SEASONALLY DRY FORESTS OF TROPICAL SOUTH AMERICA: FROM FORGOTTEN ECOSYSTEMS TO A NEW PHYTOGEOGRAPHIC UNIT

D. E. PRADO*

The Pleistocenic Arc, which must have originated from the climatic shifts in South America during the late Pleistocene, ranges from the Caatingas of north-eastern Brazil through south-eastern Brazil to the Paraguay and Paraná rivers confluence, into south-western Bolivia and north-western Argentina, and extends sporadically into dry Andean valleys of Peru or coastal western Ecuador. It is regarded as a new phytogeographic unit for South America, here named the Tropical Seasonal Forests Region, as it is characterized by a considerable number of endemic plant taxa at both generic and species level. The paradigm of the arc is the distribution pattern of *Anadenanthera colubrina* (*Fabaceae*), which, when superimposed on those of other woody species of seasonal forests, permits a reasonably accurate mapping of the new region, which might also have biogeographic implications for endemic bird taxa. The plant communities of this newly recognized unit are unique in their nature and floristic composition, when compared with other floristic areas of the continent by means of classic phytosociological and numerical analyses (PCA). These ecosystems have remained submerged within other vegetation units in South American phytogeography (such as the Chaquenian or Amazonian regions), and have been particularly neglected in conservation policies. An urgent call is made for these areas to be preserved before they disappear, because they are located in areas with some of the best agricultural soils of tropical South America, and therefore subject to clearing for farming.

Keywords. Caatingas, conservation, dry forests, Paranense province, Pleistocenic Arc.

INTRODUCTION

Cabrera & Willink's (1973) concept of the biogeographical provinces of Latin America, based mainly on the phytogeographic ideas of the first author, has remained unchallenged for nearly three decades. The currently prevailing concept of the phytogeography of the Neotropical Kingdom involves five regions (or 'dominia', in Cabrera & Willink, 1973): Caribbean, Amazonian, Guayanan, Chaquenian and Andean-Patagonian. Two of these regions are of interest for the present study: the Amazonian Region, which includes the Amazonian, Yungas, Cerrado, Paranense and Atlantic Provinces amongst others, and the Chaquenian Region, including the woody Caatingas, Chaquenian and Monte Provinces together with the Pampas grasslands.

In the course of a critical analysis (Prado, 1991) of the alleged floristic links between the vegetation of the Gran Chaco of northern Argentina, western Paraguay

---

* Cátedra de Botánica, Facultad de Ciencias Agrarias, Universidad Nacional de Rosario, PO Box 14, 2123 Zavalla, Argentina.

and south-eastern Bolivia, and that of the Caatingas of north-eastern Brazil (Andrade-Lima, 1954, 1982), a series of dot-map distributions were plotted for some of the woody species of the deciduous and semideciduous forests of tropical and subtropical South America. Whereas the Chaco-Caatingas connections proved to be a long-standing fallacy (Prado, 1991), some very interesting distribution patterns throughout South and Central America emerged, which have given rise to speculations on the influence of past wet–dry climatic fluctuations on the present-day disjunctions of seasonal forests in the continent (Prado, 1991; Prado & Gibbs, 1993). One such case is the 'Residual Pleistocenic Seasonal Formations Arc' or Pleistocenic Arc (Prado, 1991; Prado & Gibbs, 1993), which comprises a remarkable group of woody vegetation types, here regarded as seasonal forests, across central South America. The underlying hypothesis for the present study is that the Pleistocenic Arc should be regarded as a high rank phytogeographic unit itself (probably at the Region level), and its component vegetation units should therefore hold together when subjected to comparison with other formations of the continent.

The concept of seasonal forests as employed here derives mainly from Beard's (1944, 1955) 'seasonal formation series', which groups structural types of vegetation related to climatic seasonality in the tropics of South America, with a well-defined dry season of variable length. This consequently determines the physiognomy of the vegetation types involved from semideciduous to strongly deciduous, but they are also affected by light frosts in those areas that extend to a certain degree below the Tropic of Capricorn. As pointed out by Sarmiento (1972), savannas were not included by Beard in his seasonal series, despite their being definitely seasonal. However, this does not affect the present study because it is concerned with seasonal forests and woodlands; the Cerrado savannas are of interest only with regard to some components of their very rich woody flora, found in the cerradão woodlands and forests. The concept adopted here largely equates with that of 'dry forests' in Gerhardt & Hytteborn (1993), with some minor differences with regard to the length of the dry period – established as about six months by them, but which among South American seasonal forests is only surpassed by the Caatingas area but is usually much shorter – and to the quality of the soils, which are richer (Beek & Bramao, 1968) than those of the neighbouring Cerrado and Amazonian rain forests.

METHODS

In order to assess to what extent the tropical seasonal forests are interrelated to other South American formations, reliable floristic lists (i.e. without identification errors) were selected from the available literature (Table 1) and elaborated as phytosociological tables on a basis of presence-absence of genera (see Appendix). These data were then analysed following the Zürich-Montpellier approach, as modified by Mueller-Dombois & Ellenberg (1974). This consists in listing species (rows) and localities (columns; see also Table 1) and mechanically search for species with common patterns of distribution in the columns, until subsequent reshuffling of

TABLE 1. Sources of the floristic lists employed in the phytosociological analysis of the main South American seasonal forests at generic level (see Appendix)

Column	
A	The Monte province, Argentina (*sensu* Morello, 1958: 145–150).
B	Chaco *s.s.*: Sierra Chaco, Argentina (Sayago, 1969: 224).
C	Chaco *s.s.*: the lowland Chaco in its Eastern, Central and Western districts, Argentina. Floristic list from Prado (1991), excluding the species exclusive to the Sierra Chaco.
D	Austro-Brazilian Transitional Forest, Argentina (Prado, 1991).
E	'Selva de Ribera', Argentina (Prado *et al.*, 1989; Morello & Adámoli, 1974).
F	Gallery Forest, Paraná River, Argentina (Franceschi & Lewis, 1979).
G	Upper Uruguay River Valley Forests, Santa Catarina and Rio Grande do Sul, Brazil (Klein, 1972; Rambo, 1980).
H	Planalto Forest, Vassununga & Bauru, São Paulo, Brazil (Martins, 1979: 108–109; Cavassan *et al.*, 1984).
I	Subandean Piedmont Forests, in both its 'Palo blanco' and 'Tipa-Pacará' variants (Prado, 1991).
J	The Caatingas Province, Brazil (Prado, 1991).
K	Calcareous woodlands, Mato Grosso do Sul, Brazil (Ratter *et al.*, 1988: 516; Prado *et al.*, 1992).
L	Calcareous forest of Januária, M. Gerais, Brazil (Ratter *et al.*, 1978).
M	Cerrado and cerradão in Brasília, Federal District (Ratter, 1986; P. E. Oliveira, personal communication).
N	Atlantic rain forest, Ubatuba, São Paulo, Brazil (Silva & Leitão F°, 1982).
O	Amazon forest, km 30 on the road Manaus-Itacoatiara, Amazonas, Brazil (Prance *et al.*, 1976: 28–35).

columns and rows results in the grouping of certain species that seem to be exclusive to a determined group of localities (Appendix). These species groups are taken to indicate the presence of common environmental factors, hence having an ecological indicator value, and they are referred to as 'floristic groups' or FG (Mueller-Dombois & Ellenberg, 1974).

Subsequently, they were analysed through PCA (Principal Components Analysis) from the JMP IN® statistical software, an ordination technique that displays the individuals under study in hyperdimensional space along axes ('principal components') of continuous variation. These axes are numbered according to the decreasing percentage of accumulated variation they concentrate, and therefore the first one comprises the highest value of variation absorbed by any possible axis. Only the Axis 1–Axis 2 scattergram is shown and discussed here.

As emphasized by Cain & Castro (1959), probably the only procedure that reduces the usually large element of subjectivity in the designation of floristic territories is the preparation of accurate dot maps for the species of a particular flora as far as the available exsiccata and monographic studies permit; subsequently they are superimposed on a single map so as to delimit the area by a line drawn around the peripheral spots. This technique is followed in this study, though the list of mapped species is certainly not complete.

RESULTS AND DISCUSSION

The distribution of *Anadenanthera colubrina* (Vell.) Brenan (*Fabaceae–Mimosoideae*) can be taken as a paradigm of the Tropical Seasonal Forests phytogeographical unit proposed here. This tree, in its variety *cebil* (Griseb.) Altschul is one of the most common and usually dominant species in the Caatingas of north-eastern Brazil, particularly in the arboreal and shrubby formations, as evidenced by the large number of exsiccata from this area (Fig. 1). From the Caatingas area it subsequently appears more scattered within the Cerrado of central Brazil, but exclusively in mesotrophic facies cerradão and mesophilous woodlands (Ratter *et al.*, 1978) on calcimorphic soils, until it reaches the Paraguay-Paraná rivers system. Here again there is high density of exsiccata and phytogeographic records, whereas the reasonably well collected Chaco plains show an absence of this species. To the west of the Chaco there is also a remarkable concentration of dots, which coincides with a narrow fringe of strongly seasonal forests in the piedmont sector of the Subandean Mountains of north-western Argentina and south-western Bolivia, a vegetation type that has so far been submerged into the Yungas province. The distribution pattern of *Anadenanthera colubrina* var. *cebil* extends more scantily along dry interandean

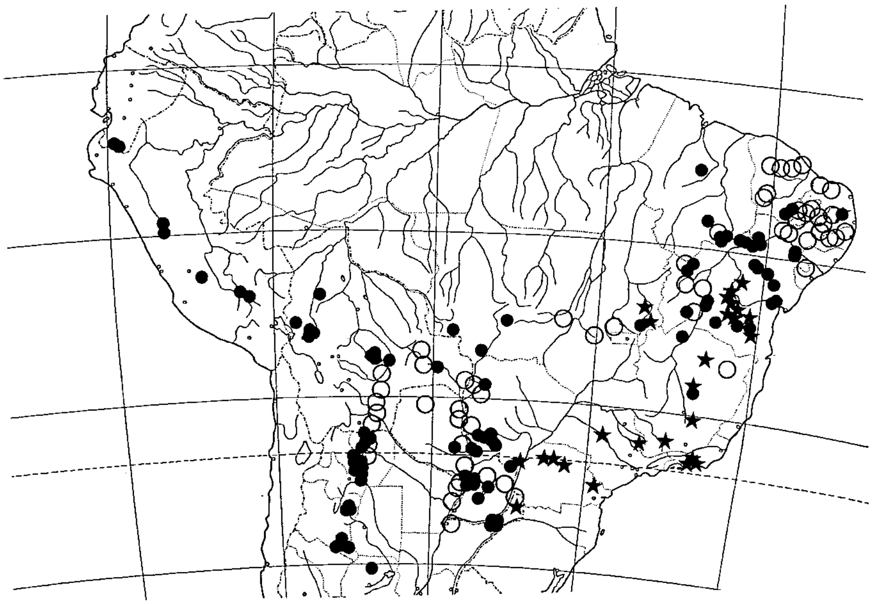

FIG. 1. Distribution map of *Anadenanthera colubrina* in tropical and subtropical South America. ★, var. *colubrina*; ●, var. *cebil* (herbarium specimens or citations in monograph); ○, var. *cebil* (citations in floristic lists).

valleys in north-western Bolivia and throughout Perú to southern Ecuador. The variety *colubrina* overlaps somewhat with var. *cebil* within the Caatingas, in rather wetter areas (e.g. Serra Jacobina in Bahia state), to subsequently form a sort of arc through Minas Gerais, Rio de Janeiro, São Paulo and Paraná states in south-eastern Brazil, until this corridor meets the Paraguay-Paraná rivers system.

This distribution pattern is very significant because it is repeated, wholly or in part, by a number of other woody species of the seasonal forests of tropical South America mapped elsewhere (Prado & Gibbs, 1993), such as *Pterogyne nitens* Tul., *Enterolobium contortisiliquum* (Vell.) Morong, *Celtis pubescens* (Kunth) Sprengel, *Amburana cearensis* (Fr. All.) A.C. Smith, etc. (Table 2). Even more indicative in this sense is the compound map of all 32 species listed in Table 2, superimposed on it (Fig. 2), which shows the actual geographical expanse of what has been named the Pleistocenic Arc (Prado, 1991; Prado & Gibbs, 1993). Three concentrations or 'nuclei' of distributions (Prado & Gibbs, 1993) can be clearly discerned: (1) the Caatingas of north-eastern Brazil, or 'Caatingas nucleus' of distribution, (2) the Paraguay-Paraná river system in north-eastern Argentina, east Paraguay and south-western Mato Grosso do Sul ('Misiones nucleus'), and (3) the Subandean Piedmont Forests of south-western Bolivia and north-western Argentina ('Subandean Piedmont nucleus').

Occasional dots occur to the west of the first nucleus into Maranhão state, where the presence of relict Caatingas outposts is still a controversial matter (cf. Galvão, 1955, and Bigarella *et al.*, 1975, vis-à-vis Eiten, 1965, 1972: 288). This area in turn can be hypothesized as linking to the Faro/Monte Alegre area close to the Amazon river in Pará, and further north to the Roraima–Guyana border area (Fig. 2). The single dot shown in the latter region corresponds to a curious collection of

TABLE 2. List of the 32 woody species following wholly or in part the Pleistocenic Arc of distribution in tropical South America, employed in the compound map of Fig. 2

Alseis floribunda Schott	*Hymenaea martiana* Hayne
Amburana cearensis (Fr.All.) A.C.Smith	*Machaerium acutifolium* Vog.
Anadenanthera colubrina (Vell.) Brenan	*Mimosa caesalpiniifolia* Benth.
Aspidosperma pyrifolium Mart.	*Myracrodruon balansae* (Engl.) Santin
Aspidosperma riedelii Muell. Arg.	*Myracrodruon urundeuva* Fr.All.
Astronium concinnum Schott	*Patagonula americana* L.
Balfourodendron riedelianum (Engl.) Engl.	*Patagonula bahiensis* Moricand
Calycophyllum multiflorum Griseb.	*Peltophorum dubium* (Spreng.) Taub.
Carica quercifolia (St.-Hil.) Hieron.	*Phytolacca dioica* L.
Celtis pubescens (Kunth) Spreng.	*Piptadenia viridiflora* (Kunth) Benth.
Combretum leprosum Mart.	*Pouteria gardneriana* (DC.) Radlk.
Commiphora leptophloeos (Mart.) Gillet	*Pterogyne nitens* Tul.
Diatenopteryx sorbifolia Radlk.	*Ruprechtia laxiflora* Meissn.
Diplokeleba floribunda N.E. Br.	*Schinopsis brasiliensis* Engl.
Diplokeleba herzogii Radlk.	*Schinopsis peruviana* Engl.
Enterolobium contortisiliquum (Vell.) Morong	*Ziziphus oblongifolius* S. Moore

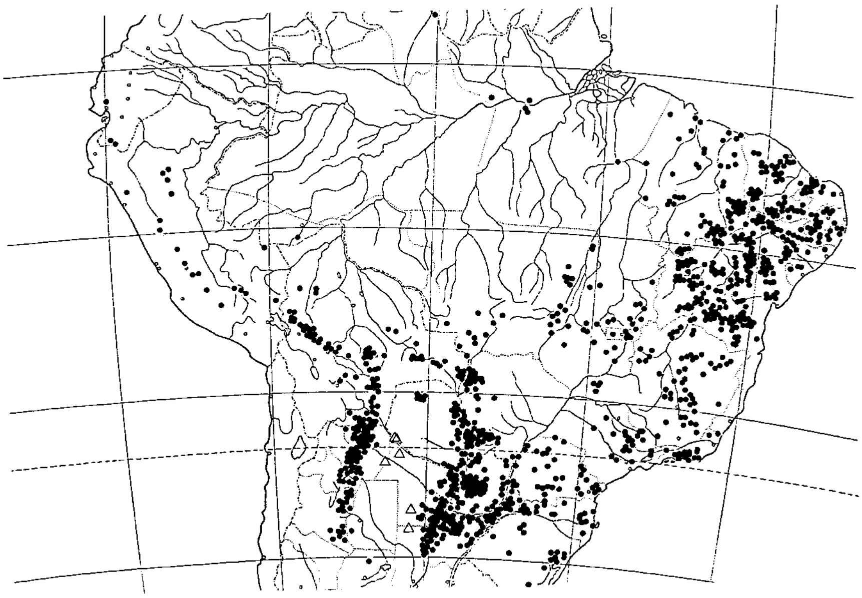

FIG. 2. Compound distribution map of the 32 species of Table 2, following wholly or in part the Pleistocenic Arc. Open triangles indicate the few intrusions of tropical elements into the Chaco plains; note also in the same space the concentration of dots in the Cerro León area in north-western Paraguay.

Commiphora leptophloeos (Mart.) Gillet by E. Ule (Prado, 1991). The first nucleus is connected to the second through two 'tracks'[1]: the northern and the southern routes. The northern track seems to cut present-day Cerrado in two halves, extending as a narrow strip from western Bahia (probably getting into Goiás via the Rio Grande valley) to the calcareous outcrops in the Federal District of Brazil and surrounding areas (Ratter *et al.*, 1978). The deciduous forests of the so-called Mato Grosso de Goiás (beginning somewhat to the east of the city of Goiânia) are part of this track, which crosses the Araguaia river at the level of Aragarças, presumably branching north from there to the Xavantina/Cachimbo and Ilha do Bananal areas, and west to the Cuiabá-north Pantanal area, later reaching the calcareous hills around Corumbá and Urucúm in Mato Grosso do Sul (Kanter, 1936; Kuhlman, 1954; Ratter *et al.*, 1988).

The southern track extends at first along the São Francisco and Jequitinhonha river valleys, and south in a wide band along the Rio das Velhas to Belo Horizonte area and the Rio de Janeiro state. The latter region has been allegedly subject to intense wet–dry climatic fluctuations during the Pleistocene (Cailleux & Tricart, 1959;

---

[1] The present author is aware that the proposed 'tracks' might simply overlap with well-collected areas or routes, instead of indicating an adjusted pattern of distribution. However, it is here believed that these tracks do suggest ancient connections between the nuclei of distribution (Prance, 1982; Prado & Gibbs, 1993).

Tricart, 1961). The southern track then goes through the states of São Paulo, Paraná and Santa Catarina, mostly via the Planalto and upper river Uruguay basin forests, until meeting the second nucleus of distribution.

The second nucleus, with a central axis in the Paraguay-Paraná system is nowadays linked to the third nucleus only through the Santiago and Chiquitos Sierras in Bolivia. This connection is interrupted between Chiquitos and Santa Cruz de la Sierra by a moderate northwards protrusion of the Chaco *s.s.* (Prado, 1993a,b), which seems to give way to humid tropical forests of direct Amazonian influence with no intervening communities of species of the Pleistocenic Arc. It is likely, however, that there were additional links in the past between the second and third nuclei, as today exemplified by the vegetation of the Cerro León in the middle of the Paraguayan Chaco plains (Fig. 2). Spichiger & Ramella (1989) and Ramella & Spichiger (1989) describe some communities on these hills and along the Timane/Lagerenza river valley, which very closely resemble the physiognomy and floristics of both the Subandean Piedmont Forests and arboreal Caatingas (Andrade-Lima, 1981), and are also very similar to the 'Caatingas' forest of calcareous hills around Corumbá (Ratter *et al.*, 1988). It is likely that when the flora and vegetation of Cerro León becomes better known, stronger links with calcareous and Caatingas vegetation will emerge. Indeed, one would predict the presence of at least some species not reported so far, such as *Schinopsis brasiliensis* Engl., *Commiphora leptophloeos*, *Piptadenia viridiflora* (Kunth) Benth., *Ruprechtia laxiflora* Meissn., *Enterolobium contortisiliquum*, *Patagonula americana* L. Any of these taxa would add to the already known presence there of *Anadenanthera colubrina* var. *cebil*, *Myracrodruon urundeuva* Freire Allemão, *Amburana cearensis*, *Pterogyne nitens*, *Aspidosperma pyrifolium* Mart. and *Calycophyllum multiflorum* Griseb. (Ramella & Spichiger, 1989; Spichiger & Ramella, 1989). It is also likely that specific and even generic endemisms would be encountered in the Cerro León or other isolated hills of the Paraguayan Chaco, such as the recently described and puzzling *Sphingiphila* Gentry (*Bignoniaceae*), known only from the type collection in the Cerro Chovoreca in northern Paraguay (Gentry, 1990).

The third nucleus stretches continuously from south-eastern Catamarca in north-western Argentina to Santa Cruz de la Sierra in Bolivia as a narrow strip of deciduous forests. It extends more tenuously but persistently along the foothills of the Andes in north-western Bolivia, and enters Perú to be present in dry interandean valleys such as those of the Apurímac, Huállaga and Marañón rivers, and just reaches south-western Ecuador. Acre state in Brazil has two species characteristic of the Pleistocenic Arc (*Amburana cearensis* and *Celtis pubescens*) and, not unexpectedly, other more widespread species have also been collected in this area, e.g. *Myroxylon balsamum* (L.) Harms and *Poeppigia procera* Presl (Prado & Gibbs, 1993).

The composite map of Fig. 2 also shows a conspicuous blank area between the second and third nuclei, which corresponds to the Chaco *s.s.* There are, however, six collections from within the Chaco (indicated with open triangles in Fig. 2) that correspond to some of the few intrusions of tropical elements into the Chaco plains via the gallery forests in the west (*Enterolobium contortisiliquum, Calycophyllum multiflorum, Anadenanthera colubrina* var. *cebil*), and via gallery forest or relictual stands of richer forest in the east (*Ruprechtia laxiflora*, *Patagonula americana*, *Phytolacca dioica* L., *Myracrodruon balansae* (Engl.) D.A. Santin). The scanty presence of these elements within the Chaco plains was regarded by some authors as 'species of non-chaquenian lineage' (Adámoli *et al.,* 1972) or 'transchaquenian elements of subtropical forests' (Morello & Adámoli, 1974: 44). In Table 3 some species of the Subandean Piedmont Forests are listed, whose presence within the Western Chaco are further evidence that these forests were more extended to the east of their present position during the climatic fluctuations of the Pleistocene (Simpson, 1971; Ab' Sáber, 1977). These forests must have extended further south as well, as the relictual presence of *Anadenanthera colubrina* var. *cebil* in the Córdoba mountains (Hunziker, 1973, and Fig. 1) seems to indicate.

Some of the species listed in Table 2 belong to monotypic genera, which are therefore genera completely restricted to the Pleistocenic Arc. At this stage it may then be postulated that the Pleistocenic Arc reflects a new phytogeographical entity, a statement that needs to be substantiated. This goal can be achieved by means of comparative analysis of floristic lists of locations inside the Pleistocenic Arc vis-à-vis other neighbouring formations, such as the Cerrado savannas, the Amazon Hylaea and the Atlantic rain forest of coastal Brazil, but also the allegedly more closely related Chaquenian formations. The scattergram of Fig. 3 shows the PCA results, which are indeed conclusive. The three clusters are clearly isolated from each other: cluster I groups the Chaco *s.s.* (Prado, 1993b) and related vegetation, isolated in the positive end of Axis 1; cluster II associates those vegetation types definitely Amazonian in character (sensu Cabrera & Willink, 1973), i.e. the Amazon (O), its closely related Atlantic forest (N), and the Cerrado vegetation (M); while on the

TABLE 3. List of woody and succulent species of the Subandean Piedmont Forests also occasionally occurring in Western Chaco

Anadenanthera colubrina (Vell.) Brenan var. *cebil* (Griseb.) Altschul
Basistemon spinosus (Chodat) Mold.
Calycophyllum multiflorum Griseb.
Carica quercifolia (St.-Hil.) Hieron.
Coursetia hassleri Chodat
Enterolobium contortisiliquum (Vell.) Morong
Jacaratia corumbensis Kuntze
Maclura tinctoria (L.) Don ex Steudel subsp. *mora* (Griseb.) V. Ávila
Manihot guaranitica Chodat & Hassler subsp. *guaranitica*
Patagonula americana L.
Pereskia sacharosa Griseb.
Phyllostylon rhamnoides (Poisson) Taubert
Pterogyne nitens Tul.
Ptilochaeta nudipes Griseb.
Quiabentia pflanzii (Vaupel) Berger

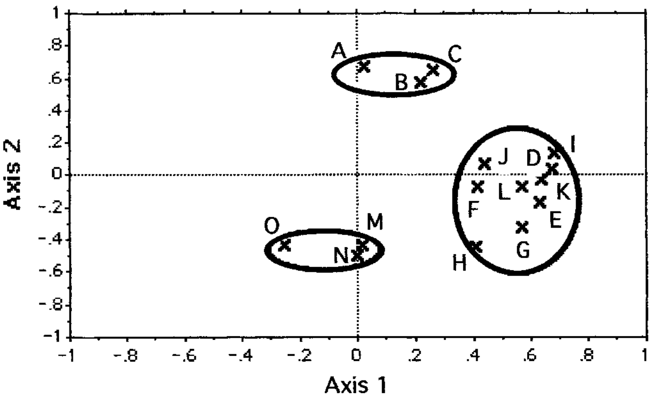

FIG. 3. Scattergram from PCA analysis of the floristic lists of Table 1. Key to the phytogeographical areas involved, and sources, in Table 1.

other hand cluster III groups together the tropical seasonal forests of South America, from the Caatingas of north-eastern Brazil (J) through the calcareous outcrops in Minas Gerais (L) and Mato Grosso do Sul (K) and the Planalto forests of São Paulo (H, rather more loosely linked), to the Upper Uruguay and Paraná river valley vegetation (D, E, F, G), and finally to one of the closest in the analysis but geographically distant of the Caatingas, the Subandean Piedmont Forests (I).

Both Axes 1 and 2 account for over 35% of the original variation, whereas the following five axes add up to 34%. Axis 1 is somewhat difficult to interpret, despite explaining over 20% of the total variation; it is likely that the different vegetation types are segregated between seasonal woodlands and forests and those which are not, e.g.: rain forests, savannas and the Monte semidesert (A), with temperate/subtropical Chaco in an intermediate position. Axis 2 can be more readily interpreted as a tropical–temperate gradient, because the Monte province occupies one of the extremes (it reaches northern Patagonia; Morello, 1958) and the Amazon forest close to Manaus the other.

The previous results are remarkably congruent with the phytosociological analysis shown in the Appendix. The Chaquenian Region (columns A–C) is well defined as a unit by the floristic groups (FG) VII, VIII, IX and X, while its links to the seasonal formations are illustrated by FG III–VI and XIII–XV. The genera endemic to or mainly restricted to the tropical seasonal forests of South America (columns D–L) are included in FG XII and especially in XVI, but also within FG XIX–XXV, XXIX, XXXII, XXXIII and XXXV. The generic links of the Upper Uruguay Forests (column G) with the Caatingas (J) are shown in FG XXIII, while those with the Subandean Piedmont Forests (I) are indicated in FG XXIV. It is noteworthy that FG XXXIII emphasizes the strong floristic contacts at generic level of solely the Caatingas and Subandean Piedmont nuclei. The floristic relationship Caatingas/Amazonian Region is shown in FG XXXIV and XXXVI, while FG XXXVII–XXXX indicate the internal coherence and close links between the formations of the Amazonian Region.

A proviso is needed: a phytogeographical entity should contain a sizeable number of endemic taxa. In this sense most authors agree in that a phytogeographic region must hold a relevant number of endemic genera and species (including those of their subordinated units), whereas the provinces consist of subdivisions of a region that should have a reduced number of monotypic or oligotypic genera and abundant specific endemism (Braun-Blanquet, 1919; Cain & Castro, 1959; Takhtajan, 1986). The Pleistocenic Arc of distribution comprises, as far as it is possible to ascertain from literature and herbarium specimens, about 11 endemic genera for the complete, or almost complete area, and some 22 genera that are endemic to the three nuclei within the arc (Table 4), and over 300 endemic species (Prado, 1991).

It is argued here that the discrete floristic nature of the Pleistocenic Arc, coupled with an appreciable level of genera and specific endemicity, supports the establishment of a new phytogeographical entity at regional level, named the Tropical Seasonal Forests Region, or 'Dominio de los Bosques Tropicales Estacionales'. It comprises at least three provinces: the Caatingas *sensu lato*, the Subandean Piedmont Forests and the Paranense. The first one is no different from the more or less established view of the present-day concept of the Caatingas (Andrade-Lima, 1981), except for the addition of a substantial part of the Bahian 'mata de cipó' (Andrade-Lima, 1966) and to the south the corridor of the Rio das Velhas in Minas Gerais. On the other hand, the other two provinces proposed involve greater changes to South American phytogeography.

It has been demonstrated elsewhere through classic phytosociological and numerical analysis (Prado, 1991) that the Caatingas province should be removed from the Chaquenian Region (Dominio Chaqueño, *sensu* Cabrera & Willink, 1973), with which it has negligible floristic links. Instead, it was proposed that it should be transferred to the Amazonian Region with which it has much stronger links, particularly because its closest formation in South America is the Subandean Piedmont Forests, a member of the Yungas province (*sensu* Cabrera & Willink, 1973, in their Amazonian Dominium). However, it is clear from this study that both seasonal formations must be in fact taken away from the Amazonian Region as well, to constitute this new region.

The Subandean Piedmont Forests province has been so far submerged as a district within the Yungas province, usually confused in the literature as 'Transitional forests' (Hueck, 1972) between neighbouring dry temperate-subtropical Chaco lowlands and the more humid 'Distrito de las Selvas Montanas' (Cabrera, 1976). In the present study this vegetation unit is recognized as one of the three nuclear areas of the Tropical Seasonal Forests Region, because of its characteristic flora (see Appendix) and physiognomy. This formation holds a very peculiar position as a wedge between two major phytogeographical units, at an intermediate altitude (350–500m in Cabrera, 1976, or 450–900m in Meyer, 1963), and also with intermediate rainfall figures (from 700 to 1000mm) of monsoonian character (Vervoorst, 1982). This

TABLE 4. Genera endemic to the Pleistocenic Arc as a whole (PA), or to the Caatingas (CA), Paranense (PE) and Subandean Piedmont Forests (SP) provinces individually

		No. of spp.	PA	CA	PE	SP
AMARANTHACEAE	*Pseudoplantago*	1			●	
ANACARDIACEAE	*Myracrodruon*	2	●			
ARECACEAE	*Arecastrum*	1			●	
ASTERACEAE	*Blanchetia*	1		●		
	Telmatophila	1		●		
BIGNONIACEAE	*Perianthomega*	1	●			
BORAGINACEAE	*Auxemma*	2		●		
	Patagonula	2	●			
BROMELIACEAE	*Neoglaziovia*	1		●		
CACTACEAE	*Brasiliopuntia*?	3	●			
	Espostoopsis	1		●		
	Leocereus	1		●		
	Quiabentia	3	●			
	Stephanocereus	2		●		
	Tacinga	2		●		
CAPPARACEAE	*Haptocarpum*	1		●		
CELASTRACEAE	*Fraunhoffera*	1		●		
EUPHORBIACEAE	*Parodiodendron*	1				●
FABACEAE	*Amburana*	1	●			
	Apuleia?	1	●			
	Bergeronia	1			●	
	Holocalyx	1			●	
	Mysanthus	1		●		
	Pterogyne	1	●			
FLACOURTIACEAE	*Aphaerema*	1			●	
MALVACEAE	*Bastardiopsis*?	1			●	
POACEAE	*Neesiochloa*	1		●		
RHAMNACEAE	*Alvimiantha*	1		●		
RUBIACEAE	*Schenckia*	1			●	
RUTACEAE	*Balfourodendron*	1	●			
SAPINDACEAE	*Athyana*	1				●
	Diatenopteryx	1	●			
	Diplokeleba	2	●			

allows for a particular kind of forest to develop with its own floristic identity. According to Sarmiento (1972), this formation has the highest proportion of deciduous species (79%) of all tropical and subtropical seasonal forests. Although this formation is mainly located in the piedmont area of the Subandean Mountains in south-western Bolivia and north-western Argentina (hence their name), its southernmost extension is actually placed in the northern extreme of the Sierras Pampeanas in south Tucumán and east Catamarca. There are two major types of forests within this unit, distributed in a north–south direction by a temperature gradient, and separated by a gap dividing the mountainous ranges (Vervoorst, in Hawkes &

Hjerting, 1969: 38), which allows the intrusion of Chaco communities into the inner dry valleys: (a) 'Palo blanco' forest, and (b) 'Tipa' and 'Pacará' forest (Prado, 1993a).

The Paranense province, as here recognized, equates partially with that delimited by Cabrera & Willink (1973), but differs in the addition of the Austro-Brazilian Transitional Forests and 'Selva de Ribera' units (Prado, 1993a,b) and the exclusion of the *Araucaria* forest of the high plateaux of south-eastern Brazil. This latter temperate forest may be considered a relict of colder paleoclimates (Andrade-Lima, 1966), as the presence of the genera *Podocarpus*, *Clethra*, *Drimys* and *Weinmannia* (Klein, 1975) and localized snowfalls seem to confirm. I agree with R. Spichiger (personal communication, and Spichiger *et al.*, 1992) that Prance's 18th Phytochorium (Prance, 1989) is a somewhat artificial unit because of the inclusion of the *Araucaria–Podocarpus* forests and woodlands in a supposedly tropical vegetation area. The main bulk of the vegetation of this modified Paranense province consists of the 'Broadleaf forest of the Paraná-Uruguay basins' (Klein, 1975), equivalent to the 'Selvas Mixtas' of Cabrera (1976) and also to the *Lauraceae–Cedrela–Chrysophyllum* tall semideciduous forest of the Paraguayan Upper Paraná (Spichiger *et al.*, 1992).

Based on the compound distribution map of Fig. 2, an attempt has been made to delimit the geographical area of the new region (Fig. 4). The scattered black dots

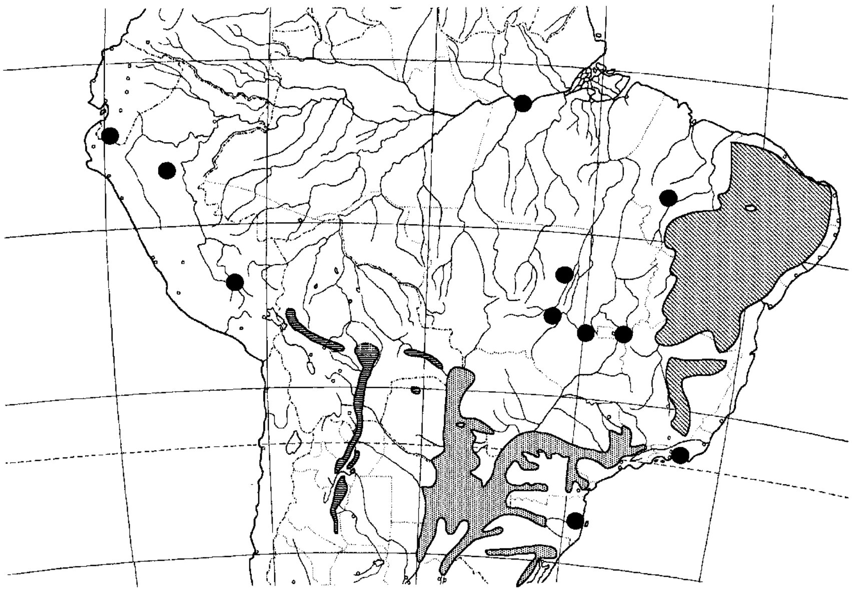

FIG. 4. Tentative mapping of the new Tropical Seasonal Forests Region of South America, based on the compound map of Fig. 2. Oblique hatching: the Caatingas province *sensu lato*; stippled: the Paranense province *sensu auctor*; horizontal hatching: the Subandean Piedmont Forests province. ●: areas with enigmatic concentration of collections that cannot be safely adscribed to the region with the present knowledge of their vegetation.

indicate some puzzling outlying collections, suggesting that the Pleistocenic Arc must have been more extensive in the geological past to areas that cannot currently be safely included as part of the Tropical Seasonal Forests Region. This region might also have important biogeographical implications; there are a number of non-migrant bird species whose distribution patterns correlate with the area shown in Figs 2 and 4, such as the monotypic genus *Myrmorchilus* and the whole genus *Melanopareia* amongst others (Formicaridae, Aves; see maps in Prado, 1991). It must be noted that the Tropical Seasonal Forests Region has been completely overlooked so far in the phytogeographical or biogeographical accounts of South America (Smith & Johnston, 1945; Cabrera & Willink, 1973; Müller, 1973; Eiten, 1974; Hueck & Seibert, 1981; Haffer, 1985; Prance, 1989).

Thus, it can be seen from the present study that the Tropical Seasonal Forests Region has usually been submerged within other regions and provinces. These seasonal forests have usually been disregarded and considered to be impoverished or 'transitional' versions of environments with higher biodiversity (such as the Atlantic Forests or the Amazon) or better known areas such as the Chaco. Scarcely a word was said about these communities of South America in a recent workshop on tropical dry forests (Gerhardt & Hytteborn, 1993, and articles thereafter). As a result the vegetation of the Tropical Seasonal Forests Region has been neglected in all serious conservation projects in South America, as evidenced by simple comparison with updated continental maps of protected areas (Barzetti, 1993: 133). With the sole exception of the Iguazú Falls area, where three national parks from three bordering countries converge (albeit with a scenic rather than conservationist approach), there is no sizeable protected area within this region. This situation is particularly critical for some sectors of the three provinces; the 'Tipa-pacará' forest has almost completely disappeared under intensive agriculture (Brown & Grau, 1993), but there is still hope for the endangered 'Palo blanco' forests that occur basically in the more extended Bolivian part of the Subandean Piedmont Forests. The situation of the Caatingas area is little better in this respect; this province has hardly benefited from the impressive and welcome thrust towards conservation of the Amazon rain forests in Brazil, and it is perhaps the harshness of climate and terrain that prevents the total disappearance of its original vegetation. An urgent call is made here for representative areas to be preserved before they disappear altogether with their genetics resources and biodiversity potentialities. The threat is great because they are located in some of the best agricultural soils of tropical South America, and despite the vagaries of their climate, they support a larger human population than rain forests in the tropics (Janzen, 1988).

ACKNOWLEDGEMENTS

This work was partially funded by CONICET (Consejo Nacional de Investigaciones Científicas y Técnicas, Argentina) and the National University of Rosario, Argentina.

REFERENCES

AB' SÁBER, A. N. (1977). Espaços ocupados pela expansão dos climas secos na América do Sul, por ocasião dos períodos glaciais quaternários. *Paleoclimas* 3: 1–19.

ADÁMOLI, J., NEUMANN, R., RATIER DE COLINA, A. D., & MORELLO, J. (1972). El Chaco aluvional salteño (Convenio INTA-Prov. de Salta). *Rev. Invest. Agrop., INTA, Serie 3,* 9: 165–237.

ANDRADE-LIMA, D. DE (1954). *Contribution to the Study of the Flora of Pernambuco, Brazil.* Recife: Universidade Rural de Pernambuco.

ANDRADE-LIMA, D. DE (1966). Vegetação. *Atlas Nacional do Brasil*, Vol. II: 11. Rio de Janeiro: Conselho Nacional de Geografia.

ANDRADE-LIMA, D. DE (1981). The Caatingas dominium. *Rev. brasil. Bot.* 4: 149–163.

ANDRADE-LIMA, D. DE (1982). Present-day forest refuges in northeastern Brazil. In: PRANCE, G. T. (ed.) *Biological Diversification in the Tropics*, pp. 245–251. New York: Columbia University Press.

BARZETTI, V. (1993). *Parques y Progreso: Areas Protegidas y Desarrollo Económico en América Latina y el Caribe.* USA: Edwards Bros, UICN-BID.

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

BEARD, J. S. (1955). The classification of tropical American vegetation-types. *Ecology* 36: 89–100.

BEEK, K. J. & BRAMAO, D. L. (1968). Nature and geography of South American soils. In: FITTKAU, E. J., ILLIES, J., KLINGE, H., SCHWABE, G. H. & SIOLI, H. (eds) *Biogeography and Ecology in South America*, pp. 82–112. The Hague: W. Junk.

BIGARELLA, J. J., ANDRADE-LIMA, D. D., & RIEHS, P. J. (1975). Considerações a respeito das mudanças paleoambientais na distribuição de algumas espécies vegetais e animais no Brasil. *Anais Acad. Brasil. Ciênc.* 47: 411–464.

BRAUN-BLANQUET, J. (1919). Essai sur les notions d'élément et de territoire phytogéographique. *Arch. Sci. Phys. Nat., 5e pér.* 1: 497–512.

BROWN, A. D. & GRAU, H. R. (1993). *La naturaleza y el hombre en las selvas de montaña.* Salta, Argentina: Proyecto GTZ.

CABRERA, A. L. (1976). *Regiones Fitogeográficas Argentinas*, 2nd edition. Buenos Aires: ACME S.A.C.I.

CABRERA, A. L. & WILLINK, A. (1973). *Biogeografía de América Latina*, 1st edition. Washington, DC: Secretaría General de la Organización de los Estados Americanos.

CAILLEUX, A., & TRICART, J. (1959). Zonas fitogeográficas e morfoclimáticas do quaternário no Brasil. *Notícia Geomorfologica, Campinas* 2: 12–17.

CAIN, S. A., & CASTRO, G. M. O. (1959). *Manual of Vegetation Analysis.* New York: Harper & Bros.

CAVASSAN, O., CESAR, O., & MARTINS, F. R. (1984). Fitossociologia da vegetação arbórea da reserva estadual de Bauru, estado de São Paulo. *Rev. brasil. Bot.* 7: 91–106.

EITEN, G. (1965). Informações preliminares sôbre a vegetação da 'Ilha de Balsas' no sudeste do Maranhão. In: SOC. BOT. DO BRASIL (ed.) *Anais do XIV Congresso Nacional de Botânica, 1963*, pp. 351–360.

EITEN, G. (1972). The cerrado vegetation of Brazil. *Bot. Rev.* 38: 201–341.

EITEN, G. (1974). An outline of the vegetation of South America. *Symposia of the 5th Congress of the International Primatological Society, Nagoya, Japan*, pp. 529–545.

FRANCESCHI, E. A. & LEWIS, J. P. (1979). Notas sobre la vegetación del valle santafesino del Río Paraná (República Argentina). *Ecosur* 6: 55–82.

GALVÃO, R. (1955). Introdução ao conhecimento da área maranhense abrangida pelo plano de valorização econômica da Amazonia. *Rev. Bras. Geogr.* 17: 239–299.

GENTRY, A. H. (1990). *Sphingiphila* (Bignoniaceae), a new genus from the Paraguayan Chaco. *Syst. Bot.* 15: 277–279.

GERHARDT, K. & HYTTEBORN, H. (1993). Natural dynamics and regeneration methods in tropical dry forests – an introduction. *J. Veg. Sci.* 3: 361–364.

HAFFER, J. (1985). Avian zoogeography of the Neotropical lowlands. *Ornith. Monogr.* 36: 113–146.

HAWKES, J. G. & HJERTING, J. P. (1969). *The Potatoes of Argentina, Brazil, Uruguay and Paraguay. A biosystematic study.* Oxford: Clarendon Press.

HUECK, K. (1972). *As florestas da América do Sul. Ecologia, composição e importancia econômica.* São Paulo: Universidade de Brasília & Editora Polígono SA.

HUECK, K. & SEIBERT, P. (1981). *Vegetationskarte von Südamerika*, 2nd edition. Stuttgart: G. Fischer Verlag.

HUNZIKER, A. T. (1973). El 'cebil' (*Anadenanthera colubrina* var. *cebil*) en la provincia de Córdoba. *Kurtziana* 7: 265.

JANZEN, D. H. (1988). Tropical dry forests: the most endangered major tropical ecosystem. In: WILSON, E. O. (ed.) *Biodiversity*, pp. 130–137. Washington, DC: National Academic Press.

KANTER, H. (1936). *Der Gran Chaco und seine Randgebiete.* Hamburg: Hamburg Universität.

KLEIN, R. M. (1972). Arvores nativas da floresta subtropical do Alto Uruguai. *Sellowia* 24: 9–62.

KLEIN, R. M. (1975). Southern Brazilian phytogeographic features and probable influence of Upper Quaternary climatic changes in the floristic distribution. *Boletim Paranaense de Geociências* 33: 67–88.

KUHLMAN, E. (1954). A vegetação de Mato Grosso. Seus reflexos na economia do estado. *Rev. Bras. Geogr.* 16: 77–122.

MARTINS, F. R. (1979). *O método de quadrantes e a fitossociologia de uma floresta residual do interior do Estado de São Paulo: Parque Estadual de Vassununga.* PhD thesis, Universidade de São Paulo, Brazil.

MEYER, T. (1963). Estudios sobre la selva de Tucumán. La selva de Mirtáceas de 'Las Pavas'. *Op. Lill.* 10: 1–144.

MORELLO, J. (1958). La provincia fitogeográfica del Monte. *Op. Lill.* 2: 5–155.

MORELLO, J. & ADÁMOLI, J. (1974). *Las grandes unidades de vegetación y ambiente del Chaco argentino. Segunda parte: Vegetación y ambiente de la provincia del Chaco.* Buenos Aires: INTA.

MUELLER-DOMBOIS, D. & ELLENBERG, H. (1974). *Aims and Methods of Vegetation Ecology.* New York: J. Wiley & Sons.

MÜLLER, P. (1973). *The Dispersal Centres of Terrestrial Vertebrates in the Neotropical Realm. A study in the evolution of the Neotropical biota and its native landscapes.* The Hague: W. Junk.

PRADO, D. E. (1991). *A critical evaluation of the floristic links between Chaco and Caatingas vegetation in South America.* PhD thesis, University of St Andrews, UK.

PRADO, D. E. (1993a). What is the Gran Chaco vegetation in South America? I. A review. *Candollea* 48: 145–172.

PRADO, D. E. (1993b). What is the Gran Chaco vegetation in South America? II. A redefinition. *Candollea* 48: 615–629.

PRADO, D. E. & GIBBS, P. E. (1993). Patterns of species distributions in the dry seasonal forests of South America. *Ann. Mo. Bot. Gard.* 80: 902–927.

PRADO, D. E., FRANCESCHI, E. A., & BIANCHI, M. B. (1989). El bosque del escarpe occidental del Río Paraná (Argentina). Composición florística y estructura. *Acta Bot. Brasil.* 3: 99–108.

PRADO, D. E., GIBBS, P. E., POTT, A., & POTT, V. J. (1992). Chaco-Pantanal transition in Southern Mato Grosso (Brazil). In: FURLEY, P. A., PROCTOR, J. & RATTER, J. A. (eds) *Nature and Dynamics of Forest–Savanna Boundaries*, pp. 451–470. London: Chapman & Hall.

PRANCE, G. T. (1982). *Biological Diversification in the Tropics*. New York: Columbia University Press.

PRANCE, G. T. (1989). American tropical forests. In: LIETH, H. & WERGER, M. J. A. (eds.) *Tropical Rain Forest Ecosystems*, pp. 99–132. Amsterdam: Elsevier.

PRANCE, G. T., RODRIGUES, W. A., & SILVA, M. F. D. (1976). Inventario florestal de um hectare de mata de terra firme km 30 da estrada Manaus-Itacoatiara. *Acta Amazônica* 6: 9–35.

RAMBO, B. (1980). A mata pluvial do Alto Uruguai. *Roessléria* 3: 101–139.

RAMELLA, L. & SPICHIGER, R. (1989). Interpretación preliminar del medio físico y de la vegetación del Chaco Boreal. *Candollea* 44: 639–680.

RATTER, J. A. (1986). *Notas sôbre a vegetação da Fazenda Agua Limpa (Brasília-DF)*. Brasília: Editora Universidade de Brasília.

RATTER, J. A., ASKEW, G., MONTGOMERY, R. & GIFFORD, D. R. (1978). Observations on forests of some mesotrophic soils in central Brazil. *Rev. brasil. Bot*. 1: 47–58.

RATTER, J. A., POTT, A., POTT, V. J., DA CUNHA, C. N. & HARIDASAN, M. (1988). Observations on woody vegetation types in the Pantanal and at Corumbá, Brazil. *Notes Roy. Bot. Gard. Edinburgh* 45: 503–525.

SARMIENTO, G. (1972). Ecological and floristic convergences between seasonal plant formations of tropical and subtropical South America. *J. Ecol.* 60: 367–410.

SAYAGO, M. (1969). Estudio fitogeográfico del norte de Córdoba. *Bol. Acad. Nac. Ciencias (Córdoba)* 46: 123–427.

SILVA, A. F. & LEITÃO F°, H. F. (1982). Composição florística e estrutura de um trecho da mata atlântica de encosta no município de Ubatuba (São Paulo, Brasil). *Rev. brasil. Bot.* 5: 43–52.

SIMPSON, B. B. (1971). Pleistocene changes in the fauna and flora of South America. *Science* 173: 771–780.

SMITH, A. C. & JOHNSTON, I. M. (1945). A phytogeographic sketch of Latin America. In: VERDOORN, F. (ed.) *Plants and Plant Science in Latin America*, pp. 11–18. Waltham, MA, USA.

SPICHIGER, R. & RAMELLA, L. (1989). The forests of the Paraguayan Chaco. In: HOLM-NIELSEN, L. B., NIELSEN, I. C. & BALSLEV, H. (eds) *Tropical Forests, Botanical Dynamics, Speciation and Diversity*, pp. 259–270. London: Academic Press.

SPICHIGER, R., BERTONI, B. S. & LOIZEAU, P.-A. (1992). The forests of the Paraguayan Alto Paraná. *Candollea* 47: 219–250.

TAKHTAJAN, A. L. (1986). *Floristic Regions of the World.* Berkeley: University of California Press.

TRICART, J. (1961). As zonas morfoclimáticas do nordeste brasileiro. *Notícia Geomorfologica, Campinas* 3: 17–25.

VERVOORST, F. (1982). Noroeste. In: SOC. ARG. BOT. (ed.) *Simposio sobre Conservación de la Vegetación Natural en la República Argentina*, pp. 9–24. Tucumán: Sociedad Argentina de Botánica.

Received 3 February 1999; accepted with revision 3 May 2000

APPENDIX

Classical phytosociological analysis of the main South American seasonal forests at generic level. FG: floristic groups *sensu* Mueller-Dombois & Ellenberg (1974). Key to the phytogeographical areas involved, and sources, in Table 1.

	Family	Genus	A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	FG
1	APOC	Aspidosperma		1	1	1			1	1	1	1	1	1	1	1	1	
2	LEGM	Mimosa	1		1			1			1	1			1			
3	BIGN	Tabebuia			1	1	1		1	1	1	1	1	1	1	1		
4	EUPH	Croton			1			1	1	1	1	1	1				1	I
5	ERYT	Erythroxylum			1				1		1	1	1		1	1		
6	RUTA	Fagara		1		1	1	1	1	1	1			1	1			
7	SOLA	Solanum			1		1		1	1	1	1			1			
8	ASTE	Gochnatia	1												1			
9	LEGM	Acacia	1	1	1	1		1	1	1	1	1	1	1				
10	ULMA	Celtis	1	1	1	1	1	1	1		1	1	1	1				
11	POLY	Ruprechtia		1	1	1	1	1	1		1	1						
12	EUPH	Sapium		1	1			1	1		1	1	1	1				
13	SAPO	Sideroxylon		1	1	1	1				1	1	1					II
14	BOMB	Ceiba			1	1			1	1	1	1	1	1				
15	LEGP	Geoffroea	1	1	1	1		1			1	1						
16	SAPI	Allophyllus			1	1	1		1	1	1		1					
17	CAPP	Capparis	1		1		1				1	1	1					
18	LEGC	Caesalpinia	1	1	1	1					1	1	1					
19	RHAM	Ziziphus		1	1	1					1	1						
20	EUPH	Jatropha	1	1	1						1	1		1				
21	ANAC	Schinus	1	1	1	1					1			1				
21	OLAC	Ximenia	1		1						1	1						
22	LEGC	Senna	1		1						1	1						III
23	CACT	Opuntia	1		1						1	1						
24	CONV	Ipomoea	1		1						1	1						
25	CELA	Maytenus	1	1	1				1		1	1	1	1				
26	CACT	Cereus	1	1	1				1		1	1	1					
27	LEGC	Bauhinia			1				1	1	1	1	1	1				
28	CACT	Pereskia			1				1		1	1						
29	BROM	Bromelia			1				1		1	1						IV
30	VERB	Aloysia	1	1	1				1	1	1							
31	CARI	Jacaratia			1				1	1	1	1	1					
32	EUPH	Sebastiania		1					1		1	1	1					
33	MYRT	Myrcianthes		1	1	1	1		1	1	1							
34	ACHA	Achatocharpus		1	1		1		1		1							V
35	EUPH	Acalypha		1	1					1								
36	FLAC	Banara		1				1	1									
37	RHAM	Scutia			1	1	1	1			1							
38	SANT	Acanthosyris			1	1	1				1							
39	SOLA	Vassobia			1		1		1		1							
40	SOLA	Cestrum			1				1		1							VI
41	CACT	Cleistocactus			1						1							
42	ASCL	Marsdenia			1						1							
43	MALV	Abutilon			1						1							
44	SANT	Jodina	1	1	1													
45	ASTE	Baccharis	1	1	1													
46	RHAM	Condalia	1	1	1													VII
47	CACT	Gymnocalycium	1	1	1													
48	LEGC	Cercidium	1	1	1													
49	ZYGO	Bulnesia	1		1													
50	LEGM	Mimoziganthus	1		1													
51	SOLA	Grabowskia	1		1													
52	ASTE	Hyalis	1		1													
53	ASTE	Cyclolepis	1		1													
54	CACT	Pterocactus	1		1													
55	CHEN	Allenrolfea	1		1													
56	CHEN	Atriplex	1		1													VIII
57	CHEN	Heterostachys	1		1													
58	CHEN	Suaeda	1		1													
59	LEGC	Zuccagnia	1		1													
60	MALP	Tricomaria	1		1													
61	MALV	Sphaeralcea	1		1													
62	RANU	Clematis	1		1													
63	ZYGO	Larrea	1		1													
64	ZYGO	Plectrocarpa	1		1													
65	ANAC	Lythraea	1	1														
66	ASTE	Flourensia	1	1														
67	ASTE	Heterothalamus	1	1														
68	ASTE	Proustia	1	1														IX
69	BROM	Deuterocohnia	1	1														
70	BROM	Puya	1	1														
71	LEGP	Ramorinoa	1	1														
72	SCRO	Monttea	1	1														

	Family	Genus	A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	FG
73	CACT	Stetsonia		1	1													
74	CACT	Echinopsis		1	1													
75	APOC	Vallesia		1	1													X
76	EUPH	Julocroton		1	1													
77	BERB	Berberis		1	1													
78	SIMA	Castela			1				1									
79	BIGN	Pithecoctenium			1				1									XI
80	LEGC	Gleditsia				1	1		1		1							
81	LEGC	Holocalyx					1		1	1								
82	ULMA	Trema					1		1		1							XII
83	ANNO	Rollinia						1	1	1	1							
84	RUTA	Pilocarpus					1		1									
85	BROM	Pseudoananas					1		1									
86	LEGM	Prosopis	1	1	1	1					1							
87	BUDD	Buddleja	1	1	1						1							
88	CACT	Trichocereus	1	1	1						1							
89	ASTE	Tessaria	1		1						1							
90	SOLA	Lycium	1		1						1							XIII
91	ASTE	Eupatorium	1	1							1							
92	BIGN	Tecoma	1								1							
93	ZYGO	Porlieria		1	1						1							
94	AREC	Trithrinax		1	1						1							
95	NYCT	Bougainvillea	1	1	1						1	1						
96	BROM	Dyckia	1	1	1						1	1						
97	EUPH	Euphorbia	1		1						1	1						
98	ANAC	Schinopsis		1	1						1	1	1					
99	VERB	Lippia		1	1						1	1						
100	STER	Ayenia		1	1						1	1						XIV
101	LEGM	Desmanthus			1						1	1						
102	MALV	Pavonia			1						1	1						
103	MALV	Sida			1						1	1						
104	AREC	Copernicia			1						1	1						
105	LEGP	Coursetia			1						1	1						
106	CACT	Quiabentia			1						1	1						
107	CACT	Eriocereus			1							1						
108	LEGC	Parkinsonia			1							1						XV
109	MALV	Wissadula			1							1						
110	BORA	Patagonula				1	1		1	1	1	1						
111	PHYT	Phytolacca				1	1		1		1	1						
112	SOLA	Brunfelsia				1	1		1		1	1						
113	BROM	Aechmea				1	1		1		1	1						
114	SAPI	Diplokeleba				1							1					
115	MORA	Maclura				1	1		1	1	1	1	1					
116	ULMA	Phyllostylon				1	1				1	1	1					XVI
117	LEGC	Peltophorum					1		1	1	1	1	1					
118	LEGC	Pterogyne					1		1		1	1	1					
119	SAPI	Sapindus					1				1	1	1					
120	ARAL	Pentapanax					1		1		1	1						
121	CARI	Carica				1	1		1		1	1		1				
122	LEGM	Anadenanthera					1				1	1	1	1				
123	LEGM	Enterolobium				1	1	1	1	1	1	1	1	1	1			
124	ANAC	Astronium				1	1			1	1	1	1	1	1			
125	NYCT	Pisonia				1	1		1	1	1	1	1		1	1		
126	SAPO	Chrysophyllum				1	1		1	1	1					1		XVII
127	MYRT	Eugenia				1	1	1	1	1	1				1	1	1	
128	LEGM	Pithecellobium				1			1	1	1	1					1	
129	SAPO	Pouteria					1	1	1		1	1		1	1	1	1	
130	MELI	Trichilia					1		1	1	1	1		1		1	1	
131	MORA	Ficus					1		1	1	1		1	1		1	1	
132	TILI	Luehea					1		1	1	1	1	1		1			
133	CECR	Cecropia					1		1	1						1	1	
134	SAPI	Cupania					1		1		1			1		1		XVIII
135	MYRS	Rapanea					1	1	1	1	1				1			
136	MORA	Sorocea					1		1							1	1	
137	LEGM	Inga						1	1	1	1					1	1	
138	COMB	Terminalia						1	1		1	1			1	1		
139	LAUR	Nectandra						1	1	1							1	
140	APOC	Peschiera						1	1	1							1	
141	MALV	Hibiscus						1	1									
142	SMIL	Smilax						1	1									XIX
143	AREC	Arecastrum						1	1									

	Family	Genus	A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	FG
144	LEGP	Erythrina						1	1		1	1	1	1				
145	LEGM	Albizia						1	1		1	1	1					XX
146	CAPP	Crateva						1				1						
147	LEGP	Lonchocarpus							1	1	1	1	1					
148	RUBI	Randia							1		1	1	1					
149	POLY	Coccoloba							1		1		1					
150	COMB	Combretum							1		1	1	1	1				XXI
151	LEGM	Calliandra							1		1	1		1				
152	VERB	Vitex							1			1	1	1				
153	MELI	Cedrela							1	1	1			1				
154	LEGM	Parapiptadenia							1	1	1	1						
155	PHYT	Seguieria							1	1	1	1						
156	RUTA	Balfourodendron							1	1		1						
157	MYRT	Campomanesia							1	1		1						
158	RUBI	Coutarea								1	1	1						
159	BIGN	Arrabidaea							1		1	1						XXII
160	BORA	Tournefortia							1		1	1						
161	EUPH	Manihot							1		1	1						
162	APOC	Rauvolfia							1		1	1						
163	STER	Byttneria							1		1	1						
164	BROM	Billbergia							1			1						
165	LEGP	Dioclea							1			1						
166	BIGN	Cuspidaria							1			1						
167	RUBI	Guettarda							1			1						XXIII
168	VITA	Cissus							1			1						
169	LEGP	Poecilanthe							1			1						
170	BIGN	Pyrostegia							1			1						
171	URTI	Urera							1	1	1							
172	PIPE	Piper							1	1	1							
173	SAPI	Diatenopteryx							1	1	1							
174	BIGN	Melloa							1		1							
175	BIGN	Macfadyena							1		1							XXIV
176	EUPH	Phyllanthus							1		1							
177	BIGN	Clytostoma							1		1							
178	BIGN	Amphilophium							1		1							
179	AMAR	Chamissoa							1		1							
180	RUTA	Esenbeckia							1	1								
181	EUPH	Actinostemon							1	1								
182	SIMA	Picramnia							1	1								XXV
183	LEGP	Sweetia							1	1								
184	FLAC	Casearia							1	1	1				1		1	
185	MYRT	Myrcia							1	1					1	1	1	
186	LEGP	Dalbergia							1	1		1			1		1	
187	SAPI	Matayba							1							1	1	
188	LAUR	Ocotea							1	1	1				1	1	1	
189	RUBI	Faramea							1								1	
190	MELI	Guarea							1	1							1	
191	LEGM	Piptadenia								1	1	1					1	
192	ANNO	Annona								1		1			1		1	XXVI
193	MELA	Miconia								1					1	1	1	
194	VOCH	Qualea								1					1	1	1	
195	RUBI	Rudgea								1						1	1	
196	STER	Sterculia									1	1	1	1			1	
197	OPIL	Agonandra									1				1		1	
198	LEGP	Swartzia									1	1					1	
199	BIGN	Cybistax							1						1			
200	BORA	Cordia							1	1	1	1	1	1		1		
201	LEGP	Machaerium							1	1	1	1	1	1	1	1		
202	BIGN	Jacaranda							1		1	1	1			1		
203	EUPH	Alchornea							1	1		1				1		XXVII
204	LEGC	Copaifera							1	1	1	1		1	1			
205	LEGC	Hymenaea								1		1			1			
206	MYRT	Siphoneugena								1	1				1			
207	COMP	Vernonia								1	1				1	1		
208	MYRT	Gomidesia							1						1	1		
209	AQUI	Ilex							1						1	1		
210	PROT	Roupala							1	1					1	1		
211	ARAL	Didimopanax							1	1					1	1		
212	LOGA	Strychnos							1						1			
213	VERB	Aegiphila							1	1					1			
214	MYRT	Calypthrantes							1	1						1		
215	MELI	Cabralea							1	1						1		XXVIII
216	MONI	Mollinedia							1	1						1		
217	AREC	Euterpe							1							1		
218	LEGP	Myrocarpus							1							1		

	Family	Genus	A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	FG
219	AREC	Acrocomia								1	1		1					
220	RHAM	Rhamnidium								1			1					
221	RUBI	Chomelia								1			1					XXIX
222	RUTA	Metrodorea								1			1					
223	PHYT	Gallesia								1		1						
224	LEGC	Dimorphandra								1					1			
225	ASTE	Piptocarpha								1					1			XXX
226	MYRT	Psidium								1					1			
227	STYR	Styrax								1					1			
228	LAUR	Cryptocarya								1						1		
229	LECY	Cariniana								1						1		
230	MYRT	Calycorectes								1						1		
231	MYRS	Ardisia								1						1		XXXI
232	FLAC	Gossiospermum								1						1		
233	LACI	Lacistema								1						1		
234	EUPH	Securinega								1						1		
235	LEGP	Amburana									1	1	1					
236	MALP	Ptilochaeta									1	1	1					XXXII
237	EUPH	Cnidoscolus									1	1	1					
238	RUBI	Calycophyllum									1		1					
239	LEGP	Myroxylon									1	1						
240	PHYT	Petiveria									1	1						
241	LEGP	Canavalia									1	1						
242	MALP	Galphimia									1	1						
243	ASTE	Lagascea									1	1						
244	FLAC	Prockia									1	1						
245	CACT	Brasiliopuntia									1	1						
246	CACT	Espostoa									1	1						
247	ASTE	Dasyphyllum									1	1						
248	EUPH	Ditaxis									1	1						XXXIII
249	LEGC	Chamaecrista									1	1						
250	MALP	Stigmatophylon									1	1						
251	OLAC	Schoepfia									1	1						
252	STER	Melochia									1	1						
253	SAPI	Serjania									1	1						
254	COCH	Cochlospermum									1	1						
255	ANAC	Loxopterigium									1	1						
256	LEGP	Aeschynomene									1	1						
257	VERB	Lantana									1	1						
258	LEGP	Sesbania									1	1						
259	BOMB	Eriotheca									1	1			1	1		
260	BOMB	Pseudobombax									1	1	1		1			
261	MALP	Heteropterys									1	1			1			
262	LEGP	Platypodium									1	1			1			
263	LAUR	Phoebe									1				1			XXXIV
264	LEGP	Pterocarpus										1				1		
265	RUBI	Alseis										1				1		
266	ASTE	Eremanthus										1			1			
267	LEGP	Acosmium										1	1		1			
268	STER	Helicteres										1	1	1				
269	BURS	Commiphora										1	1	1				
270	ANAC	Spondias										1		1				XXXV
271	POLY	Triplaris										1		1				
272	BOMB	Cavanillesia										1		1				
273	RUBI	Simira										1	1					
274	CHRY	Licania										1			1	1	1	
275	CHRY	Couepia										1			1		1	
276	LEGM	Stryphnodendron										1			1		1	
277	AREC	Syagrus										1			1		1	XXXVI
278	LEGP	Bocoa										1					1	
279	MORA	Brosimum										1					1	
280	LEGC	Peltogyne										1					1	
281	RUBI	Palicourea													1		1	
282	OCHN	Ouratea													1		1	
283	NYCT	Neea													1		1	
284	CONN	Rourea													1		1	
285	CELA	Salacia													1		1	XXXVII
286	SIMA	Simarouba													1		1	
287	DICH	Tapura													1		1	
288	CARY	Caryocar													1		1	
289	RUBI	Alibertia													1		1	
290	LEGP	Andira													1		1	

	Family	Genus	A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	FG
291	MYRI	Virola													1	1	1	XXXVIII
292	VOCH	Vochysia													1	1	1	
293	EUPH	Pera													1	1	1	
294	CHRY	Hirtella													1	1	1	
295	ANNO	Guatteria													1	1	1	
296	ANNO	Xylopia													1	1		XXXIX
297	LEGC	Sclerolobium													1	1		
298	SYMP	Symplocos													1	1		
299	ROSA	Prunus													1	1		
300	ELAE	Sloanea														1	1	XXXX
301	SAPO	Ecclinusa														1	1	
302	MORA	Pourouma														1	1	
303	MYRT	Marlierea														1	1	
304	SAPO	Micropholis														1	1	
305	OLAC	Heisteria														1	1	
306	RUBI	Coussarea														1	1	
307	ANNO	Anaxagorea														1	1	
308	LAUR	Aniba														1	1	
309	ACAN	Dicliptera	1															
310	ACAN	Justicia	1															
311	ASTE	Chuquiraga	1															
312	ASTE	Pseudobaccharis	1															
313	BROM	Abromeitella	1															
314	EPHE	Ephedra	1															
315	EUPH	Colliguaya	1															
316	LEGC	Hoffmanseggia	1															
317	LEGM	Prosopidastrum	1															
318	LEGP	Adesmia	1															
319	POLG	Bredemeyera	1															
320	RHAM	Discaria	1															
321	SOLA	Fabiana	1															
322	SOLA	Nicotiana	1															
323	VERB	Acantholippia	1															
324	VERB	Neosparton	1															
325	VERB	Verbena	1															
326	ASTE	Ophryosporus		1														
327	CACT	Acanthocalycium		1														
328	EUPH	Stillingia		1														
329	LABI	Minthostachys		1														
330	LEGP	Apurimacia		1														
331	LEGP	Collaea		1														
332	LEGP	Psoralea		1														
333	LEGP	Sophora		1														
334	LOBE	Siphocampylus		1														
335	MALP	Cordobia		1														
336	MALP	Mionandra		1														
337	POLG	Monnina		1														
338	ROSA	Kageneckia		1														
339	RHAM	Colletia		1														
340	CHEN	Holmbergia			1													
341	CACT	Monvillea			1													
342	BIGN	Dolichandra			1													
343	BIGN	Mansoa			1													
344	BORA	Cortesia			1													
345	CACT	Castellanosia			1													
346	CACT	Setiechinopsis			1													
347	CHEN	Salicornia			1													
348	LEGC	Lophocarpinia			1													
349	LEGC	Stenodrepanum			1													
350	LYTH	Heimia			1													
351	MALP	Janusia			1													
352	MENI	Cissampelos			1													
353	MENI	Odontocarya			1													
354	OLEA	Menodora			1													
355	PORT	Amphipetalum			1													
356	PORT	Grahamia			1													
357	SAPI	Urvillea			1													
358	SOLA	Capsicum			1													
359	VERB	Xeroaloysia			1													
360	CELA	Schaefferia					1											
361	STER	Guazuma					1											
362	PTER	Acrostichum					1											
363	MYRT	Hexachlamis						1										
364	RUTA	Helietta							1									
365	SAPI	Paulinia							1									
366	BIGN	Adenocalymma							1									
367	LEGC	Apuleia							1									
368	LEGP	Ateleia							1									
369	MALV	Bastardiopsis							1									

	Family	Genus	A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	FG
370	URTI	Boehmeria							1									
371	ICAC	Citronella							1									
372	LILI	Cordyline							1									
373	LEGP	Dahlstedtia							1									
374	THYM	Daphnopsis							1									
375	MONI	Hennecartia							1									
376	MYRT	Myrceugenia							1									
377	MYRT	Myrciaria							1									
378	EUPH	Pachystroma							1									
379	SIMA	Picrasma							1									
380	CAPR	Sambucus							1									
381	EUPH	Tetrorchidium							1									
382	FLAC	Xylosma							1									
383	LEGM	Zygia							1									
384	LAUR	Endlicheria								1								
385	CLUS	Callophyllum								1								
386	TILI	Christianum								1								
387	LEGP	Platycyamus								1								
388	LEGP	Centrolobium								1								
389	BIGN	Zeyhera								1								
390	LEGP	Tipuana									1							
391	SAPI	Athyana									1							
392	RUBI	Pogonopus									1							
393	COMP	Cnicothamnus									1							
394	TILI	Heliocarpus									1							
395	ASCL	Schubertia									1							
396	BIGN	Paradolichandra									1							
397	BORA	Saccelium									1							
398	CELA	Plenckia									1							
399	ASTE	Barnadesia									1							
400	ASTE	Chaenocephalus									1							
401	ASTE	Pseugynoxys									1							
402	ASTE	Senecio									1							
403	EUPH	Parodiodendron									1							
404	LEGP	Cascaronia									1							
405	NYCT	Pisoniella									1							
406	PHYT	Hilleria									1							
407	RUBI	Hoffmannia									1							
408	RUBI	Manettia									1							
409	SCRO	Basistemon									1							
410	SIMA	Alvarodoa									1							
411	ELAE	Mutingia									1							
412	APOC	Allamanda										1						
413	RHAM	Alvimiantha										1						
414	VERB	Amasonia										1						
415	CACT	Arrojadoa										1						
416	CACT	Austrocephalus										1						
417	BORA	Auxemma										1						
418	ASTE	Blanchetia										1						
419	LEGP	Calopogonium										1						
420	LEGC	Cenostigma										1						
421	RUBI	Coccocypselum										1						
422	BROM	Cottendorfia										1						
423	LEGP	Cratylia										1						
424	MALP	Dicella										1						
425	LEGC	Diptychandra										1						
426	CACT	Discocactus										1						
427	LEGP	Discolobium										1						
428	BROM	Encholirium										1						
429	CELA	Fraunhoffera										1						
430	LEGC	Goniorrhachis										1						
431	MALV	Gaya										1						
432	CAPP	Haptocarpum										1						
433	MALV	Herissantia										1						
434	BROM	Hohenbergia										1						
435	KRAM	Krameria										1						
436	CACT	Leocereus										1						
437	LEGP	Luetzelburgia										1						
438	EUPH	Maprounea										1						
439	LEGC	Martiodendron										1						
440	CACT	Melocactus										1						
441	CACT	Micranthocereus										1						
442	BROM	Neoglaziovia										1						
443	ASTE	Pectis										1						
444	CACT	Pilosocereus										1						
445	BROM	Pitcairnia										1						
446	LEGC	Poeppigia										1						
447	LEGP	Riedelella										1						
448	ANNO	Rolliniopsis										1						
449	APOC	Skytanthus										1						
450	VERB	Stachytarpheta										1						
451	CACT	Stephanocereus										1						
452	CACT	Tacinga										1						

	Family	Genus	A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	FG
453	ASTE	Telmatophila										1						
454	COMB	Thiloa										1						
455	ASTE	Wunderlichia										1						
456	VELL	Xerophyta										1						
457	CACT	Zehntnerella										1						
458	LEGP	Zollernia										1						
459	BIGN	Godmania										1						
460	CACT	Acanthocereus										1						
461	RUBI	Machaonia										1						
462	LEGP	Platymiscium										1						
463	LEGM	Chloroleucon										1						
464	BIGN	Anemopaegna										1						
465	STER	Waltheria										1						
466	SAPI	Dilodendron												1				
467	VOCH	Callisthene												1	1			
468	LOGA	Antonia													1			
469	CELA	Austroplenckia													1			
470	MYRT	Blepharocalyx													1			
471	LEGP	Bowdichia													1			
472	AREC	Butia													1			
473	MALP	Byrsonima													1			
474	CELA	Cheiloclinium													1			
475	CONN	Connarus													1			
476	MYRS	Cybianthus													1			
477	DILL	Davilla													1			
478	EBEN	Diospyros													1			
479	ICAC	Emmotum													1			
480	RUBI	Ferdinandusa													1			
481	APOC	Hancornia													1			
482	CLUS	Kielmeyera													1			
483	LYTH	Lafoensia													1			
484	MYRT	Pimenta													1			
485	LEGM	Plathymenia													1			
486	LEGP	Pterodon													1			
487	VOCH	Salvertia													1			
488	RUBI	Tocoyena													1			
489	LEGP	Vatairea													1			
490	VELL	Vellozia													1			
491	MALP	Banisteria													1			
492	RUBI	Amaioua														1		
493	EUPH	Aparisthmium														1		
494	AREC	Astrocaryum														1		
495	AREC	Attalea														1		
496	AREC	Barbosa														1		
497	RUBI	Bathysa														1		
498	CLET	Clethra														1		
499	PROT	Euplassa														1		
500	MELA	Henriettella														1		
501	EUPH	Hyeronima														1		
502	LEGP	Hymenolobium														1		
503	CUNO	Lamanonia														1		
504	EUPH	Mabea														1		
505	LEGM	Macrosamanea														1		
506	APOC	Malouetia														1		
507	LEGM	Pseudopiptadenia														1		
508	RUBI	Psychotria														1		
509	CLUS	Rheedia														1		
510	ASTE	Stifftia														1		
511	ANAC	Tapirira														1		
512	LECY	Lecythis														1		
513	SAPI	Talisia															1	
514	APOC	Ambelania															1	
515	VIOL	Amphirrox															1	
516	APOC	Anacampta															1	
517	ANNO	Bocageopsis															1	
518	BOMB	Bombacopsis															1	
519	COMB	Buchenavia															1	
520	MYRT	Calyptranthes															1	
521	RUBI	Chimarrhis															1	
522	EUPH	Conceveiba															1	
523	LECY	Corythophora															1	
524	LECY	Couratari															1	
525	LEGP	Dipteryx															1	
526	DUCK	Duckeodendron															1	
527	ANNO	Duguetia															1	
528	RUBI	Duroia															1	
529	HUMI	Endopleura															1	
530	LEGC	Eperua															1	
531	ANNO	Ephedranthus															1	
532	SAPO	Eremoluma															1	
533	VOCH	Erisma															1	
534	LECY	Eschweilera															1	
535	SAPO	Franchetella															1	

			A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	FG
	Family	Genus																
536	APOC	Geissospermum															1	
537	GNET	Gnetum															1	
538	MORA	Helianthostylis															1	
539	MORA	Helicostylis															1	
540	LECY	Holopyxidium															1	
541	MYRI	Iryanthera															1	
542	FLAC	Laetia															1	
543	VIOL	Leonia															1	
544	LAUR	Licaria															1	
545	OLAC	Liriosma															1	
546	TILI	Lueheopsis															1	
547	LEGC	Macrolobium															1	
548	MORA	Maquira															1	
549	OLAC	Minquartia															1	
550	MELA	Mouriria															1	
551	MORA	Naucleopsis															1	
552	SAPO	Neoxythece															1	
553	AREC	Oenocarpus															1	
554	CHRY	Parinari															1	
555	VIOL	Paypayrola															1	
556	EUPH	Pogonophora															1	
557	SAPO	Prieurella															1	
558	SAPO	Pseudolabatia															1	
559	QUIIN	Quiina															1	
560	SAPO	Richardella															1	
561	VIOL	Rinorea															1	
562	HUMI	Saccoglotis															1	
563	BOMB	Scleronema															1	
564	MONI	Siparuna															1	
565	BURS	Tetragastris															1	
566	STER	Theobroma															1	
567	CLUS	Tovomita															1	
568	MORA	Trimatococcus															1	
569	ANNO	Unonopsis															1	