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Shrub thicket vegetation on tropical granitic inselbergs (French Guiana)

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Abstract. In French Guiana, inselbergs are granite outcrops rising abruptly from the

surrounding rain forest. They constitute isolated islands of a special type of vegetation

restricted to this peculiar substrate. Shrub granitic vegetation, organised in thickets on open

exposed rocks of inselbergs, are described using the Braun-Blanquet method combined with

numerical analysis (Correspondence Analysis). This phytosociological study revealed only

one particular shrub community on each inselberg, including predominantly evergreen and

sclerophyllous shrubs, especially microphanerophytes, belonging to Clusiaceae, Myrtaceae

and Bombacaceae. These insular outcrop communities exhibit species endemic to the Guianas

region and also species rare in French Guiana. Affinities with flora of other inselbergs and

vegetation types in South America are examined and discussed. Reasons for observed floristic

and structural changes in each community are also discussed.

Keywords:

Correspondence Analysis; Granitic outcrops; Phytosociology;

Shrub

communities; Thickets; Vegetation dynamics.

Abbreviations: CA: Correspondence Analysis.

Nomenclature: Boggan et al. (1997).

Number of words in the ms: 4640

Introduction

Inselbergs are isolated rocky outcrops consisting generally of Precambrian granite or gneiss. The geomorphology and the geology of inselbergs have been studied worldwide, a survey being provided by Bremer and Sander (2000). These particular geomorphological formations constitute natural laboratories to address some prevailing questions concerning the past and future of biotic diversity. Inselbergs offer models for the quantitative analysis of species diversity and biotic communities in the frame of vegetation dynamics and island ecology.

Porembski and Barthlott (2000) gave a synthesis of research work done on inselberg vegetation throughout all continents. The study of plant communities on temperate inselbergs has a long tradition in North America and Australia. Such studies are lacking for South America and specially for Guianas where inselbergs need helicopter transport to be accessible. It is obvious that more extensive research needs to be done on Guianan inselbergs where only qualitative floristic data are available.

In South America, classical whale back and sugar loaf shaped inselbergs are scattered throughout Guyana and Brazilian Shields (up to East Bolivia). These outcrops rise abruptly from the surrounding plain landscape and represent singular habitats in tropical rain forests. Thus, they reflect a clear habitat fragmentation and constitute functional terrestrial islands (Prance 1996). As a consequence, insular outcrop communities are of interest because they exhibit specific, and sometimes rare, species and community types.

Some floristic studies have been carried out in French Guiana (de Granville & Sastre 1973; de Granville 1978; Sarthou 1992), in Venezuela (Steyermark et al. 1989; Steyermark et al. 1995), in Brazil (Barthlott et al. 1993; Porembski et al. 1998) and in Bolivia (Ibisch et al. 1995). Due to poorly developed soils and extreme microclimate variations, outcrop vegetation is characterised by low diversity and oligotrophic or, in some instances, xerophytic characters which contrast abruptly with surrounding rain forest vegetation. A few semi-quantitative studies described typical herbaceous communities such as monocotyledonous mats made up of Bromeliaceae and Velloziaceae, swamp vegetation and plant communities living seasonally in rock pools (Sarthou & Villiers 1998; Meirelles et al. 1999). Woody patches seem to be characteristic of Guyana shield inselbergs but they received less attention. In French Guiana, they constitute numerous shrub islands mainly composed of *Clusia* spp. on granitic outcrops (de Granville & Sastre 1973; de Granville 1978). But despite their distinctiveness and relative

simplicity of species composition, no quantitative data exist on shrub communities from Guianas inselbergs.

This paper is the first phytosociological study of shrubby thickets on French Guianan inselbergs. Phytosociological data could also provide avenues for studies on vegetation dynamics occurring within each of the three investigated plant communities.

Methods

Study area

In French Guiana, inselbergs, 100-800 m high, consist of Precambrian granites. Detailed accounts about the geomorphology and geology of rock outcrops in the study area were provided by Hurault (1963), Gruau et al. (1985) and Teixeira et al. (1989). These granitic outcrops are unique because they are located in the undisturbed rain forest while most inselbergs known in Africa, Brazil and Venezuela are situated within landscapes dominated by human activities. The open areas of exposed rocks support numerous scattered herbaceous and shrubby patches separated by bare rock, forming a mosaic called locally "savane-roche".

Data regarding inselberg flora are available in the Aublet data base (Hoff et al. 1989) but are still fragmentary. The first vegetation studies were based on qualitative field observations made in SW French Guiana (de Granville & Sastre 1973; de Granville 1978). Recently, six herbaceous and suffrutescent associations and three sub-associations have been described on the base of semi-quantitative data (Sarthou & Villiers 1998).

The field work was undertaken during the rainy season in the course of three botanical expeditions on Mont-Chauve (3° 49' N, 52° 44' W, alt. 265 m) in April 1997, Trinité (4° 35' N, 53° 21' W, alt. 400 m) in May 1998 and Nouragues (4° 3' N, 52° 42' W, alt. 410 m) in April 1999, respectively (Fig. 1). The annual average rainfall amounts to 3000-3250 mm at Mont Chauve and Nouragues and 2000-2250 mm at Trinité (Boyé et al. 1979). The studied inselbergs are dome-shaped (whale-back type). They belong to the "cyanobacteria type" i.e. the exposed rock is covered by films of cyanobacteria (Sarthou et al. 1995), in contrast to the "lichen type" which is characteristic for drier conditions (Büdel et al. 1997). Cyanobacteria films give a red-brownish to blackish-green colour to the inselberg except on areas with intense water flow.

A detailed investigation on the Nouragues inselberg showed that most extreme environmental conditions prevailed on these rocky outcrops, due to very high daily fluctuations in temperature and relative humidity (Sarthou 1992). The mean temperature ranges between 18-55°C and the mean humidity between 20-100%. The open exposed rock is submitted to intense sunlight with high evaporation rate and rapid runoff following precipitation. The temperature of the bare rock surface reaches 50°C (up to 75°C in dry season). Cyanobacteria constitute the primary factor in the establishment of nutrient cycles on the rock surface (Sarthou & Grimaldi 1992). Soils are characterised by shallowness (1-20 cm for herbaceous patches, 10-40 cm for shrubby patches), marked acidity (pH from 3.5 to 5.5), coarse material (quartz sand) and low nutrient content (Sarthou & Grimaldi 1992).

Plots

A total of 151 phytosociological relevés were made on the three inselbergs, considering the whole set of each outcrop, in floristically and structurally homogeneous thicket stands. Forty four relevés (1-44) were sampled on Mont Chauve inselberg, 50 (45-94) on Trinité and 57 (95-151) on Nouragues. Relevés were done on plots which were distributed on the whole surface of each inselberg, thus they could be considered as representing the whole population. Plot sizes were small, in accordance with the size of vegetation patches, and distances from a plot to another were also variable, folllowing vegetation distribution patterns. The area was fixed to 2 x 4 m (8m²) on Mont Chauve, to 2 x 7 m (14 m²) on Trinité and to 2 x 8 m (16 m²) on Nouragues. For each relevé, cover abundance data for all terrestrial pteridophytes and spermaphytes were recorded according to Braun-Blanquet approach (Braun-Blanquet 1964; Westhoff & van der Maarel 1973). Specimens from all plant species were collected then identified by the authors using collections from two herbaria (Cayenne and Paris). Voucher specimens were deposited at the Herbarium of French Guiana (CAY) in Cayenne and at the National Museum of Natural History in Paris (P).

A synoptic table of constancy classes (Braun-Blanquet 1979) including the three shrub communities was elaborated (Table 1). Original data, including abundance-dominance of plant species in the 151 relevés, together with slope and aspect, can be provided upon request to the corresponding author.

Analysis

For numerical analysis, cover-abundance values (according to Braun-Blanquet scale) were transformed into the 1-9 ordinal scale of van der Maarel (1979). Plots were ordinated according to their floristic composition using Correspondence Analysis, a multivariate method using the chi-square distance (Greenacre 1984). Simple correspondence analysis was used in place of detrended correspondence analysis (Hill & Gauch 1980) because not any horseshoe effect was expected to occur given our data set embracing a variety of environmental and phytogeographical conditions. This analysis was performed using the STATBOX program on a matrix crossing plant species present in at least three plots (66 taxa) with the 151 relevés. Species characterised by cover-abundance values were used as active variables (contributing to factorial axes). Passive variables, describing environmental conditions such as orientation and slope, and structural characteristics such as the total number of species, the total number of epiphytes and the number of different life forms per relevé were added to measure their degree of relationship with the factorial axes. Active and passive data were reweighted and focused (mean fixed to 20 and standard deviation fixed to 1) and each structural variable was associated with a conjugate, varying in an opposite sense (complement to 40), according to a method used by Peltier et al. (1997) for the study of plant communities. This allows factorial coordinates of variables to be proportional to their contribution to the axes, as in principal components analysis (Hotelling 1933) and gradients of global vegetation abundance to be depicted (Greenacre 1984). Thus, each species will be represented by two points, indicating higher and lower values, respectively.

Results

Flora

A total of 94 plant species were recorded in the three shrub communities (Appendix 1). The species belong to 78 genera distributed into 40 families. Dominant families are Myrtaceae (9.6% of total number of species), Bromeliaceae (8.5%) and Orchidaceae (8.5%). Other widely dispersed tropical families were also encountered, such as Rubiaceae (6.4%), Melastomataceae (4.3%), Clusiaceae (4.3%), Euphorbiaceae (4.3%) and Mimosaceae (4.3%). Well represented genera are *Myrcia*, *Clusia* and *Croton* followed by *Calyptranthes*,

Psychotria, Erythroxylum, Encyclia, Aechmea, Vriesea and Sauvagesia. Woody forms (63%) are mainly constituted by shrubs (31%), small trees (17%), climbers (10%) and lianescent sub-shrub parasites (5%) (Appendix 1). Herbaceous forms (37%) are mainly represented by erect herbs, rosettes or tussocks and by one palm species restricted to granitic outcrops in Guianas. Among life-forms, phanerophytes (49%), especially microphanerophytes, clearly dominated the communities, followed by hemicryptophytes (28%), lianas (10%), chamaephytes (7%) and parasites (5%) (Appendix 1). Geophytes were represented by only one species.

Among a total of 94 plant species, 35% were endemic to Guianas (Appendix 1). These include many species characteristic and abundant in shrub inselberg communities such as Calyptranthes lepida, Syagrus stratincola, Quapoya scandens, Rhodognaphalopsis flaviflora, Stelestylis surinamensis, Myrcia guianensis, Myrcia fallax, Myrcia saxatilis and Pitcairnia geyskesii. These insular outcrop communities are also of interest because they exhibit species rare in French Guiana such as Quapoya scandens, Rhogdophanalopsis flaviflora, Eriotheca surinamensis, Syagrus stratincola, Stelestylis surinamensis, Erythroxylum ligustrinum, Croton argyrophylloides, C. hostmannii, Zygia tetragona, Eugenia macrocalyx and Ternstroemia dentata.

Our list of 94 species includes plants also found in other habitats such as the rain forest (terrestrial or epiphyte vegetation), rocks on river sides or in the rain forest, savannas, secondary forest, white sand forest. Among inventoried species, 20% are confined to granitic inselbergs in French Guiana (Appendix 1).

Ordination

In the plane of axes 1 and 2, CA differentiates three plant communities corresponding to the three studied sites (Fig. 2). Despite the common occurrence of some taxa with a high constancy, which were generally placed not far from the origin (Table 1, Fig. 2: species with border), each community exhibits a particular floristic group described below. Given the clear delimitation of characteristic groups, no numerical classification was judged necessary to separate them. The floristic composition of the three groups is outlined in Table 1.

All shrub communities present on exposed rock surfaces are evergreen and form individualised dense thickets, 3-5 m tall, generally separated by areas of bare rock or by herbaceous communities. Occurring both on slopes (0-63%) and in depressions, they

represent the main functional woody unit of the "savane-roche" ecosystem. These communities are physiognomically dominated by Clusiaceae and Myrtaceae species. Species richness averages 12, 13, and 14 species per plot on Trinité, Mont Chauve and Nouragues respectively, which was considered similar given small differences in the size of sampling areas (varying from 8 to 16 m²). Three layers can be recognised in each of these vegetation units.

A dominant canopy stratum 3-5 m in height with rare emergents reaching 6-8 m in height is characterised by microphanerophytes (70-100% cover). Shrubs with a high constancy in all communities (Table 1), such as *Clusia nemorosa, Myrcia saxatilis, Psychotria hoffmannseggiana, Miconia ciliata* and *Erythroxylum citrifolium,* are also important structural components of the thickets. Other life forms associated with the crown space of thickets, such as lianas, parasites or epiphytes occur but with a small number of individuals. The dominant layer is complemented by a smaller stratum 0.5-1.5 m in height, typified by nanophanerophytes (5-40% cover). A herbaceous layer (50-100% cover) is often composed by dense colonies of spiny bromeliads, Cyperaceae or graminoids, small populations of orchids and species occasionally found growing in shady sites. Two species, *Pitcairnia geyskesii* and *Scleria cyperina*, occur with a high constancy and sometimes a high cover rate on the three inselbergs (Table 1).

Although above mentioned physiognomic features can be found in all investigated inselbergs, a particular community has been recognised on each inselberg, made of distinct species as well as species differing in their constancy among the three inselbergs.

The *Quapoya scandens-Rhodognaphalopsis flaviflora* community (Table 1, Fig. 2) occurs on Trinité inselberg. This shrub unit is characterised by the Guianan endemics *Quapoya scandens* and *Rhodognaphalopsis flaviflora*, two shrubs rare in French Guiana and restricted to rocky outcrops. The upper layer includes *Eugenia macrocalyx*, a tree also found in the adjacent forest. The tall shrub layer is composed of the nanophanerophyte *Turnera rupestris* var. *frutescens*, endemic to the Guianas region. The Cyperaceae *Mapania effusa* and the epilithic orchid *Encyclia granitica* predominate in the herb layer.

The *Clusia minor* community (Table 1, Fig. 2), occurring on the Nouragues inselberg, is mainly characterised by this Clusiaceae shrub species. Two Myrtaceae, *Myrcia guianensis* and *M. fallax*, endemics to the Guianas, were also found in the shrub layer. The lower layer is physiognomically dominated by populations of the Cyclanthaceae, *Stelestylis surinamensis*, 1-2m height, rare in French Guiana. The perennial grass, *Axonopus ramosus*, another Guianan endemic species, is well represented in some plots. *Anthurium jenmanii* and

Epidendrum nocturnum, also found on the Trinité inselberg, are more constant in this community (Table 1).

The *Calyptranthes lepida-Guapira sp.* community (Table 1, Fig. 2) is found on Mont Chauve inselberg. This unit is characterised by *Calyptranthes lepida*, *Guapira sp.* and the palm *Syagrus stratincola*, only found on granite outcrops in the Guianas. Lianas such as *Dioscorea pubescens* and *Dioclea virgata* are also specific to the dominant layer. The orchid *Sobralia stenophylla* grows in small populations in the herb layer. The woody species *Clusia nemorosa*, *Eriotheca surinamensis* and *Tabebuia capitata*, also found in other communities, are important structural components of this community, here more constant and with higher cover-abundance values than in other communities (Table 1). The orchid *Encyclia ionosma* and the terrestrial bromeliad *Guzmannia lingulata* are also better represented on this outcrop (Table 1).

Other marked differences in the floristic composition are reflected along axis 3 of CA, especially within the Trinité shrub unit (Fig. 3), and to a lesser extent in the Nouragues inselberg. Axis 3 could indicate a successional gradient, as suggested by the ordination of life-forms along this axis, and the fact that environmental variables such as slope and exposure contributed poorly to this axis (near to the origin, not represented in Fig. 3). Hemicryptophytes and nanophytes were projected mainly on the positive side of Axis 3, while microphanerophytes, lianas and epiphytes were projected on its negative side, suggesting a gradient in vegetation height and biodiversity, increasing from positive to negative values of Axis 3.

Discussion

The shrub vegetation of the inselbergs clearly shows a typical flora with many endemics to the Guianas region in each community. These insular outcrop communities are of interest because they exhibit specific and also rare species, due to isolation (McArthur & Wilson 1967) and particular environmental conditions. The low capacity of long-distance dispersal of most outcrop species (most species being dispersed by territorial birds and ants, personal observations) explain probably the differences in vegtation composition from an inselberg to another.

Ecological constraints, especially geology and temperature, are evident for species living in the studied rocky habitats where most extreme environmental conditions prevail

(Sarthou 1992). In contrast, in the Amazonian Basin, mountains reaching 100-200 m are scarce and humid conditions are predominant. We presume that many of the inventoried species are specifically adapted to the particular combination of high temperatures, intense runoff and chemically poor substrates which prevails on tropical granitic outcrops. Many of these species have been also found in open areas such as savannas, caatingas and also forests on white sand soils (Appendix 1).

No classification of French Guianan outcrop shrub vegetation exists owing to difficult access to inselbergs, and previous data were exclusively based on qualitative field observations. The present study constitutes the first semi-quantitative approach to the inselberg shrub flora of French Guiana, but further phytosociological analyses are required before a syntaxonomical outline can be drawn. Some authors have qualitatively described Clusiaceae thickets on Tumuc Humac inselbergs in SW French Guiana, a dryer region (< 2000 mm/year) at 450-800 m altitude (de Granville & Sastre 1973; de Granville 1978). As in our study, their results seem to confirm that, despite some common taxa, a specific floristic group can be recognised on each inselberg.

Similarly organised shrub islands have been qualitatively described on inselbergs in Venezuela (Steyermark et al. 1995), Bolivia (Ibisch et al. 1995) and Africa (Bonardi 1966; Jenik & Hall 1976). Thus, affinities with flora of saxicolous shrub communities of Venezuelan inselbergs (or lajas) was especially observed at the family and also at the genus level (Steyermark & Holst 1989; Steyermark et al. 1995). Indeed, the evergreen shrub islands on lajas harbour woody species mostly belonging to Melastomataceae, Clusiaceae, Bignoniaceae, Bombacaceae, Erythroxylaceae, Euphorbiaceae, Ochnaceae, Rubiaceae and Theaceae. Among the most important colonising herbs are also several species of Bromeliaceae and terrestrial Orchidaceae. Some genera such as *Tabebuia, Erythroxylum, Clusia, Ternstroemia* are also found on lajas. The occurrence of the gregarious palm *Syagrus orinocensis* in the understory of lajas low forest can also be compared to that of *Syagrus stratincola* in Trinité thickets. However, the flora of Venezuelan lowland granitic outcrops generally exhibits a higher level of endemism than that of French Guianan outcrops. This could be explained by higher elevation (>1000 m), a higher habitat diversity, or by hypothetical historical features, a more ancient isolation allowing more speciation.

Similarities are also noticed with the vegetation of Guianas savannas both floristically (at a genus and family level) and physiognomically. We can compare the studied communities with the sclerophyllous thickets described by Hoock (1971) in French Guianan coastal savannas. However, the life-form spectrum of outcrop shrub communities, with the

predominance of microphanerophytes and hemicryptophytes, is more similar to the peripheral forest group of coastal savannas. Outcrop communities also have affinities with some savanna-bushes described by van Donselaar (1965) and Teunissen & Wildschut (1970) in Surinam such as *Clusia-Scleria* bushes on wet white sand and *Marlierea* bushes on wet loamy sand.

Affinities may be also pointed out at the family and genus levels with other vegetation types such as low forests in French Guiana (Larpin 2001), shrublands of the Venezuelan Guyana (Huber, 1989), scrub caatingas and campos rupestres in Brazil (Pires-O'Brien 1992; Alves & Kolbek 1994; da Silva et al. 1996) and white sand and rocky substrates at the top of the Araracuara sandstone plateau in Colombian Amazonia (Duivenvoorden & Cleef 1994). Parallels in the floristic composition and structure of these vegetation types seem to be determined by particular edaphic factors. A combination of extremely poor and acid (pH<4) soil conditions and the periodic desiccation of the shallow soil profile characterises thicket vegetation on French Guianan inselbergs (Sarthou & Grimaldi 1992). Thus, periodic water stress may explain the xerophytic character of some components of this vegetation. A similar periodic water deficit has been also reported in other shrub communities described by Duivenvoorden & Cleef (1994), Steyermark et al. (1995) and Larpin (2001).

Floristic differences observed between the three studied inselbergs (Axes 1 and 2 of CA) could be related to local historical features, depending on initial outcrop colonisation. We can suppose that the neighbouring Nouragues and Mont Chauve inselbergs (projected on the positive side of Axis 1, separated by Axis 2) have a more common history of land colonisation than Trinité (projected on the negative side of Axis 1), located further north.

The presence of vegetation gradients was apparent within each shrub community, more especially at the Trinité inselberg (Axis 3 of CA). These gradients are probably associated with thicket ageing (plant succession), since orientation and exposure did not explain the variation displayed by Axis 3. But we cannot discard other factors not acounted for in our study, such as differences in edaphic constraints and runoff, for instance.

The present study pointed on the isolation of several plant communities the floristic composition of which could vary according to geographical distance. A thorough investigation of a wide range of French Guianan inselbergs will help to better discern compositional trends (gradients) at the regional scale, in order to test the hypothesis of a past development of the savane-roche in place of the present rain forest.

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Figure 1. Location of the inselbergs studied in French Guiana: Mont-Chauve (MC), Nouragues (N), and Trinité (T).

Figure 2. Correspondence analysis of the 151 relevés (sharing 66 species) combined with vegetation data on the three inselbergs: projection in the plane of the two first axes with 16.1 % and 12.3 % inertia, respectively. Trinité: Quapoya scandens-Rhodogphanalopsis flaviflora community (♠). Mont Chauve: Calyptranthes lepida-Guapira sp. Community (□). Nouragues: Clusia minor community (●). Species with border are common to all three groups (see also Table 1). Species in bold are endemic species to the Guianas. Abbreviations of taxa names: AXO: Axonopus ramosus; CAL: Calyptranthes lepida; CLM: Clusia minor; CLN: Clusia nemorosa; DIO: Dioscorea pubescens; DIV: Dioclea aff. virgata; ENG: Encyclia granitica; ERI: Eriotheca surinamensis; ERN: Ernestia granvillei; ERY: Erythroxylum citrifolium; EUG: Eugenia macrocalyx; GUA: Guapira sp.; MAP: Mapania effusa; MAT: Matelea sastrei; MIC: Miconia ciliata; MYF: Myrcia fallax; MYG: Myrcia guianensis; MYS: Myrcia saxatilis; PIT: Pitcairnia geyskesii; PPT: Piptocoma schomburgkii; PSY: Psychotria hoffmannseggiana; QUA: Quapoya scandens; RHO: Rhodognaphalopsis flaviflora; SAT: Satyria cerander; SCL: Scleria cyperina; SOB: Sobralia stenophylla; STE: Stelestylis surinamensis; SYA: Syagrus stratincola; TAB: Tabebuia capitata; TUR: Turnera rupestris var. frutescens.

Figure 3. Correspondence analysis of the 151 relevés (sharing 66 species) and associated sites: projection in the plane of the axis 2 and 3 with 12.3 % and 4.6 % inertia, respectively. Associated with correspondence analysis of passive variables: life-forms (Raunkier 1934), number of epiphytes and total number of species per relevé. Bold or italic means higher or lower values, respectively. Abbreviations: Ch: Chamaephytes; Hc: Hemicryptophytes; Na: Nanophanerophytes; Mi: Microphanerophytes; L: Lianas; TotS: total number of species per relevé; NbEp: number of epiphytes per relevé.

Table 1. Floristic composition of the shrub communities. Constancy-classes: I: 1-20%; II: 21-40%; III: 41-60%; IV: 61-80%; V: 81-100%. Species reaching only constancy class I in all the communities were omitted. Arabic numbers following indicate the range of coverabundance values. *: without epiphytes. Species with border are species in common to all three groups (see also Figure 2). Species in bold are endemic species to the Guianas region.

Inselbergs	Mont Chauve	Trinité	Nouragues
Relevés number	44	50	57
Total number of species*	44	42	50
Average species number/plot	13	12	14
Calyptranthes lepida	IV/+-2]	
Guapira sp.	IV/+-3		
Syagrus stratincola	III/+-3		
Sobralia stenophylla	III/+-3		
Dioscorea pubescens	II/+		
Dioclea aff. virgata	II/+		
		-	
Quapoya scandens		V/2-5	
Rhodognaphalopsis flaviflora		V/+-3	
Mapania effusa		V/1-5	
Eugenia macrocalyx		III/+-3	
Turnera rupestris		III/+-2	
Encyclia granitica		III/+-1	
Clusia minor			V/2-5
Stelestylis surinamensis			IV/+-4
Myrcia guianensis			III/+-2
Myrcia fallax			II/+-2
Satyria cerander			II/+-1
Axonopus ramosus			II/+-3
	•		
Clusia nemorosa	V/+-4	V/+-3	V/+-2
Myrcia saxatilis	V/+-4	V/+-3	V/+-3
Psychotria hoffmannseggiana	V/+-3	V/+-2	V/+-3
Scleria cyperina	V/+-4	IV/+-2	V/+-3
Pitcairnia geyskesii	IV/+-3	IV/+-2	V/+-4
Miconia ciliata	IV/+-3	I/+-1	IV/+-3
Erythroxylum citrifolium	II/+-2	III/+-2	IV/+-2
Matelea sastrei	I/+	I/+	II/+
Ernestia granvillei	I/+	I/+-1	II/+-2
Tabebuia capitata	III/+-2	I/+-2	I/+-1
Piptocoma schomburgkii	II/+-3	I/+-1	I /+
Paradrymonia campostyla	II/+-1	I/+-1	
Croton hostmannii		I/+-1	II/+-1
Myrcia silvatica		I/+	II/+-3
Sauvagesia aliciae		II/+-1	I/+-1
Aganisia pulchella		II/+	II/+
Epidendrum aff. nocturnum		I/+-1	II/+
Anthurium jenmanii	X7/ 2	I/+	III/+-2
Eriotheca surinamensis	V/+-3		II/+-2
Encyclia ionosma	IV/+-3		III/+-2
Guzmania lingulata	III/+-1		I/+-1

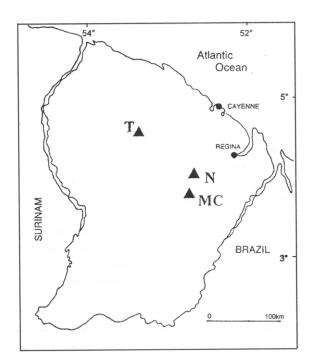


Fig. 1

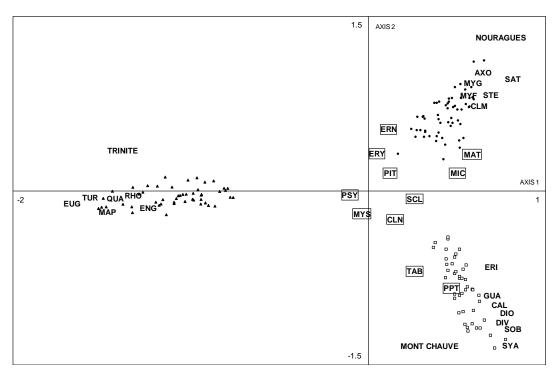


Fig. 2

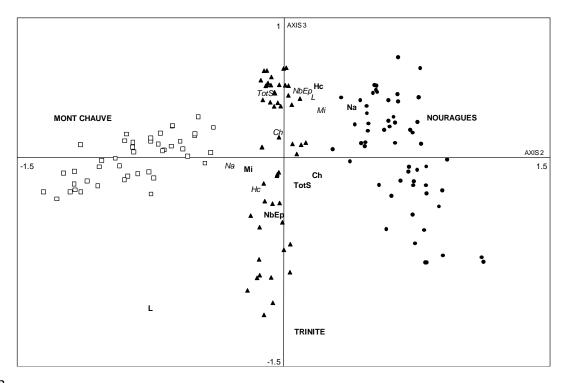


Fig. 3