

STUDY OF THE VEGETATION COMPOSITION IN THREE INSELBERGS
FROM CONTINENTAL EQUATORIAL GUINEA
(WESTERN CENTRAL AFRICA) : EFFECTS OF SITE, SOIL FACTORS AND
POSITION RELATIVE TO FOREST FRINGE

Ingrid PARMENTIER

Laboratoire de Botanique Systématique et de Phytosociologie, Université Libre de Bruxelles, CP 169,
av. F.D. Roosevelt 50, B-1050 Brussels, Belgium
(e-mail: inparmen@ulb.ac.be)

ABSTRACT. — We investigated the vegetation composition of three inselbergs from continental Equatorial Guinea in relation to six environmental variables. The most influent factors on vegetation appeared to be soil depth, pH and the position relative to the upper or lower forest fringe. There was no effect of slope or aspect. Although the three inselbergs are very close to each other (100 to 500 m), they significantly differ in their vegetation (site effect). This effect could partly be explained by the insular property of inselberg vegetation surrounded by rainforest. The position of *Afrotrilepis pilosa* (W.C.Boeck) J.Raynal, the most characteristic species of West African inselberg grasslands, along the main ecological gradient is discussed.

KEY WORDS. — Rainforest inselberg vegetation, vegetation-environment relationships, Equatorial Guinea, *Afrotrilepis pilosa*, insular ecosystems, xeric refugia.

INTRODUCTION

Inselbergs ('island hill' in German) are hills or groups of hills isolated in flat landscapes. They occur in many regions of the tropics and subtropics, as well as in temperate regions. They mainly consist of Precambrian granites and gneisses. They can vary in size from less than 100 m in both height and extent to very large and mountainous massifs approaching 1000 m in height and more than 1000 km in diameter (THOMAS 1994). Inselbergs have very particular edaphic and microclimatic conditions. Indeed, shallow soils and steep slopes cause a rapid run-off of water. The rock exposed to the sun can reach 50 °C or more (SARTHOU & VILLIERS 1998). In the rainforest landscape, inselbergs can be regarded as xeric

islands. They therefore form an excellent model system for addressing central questions of biodiversity and biogeography research, such as e.g. speciation and endemism due to geographical isolation, survival chances of insular ecosystems and refugia in the rainforest for xerophytes and orophytes.

Despite their interest as model systems, rainforest inselbergs have been poorly explored and their vegetation and ecological requirements are still little investigated. POREMBSKI & BARTHLOTT (2000) made a global biotic diversity study of tropical and temperate inselbergs. They gave interesting information on West African inselberg vegetation (dominance of *Afrotrilepis pilosa* grasslands) and general information about the plant-environment relationships on inselbergs. In

Guyana, SARTHOU & VILLIERS (1998) described six new phytosociological associations from inselbergs, resulting from different combinations of environmental factors like slope, aspect, water availability and soil depth. In Cameroon, VILLIERS (1981) made an extensive study of the Nkolsia inselberg using two different methods: the continuum method (CURTIS & MAC INTOSH 1951) and Zürich-Montpellier phytosociology (BRAUN-BLANQUET 1932). In Gabon, REITSMA *et al.* (1992) made a first study of 13 inselbergs and rock outcrops and emphasized the contrast between inselberg vegetation and the surrounding rainforest. They suggested that inselbergs could be refugia for xerophytes and orophytes, which were widely spread during the dryer and colder climates of the Pleistocene (MALEY 2002). LEJOLY & LISOWSKI (1999) published a list of vascular plants occurring on four inselbergs from Equatorial Guinea, with 128 species classified into four groups: dry grasslands, wet grasslands, grassland/forest transition and pioneer forest. A preliminary list of biotic and abiotic differentiating factors for the inselbergs of Equatorial Guinea was presented in PARMENTIER (2002), which included distance from cultivated land, buffalo grazing, and human activities. The first detailed phytosociological study of three inselbergs from this country was realized by PARMENTIER *et al.* (2001), which could distinguish several distinct vegetation units. In the present paper, we investigated the relationships between these vegetation units and environmental factors measured on the field including topography (slope, aspect), soil factors (soil depth, pH) and the position relative to the lower or upper fringe. As three inselbergs were involved in the study, and because of the insular properties of rainforest inselbergs, we also tested if the vegetation units were different in the three sites. Finally, we focused on *Afrotrilepis pilosa*, as this species is the most important mat-forming species on West African inselbergs (POREMBSKI 2000).

MATERIAL AND METHODS

STUDY AREA

Equatorial Guinea is located between Cameroon and Gabon in western central Africa (Fig. 1). This

country is composed of islands in the gulf of Guinea and of a continental part, Rio Muni. Inselbergs are frequent in the East of Rio Muni. It has an equatorial climate: annual precipitation ranges from 2000 to 3500 mm and temperature is around 25 °C all year. Primary rainforest has been replaced by secondary forest over more than 40 % of the territory (WILKS & ISSEMBÉ 2000).

The three inselbergs involved in this study, Piedra Nzas, Ncoho Biworo and Andom, are Precambrian granite outcrops enclosed in the Piedra Nzas Natural Monument (01° 27' N , 11° 02' E) (Fig. 1). They are located six kilometres away from villages and are surrounded by a plain (500 to 700 m altitude) covered by rainforest with scattered forested hills. Study sites are quite isolated from other known inselbergs of the region, but their vegetation is representative of inselbergs of eastern Equatorial Guinea (PARMENTIER & NGUEMA 2001). The three inselbergs are close to each other (100 to 500 m). The Piedra Nzas inselberg's summit and basis are 745 and 630 m height above sea level, respectively. There was no obvious sign of human activity within the study area.

SITE DESCRIPTION

Fig. 2 presents the main plant formations that can be found from the basis to the summit of rainforest inselbergs. The natural grasslands of those inselbergs strongly contrast with the surrounding rainforest. They are composed of species well adapted to harsh environmental constraints (drought, shallow soils). There is some indication that these grasslands may be submitted to occasional natural or anthropic fires. The forest fringes and the saxicolous forest (Fig. 2) shelter many species absent from the surrounding rainforest. The lower forest fringe is in direct contact with the rainforest and the upper one is bordering the upper saxicolous forest. The main vegetation units, described in PARMENTIER *et al.* (2001) are summarized hereafter.

The Afrotrilepis pilosa grasslands.

This vegetation unit, dominated by monocotyledons (Orchidaceae, Cyperaceae and Poaceae), shows a low species richness (49 species) relatively to the other rainforest inselberg vegetation units (PARMENTIER *et al.* 2001). The dominant species is *Afrotrilepis pilosa*, a caespitose chamaephyte forming dense mats of living plants, sheaths of dead roots and leaves that protect its buds from fire. This species is able to grow on bare rock, on the driest parts of the inselberg, strongly exposed to sun. There are also several species endemic to inselbergs in this vegetation unit, such as *Oreonesion*

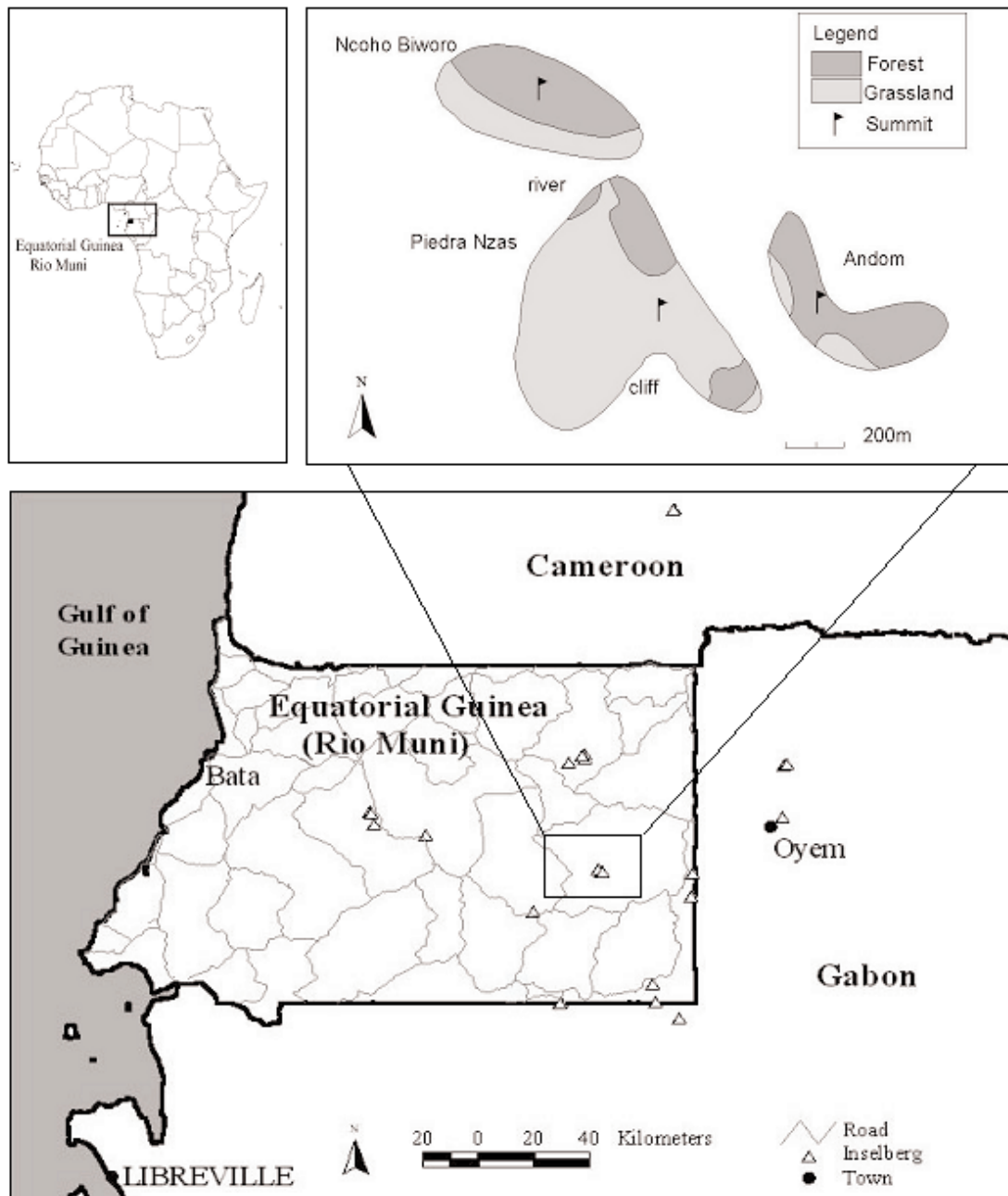


FIG. 1. — Location of Rio Muni and the Piedra Nzas Natural Monument, approximate layout of the three inselbergs inside the Piedra Nzas Natural Monument.

testui A.Raynal (Gentianaceae) and *Polystachya gabonensis* Summerh. (Orchidaceae).

The Loudetiopsis glabrata (K.Schum.) Conert *humid grasslands*

This vegetation unit is located on the slopes of the inselberg where there is a continuous water sweeping from the upper saxicolous forest, or in depressions, as most of its characteristic species are hygrophilous. It is also species-poor (36 species). The dominant species,

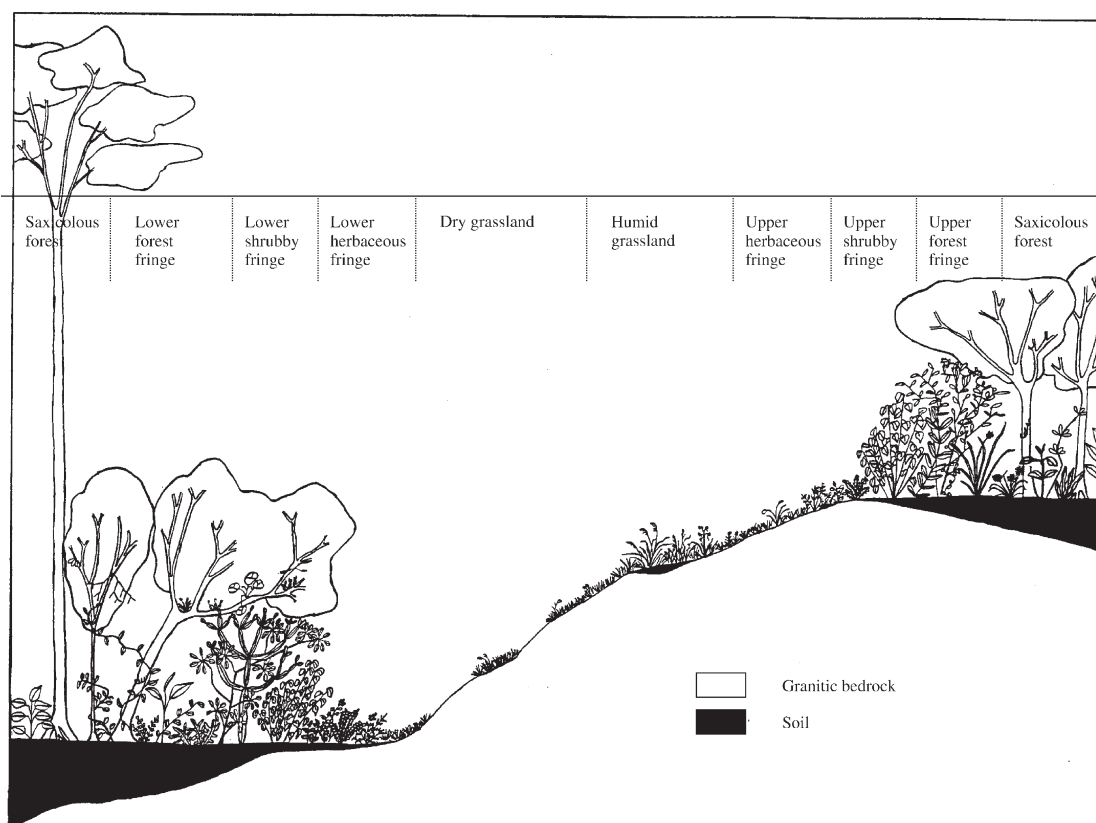


FIG. 2. — Distribution of plant formations on rainforest inselbergs.

Loudetiopsis glabrata (Poaceae) protects beneath its leaves some small herbaceous species such as *Utricularia andogensis* Welw. (Lentibulariaceae) and *Burmannia madagascariensis* Martius (Burmanniaceae) from desiccation.

The herbaceous and shrubby fringes

This vegetation unit is located in the fringe between the inselberg grassland and the surrounding rainforest, and between this grassland and the saxicolous forest of the inselberg (Fig. 2). It is dominated by shrubs like *Lanea nigriflora* (Sc.Elliot) Keay var. *nigriflora* (Anacardiaceae) and *Psychotria peduncularis* (Rubiaceae) (Salisb.) Steyerl. The most striking herbaceous species are *Calvoa pulcherrima* Gilg (Melastomataceae, inselberg endemic) and two ferns, usually epiphytic, but that grow here on the ground: *Nephrolepis biserrata* (Sw.) Schott (Nephrolepidaceae) and *Phymatosorus scolopendria* (N.L.Burm.) Pic.-Ser. (Polypodiaceae). Species richness is high (102 species).

The Memecylon collinum and Cremaspora triflora forest fringes

This vegetation unit fringes the dense forest and the saxicolous forest. The soil is not thick enough (mean soil depth is 8 cm) to enable the large, dense forest trees to grow. We find there some small tree species adapted to shallow soils, like *Memecylon collinum* Jacq.-Fél. (Melastomataceae), which is restricted to inselbergs, and *Cremaspora triflora* K.Schum. (Rubiaceae). The sunlight is still able to pass through the trees. Atmospheric humidity is high. There is a high diversity of ecological niches in this unit, due to varying conditions of soil depth and light. Epiphytic species are numerous (Orchidaceae, Begoniaceae and ferns). Species diversity is high (111 species).

The Garcinia epunctata and Coula edulis saxicolous forests

This vegetation unit is located at the summit of the inselbergs. It is composed of a large number of tree

species, but each species is represented by a few individuals. This saxicolous forest has an important role in the inselberg ecosystem because it acts as a water reserve for the other plant formations. Water accumulates in the forest soil and sweeps almost continuously alongside the inselberg between the rainfalls.

VEGETATION AND ENVIRONMENTAL DATA SAMPLING

A total of 72 vegetation relevés were realised along the three inselberg using the Braun-Blanquet's (1932) method. The inselbergs were visited in January 1999 (end of the long rainy season) and in May 1999 (end of the short rainy season). The following environmental variables were assessed for 38 of the 72 plots. Composite soil samples were collected in the superficial horizon (0-20 cm). They were air-dried and sieved to particles < 2 mm and pH_{water} was measured (1:1 soil deionised water). Soil depth corresponded to the average of the measurements at three different places, with a maximum of 45 cm. Slope was measured in percent with a clinometer. Position relatively to the lower and the upper forest fringe was noted, and categorized into two classes: low and high. A plot at an intermediate position, on the flanks hillside, received a value of 0.5 for the two categories. Aspect was categorized in eight 45° wide classes.

ECOLOGICAL INTERPRETATION OF THE VEGETATION COMPOSITION

To allow an extrapolation of the interpretation of the relationships between vegetation composition and environmental variables to the 72 plots data set, we tested if the 38 plots were representative of the whole data set (72 relevés). Therefore, a detrended correspondence analysis (DCA) was performed for the species data set with 72 and with 38 relevés separately. The scores of the 38 relevés on axis 1 to 4 of the two DCA analyses were compared using Pearson (r) and Spearman (r_s) correlation analysis. As multiple tests were involved, Bonferroni corrections were applied to test for significance (RICE 1989).

Canonical Correspondance Analysis (CCA) was used to identify the major gradients in vegetation composition and to relate them to the sampled environmental variables, using CANOCO version 4.0 (TER BRAAK & SMILAUER 2002). A Monte Carlo permutation test (999 permutations) was performed to assess the significance of the eigenvalue of the first canonical axis which specified relationships between species and explanatory variables, and the significance of the trace

statistics which gave an overall test of the effect of the environmental variables on the floristic composition (TER BRAAK & SMILAUER 2002). Forward selection and associated Monte Carlo permutation tests were applied to select the smallest set of predictor variables that could explain most of the variance of the data (TER BRAAK & SMILAUER 2002). Only the significant variables were kept for tracing the CCA plot.

As soil pH and soil depth appeared to be the most important factors explaining the variation in vegetation composition, we investigated the differences in these variables among the five vegetation units described above using one-way Analysis of Variance (ANOVA) and Neumann-Keuls multiple comparison. These analyses were performed with STATISTICA.

In order to investigate the response of *Afrotrilepis pilosa* to the main ecological gradient, we tested the distribution of its abundance on the first axis of the CCA using a regression analysis based on generalized linear models with a log function as link function. This analysis was performed with CANODRAW version 4 (TER BRAAK & SMILAUER 2002).

RESULTS AND DISCUSSION

THE 38 RELEVÉS ARE A REPRESENTATIVE SUBSET OF THE 72 RELEVÉS

Significant positive correlations were found between the scores of the 38 relevés on DCA axis 1 and 2 with all 72 and 38 relevés ($r = 0.991$ and $r = 0.849$, respectively, $p = 0.001$). On the other hand, correlation coefficients for the DCA axes 3 and 4 were not significant ($r_s = 0.011$ and $r_s = 0.096$, respectively, $p > 0.05$). As axes 3 and 4 of the two DCA only represented 5.3% (72 plots) and 6% (38 plots) of the total variation, we considered that the high correlation found for axes 1 and 2 of between the two DCA was sufficient to admit that the 38 plots were representative of the 72 plots.

ECOLOGICAL INTERPRETATION OF THE VEGETATION COMPOSITION

A summary of the results of the CCA analysis is given in Table 1. A significant correlation was found between vegetation composition data and the total set of environmental variables ($p = 0.002$). After forward selection, several variables

TABLE 1

Results of ordinations by CCA with six environmental variables, related to soil (pH, depth), site effect (Piedra Nzás, Ncho Biworo and Andom), topography (slope, aspect) and position relative to the lower or upper forest fringe: eigenvalues for the CCA with all environmental variables (total) and for the CCA f. sel., species-environment correlation coefficients for the CCA f. sel. and intraset correlation coefficients for each canonical axis. Only the significant environmental variables after the forward selection and associated Monte carlo permutation tests are given, in descending order of importance. The trace is the sum of all canonical eigenvalues. ** $p = 0.002$, *** $p = 0.001$.

Analysis	Trace	Axis 1	Axis 2	Axis 3	Axis 4
Eigenvalues					
CCA total	3251**	0.678	0.514	0.414	0.353
CCA/f. sel.	2069***	0.673	0.496	0.379	0.31
Species-environment coefficients					
	0.948	0.946	0.930	0.916	
Intraset correlation coefficients					
pH		-0.571	0.692	0.215	-0.070
Soil depth		0.809	0.441	0.196	0.082
Piedra Nzás		-0.009	0.438	-0.743	-0.348
Ncho Biworo		0.061	-0.300	0.496	0.528
Andom		0.081	-0.266	0.471	-0.243
Lower fringe		-0.178	-0.456	0.200	-0.729
Upper fringe		0.178	0.456	-0.200	0.729

were significantly related to vegetation composition: soil depth, pH, site effect, position relative to the lower or upper forest fringe. These variables only explained 22.6 % (total inertia = 9.152) of total variability whereas all variables together explained 34.5%. By including important factors like fire, animal grazing, luminosity and a good measure of water availability in our analysis, we might expect a greater part of the variance to be explained.

The ordination diagram (Fig. 3) and intraset correlation coefficients (Table 1) showed that the canonical axes were related to different environmental gradients: axis 1 was related to a decreasing pH ($r = -0.571$) and increasing soil depth ($r = 0.809$); axis 2 was related to an increasing soil pH ($r = 0.692$); axis 3 was related to site variables;

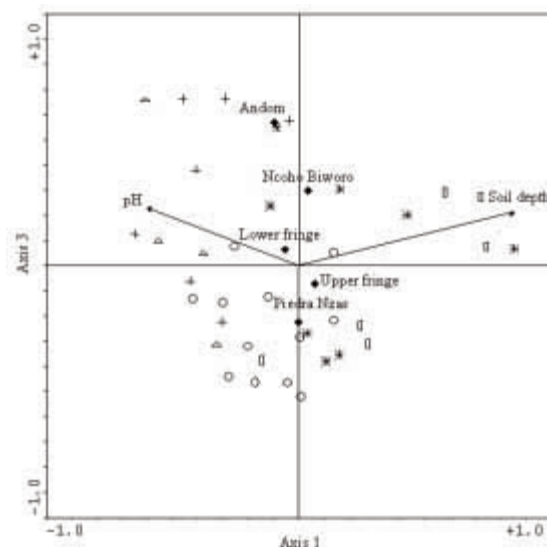


FIG. 3. — CCA ordination diagram (axes 1 and 3) for 38 plots, with the five vegetation units and the environmental variables selected by forward selection: pH and soil depth (arrows) and the nominal variables site (Piedra Nzás, Ncho Biworo and Andom) and position relatively to the upper and lower forest fringe. Eigenvalues: $\lambda_1 = 0.673$, $\lambda_3 = 0.379$. The vegetation units are represented by symbols: + *Afrotrilepis* grasslands; Δ *Loudetiopsis glabrata* humid grasslands; \circ herbaceous and shrubby fringes; * *Memecylon collinum* and *Cremaspora triflora* forest fringes; \square *Garcinia epunctata* and *Coula edulis* saxicolous forests.

axis 4 was related to site and to the position relative to the lower or upper fringe ($r = -0.729$).

Soil pH and soil depth appeared to be very important factors explaining the vegetation patterns. Significant differences in pH and depth were found among the five vegetation units when tested by ANOVA ($F = 8734$ and 17050 respectively, $p < 0.0001$ for both tests). The post-hoc multiple comparisons test indicated that pH was significantly lower ($p < 0.003$) in the forest fringes and the saxicolous forest than in the other vegetation units (Fig. 4a) and that soil depth was significantly higher ($p < 0.003$) in the saxicolous forests than in the other vegetation units (Fig. 4b). Inselberg soils are generally characterized by their low depth and high acidity. BREMER & SANDER (2000) measured pH_{KCl} from 69 soil samples of inselbergs from Ivory Coast. The median pH was 4.6 for sites with 1150 mm y^{-1} rainfall and 4.3 for

sites with 1900 mm y^{-1} . In French Guyana, with annual rainfall between 2250 and 3250 mm y^{-1} , SARTHOU & GRIMALDI (1992) measured pH_{water} values from 4.0 to 5.5 in the inselberg grasslands and pools, and around 4.0 or lower in the shrubby patches and soil depths of 1 to 3 cm for *Pitcairnia geyskesii* L.B.Sm. patches (this species has similar traits as *Afrotrilepis pilosa*), 10 to 20 cm for grasslands and 10 to 40 cm for shrubby patches. In our study sites, pH values were slightly lower (pH_{water} 3.4 to 4.8). Soil depth under *Afrotrilepis pilosa* grasslands corresponded to that of the *Pitcairnia geyskesii* patches, but the herbaceous and shrubby vegetation soil depth was lower than in shrubby patches in French Guyana. In the correspondence analysis of 74 relevés belonging to the herbaceous vegetation of the Nouragues inselberg in French Guyana, SARTHOU (2001) also interpreted the first axis as a soil depth gradient. BREMER & SANDER (2000) observed that on the edge of an inselberg, there is a relationship between thickness of the substratum, height of growth, and plant cover composition. Such a correlation was also observed by REISTMA *et al.* (1992) in their study of inselbergs from Gabon.

The significant site effect found in the CCA analysis after forward selection indicated an opposition between the relevés from Nchoho Biworo and Andom and those from Piedra Nzas (Fig. 3). Some species were only found on one or two of the 3 sites. The lower fringe of Andom and Nchoho Biworo were characterized by two inselberg endemic species: the cactus-like *Euphorbia letestui* J.Raynal (Euphorbiaceae) and *Epistemma rupestre* H.Huber (Asclepiadaceae). These species were absent from the Piedra Nzas inselberg. This unequal species repartition could originate from different properties of the inselbergs, or result from insufficient dispersal ability of the species between the three inselbergs. *Epistemma rupestre* produces anemochorous seeds, which are certainly able to cross the distance between the inselbergs. In contrast, *Euphorbia letestui* has dehiscent capsules that contain seeds without long-distance dispersal mechanism. REISTMA *et al.* (1992) observed that in the forest fringe of inselbergs, dominant species can be totally different from one site to another, although they are locat-

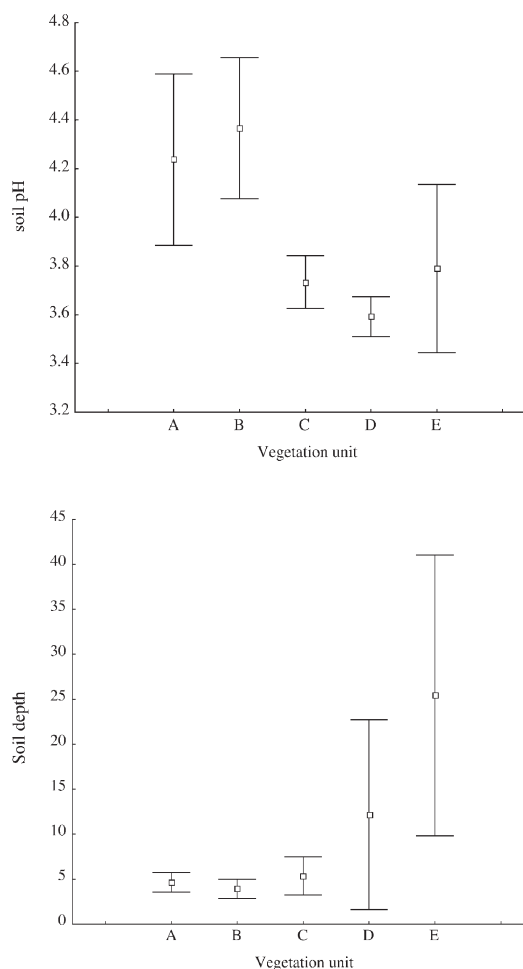


FIG. 4. — Plots showing the mean a) soil pH and b) soil depth for the five vegetation units. A : *Afrotrilepis* grasslands ; B : *Loudetiopsis glabrata* humid grasslands ; C : herbaceous and shrubby fringes ; D : *Memecylon collinum* and *Crema-sporea triflora* forest fringes ; E : *Garcinia epunctata* and *Coula edulis* saxicolous forests. Whisker = 95% confidence interval.

ed in very similar biotopes. This could be due to the isolated, even insular character of rainforest inselbergs, most of those dominant forest fringe species being (endo)zoochorous or autochorous without efficient long-distance dispersal mechanism. In their study of the vegetation of inselbergs from French Guyana, GASC *et al.* (1998) observed that some species were restricted to one inselberg or a group of inselberg and that the abundance of

any given species may greatly vary from one site to another.

The significant effect of the position relative to the lower or upper forest fringe on vegetation composition that we observed can also be explained by two main factors. Lower fringes may easily be colonised by rainforest species and receive a great quantity of runoff water coming from the slopes of the inselberg. Upper fringes on the other hand are more prone to fire.

INTERPRETATION OF THE RESPONSE OF AFROTILEPIS PILOSA AGAINST THE MAIN ECOLOGICAL GRADIENT

Afrotrilepis pilosa showed a significantly decreasing cover along the CCA axis 1 when tested with a generalized linear model analysis (Fig. 5, $p = 0.007$). This axis was negatively and positively correlated to soil depth and pH, respectively. *Afrotrilepis pilosa* grows on very shallow soil and is able to colonize bare inselberg rock. Due to several adaptations, *Afrotrilepis pilosa* resists the very high temperature and evapo-transpiration observed in this kind of habitat (SZARZYNSKI 2000). It is able to grow on steep rocky slopes, fully exposed to the sun. It spreads radially to

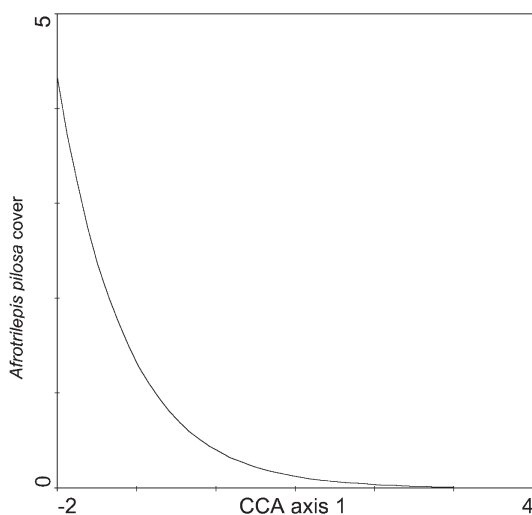


FIG. 5. — Response curve of *Afrotrilepis pilosa* along the CCA axis 1 based on a generalized linear model. The ordinate is the expected coefficient on the Braun-Blanquet scale: 1 = +, 2=1, 3=2, 4=3, 5=4, 6=5.

form almost monospecific mats that may be several hundreds years old (POREMBSKI *et al.* 1995). Those mats store rainwater and nutrients that would otherwise be rapidly lost by runoff (BIEDINGER *et al.* 2000). It is a poikilohydric species with a noteworthy capacity for recovering from drought. *Afrotrilepis pilosa* roots have a velamen radicum like those of many epiphytic species of Orchidaceae and Araceae (BIEDINGER *et al.* 2000). As a result of those adaptations, *Afrotrilepis pilosa* is highly competitive in its habitat and only leaves little space for the establishment of other species.

CONCLUSION

Amongst the variables considered in this study, the factors that explained the differences between vegetation units were soil depth, pH and the position relative to the lower or upper forest fringe. Although the three inselbergs are located very close to each other (100 to 500 m), their vegetation is however partly different. The reasons for these differences (e.g. limited dispersal, particular environmental factors, isolation) are not clear. Even if some common trends in vegetation composition, e.g. related to the above-mentioned factors could be found, each inselberg has its own plant species diversity and may be considered as island habitat in the rainforest. The presence of rare and endemic species and plant groups on the Piedra Nzas National Monument inselbergs and their function as refuge for xeric species in the rainforest, are valuable arguments to protect them for biodiversity conservation purposes. Moreover, they allow to address central questions of biodiversity research like minimum size of populations, species distribution in a discontinuous habitat or resistance of natural vegetation fragments to invasive species. Further investigations on these topics will be based on a much larger sample of inselbergs and will take additional environmental variables into account, such as inselberg area, elevation from the surrounding plains, geographical distance from villages and plantations and from other inselbergs, intensity of buffalo grazing, presence of invasive species, and type of the surrounding forest.

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