low-forest.

Further research may eventually show that this xeric facies is related to the forests of the dryer part of eastern Paraguay or central Brazil.

Species particularly well-represented are: *Ocotea puberula, Cedrela fissilis, Ocotea pulchella, Luehea candicans, Helietta apiculata, Rudgea major, Rapanea umbellata, Matayba elaeagnoides, Myrciaria ciliolata, Astronium fraxinifolium, Peltophorum dubium.*

B. Lauraceae-Luehea divaricata-Myrciaria rivularis ill-drained forests

Surveys: FU02, BS06, LCO2, SP02 (located in Ñeembucú department).

These forests are located on the lowest topographical levels of the landscape, on ill-drained and seasonally swampy soils whose texture is heavily clayey.

With regard to the height of the trees, this forest type does not differ significantly from the *Lauraceae-Cedrela fissilis*-forests. The basal area measured for 1 ha (FU02) reaches 15.9 m^2, with an average trunk diameter of 25.3 cm. 320 trees were counted. Nevertheless, the plot FU02 shows scars of former exploitation and we have to exercise caution with regard to these figures. As to the well-drained surveys, the values for 1 ha of ill-drained forest extrapolated from the Bertoni's 1/5 ha plots provide higher figures (see Chapter 3.2). These results do not allow us to conclude that the biomass values of the *Luehea divaricata* forests are significantly different from the *Cedrela fissilis* ones.

With regard to biodiversity, the species number is almost the same in one ha of ill-drained *Luehea divaricata* forest (FU02 = 58 spp.) as in one ha of well-drained *Cedrela fissilis* forest (SP01 = 60 spp.). For smaller plots (1/5 ha), the species numbers are 28 (BS06) and 25 (LCO2), i.e., lower than in well-drained forests. If we take into account the disturbed state of survey FU02 and Connell's intermediate disturbance theory (see Chapter 5), it seems possible that the biodiversity is lower in the *Lauraceae-Luehea divaricata* forests than in the *Lauraceae-Cedrela fissilis* ones.

Floristically the *Luehea divaricata-Myrciaria rivularis* ill-drained forest is characterized by the predominance of *Tiliaceae, Sapindaceae* and *Myrtaceae*. The closest floristic relationship is to be found with the *Araucaria* forests (C).

Luehea divaricata is the most characteristic species of the tall seasonally swampy forests where it is very common in the intermediate layer. According to some literature (CUNHA, 1985) the species has a south-tropical range, spreading from Brazil through to Argentina and Uruguay. This hygrophilous and heliophilous species is also a component of the succession stages.

With regard to the four species of *Sapindaceae* occurring particularly on the ill-drained substrates of the Paraguayan Alto Parana tall forests, these have a wide distribution area ranging from the Mata Atlantica through to the xerophilous Chaquean forests. However, their center of dispersion seems to be located in the Upper Parana-Upper Uruguay basins. All four of the species present show great ecological plasticity, colonizing humid, deep soils as well as rocky ones. Therefore they also constitute a prominent part of the succession stages. In the Paraguayan Alto Parana area, this plasticity allows them to colonize not only the most unfavourable soils in tall forests (swampy areas, depressions) but also the sandy or heavily clayey substrates of the low deciduous *Myrtaceae* forests.

Although *Diatenopteryx sorbifolia* is present in both tall well-drained *Lauraceae-Cedrela fissilis* (A) and in ill-drained *Lauraceae-Luehea divaricata* forests (B), the species is more frequent in the latter forest type. REITZ (1980) considers this species a very dynamic pioneer.

The significance of *Allophylus edulis* is not as clear. REITZ (1980) considers it rather to be a hygrophilous pioneer. However, the species is present in the lowest layers of several tall forest surveys. ORTEGA STUTZ (1989) considers it an element of the climacical tall forests of the Paraguayan

Alto Parana. According to SMITH & al. (1988), *A. edulis* is a co-dominant species of the underlayer of the "Floresta Estacional Decidual do Alto Uruguay" where it is frequently associated with *Sorocea bonplandii* and *Actinostemon concolor.*

Matayba elaeagnoides has one of the greatest ecological plasticities. It constitutes the intermediate and lower layers of both tall *Lauraceae-Luehea divaricata* and low *Myrtaceae* forests. The species is also particularly well represented in the *Araucaria* tall forests (see below), where it constitutes the canopy together with *Helietta apiculata.* The species is also reported to colonize the rocky "Cerros" of eastern Paraguay.

Finally, we should point out the high preponderance of a *Myrtaceae* species, *Myrciaria rivularis*, in most of the ill-drained forests. It makes up the forest underlayer where it may become strongly dominant. With *Luehea divaricata* and *Matayba elaeagnoides, Myrciaria rivularis* has to be considered a differential element of the tall ill-drained *Lauraceae*-forests. The distribution area and ecological plasticity of *Myrciaria rivularis* are similar to the ones of *Matayba elaeagnoides.* Due to their ecological plasticity, both species are recorded as frequent on ill-drained and rocky substrates.

Species particularly well-represented are: *Luehea divaricata, Matayba elaeagnoides, Myrciaria rivularis, Sebastiana brasiliensis, Patagonula americana, Diatenopteryx sorbifolia, Helietta apiculata, Nectandra megapotamica, Enneatypus tenuiflorus, Vitex cimosa, Syagrus romanzoffiana, Ocotea spectabilis.*

4.2. *Other less extended tall semi-evergreen forests*

Such forests are confined to particular substrates or are extensions of allochtonous formations inside the Paranean climacical forests.

C. *Araucaria angustifolia-Luehea divaricata swampy forests*

Survey: BS03.

This forest type has been observed only once. It grows on clayey soil, in the swampiest of the areas we surveyed. It seems to be a relict formation of the south and south-eastern Brazilian *Araucaria* forests. The very disadvantageous location in a swampy depression could prove that *Araucaria angustifolia* reaches its farthest western extension in the Paraguayan Alto Parana. Our *Araucaria angustifolia-Luehea divaricata*-forest is not vigorous enough to compete successfully on better substrates, so that it is confined to the swampier areas.

This type of forest corresponds to the *Araucario angustifoliae-Ocoteetum puberulae* association according to BOLOS & al. (1991).

In the tall swampy *Araucaria angustifolia-Luehea divaricata*-forests of the Paraguayan Alto Parana area, *Myrcianthes pungens* and *Campomanesia xanthocarpa* are abundant in the same way as in the "Zona dos Pinhais" of the southern Brazilian "Planalto" (LANDRUM, 1986). The dominance of *Myrtaceae* in this type of forest is another argument for the "Planalto" origin of the Paraguayan *Araucaria* forests.

Due to the abundance of big *Araucaria* trees, the measured basal area is the biggest we ever observed in our surveys (7.8 m² for 1/5 ha, i.e. 39 m²/ha). The maximum height of the forest corresponds to the layer formed by *Araucaria* (about 25 m). The number of trees counted in 1/5 ha is also one of the highest among our tall forest surveys: 143 for 1/5 ha, i.e. about 715 trees/ha. Unlike the biomass, the biodiversity is lower than that of the tall *Lauraceae* forests (20 spp. for 1/5 ha).

Apart from *Araucaria angustifolia* and *Luehea divaricata*, species of *Sapindaceae* as well as *Helietta apiculata* are well represented. The closest floristic relationships are consequently to be

found with the tall, ill-drained *Lauraceae* forests [*Lauraceae-Luehea divaricata-Myrciaria rivularis*-forests (B)].

Species particularly well represented are: *Araucaria angustifolia, Luehea divaricata, Matayba elaeagnoides, Ocotea puberula, Ilex paraguariensis, Helietta apiculata, Sebastiana brasiliensis, Actinostemon concolor, Diatenopteryx sorbifolia.*

D. Xerophilous Helietta apiculata-Syagrus romanzoffiana-forests

Survey: BS08.

Forests with *Helietta apiculata* seem to be native to the central part of eastern Paraguay. They grow on sandier soils, either in upland localities or on downslopes and in depressions. Their occurrence in the Alto Parana area therefore signifies an intrusion of western formations into this area. In the Paraguayan Parana region *Helietta apiculata* forests with palms occur on sandy-clayey soils in the area of Hernandaria, situated in the center of Alto Parana Department.

Helietta apiculata has a wide ecological amplitude (COWAN & SMITH, 1973): it occurs frequently in the low *Myrtaceae* forests; it is also plentiful in the tall ill-drained *Lauraceae-Luehea divaricata-Myrciaria rivularis*-forests (B) where it co-dominates with the latter species in the intermediate layer; it is reported to be abundant on the rocky substrates of the east-paraguayan "Cerros" and in the low gallery forest fringes inside the savanna areas.

In general, the presence of *Helietta apiculata* indicates an unfavourable substrate or the influence of a locally dryer environment, as is the case in the upland forest islets of the forest-savanna mosaic area [see above: *Lauraceae-Cedrela fissilis-Helietta apiculata*-forests (A.3)].

The measured basal area of such a forest is the lowest of our values for tall forests (2.7 m^2 for 1/5 ha, i.e. 13.5 m^2 for 1 ha). This low figure is due to the small trunk diameter of both of the predominent species in this forest-type, viz. *Helietta apiculata* and *Syagrus romanzoffiana.*

The highest tree layer is almost exclusively made up of *Helietta apiculata*. The clear foliage of this tree gives this forest its characteristic aspect.

The biodiversity of this survey is also the lowest of all our relevés: 14 spp. for 1/5 ha, 8 species being represented only by one tree (see Table 4).

The closest floristic relationships are to be found with the xeric facies of the *Lauraceae-Cedrela fissilis* formations (A3). Further research may show that the *Helietta apiculata-Syagrus romanzoffiana* forests are an intermediate stage between *Lauraceae-Cedrela fissilis-Chrysophyllum gonocarpum* forests (A) and *Lauraceae-Luehea divaricata-Myrciaria rivularis* forests (B).

The high frequency of *Helietta apiculata* in forest types B, C, D and A3 significantly increases the degree of floristic relationship.

Species particularly well represented include: *Helietta apiculata, Syagrus romanzoffiana, Nectandra megapotamica, Ocotea puberula, Peltophorum dubium, Matayba elaeagnoides, Styrax leprosum, Diatenopteryx sorbifolia.*

4.3. Low deciduous forests with Myrtaceae

Surveys: BS4A, BSAB, BS09, BS12.

These forests are characteristic in that their structure is lower than that of the *Lauraceae*-semievergreen forests. Their canopy does not exceed 9 m, with an average height of about 6 m. Basal areas and average trunk diameters show lower figures than those of the tall forests. Nevertheless our low forest surveys are not numerous enough to allow a significant, quantitative comparison with the tall forests.

From a phenological point of view, most of the trees loose their leaves during the dry season.

According to topographical location and substrate three types of low forests have been observed:

— typical ecoclinal formations made up of transitional belts between upland forests and downslope savannas (E1, E2);

— invasive forest-islets amidst hygromorphic savannas (E3);

— gallery-thicket fringing the seasonally flooded banks of rivulets inside savanna areas (E4).

Although the floristic composition is strongly influenced by the close, tall *Lauraceae*-forests, typical families like *Myrtaceae, Anacardiaceae* and *Myrcinaceae* characterize these formations.

Myrtaceae characterize the low deciduous forests of the Paraguayan Alto Parana. LEGRAND & KLEIN's discussion of the family with respect to the flora of Santa Catarina (1967, 1969, 1971a, 1971b, 1977a, 1977b) points out its extraordinary biodiversity in the "Mata Atlantica" and in the "Zona dos Pinhais". The *Myrtaceae* thus represent the most important western extension of the Brazilian southern "Planalto" and atlantic flora into the Paraguayan Alto Parana vegetation. This floristic influence is particularly significant in the low deciduous forests where some species are strictly confined to, and dominate, the lower and intermediate layers (3-8 m): *Myrciaria ciliolata, Eugenia uniflora, Blepharocalyx salicifolia, Myrcia multiflora, Calyptranthes concinna.*

Other species are indifferently present in low deciduous and tall semi-evergreen swampy forests *(Lauraceae-Luehea divaricata-Myrciaria rivularis*-forest and *Araucaria angustifolia-Luehea divaricata*-forest): *Myrciaria rivularis, Myrcianthes pungens, Campomanesia xanthocarpa, Eugenia* spp. As is the case in the "Mata tropical atlantica", the *Myrtaceae* are particularly well represented in the lower intermediate layer of the above-mentioned Paraguayan forests. *Myrciaria rivularis* is strikingly common in the tall semi-evergreen forests (B, C) of the depressions on ill-drained, clayey, and seasonally swampy soils (see above).

With regard to the *Myrsinaceae, Rapanea umbellata* occurs widely in the south-tropical and subtropical areas. In the Paraguayan Alto Parana it is frequent in the low *Myrtaceae* forests and in the tall *Lauraceae* forests, as well as in the secondary succession stages.

E. Myrtaceae-forests

These low *Myrtaceae* forests are probably western extensions of the south and eastern Brazilian deciduous forests (MORI & al., 1983b). Their biodiversity is lower than that observed in the tall forests. The number of species and trees of *Myrtaceae* is very important.

In the forest-savanna area the low *Myrtaceae*-forests occur as edaphoclimacical formations on sandy and xeric substrate as well as on swampy, clayey soils.

Species particularly well represented are: *Myrciaria ciliolata, Gomidesia sellowiana, Blepharocalyx salicifolia, Myrcia multiflora, Helietta apiculata, Matayba elaeagnoides.*

E1. Xeric facies with Lithraea molleoides

Survey: BS12.

In the forest-savanna area these forests are located between the upland tall *Lauraceae* forests and the downslope xeromorphic cerrado or "chamaedendrée" according to CHODAT & VISCHER (1916). They grow on the xeric and sandy slopes.

We note a strong floristic relationship with the upland tall *Lauraceae* forests [xeric facies (A3)] and with the other facies of low forests (see below).

Their most striking characteristic is the abundance of xerophilous species which are native to the Brazilian caatingas, viz. *Lithraea molleoides, Moquinia polymorpha, Schinus terebinthifolius.*

E2. Hygrophilous facies with Actinostemon concolor

Survey: BS4B.

These occur on the swampy and heavy, clayey soils of the main part of the Paranean forest, in areas where the edaphic humidity allows hydromorphic savannas to occur.

Besides trees of *Myrtaceae* and *Helietta apiculata, Actinostemon concolor* and *Terminalia triflora* are frequent. We have studied similar low formations on the foothills of the central Paraguayan hills (Cerros).

Actinostemon concolor frequently occurs in the hygrophilous low deciduous forests of the Paraguayan Alto Parana area. In eastern Paraguay it is also recorded in the low forests that grow on the "Cerros". It is a characteristic species of the underlayer of "Floresta Ombrofila Densa da costa atlântica" and of the "Floresta Estacional Decidual do Alto Uruguay" (SMITH & al., 1988). According to these authors, the species is a pioneer element of the "floresta latifoliada" colonizing the "Pinhais". It builds up gregarious monospecific populations on the rocky tops of the "chapadas" of the Serra Geral. According to SMITH & al. (1988), *Actinostemon concolor* is frequently associated with *Allophylus edulis, Sorocea bonplandii* and *Trichilia clausseni.*

E3. Mixed invasive islets

Survey: BS09.

This survey represents an invasive forest-islet inside a hygromorphic savanna. The heterogeneity of the floristic components of survey BS09 shows that this forest is evolving towards a tall *Lauraceae* forest by fostering soil-drainage.

Flora and vegetation are a mixture of *Myrtaceae-Actinostemon concolor* hygrophilous low forests and of *Lauraceae-Luehea divaricata-Myrciaria rivularis* (B) tall hygrophilous forests.

E4. Myrtaceae-gallery thicket

Survey: BS4A.

These narrow fringes are located along seasonal streams in the forest-savanna area. They occur on substrates which undergo very contrasted edaphic humidity conditions, i.e. they are overflooded during the rains and completely dried out during the dry season. This is the reason why hygrophilous species like *Inga* spp. and *Myrtaceae* spp. are to be found here next to xerophilous ones like *Cereus stegonosus* and *Bromelia* spp.

5. Discussion

Due to the many years of human interference with Paraguayan forests, the number of trees by ha and the basal area are lower (ca. 20 m^2/ha) than those observed in other more northern neotropical tall forests. Likewise the tree biodiversity is lower (ca. 60 spp./ha). According to GENTRY's theory (1982) the latter phenomenon may be correlated with the rainfall, since the Paraguayan values correspond to others provided by sites with equivalent precipitation. The highest biodiversity values among the Paraguayan Alto Parana tall forests have been observed in slightly disturbed forests, which corroborates Connell's theory of intermediate disturbance cited by GENTRY (1982).

As demonstrated above (see Chapter 3.3), the frequent occurrence of *Lauraceae, Meliaceae, Sapotaceae, Rutaceae, Sapindaceae* and *Tiliaceae* characterizes most of the Paraguayan Alto Parana tall semi-evergreen forests.

The *Lauraceae-Cedrela fissilis-Chrysophyllum gonocarpum* tall forests (see Chapter 4) are to be considered as the climacical vegetation of the Paraguayan Alto Parana area, where they grow on the best substrates. The other *Lauraceae* tall forests *(Luehea divaricata-Myrciaria rivularis* formations) have a less specific distribution and are confined to the unfavourable swampy substrates of the Paraguayan Alto Parana area. Here they can survive thanks to their high ecological plasticity.

The *Araucaria angustifolia-Luehea divaricata* tall forests and the *Helietta apiculata-Syagrus romanzoffiana* forests are allochtonous formations. The former are native to the eastern Brazilian Planalto, the latter to the western and sandier basin of the Paraguay river.

As explained above, the *Myrtaceae* low forests are western extensions of the south Brazilian Planalto (MORI & al., 1983b), of the Mata Atlantica forests and even of north-eastern Brazil. The preponderance of *Helietta apiculata* gives the low forests of the Alto Parana area their typical Paraguayan aspect.

In the past *Araucaria angustifolia* tall forests (C) might have reached a far more western range and might well have been the climacical formation of the Paraguayan Alto Parana area.

Forests made up of broad-leaved species with a wide Brazilian south-eastern distribution and with a high ecological plasticity have probably succeeded the *Araucaria* formations, driving the latter on to the most unfavourable substrates. *Lauraceae-Luehea divaricata-Myrciaria rivularis* tall forests (B) constitute this first substitution stage, with many species characterized by a wide ecological amplitude like *Matayba elaeagnoides, Helietta apiculata, Myrciaria rivularis*. At present *Lauraceae-Luehea divaricata-Myrciaria rivularis* (B) tall forests are confined to unfavourable substrates in the Paraguayan area. They seem to have been replaced, on one hand, by *Helietta apiculata* tall forests (D, A3) on rather sandy substrates and on the other hand by *Lauraceae-Cedrela fissilis-Chrysophyllum gonocarpum* tall forests (A1) on well-drained and more clayey soils. This latter formation is strongly influenced by Amazonian or peri-Amazonian elements. It can in fact be considered to be the climacical formation of the Paraguayan Alto Parana area. The low deciduous *Myrtaceae* forests (E) are probably relictual formations, like the *Araucaria* tall forests (C), being confined to substrates where the tall forests do not thrive.

The preponderant tree components of the Paraguayan Alto Parana tall forests generally have distribution areas ranging from eastern Paraguay to north-eastern Argentina and to southern and south-eastern Brazil, e.g. *Balfourodendron riedelianum, Matayba elaeagnoides* and *Luehea divaricata*. They may have taken advantage of the Parana and Uruguay rivers and of their tributaries to spread eastwards. Several other species have a wider neotropical distribution range, frequently occurring in the Paraguayan area *(Cedrela fissilis, Chrysophyllum gonocarpum)*.

The floristic specificity of the Paraguayan Alto Parana tall forest is striking among the other south Amazonian formations due to the enormous preponderance of *Cedrela fissilis* and *Chrysophyllum gonocarpum*. Both species present disjunct and almost peri-Amazonian distributions, with the highest occurrence in the Upper Parana-Upper Uruguay basins. This type of distribution may signify that the *Lauraceae-Cedrela fissilis-Chrysophyllum gonocarpum*-forests are formations that have been substituted in the past by the Amazonian Hylaea and that are currently surviving at the edges of the Amazon basin. We may also consider the Paraguayan forests to be a relay between the southern extremity of the Amazon forest and the southern area of the Mata Atlantica [see PRANCE (1989), fig. 6.3].

We agree with SMITH (1962) who considers the south-paraguayan forest a tropical forest. Although its subtropical location exposes this forest to harder mesological conditions (frost), its specific composition and structure are related to those of more northern tropical forests. Moreover, this author considers that the Paraguayan Alto Parana tall forests have invaded southern and south-eastern Brazil. Consequently we may look upon the Paraguayan Alto Parana area as the center

of a distinct neotropical flora which has extended eastwards along the Upper Parana-Upper Uruguay basins. During its eastward migration this flora would have competed successfully with the autochtonous *Araucaria*-forests and the low deciduous *Myrtaceae*-forests. Nevertheless we should also take into account BERNARDI's following opinion (1984): "... las afinidades de la flora dendrológica paraguaya son masivamente 'pan-brasileñas'".

It is surprising that in "Tropical Rain Forest Ecosystems" PRANCE (1989) does not treat the forests of the Upper Parana-Upper Uruguay basins as a distinct "Phytochorium", but includes them in his 18th Phytochorium (Soutern Brazil Regional Center) dominated by *Araucaria*-forests. Our results lead us to consider the Alto Parana tall forests as a specific tropical moist forest where *Lauraceae, Meliaceae, Sapotaceae, Sapindaceae* and *Tiliaceae* predominate.

ACKNOLEDGEMENTS

BIBLIOGRAPHICAL REFERENCES

BALSLEV, H., J. LUTEYN, B. ØLLGAARD & L. B. HOLM-NIELSEN (1987). Composition and structure of adjacent unflooded and floodplain forest in Amazonian Ecuador. *Opera Bot.* 92: 37-57.

BEARD, J. S. (1944). Climax vegetation in tropical America. *Ecology* 25: 127-158.

BENZÉCRI, J. P. & al. (1973). *L'analyse des données. II. L'analyse des correspondances.* Dunod, Paris.

BERNARDI, L. (1984). Contribución a la Dendrologia Paraguaya, parte I. *Boissiera* 35.

BOLOS, O. de, A. C. CERVI & G. HATSCHBACH (1991). Estudios sobre la vegetación de Paraná (Brasil Meridional). *Collectanea Bot.* 20: 79-182.

BOOM, B. M. (1986). A Forest Inventory in Amazonian Bolivia. *Biotropica* 18: 287-294.

CAMPBELL, D. G., D. C. DALY, G. T. PRANCE & U. N. MACIEL (1986). Quantitative ecological inventory of Terra Firme and Várzea tropical forest on the rio Xingu, Brazilian Amazon. *Brittonia* 38: 369-393.

CHODAT, R. & W. VISCHER (1916, reprint 1977). *La végétation du Paraguay.* Cramer, Vaduz.

COWAN, R. S. & L. B. SMITH (1973). Rutáceas. part I. *In:* REITZ, P. R. (ed.), *Flora ilustrada Catarinense.* Itajaí, Santa Catarina, Brasil. 89 pp.

CUNHA, M. C. da Silva (1985). Revisão das espécies do gênero Luehea Willd. (Tiliaceae). *Sellowia* 37: 5-41.

CURTIS, J. T. & R. P. McINTOCH (1951). An upland forest continuum in the prairie-forest border region Wisconsin. *Ecology* 32: 476-496.

ESKUCHE, U. (1983). *Listas florísticas de comunidades vegetales.* Exkursionsführer. Corrientes. 58 pp.

ESKUCHE, U. (1984). Vegetationsgebiete von Nord- und Mittelargentinien. *Phytocoenologia* 12: 185-199.

FAO/UNESCO (1971). *Soil map of the world.* Paris, Rome.

FISCHER, U. (1981). *Implementación de un arboretum para la escuela técnica forestal.* C. F. A. P.

GENTRY, A. H. (1982). Patterns of Neotropical Plant Species Diversity. *In:* HECHT, M. K., B. WALLACE & G. T. PRANCE (ed.), *Evolutionary Biology* 15: 1-84.

GENTRY, A. H. (1988). Tree species richness of upper Amazonian forests. *Proc. Natl. Acad. USA* 85: 156-159.

GORHAM, R. (1973). *Paraguay: ecological essays.* Academy of the Arts and Sciences of the Americas, Miami.

HAHN, W. J. (1990). *A synopsis of the palmae of Paraguay.* Thesis, Cornell University. 226 pp.

LANDRUM, L. R. (1986). Campomanesia, Pimenta, Blepharocalyx, Legrandia, Acca, Myrrhinium, and Luma (Myrtaceae). *Flora Neotropica* 45. The New York Botanical garden, New York. 178 pp.

LEGRAND, C. D. & R. M. KLEIN (1967). Mirtáceas. *In:* REITZ, P. R. (ed.), *Flora ilustrada Catarinense.* Itajaí, Santa Catarina, Brasil. 44 pp.

LEGRAND, C. D. & R. M. KLEIN (1969). Mirtáceas. *In:* REITZ, P. R. (ed.), *Flora ilustrada Catarinense.* Itajaí, Santa Catarina, Brasil. 114 pp.

LEGRAND, C. D. & R. M. KLEIN (1971a). Mirtáceas. In: REITZ, P. R. (ed.), *Flora ilustrada Catarinense.* Itajaí, Santa Catarina, Brasil. 33 pp.

LEGRAND, C. D. & R. M. KLEIN (1971b). Mirtáceas. 6. Calyptranthes Sw. *In:* REITZ, P. R. (ed.), *Flora ilustrada Catarinense.* Itajaí, Santa Catarina, Brasil. 64 pp.

LEGRAND, C. D. & R. M. KLEIN (1977b). Mirtáceas. 8. Campomanesia, 9. Feijoa, 10. Britoa, 11. Myrrhinium, 12. Hexachlamys, 13. Siphoneugena, 14. Myrcianthes, 15. Neomitranthes, 16. Psidium. *In:* REITZ, P. R. (ed.), *Flora ilustrada Catarinense.* Itajaí, Santa Catarina, Brasil. 158 pp.

LEGRAND, C. D. & R. M. KLEIN (1977a). Mirtáceas — Suplemento I. *In:* REITZ, P. R. (ed.), *Flora ilustrada Catarinense.* Itajaí, Santa Catarina, Brasil. 114 pp.

MARTINEZ-LABORDE, J. B. (1983). Revisión de las Monimiaceae austroamericanas. *Parodiana* 2(1): 1-24.

MORI, S. A., B. M. BOOM, A. M. DE CARVALHO & T. S. DOS SANTOS (1983a). Southern Bahian moist forests. *Bot. Rev.* 49: 155-232.

MORI, S. A., B. M. BOOM, A. M. DE CARVALHO & T. S. DOS SANTOS (1983b). Ecological Importance of Myrtaceae in an Eastern Brazilian Wet Forest. *Biotropica* 15(1): 68-70.

ORTEGA STUTZ, L. C. (1989). *Etude de la structure et de la composition floristique des successions forestières dans le Haut Parana (Paraguay oriental).* Thèse n° 2381, Faculté des Sciences, Université de Genève.

PENNINGTON, T. D. (1981). Meliaceae. *Flora Neotropica* 28. The New York Botanical Garden, New York.

PENNINGTON, T. D. (1990). Sapotaceae. *Flora Neotropica* 52. The New York Botanical Garden, New York.

PRANCE, G. T. (1989). American Tropical Forests. *In:* LIETH, H. & M. J. A. WERGER (ed.), *Tropical Rain Forest Ecosystems.* Elsevier, Amsterdam. 713 pp.

REITZ, R. (1974). Palmeiras. *In:* REITZ, P. R. (ed.), *Flora ilustrada Catarinense.* Itajaí, Santa Catarina, Brasil. 189 pp.

REITZ, R. (1980). Sapindáceas. *In:* REITZ, R. (ed.), *Flora ilustrada Catarinense.* Itajaí, Santa Catarina, Brasil. 160 pp.

ROHWER , J. G. (1986). Prodromus einer Monographie der Gattung Ocotea Aubl. (Lauraceae), sensu lato. *Mitt. Inst. Allg. Bot. Hamburg* 20.

SMITH, L. B. (1962). Origins of the flora of southern Brazil. *Contr. U.S. Natl. Herb.* 35: 215-249.

SMITH, L. B., R. J. DOWNS & R. M. KLEIN (1988). Euforbiáceas. *In:* REITZ, R. (ed.), *Flora ilustrada Catarinense,* Itajaí, Santa Catarina, Brasil. 408 pp.

STUTZ, L. C. (1983). Etudes floristiques de divers stades secondaires des formations forestières du Haut Parana (Paraguay oriental). Inventaire floristique d'une réserve forestière. *Candollea* 38: 542-573.

STUTZ DE ORTEGA, L. C. (1984). Etudes floristiques de divers stades secondaires des formations forestières du Haut Parana (Paraguay oriental). Dynamisme et reconstitution d'une forêt secondaire peu dégradée. *Candollea* 39: 386-394.

STUTZ DE ORTEGA, L. C. (1986). Etudes floristiques de divers stades secondaires des formations forestières du Haut Parana (Paraguay oriental). Floraison, fructification et dispersion des espèces forestières. *Candollea* 41: 121-144.

STUTZ DE ORTEGA, L. C. (1987). Etudes floristiques de divers stades secondaires des formations forestières du Haut Parana (Paraguay oriental). Structure, composition floristique et régénération naturelle: comparaison entre la foret primaire et la forêt sélectivement exploitée. *Candollea* 42: 205-262.

VATTIMO, I. DE (1979). Lauráceas part I. *In:* REITZ, P. R. (ed.), *Flora ilustrada Catarinense.* Itajaí, Santa Catarina, Brasil. 50 pp.

Address of the authors: Conservatoire et Jardin botaniques de la Ville de Genève, Case postale 60, CH-1292 Chambésy/GE.