Floristic diversity and phytogeography of the central Tuichi Valley, an isolated dry forest locality in the Bolivian Andes

MICHAEL KESSLER

&

NICHOLAS HELME

ABSTRACT

KESSLER, M. & N. HELME (1999). Floristic diversity and phytogeography of the central Tuichi Valley, an isolated dry forest locality in the Bolivian Andes. *Candollea* 54: 341-366. In English, English and Spanish abstracts.

We present a floristical survey of the dry forests of the central Tuichi Valley, dpto. La Paz, Bolivia, an isolated rain-shadowed dry forest area between 600 and 1400 m covering *ca.* 1200 km^2. We recorded 372 vascular plant species (217 genera, 71 families) in the dry forest and an additional 175 species, 80 genera and 22 families in the evergreen gallery forest. The most species-rich groups were *Leguminosae* (10.2%), *Pteridophyta* (7.8%), *Bignoniaceae* (7.3%), *Orchidaceae* (5.4%), *Bromeliaceae* (4.9%) and *Piperaceae* (4.0%). Based on full sampling of selected indicator groups (*Acanthaceae, Araceae, Bromeliaceae, Cactaceae, Palmae, Pteridophyta*) we estimate the total vascular plant number to be *ca.* 590 for the dry forest and an additional 700 for the gallery forest. Of the species in the indicator groups, 24% were endemic to Bolivia, with 3% being endemic to the Tuichi Valley. An analysis of two transects of 2 × 500 m on which all woody plants >2.5 cm d.b.h. were recorded, revealed a woody plant species richness exceeding the Neotropical average and a strong local differentiation of vegetation types within the physiognomically homogeneous Tuichi dry forest area. Phytogeographically, the Tuichi Valley showed strongest affinities to the Chiquitanía dry forests of lowland dpto. Santa Cruz, Bolivia, as well as to similar forests along the sub-Andean zone to northwestern Argentina and extending to interior southeastern Brazil. There was little affinity to dry forest areas of northern South America and to the geographically close Chaco, Cerrado and Beni savanna dry forests. Overall, the Tuichi dry forest is one of the richest such habitats documented to date in the Neotropics and probably contains the only pristine dry forest ecosystems (*ca.* 700 km^2) left in the Andes. It therefore deserves high conservation priority.

RESUMEN

KESSLER, M. & N. HELME (1999). Diversidad florística y fitogeografía del valle central del Río Tuichi, una localidad aislada de bosque seco en los Andes bolivianos. *Candollea* 54: 341-366. En inglés, resúmenes en inglés y en español.

Se presenta un análisis florístico de los bosques deciduos del valle central del Río Tuichi, dpto. La Paz, Bolivia, una localidad aislada de bosque seco en un valle en sombra de lluvia entre 600 y 1400 m cubriendo un área de aprox. 1200 km^2. Se encontraron 372 plantas vasculares (217 géneros, 71 familias) en el bosque seco y 175 especies, 80 géneros y 22 familias adicionales en bosques siempreverdes de galería. Los grupos con mayor número de especies fueron *Leguminosae* (10.2%), *Pteridophyta* (7.8%), *Bignoniaceae* (7.3%), *Orchidaceae* (5.4%), *Bromeliaceae* (4.9%) y *Piperaceae* (4.0%). Basándonos en grupos indicadores que fueron estudiados intensivamente (*Acanthaceae, Araceae, Bromeliaceae, Cactaceae, Palmae, Pteridophyta*) estimamos que el número total de plantas vasculares en el bosque seco es de aprox. 590, con unas 700 especies adicionales en el bosque de galería. De las especies de los grupos indicadores, 24% son endémicas a Bolivia, con un 3% siendo endémicas al valle del Río Tuichi. Un análisis de dos transectas de 2 × 500 m en las cuáles se registraron todas las plantas leñosas de >2.5 cm d.a.p., mostró una diversi-

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dad de especies leñosas que supera el promedio de bosques secos Neotropicales y una diferenciación local marcada de tipos de vegetación en los bosques fisonómicamente homogéneos en el valle del Río Tuichi. Fitogeográficamente, el valle del Tuichi mostró su mayor afinidad con los bosques secos de la Chiquitanía de la parte baja del dpto. Santa Cruz, Bolivia, así como con bosques similares a lo largo de la zona de piemonte Andina hacia el noroeste de Argentina y extendiéndose hasta el interior del sudeste de Brazil. Se encontró poca afinidad con los bosques secos del norte de Sudamérica y con las regiones geográficamente cercanas del Chaco, Cerrado y las Sabanas del Beni. Resumiendo, los bosques secos del Río Tuichi figuran entre los más diversos documentados hasta el presente en el Neotrópico y probablemente contienen la mayor extensión de bosque seco primario en todos los Andes (aprox. 700 km^2) por lo que se enfatiza su gran importancia de conservación.

KEY-WORDS: Flora – Diversity – Phytogeography – Dry Forests – Woody Plants – Andes – Bolivia.

Introduction

Seasonally drought-deciduous tropical forests (dry forests) are widespread in the Neotropics, occurring in western Central America (Mexico to Costa Rica), the Yucatán Peninsula, the Greater Antilles, northern Colombia and Venezuela, western Ecuador and adjacent Peru, and in a broad area extending from eastern Bolivia and northwestern Argentina through Paraguay and southern Brazil to northeastern Brazil (HUECK & SEIBERT, 1981; BULLOCK & al., 1995). Smaller dry forest enclaves are found in scattered localities in rain-shadowed Andean valleys, most notably the Magdalena and Cauca valleys, Colombia, the Marañón, Apurimac and Urubamba valleys, Peru, and numerous sites in Bolivia (Fig. 1). In the most comprehensive analysis of the composition and diversity of Neotropical dry forests conducted to date, GENTRY (1995) emphazised the homogeneity of the compostion of these forests at the generic and familial level and remarked on the regional variability of the species richness and endemism of dry forest plant communities. He concluded that the most diverse and biogeographically unique dry forests are those of western Mexico but added that "if the even more [scientifically] neglected Bolivian dry forests turn out to share this high diversity and endemism [with Mexico], as the very preliminary data suggest, then they too should share in the conservational spotlight" (GENTRY, 1995: 190).

In Bolivia, dry forests cover large areas in the central and southern lowlands and occur in at least nine isolated rain-shadowed Andean valleys (Fig. 1). Studies of the flora and vegetation of Bolivian dry forests have generally been limited. Lowland types have been described by KILLEEN & al. (1990), SALDIAS (1991) and PARKER & al. (1993) while Andean dry forests have only been treated briefly by BASTIAN (1986), GEROLD (1987), PEDROTTI & al. (1988), PARKER & BAILEY (1991), BECK & al. (1992), NAVARRO & al. (1996), NAVARRO (1997) and BACH & al. (1999). BACH & al. (1999) found a marked regional diversification of vegetation types as well as highly variable levels of species richness among different dry forest localities. Overall, the floristic diversity of Andean dry forests of Bolivia rivals that of the lowland dry forests (KESSLER & al., in press).

With an area of 1200 km^2, of which about 700 km^2 are in near-pristine state, the central Tuichi valley in northern dpto. La Paz, Bolivia, contains the largest well-preserved example of Andean dry forests remaining in Bolivia and probably anywhere in the Andes (PARKER & BAILEY, 1991; PERRY & al., 1997). A small portion of the valley was briefly studied botanically in 1990 by A.H. Gentry and R. B. Foster (in PARKER & BAILEY, 1991) during a rapid biological assessment of this region which contributed to the creation of the Madidi National Park and Integrated Natural Use Area (PNANMI Madidi) in 1995 which includes the central Tuichi Valley. Their preliminary survey documented a surprisingly rich flora and emphasized the need for further studies.

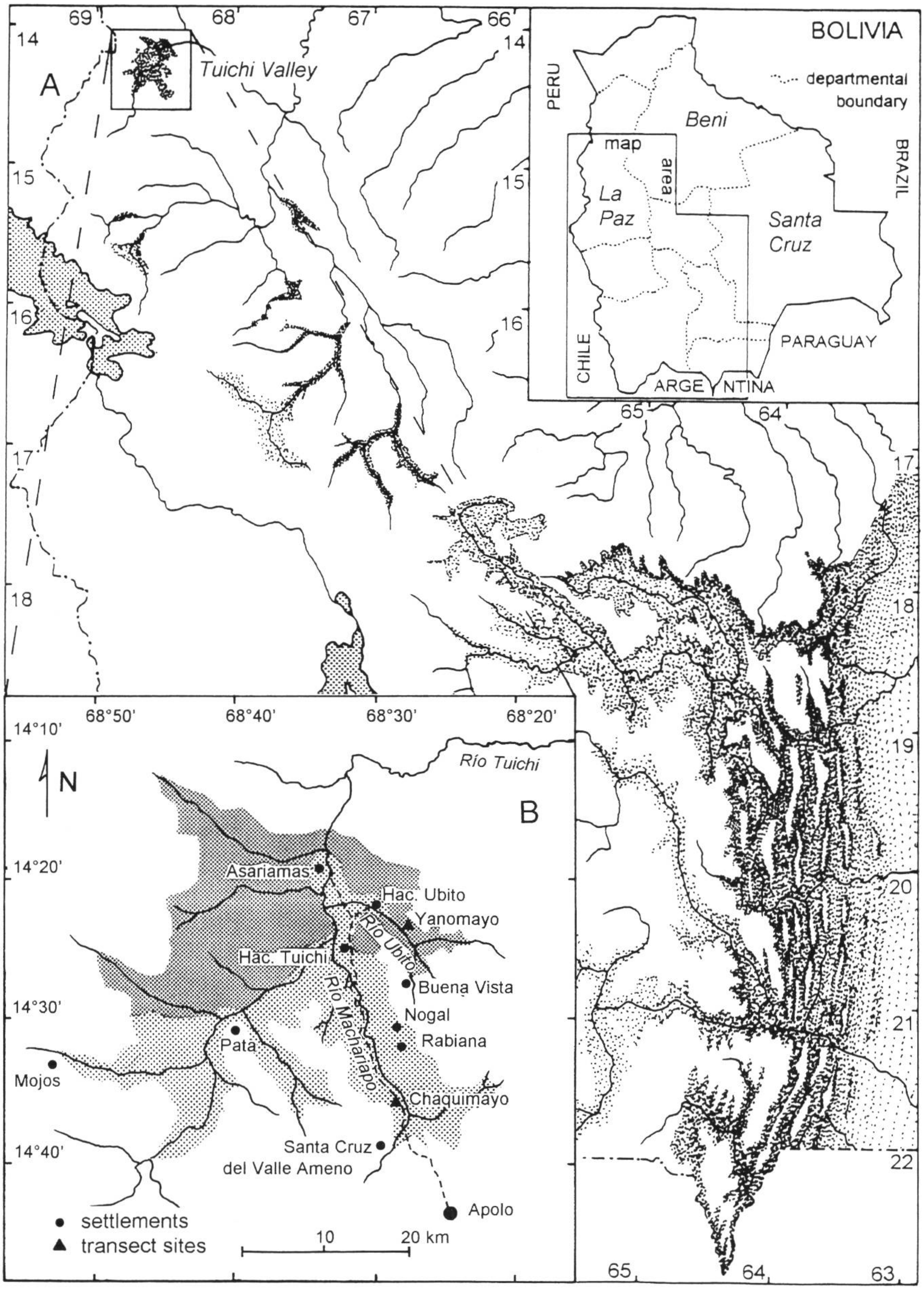

Fig. 1. – Distribution of dry forests and the study sites in **(A)** Andean Bolivia and **(B)** the central Tuichi Valley. In **(A)**, more humid dry forest areas have denser stippling. In **(B)** darker shaded areas correspond to pristine dry forest, lighter shaded areas to disturbed or degraded dry forest (modified from PERRY & al., 1997). The dashed line shows the trail from Apolo to Asariamas and roughly corresponds to the routing of the Apolo-Asariamas road currently under construction.

Based on five weeks of floristic studies conducted in 1993 in the Tuichi valley, we here present an analysis of the diversity and composition of the valley's dry forests. The analysis further includes unpublished data compiled by A. H. Gentry and made available to us by R. B. Foster.

Study area and methods

The Tuichi dry forest covers an area of about 1200 km^2 ranging from 600 to 1400 m in the rainshadowed central portion of the Tuichi Valley and several side valleys, of which the Machariapo Valley and the Ubito Valley are the most easily accessible (Fig. 1). Among the valleys in the northern Bolivian Andes the Tuichi Valley is unique because of it's broad, flat topography, very unlike the deep, V-shaped valleys typical of this region. Geologically, the area is dominated by dark gray, hard slate of Devonian age (SOUX & al., 1991) but large areas are covered by younger conglomerates and alluvial substrates cover the valley bottoms. Mean annual precipitation has been estimated to be around 1300 mm at Chaquimayo (PARKER & BAILEY, 1991), but is certainly somewhat less in the central portion of the Tuichi Valley. Rainfall is concentrated in the December-May rainy season, with the remainder of the year being much drier and characteristically receiving less than one quarter of the total annual rainfall (C. KRAFT, pers. com.). The central portion of the valley is dominated by drought-deciduous forest which gradually changes to semi-evergreen and finally evergreen forest at higher elevations and towards the northern foothills. The broad valley bottoms support groundwater-dependent evergreen gallery forests which can be up to several hundred meters wide. About 700 inhabitants lived in the area in 1993, mainly in the communities of Asariamas, Buena Vista, Nogal and Rabiana which are concentrated on the more accessible southern side of the valley (Fig. 1). Prior to the *reforma agraria* of 1953, when the large haciendas were abolished, the human population was about four times higher than at present (E. KOEHNKE, pers. com.). Agricultural areas (sugar cane, bananas, rice, yucca, maize, etc.) are concentrated on the fertile floodplains and most of the gallery forest has been destroyed or degraded. Fairly humid ridges above 1300-1400 m in the vicinity of the villages have been burnt to provide grazing grounds for cattle. As a result, in much of the Machariapo Valley, and in parts of the Ubito Valley as well as near Asariamas, the dry forest is restricted to a narrow elevational belt between the cultivated valley bottom and the burnt upper slopes. Cattle grazing is rare inside the dry forest, but coffee (*Coffea arabica*) has been planted in the understorey of some forest tracts and timber extraction has occurred in many of the more accessible places, especially historically for the distillation of alcohol from sugar cane. Access to the area is on foot or by mule, with the main trail running from Apolo along the Machariapo Valley and then along the Tuichi River to Asariamas, but a road from Apolo to Ixiamas via Asariamas was being constructed in mid-1997 (K. BACH, pers. com.). All of the dry forest is currently included in PNANMI Madidi, with the northwestern side of the valley (west of the Río Tuichi) being included in the strictly protected National Park zone while the southeastern part belongs to the Integrated Use Area where sustainable development is encouraged.

Fieldwork was conducted from 9 to 23 July and from 7 to 30 September 1993. General botanical collecting took place along the trail from Apolo to Asariamas through the Machariapo Valley and along the Río Tuichi as well as in the vicinity of Hacienda Ubito along Río Ubito and was concentrated on dry forest species, especially woody plants and members of selected plant families: *Acanthaceae, Araceae, Bromeliaceae, Cactaceae, Palmae* and *Pteridophyta* (for simplicity, pteridophytes are here considered as one family). These families were selected for their relative ease of identification, their good representation in dry forests, because they are fertile and/or identifiable even in the dry season (to which surveying was limited due to logistic reasons), and because they adequately represent the floristic relations among dry forest vegetation types (BACH & al., 1999).

A quantitative vegetation transect was established on Cerro Yanomayo (14°24'S, 68°28'W) following the method by GENTRY (1982) in which all woody plant species with >2.5 cm diameter at breast height (d.b.h.) in ten subtransects of 2×50 m each are recorded, resulting in a total sample area of 1000 m^2. On Cerro Yanomayo, our parallel subtransects were laid out on mountain slope without crossing ravines or mountain ridges at altitudes of 1020 m (3 subtransects), 1050 m, 1080 m, 1120 m, 1150 m and 1200 m (3 subtransects). The sample therefore also has characteristics of an altitudinal transect, but the habitat heterogeneity sampled was equivalent to that included by A.H. Gentry himself in his samples (pers. obs.).

All species were collected in triplicate, conserved in 70% ethanol in the field and processed at the Herbario Nacional de Bolivia, La Paz, Bolivia (LPB). Specimens have been deposited at LPB and with respective specialists (see Acknowledgements). In the woody plant transect, lianas were measured and counted, but identification (in particular of *Bignoniaceae*) was almost impossible and the liana species numbers had therefore to be estimated to a certain degree.

In addition to our data, we here include data collected by A. H. Gentry and R. B. Foster in 1990 at Chaquimayo, Machariapo Valley (14°34'S, 68°28'W, 1000 m), of which only a generalized species list and a few results from the woody plant transect have been published to date (PARKER & BAILEY, 1991; GENTRY, 1995). The woody plant transect included subtransects both in dry forest and semi-evergreen forest in ravines. A few additional species were recorded in July 1997 at the head of the Machariapo Valley by K. Bach and are also included here.

To allow comparability with GENTRY's (1982, 1995) extensive data set, data analysis of the woody plant transects followed GENTRY (1995).

The biogeographical analysis was mainly based on the six intensively studied indicator groups. Individual species maps covering the whole Neotropics were compiled for all species recorded in a 1° × 1° grid map based on records in the literature and herbarium collections at Berkeley (UC, *Pteridophyta*), New York (NY, *Pteridophyta*, *Palmae*), Saint Louis (MO, *Araceae*), Washington, D.C. (*Acanthaceae*, *Bromeliaceae*, *Pteridophyta*) in collaboration with the respective specialists (see Acknowledgements). Species ranges were then interpolated and to a lesser degree extrapolated from the specimen records by considering the ecological requirements of the species (from personal field experience, literature and specimen records) and the distribution of major vegetation units (HUECK & SEIBERT, 1991; DINERSTEIN & al., 1995). For the analysis presented here, individual species ranges were overlapped for each family.

Results

Floristic richness

A combined species list of all our collections and those by GENTRY & FOSTER (PARKER & BAILEY, 1991; R. B. FOSTER, pers. com.) includes about 547 species from 297 genera in 93 families (Appendix 1). About 372 species (217 genera, 71 families) were found in the dry forests, the other species being restricted to evergreen gallery forest along rivers and streams as well as to semi-evergreen and evergreen forest above 1250 m on Cerro Yanomayo. The most species-rich families in the dry forest were *Leguminosae* (38 species, 10.2%), *Pteridophyta* (29, 7.8%), *Bignoniaceae* (27, 7.3%), *Orchidaceae* (20, 5.4%), *Bromeliaceae* (18, 4.9%) and *Piperaceae* (15, 4.0%). However, because our visits took place in the dry season and since our collecting centered on woody plants and selected additional plant groups, some herbaceous groups (including *Compositae* and *Gramineae*) are strongly underrepresented in this list while our study groups are undoubtedly overrepresented. Despite this bias, the dominant plant families closely correspond to those of a completely sampled lowland dry forest at the Santa Cruz Botanical Garden, dpto. Santa Cruz, Bolivia (SALDIAS, 1991; PARKER & al., 1993; M. NEE & G. COIMBRA S., pers. com.) and to five of six other Neotropical sites analyzed by GENTRY (1995) (with the Antillean site showing clear biogeographical differences).

The fully sampled dry forest in Santa Cruz Botanical Garden is physiognomically fairly similar to that of the Tuichi Valley, shares the richness and broad composition of the woody plant component (Tab. 1) and belongs to the same phytogeographical unit (see below). Thus, assuming that our selected study groups have been fully sampled in the Tuichi Valley and that the floristic composition of both sites is similar, the percentage of species in our study families of the total species number can be used to extrapolate the total species number in the Tuichi Valley. The recorded percentages are 13.8% at the Santa Cruz site and 22.0% in the Tuichi dry forest, respectively. Based on a recorded number of 372 dry forest species, the total species number of vascular plant species in the area studied by us in the Tuichi Valley can be calculated to be around 590. If additional species from azonal habitats (evergreen gallery forests, rock faces) are included, then the species number rises to about 1300. Both of these estimates only consider the area actually sampled by us (about 100 km^2). Undoubtedly, the whole dry forest area (1200 km^2) contains many additional species not present at our study localities.

Woody plant transects

Both Tuichi valley woody plant transects showed values of family and species richness somewhat above the Neotropical average (Tab. 1). These values are comparable to those of tall

	Chaquimayo	Yanomayo	Tall lowland	Chaco	Neotropical average
Total no. individuals	465	339	289	392	370
Total no. tree individuals	331	278	n.a.[1]	n.a.	343
Total no. tree species	50	59	n.a.	n.a.	49
Total no. tree individuals >10 cm d.b.h.	29	63	n.a.	n.a.	65
Total no. tree species >10 cm d.b.h.	7	29	n.a.	n.a.	24
Total no. families	29	28	29	20.5	25
Total no. species	79	ca. 80	74	36.5	60
Apocynaceae	5	1	3	1.5	2.1
Bignoniaceae	10	ca. 8	12.5	1.5	6.8
Cactaceae	5	1	0.5	7	1.2
Capparidaceae	1	2	1.5	3	2.2
Euphorbiaceae	3	7	1	0.5	2.6
Leguminosae	17	14	11	6	11.0
Meliaceae	3	2	0.5	0	1.1
Myrtaceae	0	4	2.5	0	2.1
Opiliaceae	0	2	0	0.5	n.a.
Phytolaccaceae	3	5	2.5	0	0.8
Polygonaceae	0	2	0.5	2	1.6
Rubiaceae	1[2]	0[2]	2	0	4.0
Rutaceae	0	2	2	0	1.2
Sapindaceae	4	3	4.5	1	3.2
Ulmaceae	4	0	2.5	1.5	1.2

[1] n.a. = data not available.

[2] Naturalized coffee shrubs (*Coffea arabica*) present.

Table 1. – Structural data and species richness for selected plant families in the two Tuichi Valley (this study), two tall lowland (Santa Cruz Botanical Garden, Tucavaca) and two chaco-type (Curuyuqui, Yanaigua) lowland dry forests (from PARKER & al., 1993) in Bolivia, and of average Neotropical values (N = 25, after GENTRY, 1995) for woody plants >2.5 cm d.b.h. in vegetation transects of 2 × 500 m.

Bolivian lowland forest, which are among the richest dry forests in the Neotropics (GENTRY, 1995) and are much higher than those of Chaco dry forest from southern Bolivia. Numbers of woody plant individuals >2.5 cm d.b.h and of tree species and individuals per transect were comparable among the Tuichi transects and to Neotropical averages. The number of tree individuals and species >10 cm d.b.h. was conspicuously low in the Chaquimayo transect, however. As the Yanomayo transect showed typical dry forests values, it seems likely that the rarity of large trees at Chaquimayo is due to past selective tree extraction, as also suggested by GENTRY & FOSTER (in PARKER & BAILEY, 1991), and does not represent a natural characteristic of the Tuichi dry forest. The Chaquimayo transect was located in the fairly densely settled Machariapo valley which is transversed by the mule trail from Apolo to Asariamas, whereas the Yanomayo transect covered nearly pristine forest well away from any regularly used trail.

As is typical for Neotropical dry forests (GENTRY, 1995), *Leguminosae* and *Bignoniaceae* were the most species-rich woody plant families in both Tuichi transects (Tab. 1). Among the other families, however, we found several unusual trends. *Rubiaceae*, on average the third most speciose family in Neotropical dry forests, was represented by only one species in the Chaquimayo transect (plus naturalized coffee shrubs in both transects). On the other hand, *Euphorbiaceae* and *Phytolaccaceae* were unusually species-rich at Yanomayo, while *Cactaceae* and *Apocynaceae* had exceptionally high species numbers at Chaquimayo. *Euphorbiaceae* is frequently dominant in Central American and Antillean dry forests, but not in South America (GENTRY, 1995). The four species of *Myrtaceae* at Chaquimayo may indicate floristic and ecological affinities to southern subtropical dry forests where this family takes over as the most species-rich group (GENTRY, 1995).

Perhaps most surprising was the marked difference in the composition of the two Tuichi valley transects. Despite being located only about 25 km apart without any obvious separating geographical barriers at roughly the same elevation and in physiognomically similar vegetation types, only *ca*. 22 of a total of *ca*. 139 species were shared between both transects. Similarly, only four of the 12 (Yanomayo) or 11 (Chaquimayo) tree families with more than two species were shared between both samples: *Leguminosae, Meliaceae, Sapotaceae* and *Nyctaginaceae*. At Chaquimayo, a single tree species, the legume *Anadenanthera macrocarpa* (= *A. colubrina*), made up over half of the trees >20 cm d.b.h. and over two-thirds of those >30 cm d.b.h.. Opposed to this, at Yanomayo there was no single dominant large canopy tree. The three largest trees here were a *Coccoloba* sp. (85 cm d.b.h.), a *Pithecellobium* sp. (70.5 cm d.b.h.) and an *Anadenanthera macrocarpa* (61 cm d.b.h.).

While the Chaquimayo transect was certainly more anthropogenically disturbed than the Yanomayo transect, we believe that these differences mainly reflect the differentiation of vegetation communities into microhabitats. This idea is supported by the fact that, despite intensive collecting efforts, no fewer than 13 out of a total of 16 *Acanthaceae* species and nine out of 21 bromeliad species were only recorded in either the Machariapo or the Ubito valleys (Appendix 1). These mainly epiphytic and herbaceous groups are unlikely to be severely affected by the relatively moderate habitat conversion in the Machariapo Valley. Another example is provided by *Cochlospermum orinocense* which was conspicuously flowering during our visit in July 1993 but was only restricted to a small area between Haciendas Ubito and Tuichi, where it was common. The ecological factors leading to the localized distribution of species and corresponding local differentiation of vegetation types probably include a slight variability of humidity (rainfall and fog) and soils, even though no conspicuous change in the vegetation was observed at transition zones between different geological substrates (as also reported in PARKER & BAILEY, 1991).

The elevational gradient of 180 m covered by the Yanomayo transect provided another example of local vegetation differentiation (Tab. 2). Of eleven species recorded at least six times in the transect, three species were significantly more common in one half of the transect (1020-1080 m, 1120-1200 m) than in the other. Since only few species were common enough for a statistical analysis of their frequency, it seems likely that the actual number of species which were more common in one half of the transect than in the other was considerably larger. This local

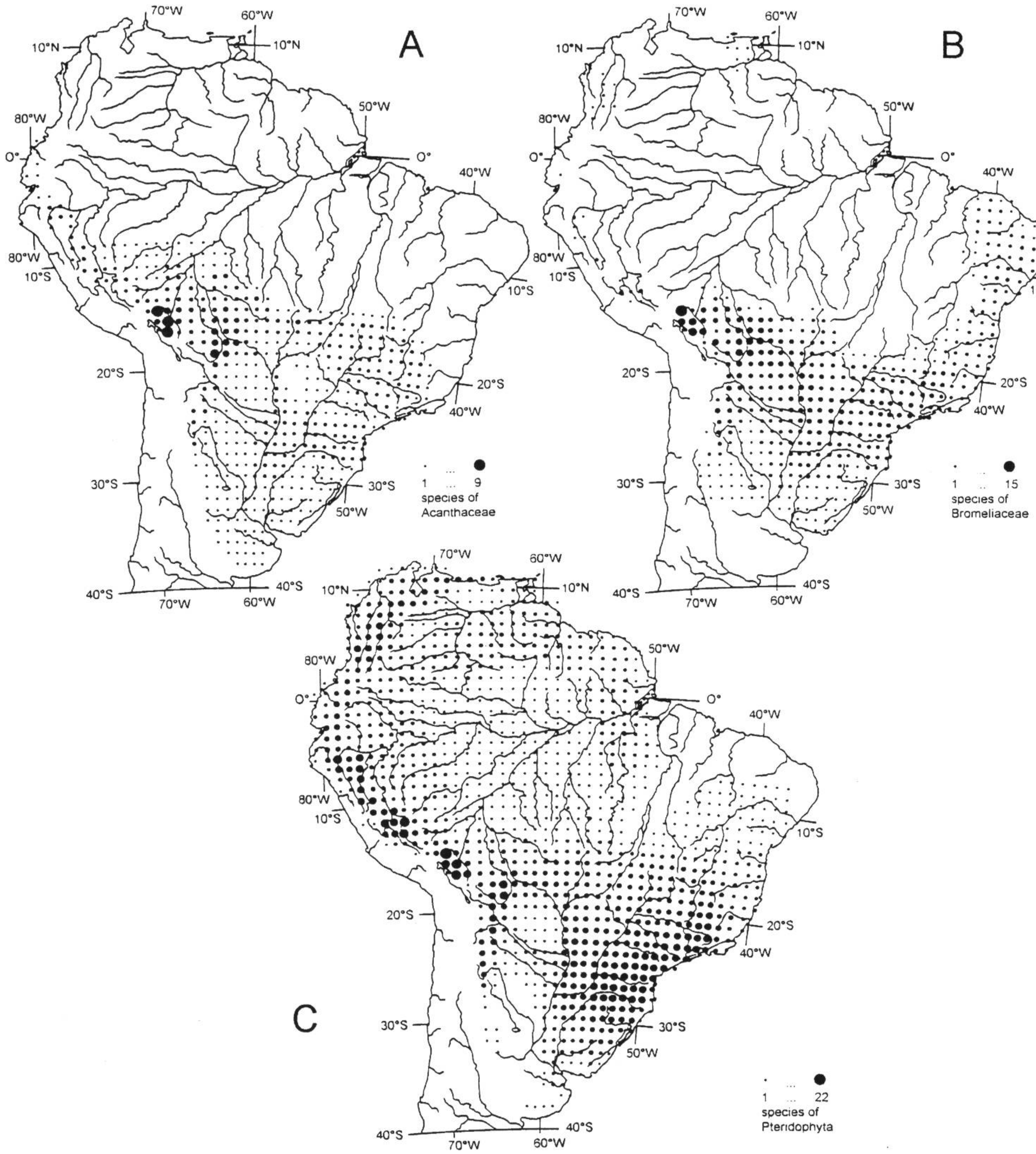

Fig. 2. – Number of *Acanthaceae* **(A)**, *Bromeliaceae* **(B)** and pteridophyte **(C)** species recorded in the Tuichi dry forest per degree square in South America. Species considered: **A:** *Dicliptera tweediana*, *Justicia boliviensis*, *J. kuntzei*, *J. magentea*, *J. ramulosa*, *J. rusbyana*, *Ruellia brevifolia*, *R. puri*, *R.* spec. nov.; **B:** *Aechmea distichantha*, *A. kuntzeana*, *Billbergia microlepis*, *Fosterella albicans*, *F. graminea*, *F. villosula*, *Pseudananas sagenarius*, *Tillandsia didisticha*, *T. kuntzeana*, *T. polystachya*, *T. spiralipetala*, *T. tricholepis*, *Vriesea maxoniana*, *Werauhia* spec. nov.; **C:** *Adiantopsis chlorophylla*, *A. radiata*, *Adiantum raddianum*, *Anemia phyllitidis*, *Asplenium dimidiatum*, *A. discrepans*, *Campyloneurum nitidissimum*, *Dicranoglossum desvauxi*, *Doryopteris concolor*, *D. pedata* var. *multipartita*, *Hemionitis palmata*, *H. tomentosa*, *Microgramma baldwinii*, *M. mortoniana*, *M. squamulosa*, *Platycerium andinum*, *Polypodium decumanum*, *P.* aff. *furfuraceum*, *P. remotum*, *P. squalidum*, *Pteris quadriaurita*, *Selaginella microphylla*, *Trachypteris pinnata*.

Lower subtransects		Upper subtransects	
Species	No. individuals	Species	No. individuals
Prunus aff. *tucumanensis*	23*	*Eugenia* sp. 3	26***
Margaritaria nobilis	18***	*Opuntia brasiliensis*	12
Opuntia brasiliensis	18	*Capparis flexuosa*	9
Capparis flexuosa	8	*Prunus* aff. *tucumanensis*	7
Trichilia sp. 1	7	*Trichilia* sp. 1	7
Capparis prisca	6	*Amburana cearensis*	5
Sapindaceae sp.	5	*Myroxylon balsamum*	5
Erythroxylon sp.	4	*Urera baccifera*	4
Croton sp. 1	4	*Metrodorea flavida*	4

Table 2. – Most frequent tree species in the lower (1020-1080 m) and upper (1120-1200 m) subtransects of the Yanomayo woody plant transect. Species significantly more frequent in one half of the transect are indicated by * ($p < 0.05$) and *** ($p < 0.001$) (two-way ANOVA).

clumping of species may not necessarily be due to elevational differences alone but may also reflect undetected soil modifications or stochastical metapopulation dynamics. Regardless of the causes, it still clearly demonstartes a strong spatial diversification of the plant communities in the Tuichi dry forest.

Biogeographic affinities and endemism

The overlapped distributional ranges of the species of *Acanthaceae* and *Bromeliaceae* found in the dry forests of the Tuichi Valley (i.e., excluding species only collected in gallery or humid montane forests) both showed the same basic biogeographical connections: Besides a close affinity to the geographically close and ecologically similar dry forest valleys of dpto. La Paz, the largest number of species was shared with the Andean foothill zone in western dpto. Santa Cruz (Fig. 2). This biogeographic track extended both further south along the Andean base to northwestern Argentina and across eastern Bolivia and Mato Grosso to eastern Paraguay and southeastern Brazil. The dry central Chaco and the arid inter-Andean valleys of central and southern Bolivia shared very few species with the Tuichi dry forest. Neither *Acanthaceae* nor *Bromeliaceae* showed strong floristic connections to dry forest areas further north. In the case of the *Acanthaceae*, a few species found in the Tuichi dry forest are more typical of humid forests, which explains a slight connection to the humid foothill zone in Peru. *Bromeliaceae*, on the other hand, shared three species with the arid Urubamba and Apurimac drainage in southcentral Peru and another three species with the Caatinga region of northeastern Brazil. *Araceae*, *Cactaceae* and *Palmae* all displayed basically similar patterns (not shown) but because of lower species numbers these were less clearly defined.

Pteridophytes showed a somewhat different pattern. Here, the largest number of species (18, 82%) was shared with the Urubamba/Apurimac drainage in Peru as well as with adjacent valley in dpto. La Paz, followed by western Santa Cruz (15, 68%), the Marañón Valley in northern Peru (14, 64%), interior southeastern Brazil (12, 55%) and the arid valleys of the Colombian Andes (11, 50%). Thus, while the fern flora displayed the floristic connections to the dry forest areas of lowland eastern Bolivia, northwestern Argentina and southeastern Brazil found in the other families, it also showed a very strong affinity to Andean dry forest areas further north. It seems noteworthy that this floristic connection is entirely Andean and does not include the physiognomically similar lowland and foothill dry forests of western Ecuador and northern Colombia and Venezuela. Generally speaking, the ferns found in the Tuichi dry forest had much wider ranges than any of the other groups and contained a small, but distinct, component of very widespread, generalistic species which are also present in Amazonia.

The phytogeographical affinities of the Tuichi dry forest to lowland dpto. Santa Cruz are further demonstrated if the woody plant species are considered. Many of the common tree species in the Tuichi dry forest, e.g., *Allophyllus edulis*, *Anadenanthera macrocarpa*, *Astronium urundeuva*, *Chrysophyllum gonocarpum*, *Maclura tinctoria*, *Myroxylon balsamum*, *Phyllostylon rhamnoides*, *Terminalia triflora*, *Trichilia clausenii* and *Urera baccifera*, are also important elements of the dry forests in lowland Santa Cruz (KILLEEN & al., 1990; PARKER & al., 1993) and further south along the sub-Andean zone to northwest Argentina (PRADO, 1993a). There are also a number of species with more northern affinities, e.g., *Capparis flexuosa* and *C.* aff. *baducca* but these are clearly a minority.

In addition to the fairly widespread dry forest species on which the above biogeographical considerations are based, the Tuichi area also contained a number of species with restricted and/or disjunct ranges. Among the 62 species from our selected study groups identified to species level, two (3%) are presumably endemic to the Tuichi Valley, nine (15%) are only shared with a few other dry forest valleys in adjacent dpto. La Paz and a further four (6%) species are limited to dry forest valleys in the Andes of central Bolivia and southern Peru. Several species show interesting disjunct ranges, most notably *Microgramma mortoniana* (*Polypodiaceae*), previously known only from northeastern Argentina (SMITH & al., in press) and *Justicia kuntzei* and *J. magentea* (*Acanthaceae*), both shared between the Tuichi valley and the sub-Andean zone in western dpto. Santa Cruz, but absent from intervening dry valleys. In addition to these dry forest specialists, we found a number of undescribed species in the gallery forest which may be endemic to the Tuichi Valley (*Chusquea* spec. nov., *Philodendron* spec. nov., *Rhipidocladum* spec. nov.).

Not surprisingly, the flora of the evergreen gallery forests showed the strongest affinity to evergreen Amazonian and, to a lesser degree, evergreen montane forests. Dry forest elements occurred only sporadically in this habitat, mainly in early secondary vegetation or on recent natural landslides which in some cases extended far onto the floodplains and allowed the development of dry forest vegetation on their little-developed soils.

Discussion

The general species list, the extrapolated species number and the woody plant transects all show that the species richness of the Tuichi valley is comparable to the richest Neotropical dry forest sites documented to date (GENTRY, 1995; DAVIS & al., 1997: 287). A direct comparison of species listings from individual sites was not attempted here because of unequal sample areas and sampling intensities. Among 18 Andean dry forest sites in Bolivia studied by Kessler and coworkers in 1995-1997 (unpubl. data), the Tuichi Valley ranks among the three most species-rich sites for all of our selected study groups except Cactaceae which are typically more diverse in the drier valleys of central and southern Bolivia (NAVARRO, 1996). Based on species richness alone, the Tuichi Valley dry forest certainly represents an area of regional or even continental conservation concern, comparable to the dry forests of western Mexico (GENTRY, 1995), western Ecuador (DODSON & GENTRY, 1991) and lowland Bolivia (PARKER & al., 1993) and superior to the well-publicized dry forests of Guanacaste, Costa Rica, (JANZEN, 1988). Despite this high richness, the 590 dry forest species estimated for the Tuichi Valley comprise only about 15% of the total number of 3400 vascular plant species estimated to occur in all Andean dry forest localities in Bolivia (KESSLER & al., in press). This discrepancy is due to the strong ecological and biogeographical differentiation (beta- and gamma-diversity, respectively, *sensu* CODY, 1986) of the Andean dry forests (BACH & al., 1999). Clearly, the conservation of the total or the majority of the dry forest flora in Andean Bolivia cannot be achieved in one or few conservation areas.

The level of national endemism of 24% found in our selected study families in the Tuichi Valley corresponds closely to the value of 23% estimated for the whole Bolivian flora by DAVIS & al. (1997: 5) and to overall levels of endemism for different Neotropical dry forest areas (GENTRY, 1995) but is lower than the average of 30% estimated for all Andean dry forests in Bolivia (KESSLER & al., in press). This difference is probably due to the close proximity of the Tuichi Valley to the Peruvian border, so that several species with restricted ranges which are shared with Peru do not qualify as national endemics.

Our study showed a marked local differentiation of the distribution of individual species and plant communities within at first glance homogeneous dry forest areas. Similar small-scale differentiation of deciduous and semideciduous forests has been observed in central and southeastern Brazil where it was related to small-scale changes in topography and soils (OLIVEIRA-FILHO & al., 1997, 1998). At somewhat larger spatial scales, as in the Tuichi Valley, changes in rainfall patterns, fog occurrence, and elevation may also play a role and lead to an even more pronounced differentiation. In Andean dry forests in Bolivia, slopes of different aspect (northeast *vs*. southwest) on average have differences of 2°C mean annual temperature and 5,5% relative air humidity, respectively (S. HOHNWALD, pers. com.). It seems likely that these differences play a more important role in dry forests than in evergreen montane forests because the higher levels of cloud and fog cover in evergreen forests lead to a higher incidence of diffuse radiation which reaches slopes of different aspect in a more equable way. Furthermore, small absolute differences of air humidity will relate to higher relative differences in dry forests than in wet forests. As a consequence, we have observed a stronger dependence of the vegetation of slope aspect in dry than in evergreen forests in the Bolivian Andes (KESSLER & al., in press).

Phytogeographically, the overall pattern emerging from our analysis was that of a pronounced affinity of the Tuichi dry forest to the tall, deciduous to semi-deciduous forests of lowland dpto. Santa Cruz. These forests have been treated as distinct from other Neotropical dry forest types (GENTRY, 1995; DAVIS & al., 1997) and have been called "Chiquitanía dry forest" (DAVIS & al., 1997: 287), "Bosque subhúmedo de las Serranías Chiquitanas" and "Bosque Semideciduo de la Región del Precámbrico" (RIBERA & al., 1996), and "Lowland well-drained tall dry forest" and "Santa Cruz lower montane dry forest" (NAVARRO, 1997). Structurally and floristically similar forests have been described from eastern Mato Grosso, Brazil (RATTER & al., 1973; EITEN, 1975), in areas adjacent to Bolivia. According to our results, the Chiquitanía dry forest (including the Tuichi dry forest) is phytogeographically probably most closely related forests along the eastern Andean base from Santa Cruz to Tucumán, Argentina, which have been called Subandean Piedmont Forests (PRADO, 1993a), Palo blanco forest (MEYER, 1944; CABRERA, 1976), Forests with *Calycophyllum multiflorum* (HUECK, 1966) or Bosque Húmedo Templado (UNZUETA, 1975), and to the semi-deciduous forests of interior southeastern Brazil (extending from Minas Gerais to Paraná, eastern Paraguay and Mato Grosso) (OLIVEIRA-FILHO & RATTER, 1995). Despite a small number of shared species and their geographic proximity, the Chiquitanía dry forests are biogeographically clearly distinct from both the edaphically different Chaco, Cerrado and Beni Savanna vegetation types (HAASE & BECK, 1989; NOVAES PINTO, 1990; PRADO, 1993b). This phytogeographic disjunction is also shown by the rather limited overlap in species composition of our study groups between these dry forest areas and the Tuichi Valley.

Among our study groups, only the ferns, which due to their spore dispersal tend to be more widespread than most other vascular plant groups (TRYON 1985), displayed a clear phytogeographic affinity of the Tuichi dry forest to the Andean dry valleys further north in Peru to Colombia (but not to the lowland dry forests). All other study groups confirmed the observation by SARMIENTO (1972) and GENTRY (1995) of a distinct biogeographic separation of northern (Peru to Venezuela) and southern (Bolivia to Brazil and Argentina) South American deciduous vegetation types. PERRY & al. (1997) similarly interpreted the Tuichi bird communities as belonging to a Bolivian-Brazilian dry forest avifaunal unit with few northern relations. The affinities of the Tuichi dry forest biotic communities to those extending across lowland Bolivia to southeastern Brazil (in several cases with vicariant species in the sub-Andean zone and Brazil) are indicative of a fairly recent montane connection, which was probably interrupted in the Plio-Pleistocene with the subsidence of the Chaco, Beni llanos and Pantanal regions (HANAGARTH, 1993; IRIONDO, 1993; SILVA, 1995).

Because of its high species richness and endemism, and especially because it contains the largest pristine examples of Andean dry forest vegetation, the Tuichi Valley represents one of the areas of highest conservation priority in the Bolivian Andes. This is probably the only Andean dry forest area left in the Andes with intact ecosystems, including large frugivores (e.g., monkeys, macaws, curassows) and predatores of higher trophic levels (e.g., jaguar and puma). In this respect, despite the legal protection of the area in PNAMNI Madidi, the construction of the Apolo-Asariamas road is highly problematic. Even if the west side of the valley is not settled any further, it has to be feared that hunting and accidental forest fires will lead to a gradual degradation of the forests. Due to their susceptibility to fires, dry forests are probably more easily degraded than evergreen forests, and therefore deserve special attention on part of the park authorities. Our observations in the area show that several forest products are already extracted locally and may represent the basis of a sustainable forest use. Such products include incense (probably from *Clusia* sp.), copal (resin of *Protium* aff. *pilosum*), balsam (bark of *Myroxylon balsamum*) and palm fruits (of *Attalea phalerata*).

Appendix 1. – Plant species recorded in the central Río Tuichi valley, dpto. La Paz, Bolivia.

Combined list from species recorded by FOSTER & GENTRY (in PARKER & BAILEY, 1991) and the present study. For brevity's sake, unidentified species in the same genus or unidentified genera in the same family are combined. The species recorded in the two woody plant transects are included under M (Chaquimayo transect) and S (Yanomayo transect) and include the number of individuals and the number of subtransects (of a total of ten subtransects) in which the species was recorded (e.g., 4/3).

Habitats and localities: M: Río Machariapo valley; D: deciduous forest, mainly in Río Ubito valley; S: semi-deciduous forest, mainly on Cerro Yanomayo; R: stunted ridge forest on Cerro Yanomayo (1100-1300 m); G: evergreen floodplain gallery forest, including agricultural areas.

Evidence: FG: listed by FOSTER & GENTRY; x: recorded in the present study (only additional species to FG); single numbers (1, 2, 3,...): number of species recorded in a particular habitat in the case of combined unidentified species; combined numbers (e.g., 3/2): number of individuals/subtransects of species recorded in the woody plant transects.

Abundance (for selected groups only): c: common (frequently recorded in suitable habitat); u: uncommon (recorded only a few times in suitable habitat); r: rare (recorded only once or twice); l: local.

Life form (after PARKER & BAILEY, 1991): t: tree (diameter-at-breast-height >10 cm, height >5 m); s: shrub; l: liana; v: herbaceous vine; h: herb; e: epiphyte.

	Habitats and localities					*Life form*
	M	*D*	*S*	*R*	*G*	
ACANTHACEAE						
Aphelandra glabrata Willd. ex Nees in DC.					lc	s
Aphelandra peruviana Wassh.					lu	s
Aphelandra sp.	FG					s
Dicliptera tweediana Nees in DC.			u			s
Justicia boliviensis (Bremek.) V. A. W. Graham		c				h
Justicia kuntzei Lindau	FG				lc	h
Justicia macrosiphon (Lindau) V. A. W. Graham					lc	h
Justicia magentea V. A. G. Graham	x					h
Justicia monopleurantha (Lindau) Wassh.					lc	s
Justicia ramulosa (Morong) Ezcurra		r				e
Justicia rusbyana Lindau	x					s
Pachystachys spicata (R. & P.) Wassh.					lu	s
Ruellia brevifolia (Pohl) Ezcurra	x					h

	Habitats and localities					*Life form*
	M	*D*	*S*	*R*	*G*	
Ruellia puri (Nees) Mart. ex Jackson	x				c	s
Ruellia sp. nov.	x				c	s
Sanchezia oblonga R. & P.	FG					h
Suessenguthia trochilophila Merxm.					lc	s
AGAVACEAE						
Furcraea sp.	x					s
AMARANTHACEAE						
Achyranthes aspera L.					x	h
Alternanthera sp.	FG				x	h
Amaranthus ? sp.	FG					h
Celosia sp. (2 spp.)	2 FG				1	h,v
Gomphrena sp.					x	h
Iresine sp.	1/1					l
Pfaffia cf. *grandifolia* (Hook.) R. E. Fr.		x				v
Pfaffia sp.					x	v
? sp.	FG					h
AMARYLLIDACEAE						
Amaryllis sp. (2 spp.)	1				1	h
? sp.	FG					h
ANACARDIACEAE						
Astronium urundeuva (Allemao) Engl.	2/2		x			t
Schinopsis brasiliensis Engl.	4/4	x				t
Schinus sp.			x			t
ANNONACEAE						
? sp.			x			t
APOCYNACEAE						
Aspidosperma sp.	2/1					t
Forsteronia spicata (Jacq.) G. Mey.	2/2					l
Forsteronia sp.	1/1	x			x	l
Prestonia (2 spp.) sp.	1/1				1	l
Stenosolen sp.			x			t
Tabernaemontana sp.	FG					s
Tabernaemontana sp.	3/1				x	t
ARACEAE						
Anthurium clavigerum Poeppig	2/2					e
Anthurium croatii Madison					x	h
Anthurium gracile (Rudge) Schott				x		e
Anthurium ottonis Krause	FG					h
Anthurium oxycarpum Poeppig		x	x		x	e,h
Anthurium paraguayense Engl.			x			h
Anthurium plowmannii Croat	FG	x	x		x	h
Anthurium scandens (Aubl.) Engl.			x	x		e
Anthurium sp. (2 spp.)	FG			1		e
Philodendron sp.	FG					e
Philodendron sp. nov.					x	h
ARALIACEAE						
Dendropanax sp.			1/1			t
Pentapanax angelicifolius Griseb.			x			t

	Habitats and localities					Life form
	M	*D*	*S*	*R*	*G*	
ARECACEAE (PALMAE)						
Astrocaryum murumuru Mart.					u	t
Attalea phalerata Mart. ex Spreng.					c	t
Chamaedorea angustisecta Burret	lc	lc			lc	s
Chamaedorea pinnatifrons (Jacq.) Oerst.				lc		s
Syagrus sancona H. Karst.	FG	r	r		u	t
ARISTOLOCHIACEAE						
Aristolochia sp.			x			v
ASCLEPIADACEAE						
Matalea sp.	FG				x	v
? sp.	FG					v
ASTERACEAE						
Chromolaena cf. *laevigata* (Lam.) R. M. King & H. Rob.					x	s
Critonia morifolia (Miller) R. M. King & H. Rob.		x			x	s
Dasyphyllum cf. *brasiliense* (Sprengel) Cabrera					x	s
Eclipta prostrata (L.) L.					x	h
Eclipta sp.					x	v
Hebeclinium macrophyllum (L.) DC.	x					s
Mikania cf. *cordifolia* (L. f.) Willd.					x	v
Pseudelephanthopus cf. *spiralis* (Less.) Cronquist					x	h
Schistocarpha eupatorioides (Fenzl.) Kuntze					x	s
Senecio cf. *hieronymi* Griseb.					x	h
Spilanthes oppositifolia (Lam.) D'Arcy					x	s
Tessaria integrifolia R. & P.					x	s
Trixis divaricata (Kunth) Spreng.	x				x	s
Verbesina sp.	FG					s
Vernonia cf. *canaminia* Gleason	x				x	s
Vernonia scorpioides (Lam.) Pers.					x	s
Wulffia baccata (L.) Kuntze					x	v
? sp. (2 spp.)					2	s,v
BEGONIACEAE						
Begonia glabra Aubl.					x	h
Begonia sp. (3 spp.)	1	1		1		h
BIGNONIACEAE						
Adenocalymna purpurascens Rusby			x			l
Adenocalymna sp. (2 spp.)			1		2	l
Amphilophium paniculatum (L.) Kunth	1/1					l
Anemopaegma sp.			x			l
Arrabidaea conjugata (Vell.) Mart.	FG					l
Arrabidaea corallina (Jacq.) Sandwith	4/3					l
Arrabidaea poeppigii A. DC.	FG					l
Arrabidaea selloi (Spreng.) Sandwith	3/3					l
Arrabidaea cf. *spicata* Bureau & K. Schum.	1/1					l
Arrabidaea sp. (2 spp.)	1FG	1		1		l
Arrabidaea ? sp.			x			l
Callichlamys latifolia (Rich.) K. Schum	FG					l
Ceratophytum tetragonolobum (Jacq.) Sprague & Sandwith	x		x		x	l
Clytostoma uleanum Kranzlin	17/8					l

	Habitats and localities					*Life form*
	M	*D*	*S*	*R*	*G*	
Jacaranda cuspidifolia Mart.					x	t
Macfadyena unguis-cati (L.) A. H. Gentry	4/4	x	x		x	l
Mansoa difficilis (Chamisso) Bureau & K. Schum.	7/2					l
Mansoa verrucifera (Schltdl.) A. H. Gentry	2/1					l
Mansoa sp.					x	l
Melloa quadrivalvis (Jacq.) A. H. Gentry	6/4					l
Paragonia pyramidata (Rich.) Bureau	2/1				x	l
Pithecoctenium crucigerum (L.) A. H. Gentry	FG					l
Schlegelia ? sp.					x	l
Tabebuia impetiginosa (Mart. ex DC.) Standl.	FG					t
Tabebuia ochracea (Cham.) Standl.	FG					t
Tabebuia serratifolia (Vahl) Nicholson	2/2					t
Tabebuia sp. (2 spp.)		1	5/4			t
Tyanthus ? sp.			x			l
BIXACEAE						
Bixa cf. *urucurana* Willd.					x	t
BOMBACACEAE						
Ceiba pentandra (L.) P. Gaertner					x	t
Ceiba sp.	3/3	x				t
Ochroma pyramidale (Cav. ex Lam.) Pers.	FG				x	t
? sp.	FG					t
BORAGINACEAE						
Cordia alliodora (R. & P.) Oken	FG				x	t
Cordia sp.					x	s
Heliotropium amplexicaule Vahl					x	s
Heliotropium cf. *indicum* L.					x	s
Heliotropium procumbens Mill.					x	s
BROMELIACEAE						
Aechmea distichantha Lem.	c	c	c	c		h,e
Aechmea kuntzeana Mez	u	lr		u		e
Billbergia cf. *microlepis* L. B. Smith	r					e
Fosterella albicans (Griseb.) L. B. Smith	lr					h
Fosterella graminea (L. B. Smith) L. B. Smith	c	c				h
Fosterella villosula (Harms) L. B. Smith	lu	lu				h
Guzmania roezlii (E. Morren) Mez	r				c	h
Pseudananas sagenarius (Arruda da Camara) Camargo	lc	lc			lc	h
Tillandsia didisticha (E. Morren) Baker	c	c	c	c	x	e
Tillandsia fendleri Griseb.					r	e
Tillandsia krukoffiana L. B. Smith					c	h
Tillandsia cf. *kuntzeana* Mez	lu					e
Tillandsia laxissima Mez					lu	h
Tillandsia polystachya (L.) L.	lu	r				e
Tillandsia rusbyi Baker				r		e
Tillandsia spiralipetala Gouda	c	c	u	u	x	e
Tillandsia streptocarpa Baker	c	c	u	c	x	e
Tillandsia tricholepis Baker		u				e
Tillandsia variabilis Schltdl.	x	c	c	c	x	e
Vriesea maxoniana (L. B. Smith) L. B. Smith	c	r	u			e
Werauhia sp. nov.	lc	lc				h

	Habitats and localities					Life form
	M	*D*	*S*	*R*	*G*	
CACTACEAE						
Acanthocereus ? sp.	2/1	x				t
Cereus sp.	1/1	x				t
Echinopsis ? sp.	FG	x				t
Epiphyllum phyllanthus (L.) Haw.	FG	x	x		x	e
Selenicereus setaceus (Salm-Dyck) Moran	2/2	x			x	e
Opuntia brasiliensis (Willd.) Haw.	60/8	x	30/10	x		t
Pereskia weberiana K. Sch.		x	x			s
Lepismium lumbricoides (Lem.) Barthlott	x	x				e
? sp.	FG					s
CAMPANULACEAE						
Siphocampylus orbignianus A. DC.					x	s
CAPPARIDACEAE						
Capparis aff. *baducca* L.		x				t
Capparis flexuosa (L.) L.			17/6			t
Capparis prisca J. F. Macbr.	33/9		8/5		x	t
Capparis sp.		x				t
Cleome sp.					x	h
Morisonia sp.		x				t
CELASTRACEAE						
Maytenus sp.	2/2	x	x	x		t
COCHLOSPERMACEAE						
Cochlospermum orinocense (H. B. K.) Steudel		x				t
COMBRETACEAE						
Combretum sp.	1/1					l
Combretum sp.	x					l
Terminalia cf. *triflora* (Griseb.) Lillo			1/1			t
? sp.	FG					s
COMMELINACEAE						
Callisia repens (Jacq.) L.		x				h
Campelia zanonia (L.) Kunth	FG	x	x		x	h
Commelina diffusa Burm. f.	x					h
Commelina erecta L.					x	h
? sp.	FG					v
CONNARACEAE						
Connarus sp.	FG					l
CONVOLVULACEAE						
Ipomoea sp.	FG				x	v
Ipomoea sp. (2 spp.)					2	v
Merremia macrocalyx (R. & P.) O'Donell					x	v
? sp.	FG					l
CUCURBITACEAE						
Psiguria ternata (M. J. Roemer) C. Jeffrey	FG	x			x	v
DIOSCOREACEAE						
Dioscorea aff. *gouanioides* (Chod. & Hassl.) R. Knuth			x			v
Dioscorea sp.	FG	x		x	x	v

	Habitats and localities					Life form
	M	*D*	*S*	*R*	*G*	
ELAEOCARPACEAE						
Muntingia calabura L.					x	t
EUPHORBIACEAE						
Acalypha sp.	1/1	x				s
Acalypha sp.	1/1		x			s
Acalypha sp.			x			s
Acidoton ? sp.			x			t
Alchornea sp.			1/1			s
Caperonia sp.					x	h
Chamaesyce hirta (L.) Millsp.					x	h
Chamaesyce sp.					x	h
Cnidoscolus urens (L.) Arthur	FG	x			x	s
Croton sp.	1/1		1/1			t
Drypetes amazonica Steyerm.			1/1			t
Euphorbia heterophylla L.					x	h
Euphorbia sp.	FG					s
Hura crepitans L.					x	t
Hyeronima sp.			1/1			t
Margaritaria cf. *nobilis* L.		x	18/4			t
Pachystroma longifolium (Nees) I. M. Johnston			3/2	x		t
Sagotia racemosa Baill.			1/1			t
Sapium sp.					x	t
? sp.	FG					s
ERYTHROXYLACEAE						
Erythroxylon sp.			4/3			s
Erythroxylon sp.			x			s
FLACOURTIACEAE						
Banara guianensis Aubl.					x	t
Banara sp.			x			t
Casearia sylvestris Sw.	FG		x	x	x	t
Casearia sp.					x	t
Casearia/Xylosma sp.			2/1			t
Xylosma sp.	1/1					t
? sp.					x	t
GENTIANACEAE						
Irlbachia alata (Aubl.) Maas					x	h
GUTTIFERAE						
Clusia sp.	FG	x				e,t
Clusia sp. (2 spp.)				1	1	t
Garcinia sp.					x	t
Vismia aff. *crassa* (Rusby) Blake					x	t
HIPPOCRATEACEAE						
Hippocratea sp.	6/4					l
ICACINACEAE						
Catatola sp.			2/2			t
LAMIACEAE						
Hyptis mutabilis (Rich.) Briq.					x	v
Hyptis odorata Benth.					x	s

	Habitats and localities					Life form
	M	*D*	*S*	*R*	*G*	
LAURACEAE						
Endlicheria sp.					x	t
Nectandra sp.					x	t
Ocotea sp.	2/2					t
? sp.	FG				x	t
LECYTHIDACEAE						
Gustavia sp.					x	t
? sp.			1/1			t
LEGUMINOSAE – CAESALPINIOIDEAE						
Apuleia ? sp.			x		x	t
Bauhinia sp. (2 spp.)		1	2			l
Caesalpinia sp.			x			t
Caesalpinia ? sp.	1/1					t
Sclerolobium ? sp.			x			t
Senna cf. *obtusifolia* (L.) Irwin & Barneby					x	s
Senna spectabilis (DC.) Irwin & Barneby					x	t
Senna sp. (2 spp.)					2	t,s
? sp.			x			t
LEGUMINOSAE – MIMOSOIDEAE						
Acacia sp.	3/3	x	1/1			t
Acacia sp.	1/1					t
Acacia sp.	22/7					l
Acacia sp.					x	s
Acacia ? sp.	8/3					l
Albizia niopioides (Spruce ex Benth.) Burkart	3/2					t
Anadenanthera colubrina (Vell. Conc.) Benth.	24/7	x	4/4		x	t
Inga cf. *edulis* Mart.	FG					t
Inga sp. (7 spp.)	4/3		2		5	t
Piptadenia communis Benth.	FG					l
Piptadenia flava (Spreng. ex DC.) Benth.	FG					l
Piptadenia peruviana (J. F. Macbr.) Barneby			1/1			t
Piptadenia sp.			1/1			l
Prosopis sp.			1/1			t
Stryphnodendron sp.			2/1			t
? sp.	4/4					t
? sp.	2/2					t
LEGUMINOSAE – PAPILIONOIDEAE						
Amburana cearensis (Allemao) A. C. Smith	FG		6/5			t
Chamaecrista desvauxii (Colladon) Killip		x				s
Crotalaria nitens Kunth					x	h
Diplotropis ?					x	t
Desmodium sp.					x	h
Erythrina cf. *poeppiginana* (Wallp.) O. F. Cook		x				t
Erythrina sp.			1/1		x	t
Lonchocarpus sp.	FG		2/2			t
Machaerium sp.	2/1		1/1		x	t
Machaerium sp.	3/3				x	l
Machaerium sp.	3/1					l

	Habitats and localities					Life form
	M	D	S	R	G	
Machaerium/Dalbergia sp.	12/7					l
Myroxylon balsamum (L.) Harms	12/4	x	8/5		x	t
Platymiscium aff. *cochabambense* Rusby			x			t
Platymiscium sp.	1/1		x		x	t
Pterocarpus sp.	3/2		1/1			t
Swartzia ? sp.	1/1					t
LEMNACEAE						
Lemna sp.					x	h
LILIACEAE						
Herreria sp.		x				h
LOGANIACEAE						
Buddleja sp.					x	s
Priva lappulacea (L.) Pers.					x	h
LORANTHACEAE						
Phoradendron aff. *bathyoryctum* Eichler		x				e
Phoradendron inaequidentatum Rusby	FG					e
Phoradendron liga (Gillies) Eichler					x	e
Phoradendron mucronatum (DC.) Krug & Urb.			x	x		e
LYTHRACEAE						
Cuphea sp.					x	h
MALPIGHIACEAE						
Banisteriopsis muricata (Cav.) Cuatrec.					x	l
Hiraea cf. *grandifolia* Sandl. & E. O. Williams		x			x	l
Stigmaphyllum sp.					x	l
MALVACEAE						
Abutilon aff. *ramiflorum* St. Hilaire					x	s
Pavonia paniculata Cav.					x	h
Sida sp.					x	h
Sidastrum paniculatum (L.) Fryxell					x	s
Wissadula cf. *boliviana* R. E. Fr.					x	s
MELASTOMATACEAE						
Clidemia hirta (L.) D. Don					x	s
Miconia longifolia (Aubl.) DC.					x	s
Miconia molybdaea Naud.					x	t
Miconia sp.					x	s
Tibouchina longifolia (Vahl) Baillon					x	s
? sp.					x	s
MELIACEAE						
Cedrela sp.	FG					t
Guarea guidonia (L.) Sleumer					x	t
Trichilia claussenii C. DC.		x	x	x	x	s0
Trichilia elegans Adr. Juss.	3/2		1/1			t
Trichilia pleeana (Adr. Juss.) C. DC.	6/2					t
Trichilia sp.	7/4		14/7		x	t
MORACEAE						
Cecropia polystachya Trécul	FG				x	t
Cecropia sp.	FG				x	t
Clarisia biflora R. & P.	FG		x		x	t

	Habitats and localities					*Life form*
	M	*D*	*S*	*R*	*G*	
Coussapoa cf. *ovalifolia* Trécul					x	e
Coussapoa sp.					x	t
Ficus citrifolia Miller	FG					t
Ficus insipida Willd.					x	t
Ficus maxima Miller					x	t
Ficus obtusifolia H.B.K.			1/1			t
Ficus trigona L.f.	1/1		x			e
Ficus sp.	x					t
Maclura tinctoria (L.) D. Don ex Steudel	1/1				x	t
MUSACEAE						
Heliconia sp.					x	h
MYRSINACEAE						
Myrsine sp.				x		t
MYRTACEAE						
Eugenia sp.			29/8			s
Eugenia sp. (2 spp.)					2	s
? sp.			1/1			s
NYCTAGINACEAE						
Boerhavia coccinea Mill					x	s
Bougainvillea sp.	3/3					s
Neea aff. *hermaphrodita* S. Moore			x			s
Neea sp.	7/4	x	3/1	x		s
Neea sp.			3/2		x	s
Neea ? sp.					x	s
Pisonia sp.	FG	x				t
? sp.	FG					t
OLACACEAE						
Ximenia americana L.	1/1					t
ONAGRACEAE						
Ludwigia cf. *affinis* (DC.) H. Hara					x	h
Ludwigia leptocarpa (Nutt.) H. Hara					x	h
Ludwigia sp.	FG					h
ORCHIDACEAE						
Comparettia sp.	x	x				e
Epidendrum paniculatum R. & P.			x			h
Ionopsis utricularioides (Sw.) Lindl.	FG					e
Notylia sp.	FG					e
Oeceoclades maculata (Lindl.) Lindl.	FG					e
Pleurothallis sp.				1		e
Stelis sp.				1		e
Orchidaceae (15 spp.)		1	2	8	2	e, h
OPILIACEAE						
Agonandra cf. *brasiliensis* Miers ex Benth.			2/2			t
Agonandra cf. *excelsa* Griseb.			1/1			t
Agonandra sp.	17/8				x	t
PASSIFLORACEAE						
Passiflora coccinea Aubl.					x	l
Passiflora rubra L.					x	l
Passiflora sp. (3 spp.)		1	1		1	l

	Habitats and localities					Life form
	M	*D*	*S*	*R*	*G*	
PHYTOLACCACEAE						
Achatocarpus nigricans Triana	3/3		3/2			t
Achatocarpus cf. *praecox* Griseb.			1/1			t
Achatocarpus sp.	FG					t
Gallesia integrifolia (Sprengel) Harms	1/1		1/1		x	t
Microtea debilis Sw.					x	h
Petiveria alliacea L.	FG	x			x	s
Seguieria aculeata Jacq.	12/8		1/1			t
Seguieria macrophylla Benth.	FG					l
Seguieria sp.			x			l
Schindleria densiflora H. Walter		x				s
PIPERACEAE						
Peperomia aceroana C. DC.				x		e
Peperomia cf. *circinnata* Link				x		e
Peperomia cf. *macrostachya* (Vahl) A. Dietr.				x		h
Peperomia pseudo-umbilicata Yunck.	x					h
Peperomia cf. *saxicola* C. DC.					x	h
Peperomia cf. *serpens* (Sw.) Loudon					x	h
Peperomia aff. *vestita* C. DC.		x				h
Peperomia sp. (8 spp.)	2	1	1	2	4	h,e
Piper aduncum L.					x	s
Piper arboreum Aubl.			x		x	s
Piper cf. *heterophyllum* C. DC.			x			s
Piper cf. *hieronymi* C. DC.			x		x	s
Piper medium Jacq.	2/1					s
Piper sp.	FG		2/1			s
Pothomorphe peltata (L.) Miq.					x	s
PLUMBAGINACEAE						
Plumbago scandens L.		x			x	v
POACEAE						
Chusquea sp. nov.	lc	lf	lc	lc	lc	s
Guadua weberbaueri Pilger					lc	s
Gynerium sagittatum (Aubl.) P. Beauv.	c				c	s
Lasiacis sp.		x	x	x	x	s
Olyra latifolia L.	FG				f	h
Rhipidocladum sp. nov.	lc		lc	lc		s
POLYGALACEAE						
Polygala acuminata Willd.					x	h
POLYGONACEAE						
Coccoloba sp.			2/2			t
Coccoloba sp. (2 spp.)			1		1	t
Polygonum punctatum Buch.-Ham.					x	h
Triplaris americana L.	2/2	x	3/1		x	t
PORTULACACEAE						
Portulaca ? sp.	FG					h
Clematis dioica L. var. *brasiliana* (DC.) Eichler					x	v
PTERIDOPHYTA						
Adiantopsis chlorophylla (Sw.) Fée	x					h

	Habitats and localities					*Life form*
	M	*D*	*S*	*R*	*G*	
Adiantopsis radiata (L.) Fée			x			h
Adiantum raddianum Presl	x		x		x	h
Asplenium auritum Sw.					x	h
Asplenium dimidiatum Sw.			x			e
Asplenium discrepans Rosenst.	x					h
Asplenium myriophyllum (Sw.) Presl				x		h
Asplenium raddianum Gaud.	x					e
Asplenium serra Langsd. & Fisch.				x		h
Asplenium serratum L.					x	e
Asplenium tetraphyllum Willd.					x	h
Asplenium sp. (2 spp.)			1	1	1	h
Anemia phyllitidis (L.) Sw.	x					h
Blechnum occidentale L.					x	h
Bolbitis serratifolia (Kaulf.) Schott					x	e,h
Campyloneurum brevifolium (Link) Link					x	e
Campyloneurum nitidissimum (Mett.) Ching			x	x		e
Dicranoglossum desvauxii (Klotsch) Proctor			x	x		e
Doryopteris concolor (Langsd. & Fisch.) Kuhn			x			h
Doryopteris pedata (L.) Fée var. *multipartita* (Fée) R. M. Tryon			x		x	h
Hemionitis palmata L.		x			x	h
Hemionitis tomentosa (Lam.) Raddi	x				x	h
Lycopodiella cernua (L.) Pic.-Ser.	x				x	h
Lygodium venustum Sw.					x	v
Microgramma mortoniana Sota	x					e
Microgramma percussa (Cav.) Sota					x	e
Microgramma squamulosa (Kaulf.) Sota		x		x		e
Nephrolepis cordifolia (L.) Presl.					x	e
Pecluma plumula (Willd.) Price				x		e
Phlebodium decumanum (Willd.) J. Sm.			x	x	x	h
Platycerium andinum Baker	FG	x	x		x	e
Pityrogramma calomelanos (L.) Link	x				x	h
Pityrogramma trifoliata (L.) Tryon					x	h
Pteridium arachnoideum (Kaulf.) Maxon					x	h
Pteris denticulata Sw.					x	e
Pteris quadriaurita Retz			x			h
Polypodium fraxinifolium Jacq.					x	e
Polypodium furfuraceum Schlecht. & Cham.					x	e
Polypodium aff. *furfuraceum* Schlecht. & Cham.	x		x			h
Polypodium remotum Desv.			x	x	x	e
Polypodium squalidum Vell.			x	x	x	e
Selaginella microphylla (H. B. K.) Spring	x					h
Selaginella sulcata Spring					x	h
Thelypteris cf. *juruensis* (C. Chr.) R. Tryon & Conant					x	h
Thelypteris sp. (2 spp.)					2	h
Trachypteris pinnata (Hooker f.) C. Chr.		x				h
RHAMNACEAE						
Gouania sp.	FG				x	l

	Habitats and localities					*Life form*
	M	*D*	*S*	*R*	*G*	
ROSACEAE						
Prunus aff. *tucumanensis* Lillo			30/8			t
RUBIACEAE						
Coffea arabica L.	37/4		1/1			s
Manettia sp.					x	v
Palicourea crocea (Sw.) Roemer & Schultes					x	s
Palicourea cf. *guianensis* Aubl.			x			t
Pittoniotis sp.	FG					t
Psychotria marginata Sw.					x	s
Psychotria ? sp.		x			x	s
Randia sp.	FG		x			s
RUTACEAE						
Angostura cf. *pilocarpoidea* (Rusby) Albuquerque			x			t
Dictyoloma peruvianum Planch.	x				x	s
Erythrochiton fallax Kallunki		x			x	s
Esenbeckia almawillia Kaastra			x			t
Metrodorea flavida K. Krause			4/1			t
Pilocarpus peruvianus (J. F. Macbr.) Kaastra			4/3	x		t
Zanthoxylon sp.					x	t
SALICACEAE						
Salix humboldtiana Willd.					x	t
SAPINDACEAE						
Allophyllus cf. *edulis* (A. St. Hil.) Radlk.	6/4		4/3			t
Allophyllus sp.	5/3					t
Paullinia sp.		x				l
Sapindus saponaria L.	1/1	x	x		x	t
Serjania cf. *lethalis* A. St.-Hil.			x			l
Serjania sp. (2 spp.)	2 FG					l
Thinouia ? sp.	3/3					l
Urvillea ? sp.	FG					l
? sp.			7/4			t
SAPOTACEAE						
Chrysophyllum gonocarpum (Mart. & Eichler) Engl.	1/1		1/1		x	t
Pouteria sp.	1/1		3/3			t
Pouteria sp.					x	t
SCROPHULARIACEAE						
Lindernia sp.					x	h
Scoparia dulcis L.					x	h
SIMAROUBACEAE						
Simarouba amara Aubl.					x	t
SOLANACEAE						
Cestrum strigillatum R. & P.					x	s
Cestrum sp.		x				s
Juanulloa parasitica R. & P.				x		l
Physalis pubescens L.					x	h
Solanum myrianthum Rusby					x	s
Solanum (7 spp.)	1		1	1	4	s

	Habitats and localities					Life form
	M	D	S	R	G	
STERCULIACEAE						
Guazuma ulmifolia Lam.	FG					t
Helicteres ihotzkyana (Schott & Endl.) Schumann	FG	x				s
THEOPHRASTACEAE						
Clavija cf. *peruviana* B. Stahl			x			s
Clavija tarapotana Mez	35/10	x	1/1	x	x	s
TILIACEAE						
Luehea cf. *grandifolia* Mart.	FG					t
Luehea splendens Rusby					x	t
Triumfetta sp.					x	s
TRIGONIACEAE						
Trigonia sp.	2/1					t
ULMACEAE						
Ampelocera sp.	1/1					t
Celtis iguanea (Jacq.) Sarg.	1/1	x			x	l
Celtis sp.	1/1				x	l
Phyllostylon rhamnoides (Poisson) Taubert	6/4					t
Trema micrantha (L.) Blume					x	t
URTICACEAE						
Phenax angustifolius (Kunth.) Wedd.					x	s
Urera baccifera (L.) Gaudich.	9/7		5/4			s
Urera caracasana (Jacq.) Gaudich. ex Griseb.	FG					s
? sp.					x	t
VERBENACEAE						
Aegiphila sp.					x	s
Lantana sp.					x	s
Stachytarpheta cayannensis Loes.					x	h
VITACEAE						
Cissus sicyoides L.					x	v
ZINGIBERACEAE						
Costus sp.					x	h
Renealmia sp.					x	h

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Addresses of the authors: M. K.: Albrecht-von-Haller-Institut für Pflanzenwissenschaften, Abteilung Systematische Botanik, Untere Karspüle 2, D-37073 Göttingen, Germany.

N. H.: P.O. Box 22652, Scarborough, 7975, South Africa.