

Diversity and complexity of the Araracuara sandstone flora and vegetation in the Colombian Amazon

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Insular open vegetation of the western Guayana Shield in Colombia (c.150-1000 m) surrounded by NW Amazon rain forest (over 3000 mm annual precipitation) has been botanically unexplored until the early 1990's. During recent botanical exploration of the sandstone plateaus of the Araracuara region a total of 381 vascular species belonging to 205 genera and 77 families have been documented. This is much less than in the same altitudinal interval of the floristically rich core area of the Central Guayana Province in southern Venezuela. The lowermost sandstone plateaus of the Araracuara region (West Guayana Province) offer an array of different habitats for 1) pioneer-like herb vegetation (at least 18 plant communities) and 2) shrubland and low thin-stemmed forest (5 plant communities). Basically three types of sandstone habitats occur: gently sloping rock, concave and convex sandstone surfaces. Microtopography in combination with substrate thickness and organic matter content and degree of water supply have created a number of different microhabitats, which account for a large number of different plant communities. Low herbaceous vegetation structure consisting of main lifeforms such as chamaephytes, hemicytrophites and therophytes combined with a limited number of species per vegetation type resulted in a low alpha diversity and a relatively high beta diversity (especially in open pioneer-like and herbaceous vegetation). Similar evidence with a high diversity of habitats has also been found in another landscape dominated by extreme environmental conditions: the high Andean paramo. In contrast to paramo West Guayanan sandstone flora and vegetation have a much longer historical record. The present highly specialized vegetation of West Guayana must have been derived by selection and adaptation to the harsh conditions of the equatorial sandstone surfaces with many different habitats. Plant strategies developed involve: 1) conservative use of limited amount of nutrients, 2) xeromorphic structures, 3) different photosynthesis pathways, 4) long distance seed dispersal by wind and fauna, 5) longtime investment in strategic growth forms such as branched and unbranched ground rosettes, caulescent rosettes, tufted herbs with long needle like leaves or short thick coriaceous leaves, 6) development of many therophytic species adapted to cyclic flooding and drought.

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Introduction

Inselbergs have recently been reviewed worldwide in terms of the biodiversity of the flora and vegetation (Porembski & Barthlott 2000). Only a few studies however deal with aspects of ecosystem processes on rocky surfaces and outcrops.

The Colombian sector of the Guayana Shield is considered by Huber (1994, 1995) as the westernmost part of the phytogeographical Province of West Guayana. The south to north-western delimitation of this Province is still under discussion, but the lowermost ridges and plateaus of the Serranía de la Macarena support a genuine Guayana-derived outcrop flora and vegetation (D. Cárdenas, pers. comm.) as do partially also the rocky surfaces of the Sierra de La Lindosa near Guaviare (López & Betancur 1999). Guayanan species have also been reported from the tropical Andes, *e.g.* from the Cordillera del Cóndor in south Ecuador and in Chachapoyas of northern Perú (Schulenberg & Awbrey 1997, Conservación Internacional Perú 1999, Fundación Natura *et al.* 2000). On the other hand genuine Andean taxa have also been reported from the Venezuelan tepuis (Berry *et al.* 1995). As everywhere in the West Guayana province, the insular sandstone plateaus of the Araracuara region in the Colombian Amazon are surrounded by rain forests.

The earliest botanical exploration of the Mesa of Araracuara was in January 1820 by Carl F. Ph. von Martius, when he reached the Canyon of Araracuara of the Caquetá river upstream from the Amazon river. From 1944 onwards, the systematic (ethno-) botanical exploration of the Colombian Amazon initiated by Richard E. Schultes and coworkers lasted for almost half a century (*e.g.* Schultes 1944, 1945).

The present botanical exploration in the Middle Caquetá started in the 1980's with stud-

ies of *e.g.* Palacios (1986), Cleef and Duivenvoorden (1994), Duivenvoorden and Cleef (1994), Duivenvoorden and Lips (1993, 1995), Urrego (1997), Vester and Cleef (1998), Arbeláez and Callejas (1999), Londoño and Álvarez (1997), Sánchez (1997), Duivenvoorden *et al.* (2001), Quiñones (2002), Arbeláez (2003), Duque *et al.* (2002, 2003), Berrío *et al.* (2003) and Arbeláez and Duivenvoorden (2004).

Earlier, Sastre and Reichel (1978) were the first to report on the Aduche sandstone plateau, south of Araracuara. Also other parts of the outcrops of the Colombian sector of the Guayana Shield were botanically explored during the 1990's: the Serranía de Chiribiquete (Estrada & Fuertes 1993; Rangel *et al.* 1995; Cortés & Franco 1997) and the departments of Guaviare, Vaupés y Guainía (López & Betancur 1999; Martínez & Galeano 1999, Etter 2001).

In this study we provide an overview of the diversity and complexity of the flora and vegetation of the lowland Araracuara sandstone plateaus in order to provide key data on this topic for the Western Guayana Province and to discuss its biogeographical and ecological basis. Equatorial sandstone surfaces seem extremely inhospitable for plant growth in terms of air and rock surface temperatures and water and nutrient supply. Because the study area is part of the Guayana Shield we are interested to know (1) how plant taxa are distributed over the extension of sandstone plateaus surrounded by rainforests; (2) how species assemblages perform to colonize, to develop to open and closed herbfields and how shrub and dwarf forests grade into the surrounding rain forests; (3) as already established in Central and East Guayana (mainly on granitic substrates), here we are interested to see how species assemblages perform in the different vegetation types in terms of main life and growth forms, alpha diversity and vegetation diversity and phytogeographical patterns.

Environmental stress

Environmental stress on top of the sandstone surfaces of the study area has thus far not been documented. Only nutrient availability of different sandy and organic substrates has been analyzed showing extremely low nutrient contents and low pH values (Duivenvoorden & Cleef 1994; Arbeláez 2003; Arbeláez & Cleef, in prep.). Weathering of the sandstone surface does not release substantial amounts of nutrients. Nutrient limitation is surely a serious environmental stress, causing strong root competition (in dense vegetation) and the nutrient capital of a habitat is materialized in living and dead biomass (Duivenvoorden & Cleef 1994; Duivenvoorden & Lips 1993, 1995).

The sandstone surfaces in the regional matrix of NW Amazonian rain forests with over 3000 mm annual precipitation are subject to repetitive heavy showers and intermittent short dry spells. Torrential rain causes swollen streams which are loaded with sediment and organic debris. During showers, large and almost level or gently sloping sandstone surfaces experience a 5-15 cm thick sheet of swiftly moving water. Flood-marks can be found everywhere, but especially along the border of vegetation patches such as that of insular water-logged *Bonnetia martiana* shrub more or less in slightly concave physiographic conditions. Water action is apparently important for the dispersal of seeds and diaspores, invertebrate and small ground dwelling vertebrate fauna, and for the mineral and organic accretion of insular vegetation patches allowing for vegetation expansion, especially in the early stages of successional development (Berrio *et al.* 2003).

Environmental dryness is most prominent from December to March, although monthly precipitation is still over 100 mm. Plant species seem well adapted to dryness, i.e. by a xerophytic morphology (Groeger 1995; Porembski & Barthlott 2000). This is expressed by *e.g.* thick coriaceous leaves in a limited number, or

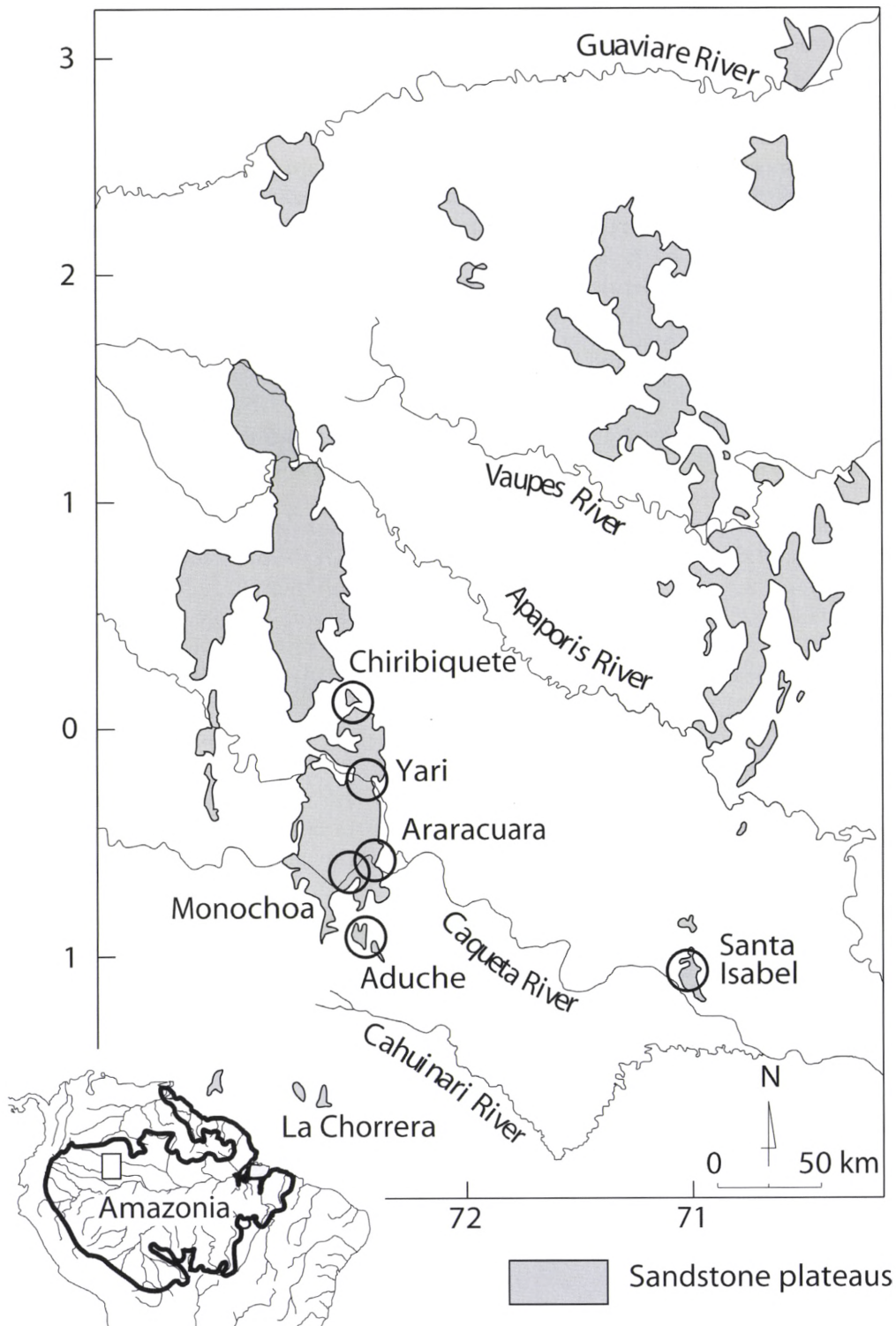
small xeromorphic foliage (but numerous leaves), pachycaulous stems, vertical leaf orientation, therophytic strategy adapted to flooding and subsequent evaporation, facultative C3-CAM photosynthesis, among a number of other special adaptations to these extreme habitats which, in addition, also are characterized by strongly limited nutrient availability.

Gröger (1995) carried out daily climate measurements on granitic inselbergs along the Orinoco river, which showed an interesting pattern of high relative humidity levels of about 70% between 4.00 and 8.00 hr and lowest values of about 30% between 13.00 and 14.00 hr. Opposite values were recorded for aerial temperature with lowermost values of 23-25° C in the early morning (6.00-8.00 hr) and highest temperatures of about 45° C around 13.00 hr. A similar repetitive daily temperature and relative humidity sequence is expected above the Araracuara sandstone plateaus.

Study area

The study area of the sandstone plateaus of the Araracuara region (about (72° 30' – 71° 00' W, 0° 04' N – 1° 10' S) reaches from Serranía de Chiribiquete southwards for 25-30 km to the Aduche sandstone plateau south of the village of Araracuara (Fig. 1): These sandstone plateaus reach altitudes between about 150 m and 300 m a.s.l., they are insular plateaus and surrounded by Amazonian rain forests, and deeply dissected with deep escarpments and gorges. The Caquetá and Yarí rivers dissect the plateau with deep canyons near Araracuara. Most of the sandstone surface is level or slightly sloping up to 3-5 degrees and only rarely steeper parts are found.

Geologically the sandstone formation of Araracuara is of Paleozoic age and developed on top of the Precambrian shield. Soils related to the sandstone are relatively shallow (mostly less than 10 cm, and rarely up to 1 m), acidic,



grayish, sandy, podzolic and extremely low in nutrient content. Under shrub and low forest formations a distinct superficial reddish root-mat is developed under a thick litter layer of mainly coriaceous leaves. Duivenvoorden and Lips (1993) classified the soil as typic Psammaquents. Large parts of the sandstone surface are outcrops, but substantial portions are also covered by fluvial or aeolic white sand deposits, specially in the Aduche sandstone plateau.

The climate is that of equatorial lowland rainforest with unimodal annual precipitation of over 3000 mm and all months receive over 100 mm precipitation although drier conditions may prevail from December to March. During the daytime air temperature fluctuates between 29-32° C; during the night between 21-23° C (Duivenvoorden & Lips 1993; Tobón 1999). The Köppen classification ranks the regional climate as Afi.

Methods

The botanical exploration of the sandstone plateaus consisted of gathering representative plant collections (vouchers in herbaria COAH in Bogotá and HUA in Medellín) and representative relevés of the non-forest vegetation (including dwarf forests up to 8-10 m in height) following the Zürich-Montpellier method as applied by Cleef (1981), Duivenvoorden and Cleef (1994), Arbeláez (2003) and Arbeláez and Duivenvoorden (2004). Estimates of cover percentages were based on assessment of the ground cover of each species using the peripheral outline. In total 227 relevés were collected with about two thirds of them located in the southern half of the study area and one third in the northern half. They were selected to represent the variation in structure and composition of the vegetation. The phytosociological associations in this study is not a validation of their syntaxonomical names (Arbeláez & Cleef, in prep.).

Results

Phytogeography

On the sandstone plateaus of the Araracuara region a total of 381 vascular species in 205 genera and 77 families were documented. The percentage of species belonging to each of four phytogeographic categories was calculated for 301 species, 205 genera and 77 families; for which phytogeographical origin was known (Fig. 2). The proportion of both the endemic Guayana Shield and the Neotropical element accounts for more than 90% at the species level. Only the Guyana Shield element attains almost 40% of the vascular species. Phytogeographic evaluation of genera referred above as 'important in the study area because of prominence and dominance', such as: *Gongylolepis*, *Bonnetia*, *Clusia*, *Euceraea*, *Monotrema*, *Schoenocephalium*, *Brocchinia*, *Navia*, emphasize a strong affinity with the Guayana Shield region.

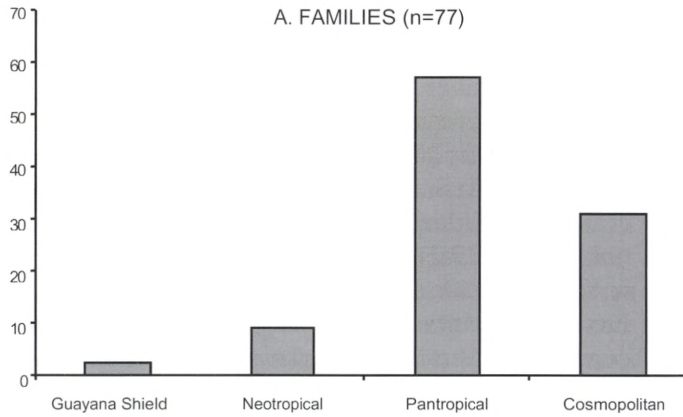
Vegetation diversity

The sandstone plateaus of the Araracuara region include an array of different habitats with pioneer-like herbaceous vegetation. Low shrub formations and open and dense thin-stemmed dwarf forests are associated as well.

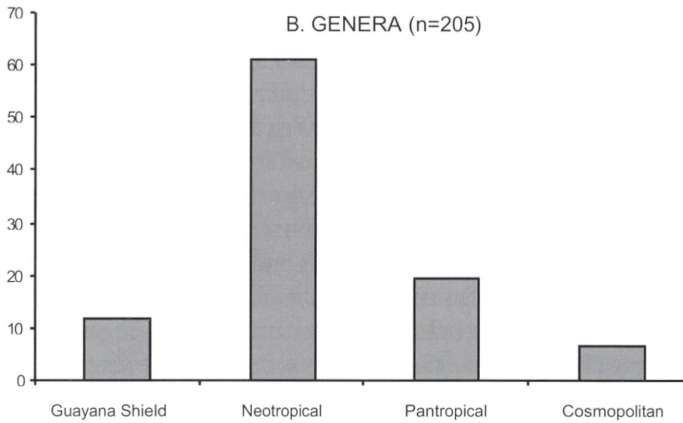
Basically three main sandstone habitats occur on the sandstone plateaus of the Araracuara region: level to gently sloping rock, concave and convex sandstone surfaces (Fig. 3, 1-4). Sandstone rock surfaces are in general more or less smooth. In combination with white sand bodies the number of habitats increases. Microtopography in combination with substrate thickness, organic matter content and degree of water supply create a number of different habitats, which account for many distinct plant communities, especially in pioneer-like and herb-dwarf-shrub vegetation.

Other less studied habitat types include prominent escarpments with dry, mesic and

Proportion of all families (%)



Proportion of all genera (%)



Proportion of all species (%)

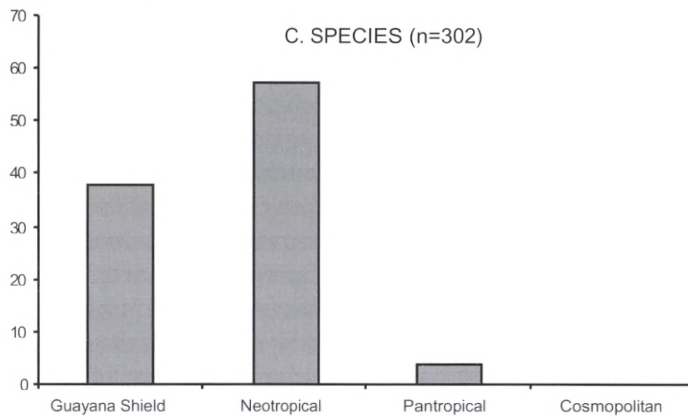


Fig. 2. Phytogeographic breakdown at family, genus and species level of the vascular flora of the sandstone plateaus of the Aracuara region.

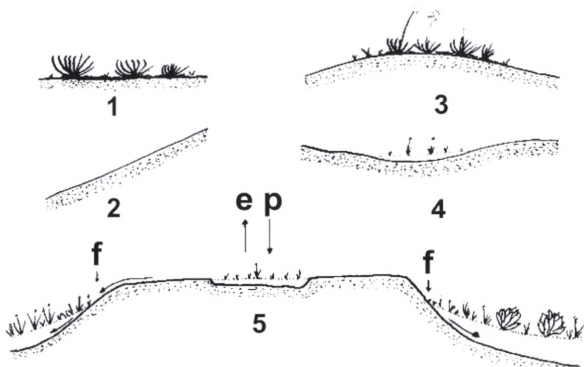


Fig. 3. Basic habitat types of sandstone plateaus of the Araracuara region: 1, level. 2, slope. 3, convex. 4, concave. Assemblages with sand bodies (as the example 5 from Aduche). In 5: p, precipitation; e, evaporation; f, flow.

humid to wet substrate (also according to presence and quality of shading), mostly shaded evergreen wet bryophyte-herb communities along streams and drainage channels, deep and filled-in crevices mostly with woody growth in line patterns, and small seepage patches of a few square meters consisting of organic accumulation (more than 50 cm) with growth of an unknown *Juncus* species with *Xyris lomatophylla* (Aduche locality).

At least 18 pioneer and herbaceous plant communities at the phytosociological association level have been recognized thus far. In addition, for shrub-land and thin-stemmed low

Table 1. The phytosociological associations of the open vegetation of the sandstone plateaus of the Araracuara region. The names of the associations discussed in the text are in *italic*. The associations without author name will be published soon by Arbeláez and Cleef (in prep.).

Pioneer/ephemeral vegetation

P 1 *Clusio chiribiquetensis-Navietum garcia-barrigae*

P 2 *Axonopodo schultesii-Navietum garcia-barrigae*

P 3 *Utricularietum neottioides* J. F. Duivenvoorden & A. M. Cleef 1994.

P 4 *Siphuletum carassanae*

P 5 *Siphanthero hostmannii-Xyridetum paraensis* J. F. Duivenvoorden, A. M. Cleef, J. C. Murillo & M. V. Arbeláez 1994.

Herbaceous vegetation

H 1 *Pachiro coriacea-Axonopodetum schultesii*

H 2 *Syngonantho humboldtii-Paspaleetum tillettii*

H 3 *Syngonantho vaupesana-Xyridetum wurdackii*

H 4 *Xyrido wurdackii-Paspaleetum tillettii* J. F. Duivenvoorden & A. M. Cleef 1994

H 5 *Xyris mima-Lagenocarpus verticillatus*

H 6 *Syngonantho humboldtii-Panicetum orinocanum*

H 7 *Xyrido lomatophyllae-Paspaleetum tillettii*

H 8 *Sauvagesio fruticosae-Brocchinietum hechtioides*

H 9 *Axonopodo schultesii-Schoenocephalietum martiani* J. F. Duivenvoorden & A. M. Cleef 1994.

H 10 *Bulbostylido lanatae-Rhynchosporietum globosae*

H 11 *Burmannio bicoloris-Monotremetum xyridioides*

H 12 *Schoenocephalio martianum-Ourateetum roraimae*

H 13 *Epistephio parvifolium-Crotonetum*

Low shrub formation and dwarf forest

A 1 *Tepuiantho colombiani-Euceraetum nitidi*

A 2 *Ocoteo esmeraldanae-Clusietum opacae*

A 3 *Everardio montanae-Bonnetietum martiana*

A 4 *Brocchinio hechtioides-Bonnetietum martiana*

A 5 *Macaireo rufescentis-Bonnetietum martiana* J. F. Duivenvoorden & A. M. Cleef 1994

Table 2. Alpha diversity, growth form, photosynthesis pathway and habitats of some selected vegetation types (Table 1) of the vegetation of the sandstone plateaus of the Araracuara region.

Structure-substrate	Habitat	Soil depth (cm)	Alpha diversity		Predominant growth form		C3-C4-CAM	pH
			mean	total	Monocot	Dicot		
<i>Pioneer</i> (Veg. 50 cm)								
(1) sandstone		< 12	8 – 47		rare dwarf scrubs	ground rosettes	CAM-C3-C4	4.2
(7) sand	(f)	< 8	8 – 14		ephemerals	tufts	C3-C4	5.4
<i>Herb field</i> (Veg. 100 cm)								
(15) sand		< 45	8 – 27		ground rosettes	xeromorphic scrub/carnivorous herbs	C3	5.5
(12) sand		< 40	13 – 46		tufts		C3 – CAM	4.5
(11) sand	(s)	? 1 – 8	11 – 58		ground rosettes	xeromorphic scrub	CAM – C3	5.5
<i>Shrub-dwarf forest</i> (Veg. 3-4 m)								
(a5) sand	(s)	< 100	17 – 113		ground rosettes	woody branched rosettes	C3 (+CAM)	3.2
(a1) sand		< 80	20 – 113		mixture	mixture	C3	5

f: periodically flooded and subsequent evaporation
s: seepage

(1): *Clusia chiriquetensis* – *Navia garcia-barrigae*
(7): *Siphantera hostmanii* – *Xyris paraensis*
(11): *Sauvagesia fruticosa* – *Brocchinia hechtiioides*
(12): *Axonopus schultesii* – *Schoenocephalum martianum*
(15): *Schoenocephalum martianum* – *Ouvatea voraimae*
(a5): *Macairea rufescens* – *Bonnetia martiana*
(a1): *Tepuianthus colombianus* – *Euceraea nitida*

forest, five plant communities at the association level have been classified (Table 1). However, some herbaceous and shrub communities still remain undescribed because of incomplete relevé data.

Because of its low structure, it is likely that habitat diversity is more easily reflected by herbaceous vegetation diversity as opposed to taller vegetation types (Duivenvoorden and Cleef 1994, Arbeláez 2003). Our data indicate a complex vegetation mosaic consisting of different (micro-)habitats, each of which is characterized by a proper combination of plant species.

The same complexity repeats itself on a mesic landscape scale (i.e. surveys dealing with a mapping scale of 1:10 000 to 1:100 000), and complexity is even increased specially in combination with white sand deposits (Duivenvoorden & Cleef 1994). White sand bodies of different thickness and different water supply, i.e. permanently or periodically with seepage or water-logged, create more habitats on top of the sandstone surfaces. Habitat dynamics by wind and water erosion and deposition are also frequent and cause substantial stress and fragmentation of communities. Therophytes and

Table 3. The ten most species rich plan families in this study compared to other studies on hard rock formations in the Amazon basin. Differences in study area were not taken into account in this compilation.

Sandstone plateaus in the Araracuara study area; < 350 m snm. (Arbeláez 2003)	Sandstone plateaus in Sierra de Chiribiquete, Colombian Guayana; 580-800 m snm. (Cortés <i>et al.</i> 1998).	Sandstone plateaus in the Venezuelan Guayana; 0-3000 m snm. (Berry <i>et al.</i> 1995)	Granitic Inselbergs in Venezuela; < 500 m snm. (Gröger 2000; Gröger & Barthlott 1996)	Granitic Inselbergs in the Guianas; 360 y c. 550 m snm. (Raghoenandan 2000)
Cyperaceae (28)	Rubiaceae (32)	Orchidaceae (689)	Cyperaceae (40)	Poaceae (23)
Orchidaceae (24)	Melastomatoc. (31)	Rubiaceae (530)	Rubiaceae (40)	Cyperaceae (15)
Melastomatoc. (22)	Orchidaceae (25)	Poaceae (420)	Melastomatoc. (36)	Orchidaceae (14)
Xyridaceae (22)	Bromeliaceae (22)	Melastomat. (397)	Orchidaceae (33)	Bromeliaceae (10)
Rubiaceae (21)	Euphorbiaceae (19)	Fabaceae (319)	Poaceae (31)	Rubiaceae (10)
Bromeliaceae (16)	Moraceae (16)	Bromeliaceae (273)	Bromeliaceae (20)	Euphorbiaceae (8)
Poaceae (15)	Cyperaceae (14)	Asteraceae (257)	Apocynaceae (18)	Melastomatoc (7)
Apocynaceae (15)	Apocynaceae (13)	Cyperaceae (243)	Caesalpiniaceae (18)	Cactaceae (7)
Eriocaulaceae (11)	Poaceae (13)	Euphorbiac. (237)	Fabaceae (17)	Eriocaulaceae (5)
Euphorbiaceae (10)	Araceae (12)	Caesalpiniac. (203)	Euphorbiaceae (15)	Araceae (5)

small tufted hemicryptophytes (*e.g.* small *Xyris* spp.) suffer most; large hemicryptophytic ground rosettes (*e.g.* *Navia*, *Brocchinia*, *Abolboda*, *Syngonanthus*) are the most resistant elements (to wind and water force) of the open ground layer.

Life forms

Duivenvoorden and Cleef (1994) visualized the Raunkiaer life form spectra and the relative contribution of lichens, ferns, monocots and dicots for six plant communities. In mixed shrub communities (*Dimorphanda cuprea-Ilex divaricata*) phanerophytic and dicots have the highest values of over 60% of the species. Other life-forms and phanerogamic and cryptogamic species contribute only up to 10%. In the *Macaireo rufescentis-Bonnetietum martianae* shrub association the proportion of therophytes (c. 20%) and monocots (c. 25%) increased. The herbaceous associations *Axonopodo schultesii-Schoenocephalietum martiani* and *Xyrido wurdackii-Paspaleetum tillettii* show a marked decrease of the proportions of both phanerophytes and dicots versus high values for monocots (resp. c. 45% to 35%) and

hemicryptophytes (resp. c. 30% and 20%). Therophytes (c. 45%) and lichens (c. 25%) rank high in the *Xyrido wurdackii-Paspaleetum tillettii* herbfield. It is striking that ferns are almost absent. In the association *Siphanthero hostmannii-Xyridetum paraensis* occupying a harsh habitat (temporarily flooding and evaporation) therophytes and monocots (both almost 50%) and chamaephytes (> 20%) attain the highest proportions. Phanerophytes and ferns are absent. The sandstone surface pioneer association *Navio garcia-barrigae-Lagenocarpetum* (presently *Clusio chiribiquetensis-Navietum garcia-barrigae* according to Arbeláez 2003) shows up with the highest proportion of lichens (c. 25%) and of therophytes and dicots (c. 40%).

Growth forms

Growth forms refer to the same physiognomic morphological aboveground structures of vegetation and approaches also the concept of functional groups (Díaz & Cabido 1997) in vegetation. Growth forms used in this study are defined as vascular plant structures of similar physiognomy and morphology, which belong

to the same or different taxonomic entity. They are mostly shaped as such by specific environmental conditions. We did not look in a systematic and detailed way to all the species and growth forms involved of the sandstone communities, but some remarkable growth forms could be detected. Among them rosettes, tufts, tiny delicate one-stemmed herbs, shrub and low slender-stemmed trees of all sizes from dwarf to 5-6 m with few large coriaceous leaves or with numerous small sclerophyllous leaves. Lichens were also prominent, especially species of *Cladina* and *Cladonia*. Bryophytes, ferns and fern allies were rare; lianas and epiphytes were limited in occurrence.

In pioneer-like communities a marked proportion of ground rosettes and stem rosettes were present. A special feature are rosettes which are horizontally branched and lay on the sandstone substrate (*Navia garcia-barrigae*) and branching on stems (*Vellozia lithophila*). Both growth forms also display a number of xeromorphic adaptations. Ground rosettes are mostly broad-leaved and less xeromorphic in herb fields and under open shrub. All belong to different monocot families like Bromeliaceae, Eriocaulaceae, Velloziaceae and Xyridaceae.

All meadow communities are dominated by tufts. Large-leaved or short-leaved monocot genera prevail according to the water and/or nutrient supply. Large tufts occur in habitats with most water availability (not flooded); small tufts suffer long-term water stress and may be periodically flooded (and experience long term evaporation) after rain. The amount of nutrients also influences growth forms. More nutrient contents are 'translated' in larger growth forms and thus more structure and biomass. Mesic to humid conditions with sufficient nutrient availability allow species with 2-4 mm wide, more or less flat blades. This can be observed in a number of species of *Xyris* (e.g. *X. fallax*, *X. lomatophylla*) and Rapateaceae (e.g. *Monotrema arthrophylla*, *Schoenocephalum*

martianum). Increasing humidity also favors the ground rosette growth form (e.g. *Abolboda*, *Brocchinia*, *Macairea*, *Vriesea*).

Woody communities are either shrub formations or thin-stemmed low forests. *Bonnetia martiana* shrub seems successional to Rapateaceae herb field (Berrío *et al.* 2003). Low dwarf forest of waterlogged *Bonnetia martiana* is apparently the climax of this series. A characteristic feature are the relatively thick stems up to maximally 6-7 m in height with a prominent rough bark and the limited number of thick coriaceous leaves. On the branches of *Bonnetia*, leaves are concentrated in small tufts. This allows much more light in the understory as compared with other mixed shrub and low forest communities. In open *Bonnetia martiana* dwarf forest however, the thick coriaceous litter layer is counteracting the effect of incoming light: only few inconspicuous herb species persist in this dense litter layer covering wet, shallow sandy substrate. We consider this thick-stemmed dwarf forest type, present in small patches in the study area, at least as one line of the climax of *Bonnetia martiana* succession. *Gongylolepis martiana* may occur in small mono-dominant patches (dense dark understory) and *Euceraea nitida* in a more open true dwarf forest type on thin soil on wet sandstone surfaces. The numerous stems of *Gongylolepis* are thin and prevent easy penetration of these thickets. Highest alpha diversity of the vegetation is documented with more than 100 vascular species per community for both *Bonnetia martiana* shrub associations (*Everardio montanae-Bonnetietum martiana*, *Macaireo rufescentis-Bonnetietum martiana*) grading into low forest of *Tepuiantho colombiani-Euceraeetum nitidi* (Duivenvoorden & Cleef 1994; Arbeláez 2003; Arbeláez & Cleef in prep.).

Alpha diversity

The seven sandstone plant communities (associations) selected include two pioneer communities, three herbaceous communities and two

shrub/low forest communities (Table 2). The mean number of vascular species shifts from eight in pioneer communities to 11-13 species in well developed meadows, to 17-20 species in shrub and low forest.

Total alpha diversity at the association level has been summarized from the phytosociological tables (Arbeláez 2003; Arbeláez & Cleef in prep.). For the *Clusia chiribiquetensis-Navia garcia-barrigae* pioneer community alpha diversity has been established at 47 species in total. The remaining six associations indicate a range of increasing species numbers, from 14 to 113. The discrepancy of a high total species number for the pioneer community (P_1) can be explained by the small patchy or mosaic-like occurrence of this vegetation type. Rectangular plots without doubt supposedly have included a number of species of other neighboring rock dwelling communities. The subassociation of *Clusia opaca* of the association *Clusia chiribiquetensis-Navietum garcia-barrigae* refers to a pioneer community with in total 18 vascular species; nine occasional and nine frequent.

Discussion

Floristic patterns

Open vegetation was specified as pioneer and herbaceous growth. In closed thin-stemmed vegetation most species are arborescent. Terrestrial species of bryophytes are limited, except in the low forest of *Euceraea nitida*. Terrestrial lichens in contrast, are much more abundant and are diverse (Sánchez 1997). In the Chiribiquete region (probably underexplored) Cortés *et al.* (1998) found three genera and three species (one a forest species) of Rapateaceae while in our study in Araracuara we found four genera and five species. Xyridaceae are represented with two genera and 23 species on top of the Araracuara sandstone surfaces versus 11 species in Chiribiquete highlands. Asclepiadaceae and Rhamnaceae have not

been documented in Chiribiquete up till now. Thus far species of *Bulbostylis* (Cyperaceae) have not been reported.

Gröger (1995, 2000) studied the vegetation of numerous granitic outcrops in the lowlands of southwestern Venezuela, mostly along the Orinoco River. His study area extended from central Venezuela to the southwest border along the upper Rio Negro under both a savanna climate (five dry months annually and less than 1500 mm precipitation) and an Amazon rain forest climate of over 3000 mm annual precipitation. In total he recorded 614 species belonging to 344 genera and 107 families. Cyperaceae, Orchidaceae, Melastomataceae, Rubiaceae and Poaceae are about as rich in taxa as in the Colombian sector of the West Guayana province. Xyridaceae are rather poorly represented and Leguminosae are outstandingly rich in species (35). Cactaceae (8) and Portulacaceae (7) have also been reported from the northernmost granitic inselbergs. Scrophulariaceae genera like *Bacopa* and *Lindernia* have also been documented here. Gröger (l.c.) referred to the assemblage of Apocynaceae, Erythroxylaceae and Portulacaceae as the most diagnostic families of the granitic outcrops along the Orinoco. Berry *et al.* (1995) considered the vascular flora of Central Guayana and Pantepui Provinces of southern Venezuela. In total c. 9400 species have been considered belonging to all types of habitats representing an area about 454,000 km² forest and non-forest; dry and aquatic. The most species rich is the orchid family (many epiphytes) and the Rubiaceae family (mainly forest species). The order of species richness in families is mainly determined by forest species. Raghoenandan (2000) reported 157 species from granitic outcrops in the of Sipalawini and the Voltzberg area in Suriname located in the central part of East Guayana Province. The families arranged according to their species richness are: Poaceae, Cyperaceae, Orchidaceae, Bromeliaceae, Rubiaceae, Euphor-

biaceae, Melastomataceae, Cactaceae, Araceae and Eriocaulaceae. Xyridaceae are less important and Rapateaceae are absent (Table 3).

It is difficult to obtain a good idea about the floristic diversity elsewhere in the Central Guayana Province in this altitudinal interval concerning non-forest vegetation. When we use the information provided by Berry *et al.* (1995), they refer to 138 endemic (forest and non-forest) plant genera of the Guayana Shield. Of these, 118 have been documented for Venezuela and 34 for Colombia. Almost all Colombian endemic genera are shared with Venezuela. All the vascular genera in the Araracuara sandstone region probably also occur in Venezuela except for the newly discovered undescribed genus and species of Rhamnaceae (M.V. Arbeláez # 1145) on the Yarí sandstone plateau north of Araracuara (Fig. 1). Further, Berry *et al.* (1995) list the earlier mentioned 138 endemic genera in distribution and in altitude in the countries of the Guayana Shield. However, these numbers refer to genera both of forest and non-forest habitats and landscapes. In the altitudinal interval below 500 m, 53 genera out of 118 have been recorded for the Venezuelan Guayana as a unit (Central Guayana Province > 500 m) including the Neblina summit at 3014 m. In the Colombian sector only 34 endemic genera have been documented up to the ca. 900 m summits of Chiribiquete. The country of Guyana possesses 61 endemic genera, a larger part of which is to be found on the slopes of Roraima. Suriname and French Guyana only have 13 and 10 endemic genera; they only share 6 of them. Almost 40% of the species and over 10% of the genera of the Araracuara sandstone region is ranked with Guayana Shield affinity (Fig. 2).

Vegetation diversity and succession

A total of about 25 plant communities at the phytosociological association level have been reported from the Araracuara region study

area (Arbeláez 2003, Arbeláez and Cleef, in prep.). First colonization as a rule is by Cyanobacteria and lichens including micro-colonial fungi forming biofilms (Büdel *et al.* 2000). It is believed that the vascular colonizers of this habitat persist for a very long time. On slightly convex and almost level sandstone surfaces (in the absence of deeper soils) the succession pathway is supposed to stay a long time in the colonist phase. Succession towards structural more developed vegetation takes place on deeper soils. Though erosion at the sandstone surface is ongoing, the chance that erosion material (sand) remains in situ has a low probability because of splash erosion and the high frequency of torrential rain. In some cases, like on the sandstone plateau of Aduche sand bodies can be found on top of level rock surfaces. Erosion and accumulation by water and wind are the main factors shaping the present day rocky surfaces and sand bodies here (Fig. 3). This configuration of sand bodies and sandstone rock surfaces with soil moisture and seepage, are the main factors causing habitat diversity.

On much smaller granitic surfaces of three dome-shaped inselbergs surrounded by rain forest in French Guyane Sarthou and Villiers (1998) documented six associations based on similar field methods. Annual precipitation is also between 3000 and 3250 mm (except for Roche Dachine, 2250-2500 mm) as in the Araracuara study area. The number of species and communities may be explained by the difference in size of the rock surfaces between both areas, the convex, dome-shaped inselbergs not allowing for accumulation of sand bodies as in the Araracuara study area, thus less habitat diversity on the inselbergs.

Succession pathways are complex and not easy to unravel at the plant community level with a high resolution. Succession is supposed to develop from initial colonizing plant communities to meadows vegetation types and

finally according to physiographic position, moisture supply and soil depth to shrub-land communities and low thin-stemmed forest. On sloping sandstone surface succession from Rapateaceae dominated meadow communities to structurally more complex shrub and dwarf forest of *Bonnetia martiana* may only take some 50 years as Berrío *et al.* (2003) demonstrated with a radiocarbon controlled pollen diagram. Increased water supply (by changing drainage patterns) may also contribute to this successional change of vegetation structure.

On top of the sandstone of the lowermost part of a wet concave slope organic and mineral material collects and a well developed *Bonnetia martiana* shrub is present on top of wet mineral soils between 30 and 50 cm depth.

Deeper and more aerated soils give rise to mixed stands of low forest. Woody elements of this forest type follow the deep crevices pattern in the sandstone landscape, when they are filled up with sandy deposits originating by erosion. Increasing soil depth increases structure and alpha diversity from shrub to dwarf forest and low rain forest. A herb layer of species of Marantaceae dominates in low, thin-stemmed rain forest up to 10-12 m in height with a mineral soil depth of about 75 cm.

Comparison to paramo

Comparing the vegetation of the sandstone plateau with another neotropical landscape that suffers from harsh environmental conditions (the open Andean paramo) some striking resemblance can be identified. Also in the paramo a daily climate type is experienced, though with markedly lower mean temperatures according to the altitude above sea level. Values of atmospheric relative humidity follow comparable patterns in the short dry season and prolonged wet season (Gröger 1995, Witte 1994). Annual precipitation in paramo (except in ecotonic bamboo paramos) is less than at the Araracuara study area, but evapotranspira-

tion is expected to be similarly less (Cleef 1981, Bekker & Cleef 1989). For floristic affinities between both equatorial ecosystems the reader is referred to Cleef *et al.* (1993).

The Guayana Shield rock surfaces including those of Pantepui were present long before the rise of the northern Andes. The same applies to the flora of the Brazilian Shield. The flora of the study area must be much older than the early paramo flora dating back from the proto paramo of the Middle and Upper Pliocene (van der Hammen & Cleef 1986). The oldest palynological sections on tepuis and in the Gran Sabana in Venezuela are not much older than c. 8000 BP (Rull 1991). It is however, very difficult to obtain good palynological sections from the rocky lowland part of the Guayana Shield (Berrío *et al.* 2003) in order to understand the history of vegetation and climate over much longer time.

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Literature cited

- Arbeláez, M.V. & Callejas, R. 1999. *Flórula de la Meseta de Arenisca de la Comunidad de Monochoa*. Estudios en la Amazonia Colombiana. XIX. Tropenbos-Colombia. Bogotá.
- Arbeláez, M.V. 2003. Diversity and dynamics of the vegetation on West Guayanan sandstone plateaus in the Middle Caquetá Region, Colombian Amazonia. Thesis University of Amsterdam, The Netherlands.
- Bekker, R.P. & Cleef, A.M. 1989. La vegetación del páramo

- de la Laguna Verde (Municipio de Tausa, Cundinamarca). *Análisis Geográficos 14*. IGAC, Bogotá, Colombia.
- Berrio, J.C., Arbeláez, M.V., Duivenvoorden, J., Cleef, A. & Hooghiemstra, H. 2003. Pollen representation and successional vegetation change on the sandstone plateau of Araracuara, Colombia Amazonia. *Rev. Palaeobot. Palynol.* **126**: 163-181.
- Berry, P. E., Huber, O. & Holst, B. K. 1995. Floristic analysis and phytogeography *In*: Steyermark, J. A., Berry, P. & Holst, B. K. (eds.), *Flora of the Venezuelan Guayana, Vol. 1*. Portland, Oregon, U.S.A.
- Büdel, B., Becker, U., Follmann, G. & Sterflinger, K. 2000. Algae, Fungi, and lichens on Inselbergs *In*: Porembski, S. & Barthlott, W. (eds.), *Inselbergs*. Ecological Studies 146. Berlin, Heidelberg, Germany.
- Cleef, A. M. 1981. The vegetation of the paramo of the Colombian Cordillera Oriental. *Dissertationes Botanicae 16*. J. Cramer, Vaduz.
- Cleef, A. M., van der Hammen, T. & Hooghiemstra, H. 1993. The savanna relationship in the andean paramo flora. *Opera Bot.* **121**: 285-290.
- Cleef, A. M. & Duivenvoorden, J. F. 1994. Phytogeographic analysis of a vascular species sample from the Araracuara sandstone plateau, Colombian Amazonia. *Mém. Soc. Biogéogr.* **4**: 65-81.
- Conservación Internacional Perú. 1999. *Biodiversidad de la Cordillera del Cóndor: Referencias Técnicas para su Conservación*. Lima.
- Cortés, R. & Franco, P. 1997. Estudio florístico y análisis panbiogeográfico de la flora de Chiribiquete, Colombia. *Caldasia* **19**: 465-478.
- Cortés, R., Franco, P. & Rangel, O. 1998. La flora vascular de la Sierra de Chiribiquete, Colombia. *Caldasia* **20**: 103-141.
- Díaz, S. & Cabido, M. 1997. Plant functional types and ecosystem function in relation to global change. *J. Veg. Sci.* **8**: 463-474.
- Duivenvoorden, J. F. & Lips, J. M. 1993. *Ecología del Paisaje del Medio Caquetá. Memoria Explicativa de los Mapas*. Estudios en la Amazonia Colombiana. III A – III B. Tropenbos-Colombia. Bogotá. 301 pp. + mapas.
- Duivenvoorden, J. F. & Cleef, A. M. 1994. Amazonian savanna vegetation on the sandstone plateau near Araracuara, Colombia. *Phytocoenologia* **24**: 197-232.
- Duivenvoorden, J. F. & Lips, J. M. 1995. A Land-Ecological Study of Soil, Vegetation, and Plant Diversity in Colombian Amazonia. Tropenbos Series 12.
- Duivenvoorden, J.F., Balslev, H., Cavelier, J., Grandes, C., Tuomisto, H. & Valencia, R. (eds.), 2001. *Evaluación de Recursos Vegetales no Maderables en la Amazonia Noroccidental*. IBED, Universiteit van Amsterdam, Amsterdam; the Netherlands.
- Duque, A., Sánchez, M., Cavelier, J. & Duivenvoorden, J. 2002. Differential floristic patterns among understory and canopy woody plants in Colombian Amazonia. *J. Trop. Ecol.* **18**: 499-525
- Duque, A., Cárdenas, D. & Rodríguez, N. 2003. Dominancia florística y variabilidad estructural en bosques de tierra firme en el noroccidente de la Amazonia colombiana. *Caldasia* **25**:139-152.
- Estrada, J. & Fuertes, J. 1993. Estudios botánicos de la Guayana colombiana, IV. Notas sobre la vegetación y la flora de Chiribiquete. *Revista de la Academia Colombiana de Ciencias Exactas, Físicas y Naturales* **18(71)**: 483-493.
- Etter, A. (ed.). 2001. Punawai y Nukak. Caracterización Ecológica General de Dos Reservas Nacionales Naturales de la Amazonia Colombiana. Ambiente y Desarrollo. Serie de Investigación 2. Instituto de Estudios Ambientales para el Desarrollo -IDEADE-. Bogotá, Colombia.
- Fundación Natura, Ministerio del Ambiente, CDC-Ecuador & Fundación Arcoiris. 2000. *Parque El Cóndor: Estudios y Propuestas*. Fundación Natura, Quito, Ecuador.
- Gröger, A. 1995. Die Vegetation der Granit-Inselberge Südvenezuelas: ökologische und biogeographische Untersuchungen. Ph.D. thesis. Botanical Institute, University of Bonn, Germany.
- Gröger, A. 2000. Flora and vegetation of Inselbergs of Venezuelan Guayana *In*: Porembski, S. & Barthlott, W. (eds.), *Inselbergs*. Ecological Studies 146. Berlin Heidelberg, Germany.
- Huber, O. 1994. Recent advances in the phytogeography of the Guayana region, South America. *Mém. Soc. Biogéogr.* **4**: 53-63.
- Huber, O. 1995. Geographical and physical features *In*: Steyermark, J. A., Berry, P. & Holst, B. K. (eds.), *Flora of the Venezuelan Guayana, Vol. 1*. Missouri Botanical Garden. St Louis, Missouri, and Timber Press, Portland, Oregon.
- Londoño, C. & Álvarez, E. 1997. Composición florística de dos bosques (Tierra firme y varzea) en la región de Araracuara, Amazonia colombiana. *Caldasia* **19**: 431-463.
- López, R. & Betancur, J. 1999. *Flora y vegetación de la Seranía de La Lindosa (Guaviare, Amazonia colombiana)*. Instituto Amazónico de Investigaciones Científicas (SINCHI)-Instituto de Ciencias Naturales, Universidad Nacional de Colombia. Libro de Resúmenes del Primer Congreso Colombiano de Botánica.
- Martínez-A, X.A. & Galeano, M.P. 1999. *Composición florística de dos ecosistemas naturales sobre arenas blancas en la campina baja de Timbó y en el arco de tierras altas de Mandí y los Cerros. Vaupés*. Amazonia colombiana. W & C de Colombia Ltda-Universidad Javeriana. Libro de Resúmenes del Primer Congreso Colombiano de Botánica.
- Urrego, L.E. 1997. *Los Bosques Inundables del Medio Caquetá: Caracterización y Sucesión*. Estudios en la Amazonia Colombiana. XIV. Tropenbos-Colombia. Bogotá, Colombia.

- Palacios, P.A. 1986. Observaciones sobre la vegetación de la escarpa de Araracuara. *IV congreso Latinoamericano de Botánica. Resúmenes*. Medellín; Colombia.
- Porembski, S. & Barthlott, W. (eds.), 2000. *Inselbergs*. Ecological Studies 146. Berlin, Heidelberg, Germany.
- Quiñones, M. 2002. *Polarimetric Data for Tropical Forest Monitoring*. Studies at the Colombian Amazon. Tropenbos series 21.
- Raghoenandan, U.P.D. 2000. The Guianas (Guyana, Suriname, French Guiana) *In: Porembski, S. & Barthlott, W. (eds.), Inselbergs*. Ecological Studies 146. Berlin Heidelberg, Germany.
- Rangel, J.O., Franco, P. & Betancur, J. 1995. La Serranía de Chiribiquete: Un mosaico botánico para la ciencia. *Revista del Sistema de Parques Nacionales de Colombia* **1**(1): 7-10.
- Rull, V. 1991. Contribución a la paleoecología de Pantepui y la Gran Sabana (Guayana venezolana): clima, biogeografía y ecología. *Scientia Guianae* 2.
- Sánchez, M. 1997. *Catálogo Preliminar Comentado de la Flora del Medio Caquetá (Amazonia Colombiana)*. Estudios en la Amazonia Colombiana. XII. Tropenbos-Colombia. Bogotá; Colombia.
- Sarthou, C. & Villiers, J.-F. 1998. Epilithic plant communities on inselbergs in French Guiana. *J. Veg. Sci.* **9**: 847-860.
- Sastre, C. & Reichel, D. H. 1978. Notas botánicas sobre la región de Araracuara (río Caquetá, comisaría del Amazonas, Colombia). *Bulletin de l'Institut Français d'Études Andines* 7: 105-117.
- Schulenberg, T. S. & Awbrey, K. (eds), 1997. *The Cordillera del Cóndor Region of Ecuador and Peru: A Biological Assessment*. Rapid Assessment Program Working Papers No. 7. Conservation International, Washington, DC.
- Schultes, R.E. 1944. Plantae Colombianae, IX. *Caldasia* **3**:121-130.
- Schultes, R.E. 1945. Glimpses of the little known Apaporis River in Colombia. *Chronica Bot.* **9**: 123-127.
- Tobón, C. 1999. *Monitoring and Modelling Hydrological Fluxes in Support of Nutrient Cycling Studies in Amazonian Rain Forest Ecosystems*. Tropenbos Series 17. Wageningen.
- Van der Hammen, T. & Cleef, A. M. 1986. Development of the high andean paramo flora and vegetation. *In: Vuilleumier, F. & Monasterio, M. (eds.), High Altitude Tropical Biogeography*. New York/Oxford.
- Vester, H. F. M. & Cleef, A. M. 1998. Tree architecture and secondary tropical rain forest development. A case study in Araracuara, Colombian Amazonia. *Flora* **193**: 75-79.
- Witte, H.J.L. 1994. Present and past vegetation and climate in the Northern Andes (Cordillera Central, Colombia): A quantitative approach. Ph.D Dissertation, University of Amsterdam; the Netherlands.

