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The mixed dense forest of the Southern Chaco. Contribution to the study of flora and vegetation of the Chaco. VIII.

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ABSTRACT

LEWIS, J. P., E. F. PIRE & J. L. VESPRINI (1994). The mixed dense forest of the Southern Chaco. Contribution to the study of flora and vegetation of the Chaco. VIII. *Candollea* 49: 159-168. In English, English and French abstracts.

The Santa Fe Forest Wedge is the southernmost portion of the Eastern Chaco. Plant communities form toposequences perpendicular to rivers and "esteros" and in the upper part of the elevation gradient there are mixed dense forests (Chaquenian forest). In this paper we analyse the structure and variation along the S.-N. geographic gradient of the mixed dense chaquenian forest. The tree canopy is almost continuous and its structure is complex with two or more united tree layers and a very sparse herbaceous stratum. Floristic composition varies along the geographical gradient, northwards this forest becomes floristically richer and amazonian species appear in it.

RÉSUMÉ

LEWIS, J. P., E. F. PIRE & J. L. VESPRINI (1994). La forêt dense mixte du Chaco méridional. Contribution à l'étude de la flore et de la végétation du Chaco. VIII. *Candollea* 49: 159-168. En anglais, résumés anglais et français.

Le coin forestier Santa Fe est la partie la plus méridionale du Chaco oriental. Les groupements végétaux forment des toposéquences perpendiculaires aux fleuves et "esteros". La partie supérieure du gradient altitudinal est colonisée par des forêts denses mixtes (forêt "chaquénienne"). La structure et la variation le long du gradient S-N géographiques des forêts mixtes denses du Chaco sont analysées. La cime des arbres est presque continue et sa structure est complexe, avec deux ou plusieurs étages et une strate herbacée très éparse. La composition floristique varie le long des gradients géographiques: vers le nord, la richesse floristique de la forêt augmente avec l'apparition des espèces amazoniennes.

KEY-WORDS: Argentina — Chaco — Forests — Floristic richness — Gradients — Mixed forests — Vegetation structure.

Introduction

The whole of the Chaco covers about 1.000.000 km^2 on E. Bolivia, W. Paraguay, N. Argentina and a very small part of S. Brasil, from parallel 15°S to 35°S. It is a huge sedimentary alluvial plain with a very gentle slope from SE. to NW. with hills and relatively low mountains in the west. The Paraguay and the Paraná rivers run along the east boundary and on the western one pre-Andean high mountains stand.

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Climate is warm temperate humid in the east, semiarid in the west. Mean annual temperature ranges from 18°C in the south to 26°C in the north with an absolute maximum of summer temperature of 48°C and winter frosts. Annual rainfall varies from 1300 mm in the east to less than 500 mm in the west, whereas it increases when approaching the western high mountains. Most rainfall occurs during summer and there is a long winter drought of variable length (BURGOS, 1970; SPICHIGER & RAMELLA, 1989).

Three main river systems cross the Chaco from NW. to SE.; from north to south they are the Pilcomayo, Bermejo and Juramento-Salado. The river Pilcomayo separates the Northern Chaco from the Austral Chaco. Most authors segregate a humid Chaco in the east from a dry Chaco in the west (RAGONESE & CASTIGLIONI, 1970; CABRERA & WILLINK, 1980; RAMELLA & SPICHIGER, 1989). CABRERA (1971) divides the Austral Chaco in an Eastern district characterized by the presence of *Schinopsis balansae*, a Western one characterized by the presence of *Schinopsis lorentzii* and the Serrano district by *Schinopsis haenkeana*. In the south between the Eastern and Western sectors there is a large depression, the Submeridional Lowlands, characterized by *Spartina argentinensis* grasslands and the scarcity of trees (LEWIS & al., 1990). A general study of the Austral Chaco vegetation and environment was made by MORELLO & ADÁMOLI (1968).

The southernmost segment of the Eastern Chaco is the Santa Fe Forest Wedge ("Cuña Boscosa") which is situated between the Submeridional Lowlands and the river Paraná from 28° to 30°30'S. Its vegetation is a mosaic of forests, savanna grasslands and hygrophilous communities. The most important plant communities are ordered along moisture and salinity gradients correlated with topographic elevation forming different types of toposequences (SPICHIGER & al., 1991). The river valleys are covered by *Copernicia australis* savannas with an herbaceous layer of *Panicum prionitis* or *Spartina argentinensis*, and then following the elevation gradient there are forests of *Prosopis nigra* var. *ragonesei* ("algarrobal"); open forests of *Schinopsis balansae* ("quebrachal") and on the highest part of the gradient mixed dense forests ("bosque chaqueño") (Fig. 1). The "esteros" (senescent waterways) are covered by a mosaic of hygrophilous communities sometimes flanked or pervaded by *Spartina argentinensis* grasslands and then following the elevation gradient the "algarrobal", "quebrachal" and "bosque chaqueño" (Fig. 2) (LEWIS & PIRE, 1981).

The object of this paper is to analyse the floristic composition and structure of the mixed dense forest ("bosque chaqueño") which is on the higher, most evolved and better drained soils of the Santa Fe Forest Wedge.

Material and methods

Nine stands of the mixed dense forest located at different latitudes were sampled with point centered quarter method (COTTAM & CURTIS, 1956) and relative frequency was calculated for all tree species. Additional species present in the stand but not sampled were recorded. On four stands cartographic quadrats and vegetation profiles (DAVIS & RICHARDS, 1933) were drawn for 25 × 10 m plots, two of them are shown in Figures 6 and 7.

Data were classified with Ward's method using euclidean distance as dissimilarity measure and then ordinations were made with Detrended Correspondence Analysis (DECORANA) and Principal Component Analysis (PCA) using a correlation matrix. In all cases PC-ORD programs were used (McCUNE, 1991).

Results

On Table 1 the floristic composition of the stands is shown ordered by increasing latitude. Species with + symbol are those present in the stand but not sampled with the point centered quarter method. Floristic richness increases linearly from south to north and there is a significant correlation (r = 0.68) between latitude and the number of species (LEWIS, 1991).

	1	2	3	4	5	6	7	8	9
1 *Geoffroea decorticans*	25.0	2.5	5.5	5.0			2.5		
2 *Bumelia obtusifolia*	7.5	7.5	7.5	17.5	+	+	+		+
3 *Prosopis* sp.	17.5	17.5	12.5	7.5	5.0	+	+	+	+
4 *Schinopsis balansae*	20.5	27.5	7.5	+	+	+	5.0		+
5 *Acacia aroma*	5.0		2.5				+		
6 *Aspidosperma quebracho-blanco*	5.0	7.5	15.0	5.0	+	7.5	2.5		
7 *Acacia praecox*	5.0	5.0	22.5	20.0	5.0	12.5	7.5	+	+
8 *Achatocarpus praecox*	15.0	5.0	17.5	7.5	5.0	20.0	2.5	+	12.5
9 *Sapium haematospermum*		5.0		5.0				+	2.5
10 *Zizyphus mistol*			2.5	7.5		+			
11 *Phytolacca dioica*		+	5.0	5.0			+	+	+
12 *Capparis retusa*		10.0	2.5	2.5	2.5	+	+		
13 *Myrcianthes cisplatensis*		12.5		7.5	10.0	15.0	7.5	7.5	7.5
14 *Acanthosyris falcata*				2.5			+		
15 *Gleditsia amorphoides*				7.5	12.5	+	5.0	7.5	27.5
16 *Caesalpinia paraguariensis*		+		+	5.0	5.0	5.0		
17 *Ruprechtia laxiflora*					30.0	17.5	17.5	7.5	7.5
18 *Eugenia uniflora*					22.5	12.5	12.5	27.5	15.0
19 *Patagonula americana*					2.5	+		+	2.5
20 *Scutia buxifolia*		+			+	10.0	12.5	25.0	15.0
21 *Fagara naranjillo*							10.0		
22 *Rapanaea lorentzii*							10.0		
23 *Allophyllus edulis*						+	+	22.5	5.0
24 *Terminalia triflora*								2.5	5.0
25 *Hexachlamis* sp.									2.5
26 *Psidium* sp.									2.5
27 *Acacia caven*	+	+				+	+		+
28 *Jodinia rhombifolia*			+						
29 *Carica quercifolia*				+					
30 *Pisonia zapallo*				+					
31 *Aspidosperma triternata*					+				
32 *Eugenia pyriformis*							+		
33 *Fagara hyemalis*								+	
34 *Arecastrum romanzoffianum*									+
35 *Ficus monckii*									+
36 *Tabebuia heptaphylla*									+
37 *Pithecellobium scalare*									+
38 *Enterolobium contortisiliquum*									+
39 *Holocalyx balansae*									+
Recorded species	8	10	11	13	10	8	13	7	12
Total species	9	14	12	16	15	16	22	14	24

+ Species present in the stand but not sampled.

Table 1. — Floristic composition of the stands. Ordered from South (1) to North (9).

Relative floristic composition varies as well with latitude. When stands are classified (Fig. 3) two main clusters are formed, a southern one characterized by *Prosopis* sp., *Bumelia obtusifolia* and *Geoffroea decorticans* and a northern one characterized by *Ruprechtia laxiflora*, *Eugenia uniflora* and to a lesser degree by *Gleditsia amorphoides*. The northern cluster is formed by two distinct clusters of lower hierarchy, one characterized by *Caesalpinia paraguariensis* and another which has the northernmost stands with *Allophylus edulis* and *Terminalia triflora*. The southern cluster is also formed by two clusters which differ from each other by the relative frequency of *Schinopsis balansae* and *Acacia praecox*. It must be pointed out that in the northern stands there is hardly any individual of *Schinopsis balansae*.

The PCA scatter diagram based on the analysis of a correlation matrix (Fig. 4) is almost the same as the one based on the analysis of a covariance matrix (LEWIS, 1991) and it shows that axis I segregates the northern clusters from the southern ones which are further divided by axis II. Clusters are arranged along a horse shoe gradient mainly defined by the first axis with the SW and NE clusters at both extremes. DECORANA (Fig. 5) also scatter the clusters along a gradient mainly defined by the first axis.

Cartographic diagrams (Fig. 6) show that the stands of this forest have an almost continuous canopy with small gaps of different sizes resulting from clumped distribution of trees, presence of small treeless depressions and treefalls. Vegetation profiles (Fig. 7) show that the structure of this forest is rather complex. There is a tall mixed tree layer more than 10 m high of the dominant species and a lower tree layer of about 5 m high where *Eugenia uniflora* is frequent accompanied by renewals of most of the tree species. Below the lower tree layer there is a layer with shrubs and the younger renewals of tree species. Often all layers are united so that they can not be distinguished from each other and woody species form a vertical continuum of different species and individuals heights. In some places of the northern stands *Ficus monckii* is an epiphyte on trees, that outgrows and finally kills its hosts occupying their place forming an emergent tree layer 15 m high. The herb layer is not very conspicuous, and in dense shade bromeliads such as *Bromelia serra* can be abundant. Lianas and epiphytes are present but they are not very abundant.

Discussion

In the south of the area there are no marked differences between this forest and the quebrachal. Northwards although both types of forest become floristically richer they differenciate from each other in structure and floristical composition.

The Santa Fe Forest Wedge "quebrachal" is a xerophytic open and clear forest quite different from the quebrachal of the western Chaco (ADÁMOLI & al., 1972) or the Paraguayan Chaco (RAMELLA & SPICHIGER, 1989; SPICHIGER & al., 1991), while the mixed dense forest ("bosque chaqueño") is a dense, shady and more hygrophilous type of forest.

Schinopsis balansae, *Aspidosperma quebracho-blanco*, *Acacia praecox* and *Prosopis* sp. are fairly abundant in the quebrachal and in the southern stands of the "bosque chaqueño", but become rarer on the northern stands of the latter. In fact in the far northern stands these species, especially *Schinopsis balansae* are almost absent and grow preferentially in the internal or external edges of the forests, that is in canopy gaps around ponds or internal depressions or in the transition zone with the "quebrachal" or savanna grasslands which thrive on depressed areas next to the forests.

While in the quebrachal *Aspidosperma quebracho-blanco* and especially *Schinopsis balansae* seedlings, saplings and renewals are very abundant they are absent altogether in the mixed dense forest. Inside this forest *Schinopsis balansae* individuals, if present, are very old and do not regenerate when felled. Important species from the quebrachal are large-gap species while those from this type of forest must be small-gap or understorey specialists (DENSLOW, 1980).

The temperature gradient of the Chaco can be correlated with the latitudinal gradient, therefore the northward increase in floristical richness by a 2.5 factor over this segment may be correlated with high temperatures. However, floristic richness may also be correlated to moisture, as those stands at similar latitudes are floristically richer when they are closer to the Paraná river. Along

the banks of the Paraná river valley there are even more hygrophilous forests of different nature dominated by *Holocalyx balansae*, *Pouteria gardneriana* and *Chrysophyllum gonocarpus* (PRADO & al., 1989).

In the south the mixed dense forest species are mainly chaquenian, but when they become richer towards the north they get some amazonian (sensu CABRERA & WILLINK, 1980) or more precisely Austro-Brazilian species such as *Arecastrum romanzoffianum*, *Holocalyx balansae*, *Allophylus edulis*, *Tabebuia heptaphylla*, *Ficus monckii*, etc.

These forests are placed over long narrow hills or on levees ("albardones") associated to active or senescent waterways; so they may be some sort of intermediate forests between an impoverish gallery forest and humid Chaco forests (SENNHAUSER, 1991), but appart from anthropic destruction they seem to be very stable.

Although throughout the Forest Wedge, the floristically poor, xerophilous "quebrachal" is more widespread than the mixed dense forest ("bosque chaqueño"), the "Bosque chaqueño" seems to be a more evolved type of forest and as its stands are more tropical and hygrophilous forests the question arises if these are really chaquenian forests or they are an amazonian intrusion within the Chaco, as hinted by PRADO (1991).

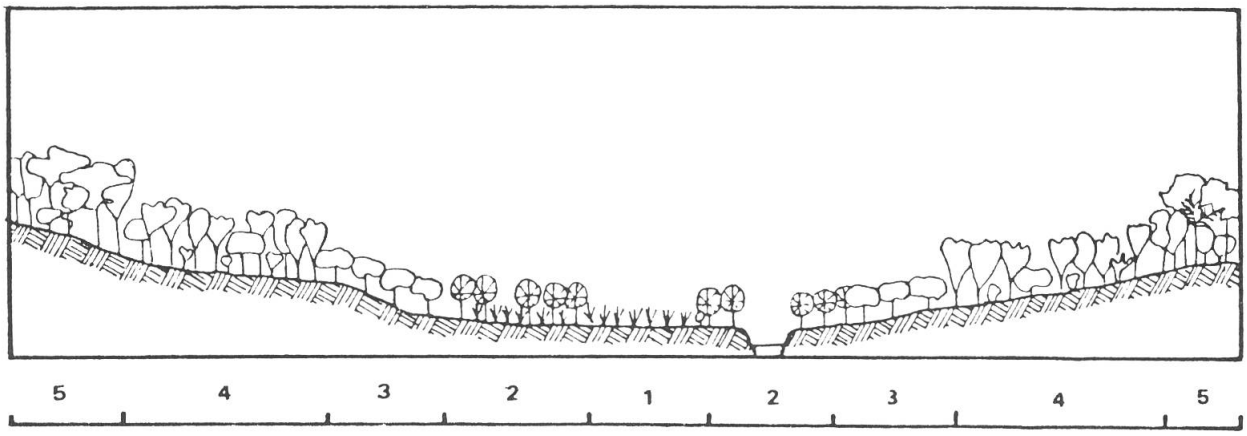

Fig. 1. — Plant communities of the Santa Fe Forest Wedge along an elevation gradient perpendicular to a river. **1)** *Panicum prionitis* tall grassland; **2)** Palm *(Copernicia australis)* groves; **3)** *Prosopis nigra* var. *ragonesei* forest; **4)** *Schinopsis balansae* quebrachal; **5)** Mixed dense forest (Bosque chaqueño).

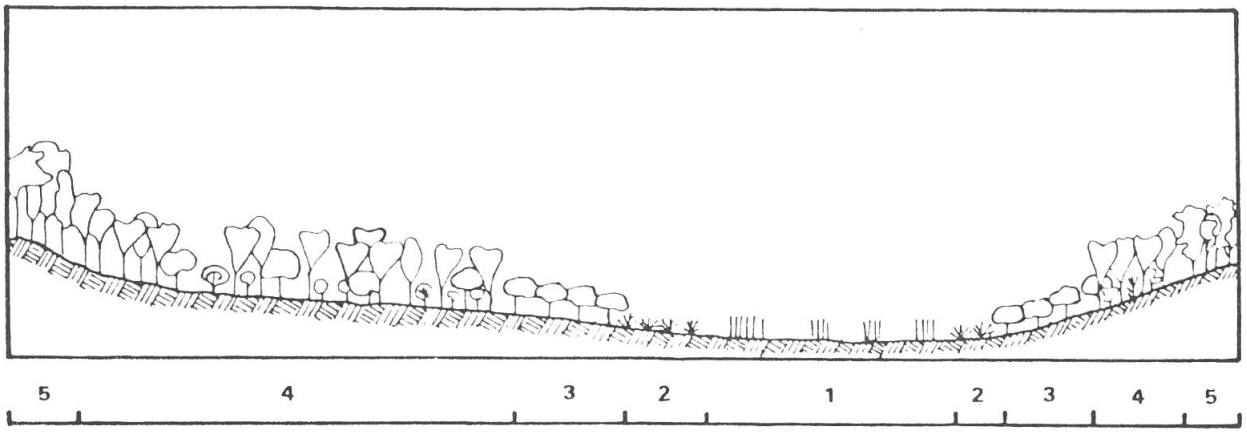

Fig. 2. — Plant communities of the Santa Fe Forest Wedge along an elevation gradient perpendicular to an "estero". **1)** Mosaic of hygrophilous communities on the bed of the estero; **2)** *Spartina argentinensis* tall grassland; **3)** *Prosopis nigra* var. *ragonesei* forest; **4)** *Schinopsis balansae* quebrachal; **5)** Mixed dense forest (Bosque chaqueño).

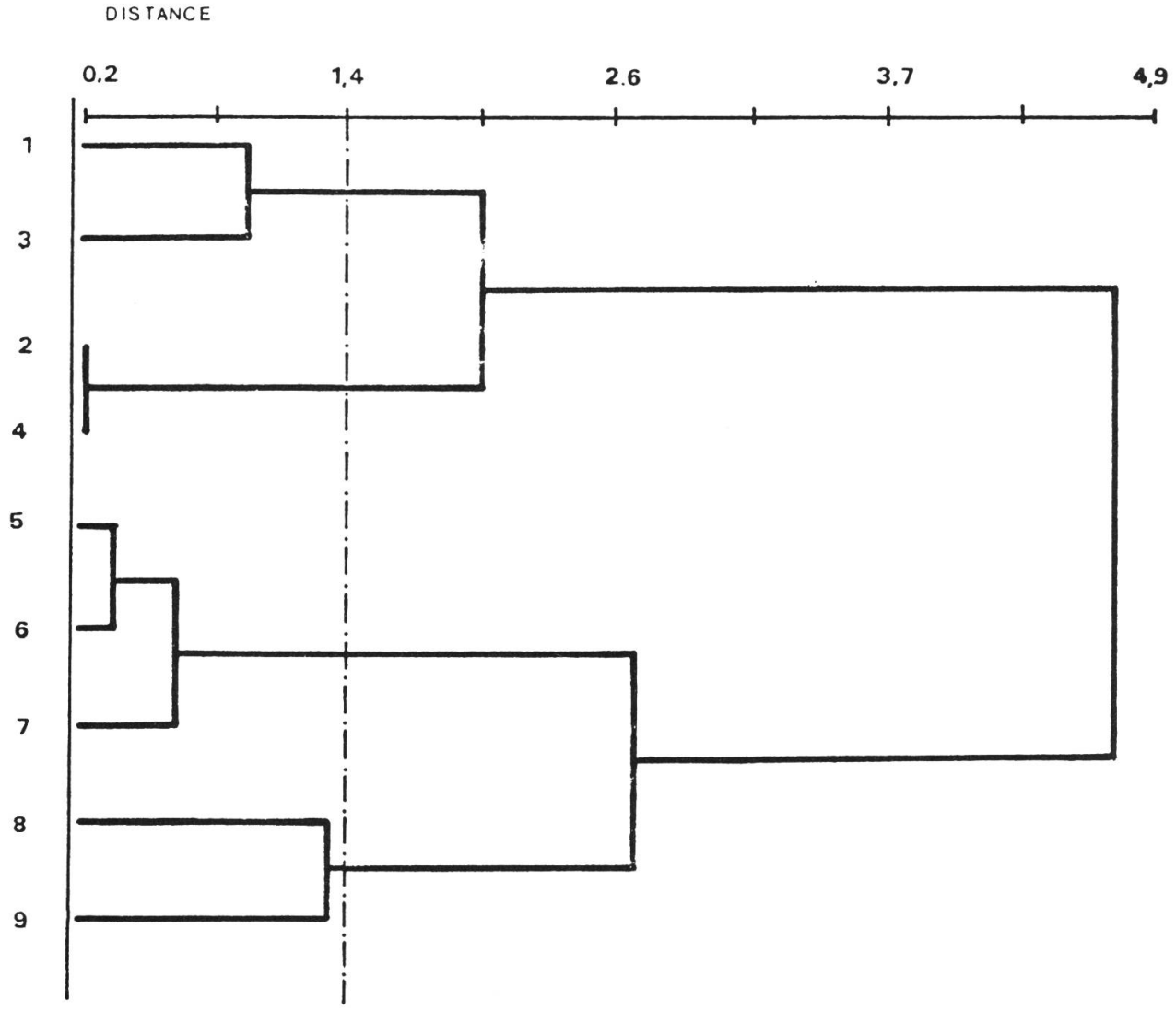

Fig. 3. — Dendrogram of the stands classified with Ward's method.

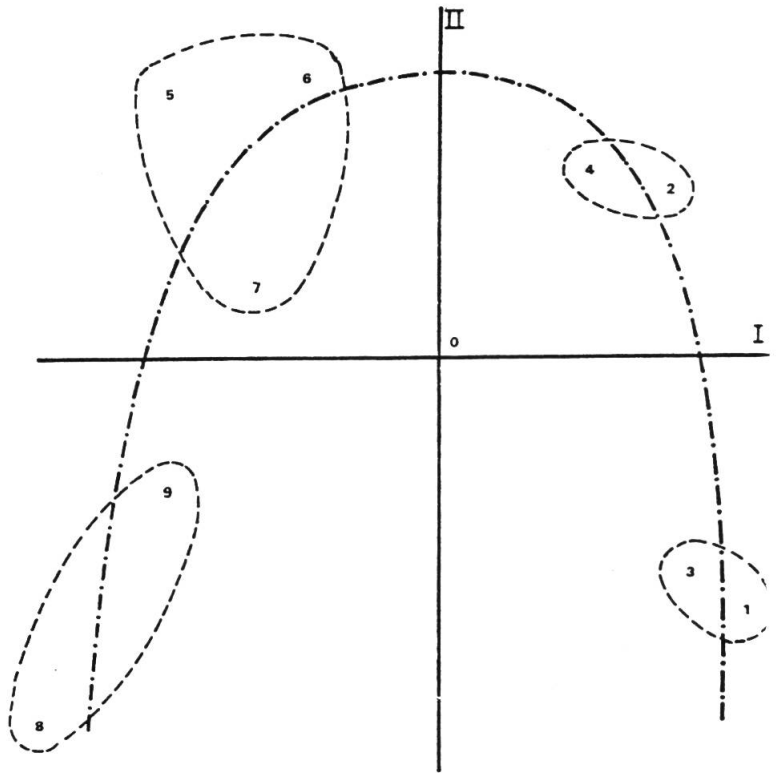

Fig. 4. — Principal Component Analysis scatter diagram of the stands on the plane of axes I and II.

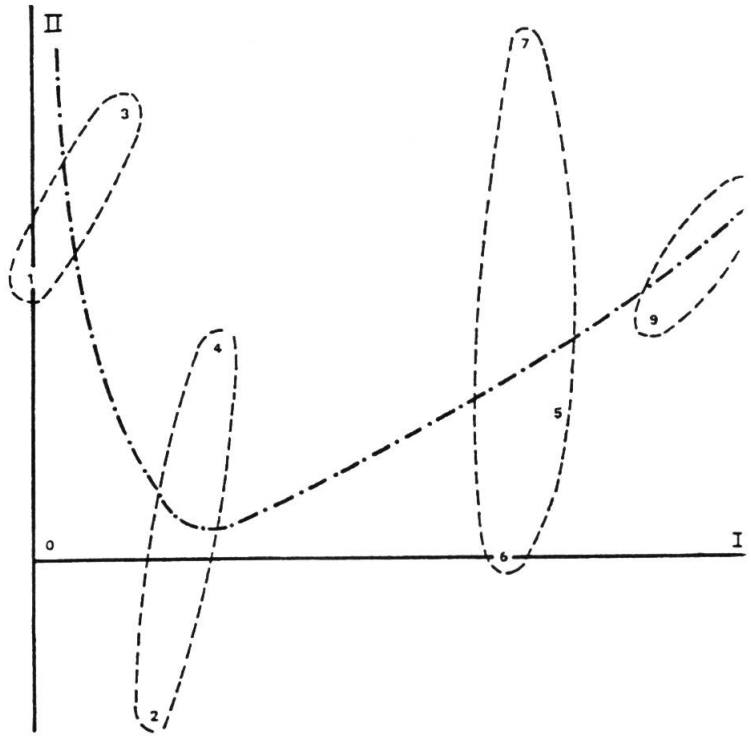

Fig. 5. — DECORANA scatter diagram of the stands on the plane of the first two axes.

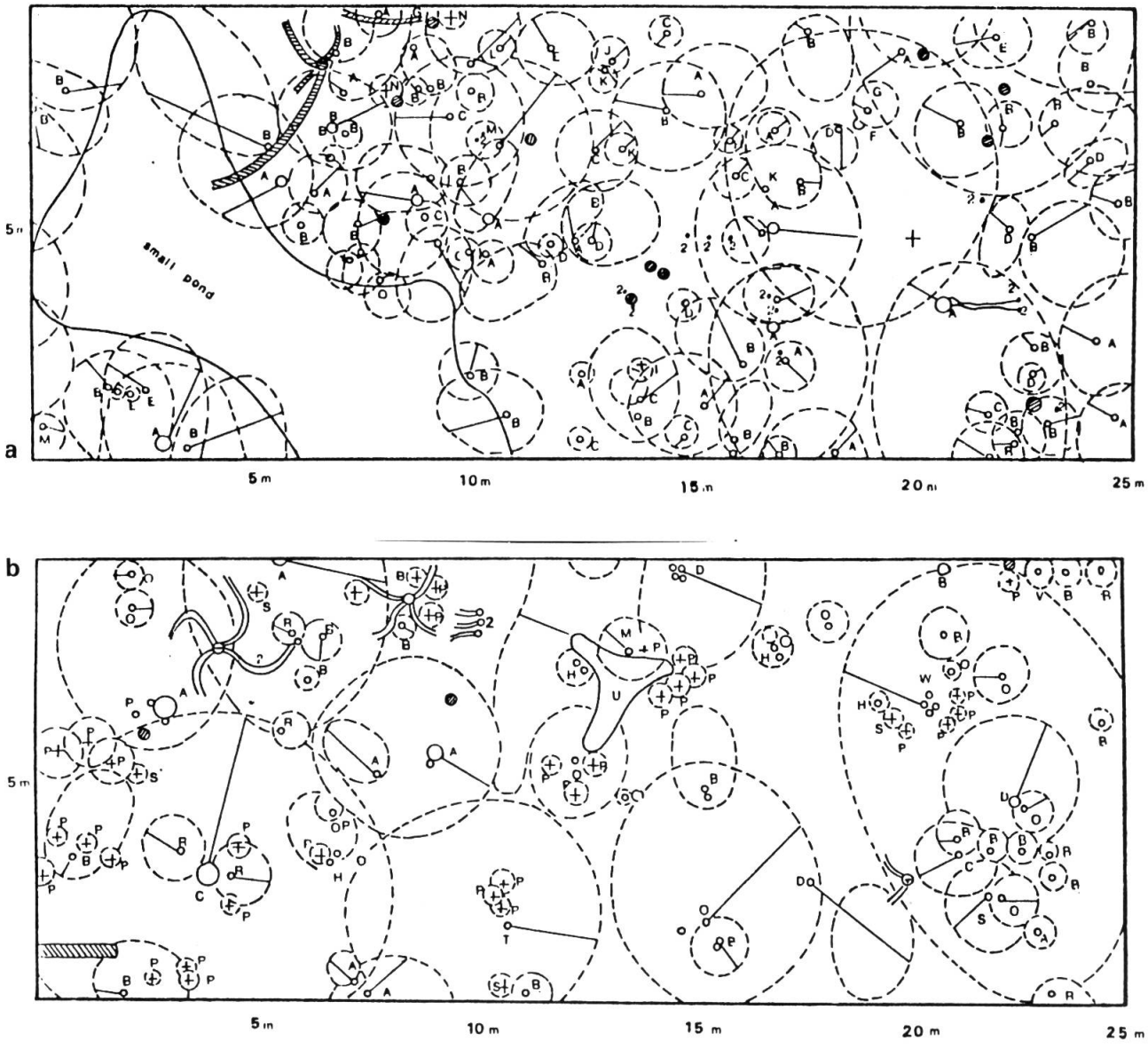

Fig. 6 a and b. — Cartographic diagrams of two forests. **(a)** near Colmena and **(b)** further north near Villa Guillermina. Symbols: **A** *Ruprechtia laxiflora*, **B** *Eugenia uniflora*, **C** *Gleditsia amorphoides*, **D** *Achatocarpus praecox*, **E** *Acacia praecox*, **F** *Aspidosperma quebracho-blanco*, **G** *Jodinia rhombifolia*, **H** *Allophyllus edulis*, **I** *Coccoloba alagoensis*, **J** *Poligonaceae* (undetermined), **K** *Capparis retusa*, **L** *Geoffroea decorticans*, **M** *Myrciantes cisplatensis*, **N** *Celtis* sp., **O** *Scutia buxifolia*, **P** *Bumelia obtusifolia*, **Q** *Eugenia* sp., **R** *Patagonula americana*, **S** *Rapanaea lorentzii*, **T** *Euphorbiaceae* (undetermined), **U** *Phytolacca dioica*, **V** *Ficus monckii*, **W** *Arecastrum romanzoffianum*, **1**, Stump, **2**, liana, **3**, dead stem.

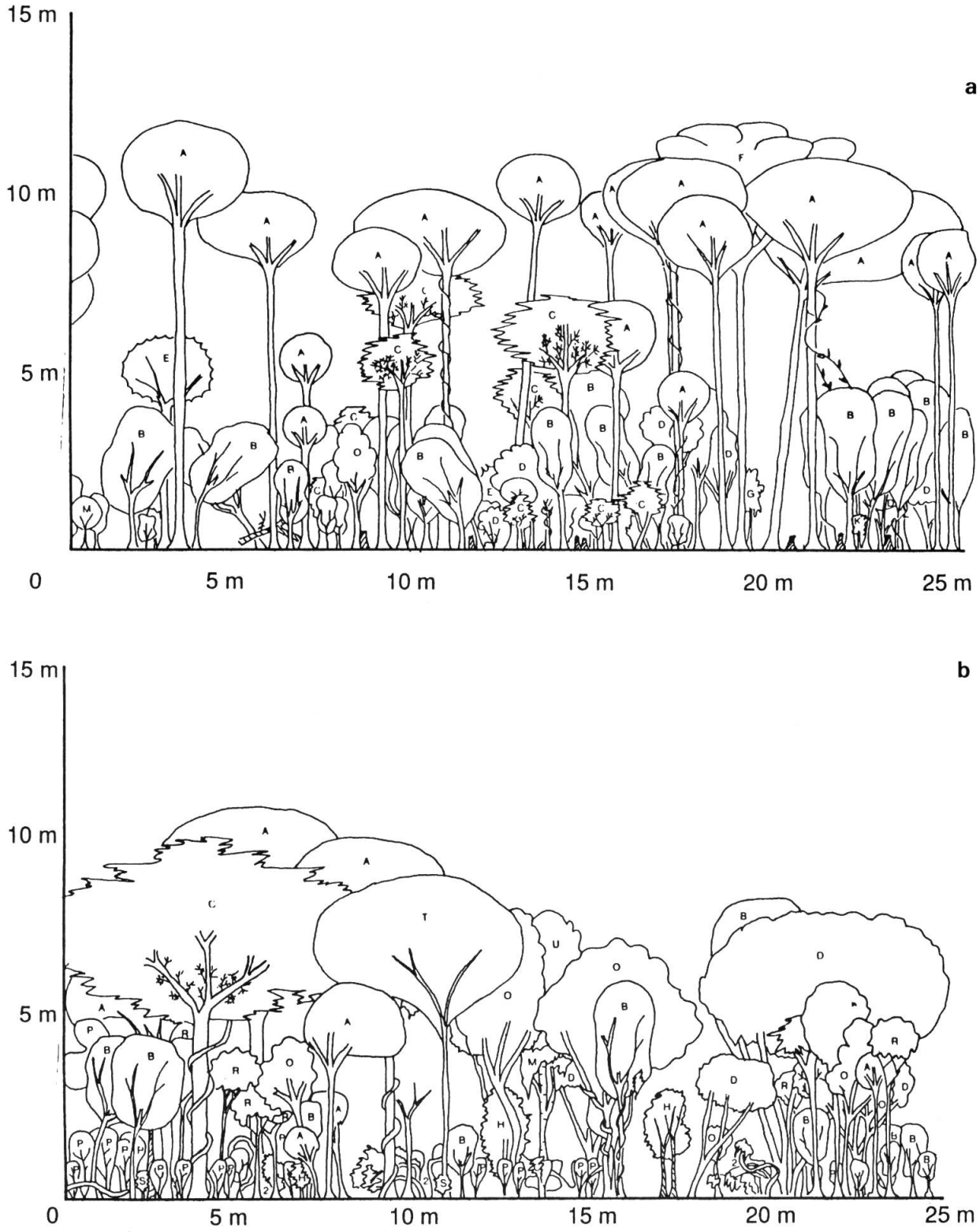

Fig. 7 a and b. — Vegetation profiles of the same forests as in figure 6. Symbols as in figure 6.

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