A PHYTOGEOGRAPHIC ANALYSIS OF THE WOODY ELEMENTS OF NEW WORLD SAVANNAS

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An analysis was made of the floristic composition of 45 savanna sites located throughout the southern neoarctic and neotropics. A total of 533 woody species were recorded from published and reliable unpublished floristic lists; of these, 234 species (44%) were from 10 Brazilian cerrado sites, with 187 (80%) of them restricted to the cerrado biome. The cerrados were clearly shown to be the most diverse New World savanna system with a high degree of endemism. The data were analysed using two multivariate techniques: TWINSPAN and DCA. Four phytogeographic zones were identified: Central Brazil and Bolivia extending to Southern Amazonia; north of Amazonia extending across the isthmus of Central America and including the Caribbean; Belize, Guatemala and Southern Mexico; and north of the Mexican Plateau. The analyses revealed gradients of floristic variation associated with latitude and longitude, and showed the great heterogeneity of savanna vegetation.

Keywords. Biodiversity, cerrado, floristic patterns, multivariate analysis, tropical plant biogeography.

INTRODUCTION

The conservation–development debate about tropical vegetation predominantly concerns moist evergreen forest (Huntley & Walker, 1982; Stott, 1991; Furley, 1994). However, savannas occupy the greater area of the southern continents and are biologically diverse (Ratter *et al.*, 1996). They are home to about 25% of the world's population (Stott, 1991) and suffer great anthropogenic pressure particularly from agricultural development (Ratter *et al.*, 1997). Conservation of savanna systems is a priority although a lack of understanding of distribution patterns in their diversity impedes planning. In the Americas, for example, information on savanna diversity patterns are available only for the cerrado biome (tree savanna) of Brazil (Ratter & Dargie, 1992; Ratter *et al.*, 1996).

The present work collates floristic data encompassing much of the latitudinal range of American savannas and attempts to identify patterns of diversity and define floristic links.

MATERIALS AND METHODS

Data collection

A site–species data matrix was compiled using information from published (and reliable unpublished) floristic surveys of neotropical and neoarctic savannas, with

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the data expressed as presence/absence. The geographic positions of the 45 sites are shown in Fig. 1 and other details in Appendix 1. Restraints on the data include in some cases insufficient sampling area and inconsistent levels of recording, due to differences in field sampling techniques and thoroughness of the studies undertaken.

Only species of trees and large shrubs have been used in the study as insufficient data are available for herbaceous and subshrub species.

Data analysis

The approach used in this research follows that of Ratter & Dargie (1992), Oliveira-Filho & Ratter (1995) and Ratter *et al.* (1996). Two multivariate analyses were used. The techniques were: i, a divisive hierarchical classification using TWINSPAN (Two-Way Indicator Species Analysis) (Hill, 1979); and ii, an ordination using DCA (Detrended Correspondence Analysis (Hill & Gauch, 1980).

Floristic matrices were analysed by these two techniques at species level omitting unicates, i.e. species that occur at only one site (Appendix II). These were removed as they provide no basis for comparison (Oliveira-Filho & Martins, 1991; Ratter & Dargie, 1992; Oliveira-Filho *et al.*, 1994). In addition, unicate records can produce misleading results, as they can include various types of errors such as scoring species from adjacent non-savanna vegetation, misidentifications and unrecognized synonyms (Ratter *et al.*, 1996).

RESULTS AND DISCUSSION

A total of 533 species was recorded at the 45 sites (Appendix II). Of these, 347 (65%) were unicates, illustrating the great floristic heterogeneity of savanna systems. No species occurred at all the sites. However, two species showed a cosmopolitan distribution, with *Curatella americana* L. occurring at 30 (67%) of the sites and *Byrsonima crassifolia* (L.) Kunth at 29 (64%) of the sites. These widespread species are bird-dispersed and both are tolerant of a wide range of ecological and environmental conditions, most importantly being their ability to withstand temporary or seasonal inundation (Ratter *et al.*, 1996).

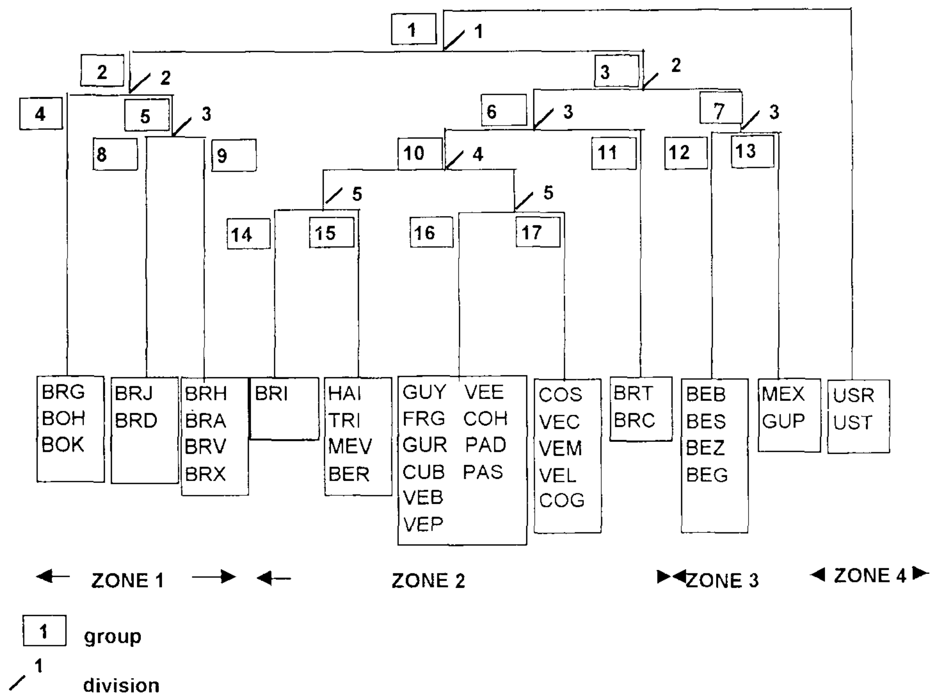
The cerrado sites of Central Brazil showed the greatest diversity of woody species of all the New World savanna systems, with all sites (BRJ, BRD, BRV and BRX) having more than 50 woody species recorded; one site (BRX) showed a diversity of 121 species. Only one other savanna site from Belize (BER, with 59 species) showed a comparable species diversity. The cerrados also showed a high degree of endemism, with 80% of the 234 species recorded occurring only at these sites.

Multivariate analyses

The results from the two analytical techniques show a significant degree of coincidence and their similarity suggests that they reflect a true phyogeographic pattern.

FIG. 1. Location of sites used in this study.

i. TWINSPAN. The TWINSPAN analysis was run to five divisions (Fig. 2); however, four phytogeographic zones clearly show after three divisions (shown geographically, Fig. 3). Six sites (COA, BAR, ANT, DOM, USC and USH) were not



The groups and divisions in the dendogram follow the standard TWINSPAN numbering.

ZONE 1	Group 4	Humaitá (site 4) and both Bolivian sites
	Group 8	Jardim Bôtanico de Brasília; Brasília National Park (both Brazil)
	Group 9	Alter do Chão; Vale do Songos; Nova Xavantina; Humaita (site 3) (all Brazil)
ZONE 2	Group 14	Maracá (Brazil)
	Group 15	Haiti/Dominican Republic; Trinidad; Veracruz; Mexico; RBCMA, Belize
	Group 16	Rupununi, Guyana and Guyana (site 16); French Guiana; Cuba; Palma Sola Ranch, Venezuela; southern Venezuela; Venezuela; high plains of Colombia; Darién; Santiago Plain Veraguas (Panama)
	Group 17	Comelco and NW Costa Rica; Llanos and Calabozo, Venezuela
	Group 11	Tartarugalzhino and S of Calçoene (both Amapá, Brazil)
ZONE 3	Group 12	Mountain Pine Ridge; Spanish Lookout; Belize Zoo; Gracey Rock (all Belize)
	Group 13	Mexico and Petén, Guatemala
ZONE 4		Rio Grande Plains, southern Texas, both in the USA

FIG. 2. Site hierarchy derived from TWINSPAN data analysis.

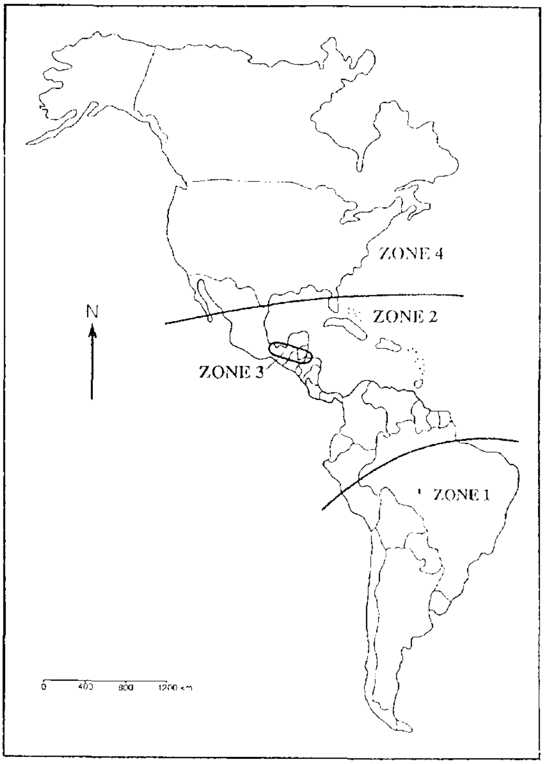


FIG. 3. Phytogeographic patterns of the sites, as defined by TWINSPAN. Zone 1, Central Brazil and Bolivia extending into Southern Amazonia; zone 2, from Northern Amazonia extending across the isthmus of Central America and including the Caribbean; zone 3, Belize, Guatemala and Southern Mexico; zone 4, north of the Mexican plateau.

included in the analysis, as these consisted entirely of unicate species. The initial run of TWINSPAN included two North American sites and this caused excessive clumping of the other sites in the study. As a distinct outlying zone was formed by North American sites (USR, UST) they were omitted from a second analysis of the Central and South American sites. Fig. 2, however, shows a combination of both analyses.

Zone 1. The first division separates Southern Amazonian, Central Brazilian and Bolivian cerrado sites from species-poor sites in Venezuela, Colombia and Central America. Cerrados predominantly occur on dystrophic soils, although mesotrophic cerrados can occur (Furley & Ratter, 1988). Group 9 of zone 1 appears to represent the latter element to a certain extent with some sites containing a high percentage of mesotrophic indicator species, as indicated by Ratter *et al.* (1996).

Zone 2. This zone, stretching from north of the Hylaea to the Mexican Plateau and including the Caribbean region shows, a high degree of internal heterogeneity.

Zone 3. This is a grouping of Southern Mexican, Petén and Belizean sites which separate from the rest of Central America.

Zone 4. This zone was created at the first division, confirming the expected distinct floral differences between North America and Central and South America. The boundary of this zone corresponds well with the topographic barrier represented by the edge of the Mexican Plateau.

ii. DCA. The ordination for the sites on the two principal axes, which explain the greatest amount of variation in the data (Jackson & Somers, 1991), is shown in Fig. 4.

The zones and groups produced in the ordination show close agreement to those produced by TWINSPAN. As for TWINSPAN, the six sites consisting entirely of unicate species were not included in the analysis. In addition, the remaining two outlying North American sites were not entered in the analysis as their inclusion caused excessive clumping of the other sites.

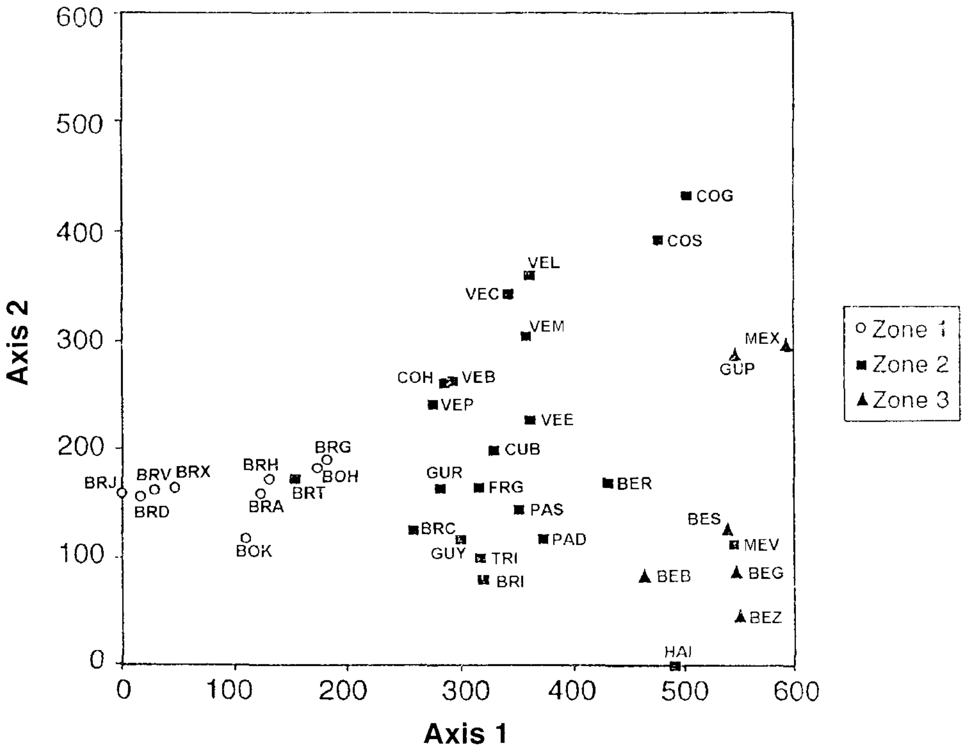


FIG. 4. Principal ordination of the sites. To avoid excessive clumping, outliers (USR and UST) and misclassified sites (DOM, BAR, ANT and COA) are not included. Symbols follow zones indicated by TWINSPAN.

Axis 1. The ordination of sites along Axis 1 follows a south–north sequence, reflecting variation in floristic composition with increasing latitude. The cerrados of central and southern Amazonian Brazil and the savannas of Bolivia are clustered at the lower end of the axis. Sites from Southern Mexico, Petén and Belize are clearly shown at the upper end of the axis. The remaining sites take up the central space of the triangle, representing floristic transitional stages.

Axis 2. The variation represented in Axis 2 may be caused by a number of environmental variables relating to changes in longitude. However, reliable environmental data for the sites are limited so it was not possible to correlate these variables with this axis. There are considerable limitations in extracting environmental information from literature. Differing survey objectives affect the type and detail of data collection. Some papers describe climate in detail, whereas others put more emphasis on edaphic features. Differences in the times of year that surveys were conducted also hinders direct comparison of soil and climatic data.

This study suggests the existence of four distinct phytogeographic subprovinces within neotropical and southern neoarctic savannas. These are: a, Central Brazil and Bolivia, extending into Southern Amazonia (zone 1); b, north of Amazonia extending across the isthmus of Central America and including the Caribbean (zone 2); c, Belize, Guatemala and Southern Mexico (zone 3); and d, north of the Mexican Plateau (zone 4).

Although the two analyses complemented each other, suggesting strong phytogeographic patterns throughout American savannas, problems were encountered. Standardization of techniques used in floristic data collection would have increased the comparability of the data. Ideally, environmental data should have been available for each site to enable CCA (Canonical Correspondence Analysis) or DCCA (Detrended CCA) ordinations. These offer a more sophisticated analysis of the relationships between plants and their environment. However, the present work demonstrates the value of running analyses to define preliminary phytogeographic groupings, even with relatively imperfect data.

The zonation reflects the distribution of individual species that are restricted to one or more areas. However, widespread species such as *Curatella americana* and *Byrsonima crassifolia* occur in a large number of sites. In contrast, *Berberis trifoliolata* Moric. is found only in the northern hemisphere from Texas to Arizona. Similarly, *Qualea grandiflora*, being endemic to the cerrado vegetation of South America, is indicative of the division of phytogeographic zone 1 from zones 2, 3 and 4.

The ultimate historical explanations of these distribution patterns are complex and beyond the scope of this paper. They may reflect both Pleistocene climatic changes, where savanna areas may have reverted to forest (e.g., Raven & Axelrod, 1974; Colinvaux, 1991), and more ancient events such as the closure of the Isthmus of Panama which created a terrestrial migration path between North and South America. Whatever the explanation for the patterns of endemism noted in this work, they need consideration in conservation planning for Neotropical savannas.

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APPENDICES

Appendix I. Areas of savanna compared in the study

Site BER was surveyed by the authors in 1996. The other survey results come from publications or reliable unpublished reports.

Site no.	Site code	Locality	No. of species	References
1	BOH	Bolivia	44	Haase & Beck, 1989; Haase, 1990
2	BOK	Bolivia	40	Killeen, 1997
3	BRH	Humaitá, AM, Brazil	46	Janssen, 1986
4	BRG	Humaitá, AM, Brazil	17	Gottsberger & Morawetz, 1986
5	BRJ	Jardim Botânico, DF, Brazil	78	Fundacão Zoobotânica, 1990

6	BRD	Brasília, DF, Brazil	52	Felfili & Silva Jr, 1993
7	BRA	Alter do Chão, PA, Brazil	49	Sanaiotti, 1991; Branch & Silva, 1983; Miranda, 1993
8	BRI	Ilha da Maracá, RR, Brazil	27	Milliken & Ratter, 1989
9	BRV	Vale de Sonhos, MT, Brazil	72	Ratter *et al.*, 1977
10	BRX	Nova Xavantina, MT, Brazil	121	Ratter *et al.*, 1973
11	BRT	Tartarugalzinho, AP, Brazil	7	Sanaiotti *et al.*, 1997
12	BRC	south of Calcoene, AP, Brazil	6	Sanaiotti *et al.*, 1997
13	COH	high plains – Colombia	14	FAO, 1966
14	COA	alluvial plains – Colombia	6	FAO, 1966
15	FRg	French Guiana	8	Beard, 1953
16	GUY	Guyana	8	Beard, 1953
17	GUR	Rupununi, Guyana	15	Goodland, 1964
18	VEB	Venezuela	11	Beard, 1953
19	VEC	Calabozo, Venezuela	17	Blydenstein, 1962
20	VEM	Venezuela	10	Myers, 1933
21	VEE	southern Venezuela	9	Eden, 1974
22	VEL	Venezuelan Llanos	12	Monasterio & Sarmiento, 1976; Sarmiento, 1984
23	VEP	Palma Sola Ranch, Venezuela	16	Farji Brener & Silva, 1995
24	PAD	Darién, Panama	5	Graham, 1973
25	PAS	Santiago Plain, Veraguas, Panama	5	Graham, 1973
26	COS	Comelco, Costa Rica	7	Frankie *et al.*, 1974
27	COG	Guanacaste, Costa Rica	19	Daubenmire, 1972
28	TRI	Trinidad	28	Schwab, 1988
29	BAR	Barbuda, Lesser Antilles	2	Beard, 1953
30	ANT	Antigua	2	Beard, 1953
31	DOM	Dominica	5	Beard, 1953
32	HAi	Haiti/Dominican Rep.	41	Pollacci, 1936
33	BEb	Mountain Pine Ridge, Belize	14	Kellman, 1989
34	BES	Spanish Lookout, Belize	7	Ratter in Munro, 1989
35	BEZ	Zoo, Belize	11	Ratter in Munro, 1989
36	BEG	Gracey Rock, Belize	10	Ratter in Munro, 1989
37	BER	RBCMA, Belize	59	Bridgewater *et al.*, 1997
38	GUP	Petén, Guatemala	12	Lundell, 1937
39	MEx	Mexico	8	Rzedowski, 1978
40	MEV	Veracruz, Mexico	10	Gómez-Pompa, 1972
41	CUB	Cuba	8	Beard, 1953
42	USR	Rio Grande Plains, Texas, USA	9	Barnes & Archer, 1996
43	UST	Texas, USA	14	Scanlan, 1988; Coffey, 1986
44	USC	California	3	Momen *et al.*, 1994
45	USH	Howes Prairie, In, USA	11	Cole & Taylor, 1995

Appendix II. Species occurring at more than one of the 45 sites

Those with a single occurence have been omitted. The figures give the number of locations at which each species is recorded.

Acacia farnesiana W.Wall. 2
Acoelorraphe wrightii H. Wendl. ex Becc. 4
Acosmium dasycarpum (Vogel) Yakovlev 3
Acrocomia aculeata (Jacq.) Lodd. ex Mart. 2

A. mexicana Karw. ex Mart 3
Aegiphila lhotskyana Cham. 2
Agonandra brasiliensis Miers 2
Alchornea schomburgkii Klotzsch 2
Alibertia edulis (L. Rich.) A. Rich. 4
A. sessilis (Cham.) K. Schum. 2
Anacardium occidentale L. 7
Andira cuiabensis Benth. 2
A. inermis Kunth 3
A. vermifuga Mart. 2
Antonia ovata Pohl 3
Apeiba tibourbou Aubl. 3
Aspidosperma macrocarpon Mart. 5
A. multiflorum A. DC. 2
A. tomentosum Mart. 4
Astronium fraxinifolium Schott 4
Austroplenckia populnea (Reiss.) Lundell. 2
Bauhinia rufa (Bong.) Steud. 4
Berberis trifoliolata Moric. 2
Blepharocalyx salicifolius (Kunth) Berg 2
Bowdichia virgilioides Kunth 13
Bredemeyera altissima A.W. Benn. 2
Brosimum gaudichaudii Trécul 4
Byrsonima coccolobifolia Kunth 10
B. crassa Nied. 2
B. crassifolia (L.) Kunth 29
B. pachyphylla A. Juss. 2
B. spicata Rich. ex A. Juss. 2
B. verbascifolia Rich. ex A. Juss. 12
Callisthene fasciculata (C. K. Spreng.) Mart. 2
Caryocar brasiliense Cambess. 4
Casearia grandiflora Cambess. 2
C. sylvestris Sw. 7
Cassia diphylla L. 2
Celtis pallida Torr. 2
Chamaecrista nictitans (L.) Moench. 2
Chomelia ribesioides Benth. 3
Chrysobalanus icaco L. 4
C. pellocarpus Mey. 2
Citharexylum caudatum L. 2
Clidemia hirta D. Don. 2
C. sericea D. Don. 2
Clitoria nemorosa G. F. W. Mey. 2
Coccoloba pubescens L. 2
Cochlospermum regium (Schrank) Pilg. 3
C. vitifolium (Willd.) Spreng. 7
Connarus suberosus Planch. 4
Copaifera langsdorfii Desf. 4
C. martii Hayne 2
Copernicia tectorum Mart. 2
Cornutia pyramidata L. 2
Couepia grandiflora (Mart. & Zucc.) Benth. 3
Crescentia alata Kunth 2
C. cujete L. 4
Crotalaria sagittalis L. 2
Curatella americana L. 30
Cybistax antisyphilitica Mart. 2
Dalbergia miscolobium Benth. 3
Davilla elliptica A. St.-Hil. 4
Didymopanax distractiflorum Harms 4
D. macrocarpum (Cham. & Schltdl.) Seem. 3
Dimorphandra mollis Benth. 3
Diospyros texana Scheele 2
Duguetia furfuracea (A. St.-Hil.) Benth. & Hook. 3
Emmotum nitens (Benth.) Miers 4
Enterolobium cyclocarpum Griseb. 2
Eremanthus glomerulatus Less. 2
Eriotheca gracilipes (Schum.) Robyns 2
E. pubescens (Mart. & Zucc.) Schott. & Endl. 2
Erythroxylum daphnites Mart. 2
E. deciduum A. St.-Hil. 2
E. suberosum A. St.-Hil. 7
E. tortuosum Mart. 4
Euplassa inaequalis (Pohl) Engl. 2
Ferdinandusa elliptica Pohl 2
Genipa americana L. 2
Gliricidia sepium Kunth 2
Godmania macrocarpa Hemsl. 3
Guazuma ulmifolia Lam. 3
Guettarda scabra Lam. 2
Haematoxylum campechianum L. 2
Hancornia speciosa Nees & Mart. 4
Himatanthus obovatus (Müll. Arg.) Woodson 3
Hirtella ciliata Mart. ex Zucc. 3
H. glandulosa Spreng. 3
H. racemosa Lam. 3
Humiria balsamifera A. St.-Hil. 2
Hymenaea courbaril L. 2
H. stigonocarpa Mart. ex Hayne 4
Ilex guianensis Kuntze 2
Inga venosa Griseb.
Kielmeyera coriacea (Spreng.) Mart. 4
K. rubriflora A. St.-Hil. 2
K. speciosa A. St.-Hil. 2
Lacistema aggregatum (Berg) Rusby 3
Lafoensia pacari St. Hil. 4
Licania humilis Cham. & Schltdl. 2
Luehea paniculata Mart. 3
L. speciosa Willd. 2

Machaerium acutifolium Vogel 3
M. opacum Vogel 2
Magonia pubescens A. St.-Hil. 2
Maprounea guianensis Aubl. 3
Matayba guianensis Aubl. 3
Mauritia flexuosa L.f 2
Melochia villosa (Mill.) Fawc. & Rendl. 2
Miconia albicans (Sw.) Triana 9
M. ciliata (Rich.) DC. 2
M. ferruginata DC. 2
M. pohliana Cogn. 2
M. rubiginosa (Bonpl.) DC. 2
M. rufescens (Aubl.) DC. 2
M. stenostachya DC. 4
M. tiliaefolia Naud. 3
Mimosa albida H. & B. ex Willd. 2
M. obovata Benth. 2
Morinda elliptica Mart. 2
Myrcia cerifera L. 2
Ouratea hexasperma (A. St.-Hil.) Benth. 6
O. spectabilis (Mart.) Endl. 3
Palicourea rigida Kunth 5
Paurotis wrightii (Griseb. & Wendl.) Britton 2
Physocalymma scaberimmum Pohl 3
Pinus caribaea Morelet 4
Piptocarpha rotundifolia (Less.) Baker 5
Pisonia noxia Netto 2
Pithecellobium saman Benth. 2
Plathymenia reticulata Benth. 3
Plumeria alba Aubl. 2
Pouteria ramiflora (Mart.) Radlk. 3
P. torta (Mart.) Radlk. 2
Prosopis glandulosa Torr. 2
Protium heptaphyllum (Aubl.) E. K. Marchal 3
Pseudobombax longiflorum (Mart. & Zucc.) Robyns 2
P. tomentosum (Mart. & Zucc.) Robyns 2
Psidium cf. *guineese* Sw. 2
P. guajava L. 2
P. salutare Berg. 2
Pterocarpus podocarpus Blake 2
Pterodon pubescens Benth. 4
Qualea grandiflora Mart. 7
Q. multiflora Mart. 5
Q. parviflora Mart. 6
Quercus oleoides Schltdl. & Cham. 5
Rapanea guianensis Aubl. 3
Roupala complicata Kunth 2
R. montana Aubl. 10
Rourea induta Planch. 2
Sabal morrisiana Bartlett 2
Salacia crassifolia (Mart.) Peyr. 3
Salvertia convallariodora A. St.-Hil. 4
Schaefferia cuneifolia A. Gray 2
Sclerolobium paniculatum Vogel 5
Senna uniflora (P. Mill.) Irwin & Barneby 2
Simarouba amara Aubl. 3
S. versicolor A. St.-Hil. 2
Siparuna guianensis Aubl. 4
Strychnos pseudoquina A. St.-Hil. 4
Styrax ferrugineus Nees & Mart. 3
Swartzia laurifolia Benth. 2
Syagrus flexuosa (Mart.) Becc. 3
Tabebuia aurea Benth. & Hook. 4
T. ochracea (Cham.) Standl. 5
Tapirira guianensis Aubl. 4
Terminalia argentea Mart. & Zucc. 3
T. brasiliensis Eichler 2
Terstroemia tepezapote Schldl. & Cham. 2
Tetragastris unifoliolata (Engl.) Cuatrec. 2
Tibouchina aspera Aubl. 2
Tocoyena formosa (Cham. & Schltdl.) Schum. 4
Vatairea macrocarpa (Benth.) Ducke 4
Vernonia ferruginea Less. 2
Virola sebifera Aubl. 4
Vismia cayennensis (Jacq.) Pers. 2
Vochysia elliptica (C. K. Spreng.) Mart. 2
V. haenkeana Mart. 3
V. rufa (C. K. Spreng.) Mart. 2
V. thyrsoidea Pohl 2
Xylopia aromatica Lam. 8
X. frutescens Aubl. 3
Zanthoxylum fagara Sarg. 2
Ziziphus obtusifolia (T. & G.) Gray. 2