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REGULAR PAPER

Shrubby and forest fringe communities of the inselberg - rainforest ecotone in Atlantic Central Africa

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Background and aims – Inselbergs are rock outcrops standing out from the surrounding plains. In the rainforest landscape they can be considered as forming "xeric islands". Plants on inselbergs endure very harsh edaphic and microclimatic conditions. The inselberg - rainforest ecotone is characterized by the spatial transition from monocotyledonous mats and grasslands to an herbaceous fringe, a shrubby fringe, a forest fringe and a saxicolous forest. We describe here the plant communities of the shrubby and forest fringes of 25 sites in Southern Cameroon, Equatorial Guinea and Gabon. We identify their affinities with other inselberg plants communities described in West and Central Africa and evaluate their conservation value.
Methods – We used cluster analysis and ordination to classify 191 phytosociological relevés into plant communities, as well as the IndVal method to highlight the character species of each plant community.
Key results – A total of 709 vascular plant species and 394 morpho-species were recognized within the 191 plots. The four plant communities recognized correspond to three groups of inselbergs distinct by their geographical location, mean annual rainfall, altitude, rock substrate and the presence of buffaloes. They differ from plant communities described in other habitats in Central Africa and from the rock outcrop and inselberg plant communities described in West Africa. A limited number of species are restricted to the inselberg habitat or endemic to the study area.
Conclusions – Inselbergs contribute to the regional biodiversity through (i) the presence of some endemic species restricted to the inselberg habitat and to Atlantic Central Africa, (ii) the presence of species that inside the rainforest zone, can only be found on inselbergs, their main distribution being in the savannas or on mountains at higher elevations and (iii) their unique species assemblages. To preserve the inselberg flora and plant communities in Atlantic Central Africa, several sites and the surrounding rainforest should be protected within each of the three ecogeographical groups identified.

Key words – inselberg, insularity, forest fringe, vegetation, endemics, Central Africa, ecotone, IndVal, rainforest.

INTRODUCTION

Inselbergs are rocky outcrops standing out from surrounding plains, shaping more or less isolated hills or groups of hills. Environmental conditions on inselbergs can be extremely harsh for plant life. On the naked rock and shallow soils, rainfall is largely lost to runoff, limiting water retention. Moreover, a large proportion of solar radiation is absorbed at the rock surface causing high temperature and high evapotranspiration rates (Szarzynski 2000). On the contrary, there might be places on inselbergs where water flows and accumulates (i.e. down the slopes and in rock depressions). Steep inselberg slopes can also result in air humidity saturation at lower elevation than expected (Vesey-Fitzgerald 1940). Hence, inselbergs generate a range of microhabitats where ecological conditions contrast moderately to extremely from the surrounding landscape (the 'matrix'). The degree of contrast depends on the position of the local habitat along the inselberg-matrix ecotone, on topographic features as well as on the regional climate and edaphic characteristics of the matrix (Burke 2003). In the rainforest landscape, the inselberg - rainforest ecotone is characterized by very steep ecological gradients occurring on short distances (20 to 100 m):

increasing soil depth, soil and air humidity, water availability and decreasing light intensity. These gradients are correlated with a succession of plant formations (turnover in the relative abundance of life forms) and an important species turnover (Larpin 2001, Parmentier 2003, Parmentier et al. 2005). Microclimatic measurements realized along the inselberg-forest ecotone in Cote d'Ivoire (Szarzynski 2000) have shown that the maximum of global solar radiation on the forest floor of a dense, semi-deciduous, humid forest was only 5% of that on the adjacent inselberg (dry season values). On the inselberg, diurnal amplitude of air temperature (18–37°C) and relative humidity (28–100%) were extremely high while limited in the rainforest (18–26.5°C and minimum relative humidity 70%). Maximum temperature at the rock surface reached 55°C. Vapor pressure deficit, a very important water stress factor for plants, was four times higher on the inselberg than within the rainforest. Hence, in tropical rainforest landscapes, inselbergs can be regarded as habitat islands (Whittaker 1998) providing shelter for azonal vegetation types associated with azonal edaphic and climatic conditions.

Inselbergs have been used by humans for everyday life and for outstanding religious or profane purposes (Seine 2000). The intensity of these human uses and their consequences on the inselberg fauna and vegetation differ according to the region. In Atlantic Central Africa (ACA), this influence is moderate, with the exception of the inselbergs surrounding the Cameroonian capital Yaoundé. Inselbergs are used to dry food or clothes, to hunt, to collect worms used as baits for fishing etc. Hunters sometime set fire to the inselberg grasslands to hunt rodents. Inselbergs are also a source of rock and some inselbergs are used as artisanal or industrial quarries, the latter having a strong negative influence on the inselberg habitat (Parmentier 2001). Inselbergs can also be touristic attractions. Some sites have a Christian cross or statue at their summit and people climb there; other sites are regularly visited by naturalists. In several places in ACA, inselbergs are considered the ancestors' domain and are therefore sacred; special ceremonies are necessary to enter them (Villiers 1981).

Inselbergs play an important role for the fauna (Mares & Seine 2000). They harbour rock specialists such as the cock of the rock (*Rupicola rupicola*) in the Guyanas, the picatarthe (*Picathartes oreas*) in ACA, or bat colonies in inselberg caves and crevices, and they provide shelters, hunting and foraging sites for rainforest animals. In ACA, rainforest buffaloes frequently rest and graze in the inselbergs grasslands, and many animals like hornbills and monkeys feed on fruits in the rainforest-inselberg fringe. Rainforest inselbergs also are a refuge for species adapted to drier climatic conditions and they often harbour endemic plant and animal species (Villiers 1981, de Granville 1982, Reitsma et al. 1992, Mares & Seine 2000, Parmentier 2003).

Several authors have studied inselberg plant communities in West Africa and ACA. For a literature review, see Parmentier & Müller (2006) and Müller (2007). In ACA, six main plant formations, defined by their structural characteristics, are recognized along the ecotone. They typically form the following sequence from the surrounding forest to the bare rock (for a graphic presentation and more details, see Parmentier 2001): (1) a saxicolous forest that is fringing the inselberg where trees are generally smaller and the structure is more open than in the surrounding forest on deeper soils; (2) the forest fringe that has a width of about 5 m and is the part of the forest where lateral sunlight still reaches the ground. It is composed of small trees, shrubs, herbaceous species and epiphytes; (3) the shrubby fringe that is mainly composed of shrubs and a dense cover of lianas and herbaceous species; (4) the herbaceous fringe; (5) the grasslands, limited to sweeping zones and small depressions where humidity may be conserved between rainfall events; (6) the monocotyledonous mats constituted of *Afrotrilepis pilosa* (Cyperaceae), on shallow soils and on the bare rock. The same sequence of plant formations occurs at the summit of the inselberg in cases where it is covered by a saxicolous forest. These upper saxicolous forests act as water reserves. The water sweeps gently from them almost continuously during the rainy season, allowing hygrophilous species to grow on inselberg slopes and in the grasslands fringing these upper saxicolous forests. At a local scale, species composition is best explained by the spatial transition from one plant formation to another along the ecotone. At a regional scale, similar ecological niches along the ecotone are occupied by different species depending on the available local species pool (Parmentier et al. 2005, Parmentier & Hardy 2009).

Inselberg plant communities in ACA have been described for the monocotyledonous mats and the grasslands and herbaceous fringes (Parmentier et al. 2006, Parmentier & Müller 2006), but so far, plant communities in the shrubby and forest fringes have not been studied in detail at a large number of sites. Based upon our own data from 25 sites in three countries, we propose a description of the plant communities of the shrubby fringes and forest fringes on inselbergs in ACA. The ecology and the geographical distribution of the character species of these plant communities are discussed, and the influence of environmental variables and geographical location on the floristic composition are analysed. The plant communities are compared with the existing literature in West and Central Africa. The following questions and topics are discussed:

1. Are the plant communities similar in different ecogeographical regions of ACA?
2. What are the floristic affinities of these plant communities with those described on inselbergs in Central and West Africa?
3. Did endemic taxa evolve in inselberg shrubby fringes and forest fringes? What is the conservation value of these plant communities?

MATERIALS AND METHODS

Study area

The study area in ACA comprises parts of Equatorial Guinea, Gabon and Southern Cameroon (fig. 1). It extends approximately 270 km in longitude and 280 km in latitude and belongs to the Guineo-Congolian region, more precisely to the Lower Guinea subcentre of endemism (White 1983). Climate is equatorial. Annual rainfall is affected by the distance to the ocean and the altitude, ranging from 1625 mm to more than 2360 mm (WorldClim annual precipitation, Hijmans

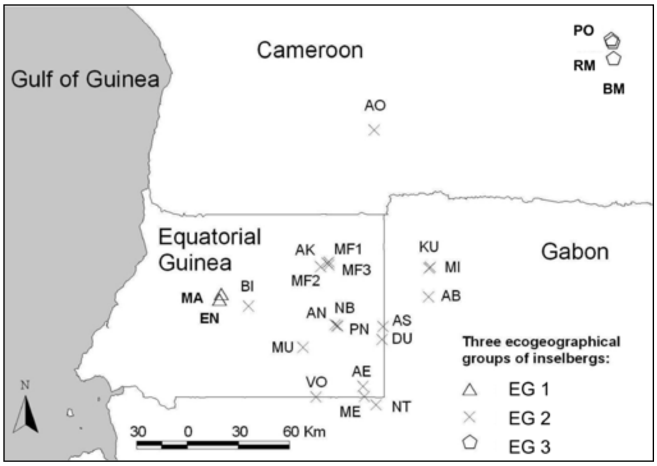

Figure 1 – Study sites: 25 inselbergs belonging to three ecogeographical groups.

et al. 2005). There are generally two dry months: July and August in the southern range of the study area, January and July in the central range, and December and January in the north-east. Temperatures remain between 23 and 26°C all year round. Inselbergs are scattered in the landscape. Some are isolated while others are grouped. Twenty-five inselbergs were included in this analysis (table 1). The altitude of the inselberg summits varies between 580 and 800 m a.s.l., and their elevation above the surrounding plains does not exceed 150 m. The rock outcrops of Monte Alén and Engong are exceptions as they are located in the Niefang mountain range at 1130 m altitude. They are surrounded by submontane forest (Senterre et al. 2004, Senterre 2005). All inselbergs consist of granitic rocks except in the Dja Faunal Reserve (Bouamir, Palme d'Or, Rocher Mba) where they are made of chloritic schist with quartzite (Letouzey 1968). Wild herds of buffaloes graze intensively the grasslands of the Dja Faunal Reserve and of the Monte Alèn and Engong rock outcrops.

Table 1 − Geographical location, characteristics and number of relevés for the 25 studied inselbergs.
CA = Cameroon; EG = Equatorial Guinea; GA = Gabon; A.R. = mean annual rainfall [mm]; Alt. = mean altitude above sea level [m]; N.R. = number of relevés; E.G. = ecogeographical group; Subs. = substrate; G = granite; S = schist.

Country	Name	Abbreviation	Coordinates	Alt.	N.R.	A.R.	E.G.	Subs.	Buffaloes
CA	Ako Okas	AO	02°43'N 11°16'E	690/750	10	1775	2	G	
CA	Bouamir	BM	02°43'N 12°48'E	650/730	11	1637	3	S	yes
CA	Palme d'Or	PO	03°18'N 12°47'E	620/660	5	1628	3	S	yes
CA	Rocher Mba	RB	03°17'N 12°48'E	615	1	1633	3	S	yes
EG	Akoak Ebanga	AE	01°04'N 11°12'E	570/590	7	1877	2	G	
EG	Akuom	AK	01°50'N 10°56'E	620	12	2004	2	G	
EG	Andom	AN	01°27'N 11°02'E	600/720	2	2027	2	G	
EG	Asoc	AS	01°27'N 11°20'E	600/640	12	1869	2	G	
EG	Bicurga	BI	01°35'N 10°28'E	610/775	18	2330	2	G	
EG	Dumu	DU	01°22'N 11°19'E	605/800	8	1871	2	G	
EG	Engong	EN	01°37'N 10°18'E	1080/1110	9	2362	1	G	yes
EG	Mfuin 1	MF1	01°52'N 10°59'E	590/650	5	1964	2	G	
EG	Mfuin 2	MF2	01°51'N 10°59'E	640/780	8	1975	2	G	
EG	Mfuin 3	MF3	01°52'N 10°58'E	660/680	4	1975	2	G	
EG	Monte Alén	MA	01°40'N 10°17'E	1100/1130	10	2354	1	G	yes
EG	Mungum	MU	01°19'N 10°49'E	705/760	7	2196	2	G	
EG	Ncoho Biworo	NB	01°28'N 11°01'E	635/800	4	2039	2	G	
EG	Piedra Nzas	PN	01°27'N 11°02'E	630/745	22	2027	2	G	yes
GA	Assep Bengong	AB	01°39'N 11°38'E	615/710	10	1782	2	G	
GA	Féné	FE	01°00'N 10°54'E	500/610	2	2039	2	G	
GA	Kum	KU	01°50'N 11°38'E	590/740	12	1762	2	G	
GA	Mengong	ME	00°57'N 11°17'E	670	2	1802	2	G	
GA	Miwa	MI	01°50'N 11°38'E	650/725	5	1762	2	G	
GA	Ntan	NT	01°00'N 11°13'E	600/790	4	1865	2	G	
GA	Voma	VO	01°00'N 10°54'E	600	1	2040	2	G	

The presence of buffaloes has several effects: grazing, trampling, transportation of seeds and excrements which result locally in higher nutrient concentrations. These inselbergs are surrounded by primary rainforests, secondary forests or fields. With the exception of stone quarries on two inselbergs (Miwa and Andom), and of touristic climbing on one inselberg (Koum), human activities on the inselbergs themselves are very limited (hunting paths). However, the proximity of agricultural fields results in some cases in the destruction of parts of the lower saxicolous forest and the forest fringe. Both, the proximity of fields and the presence of quarries increase the probability of fire events lit by humans and favour the intrusion of weeds. The 25 inselbergs belong to three ecogeographical groups (fig. 1, table 1) that were previously identified in Parmentier & Müller (2006): a) group 1, granitic rock outcrops in the Niefang mountain range, surrounded by submontane forest, intensively grazed by buffaloes; b) group 2, granitic inselbergs surrounded by lowland forest; c) group 3, schistose inselbergs surrounded by lowland, intensively grazed by buffaloes and with lower mean annual precipitation than ecogeographical group 2.

Data collecting and floristic nomenclature

Field work was carried out throughout the year, from 1998 to 2002. The floristic structure of the vegetation was documented with 191 phytosociological relevés from 25 sites. All relevés were located randomly in the inselberg shrubby fringes or forest fringes (stratified sampling). For each relevé, a species list was established and the plot size was increased until no new species could be added, or until the entire continuous patch occupied by the plant formation was investigated. Mean plot size was 122 m^2 (158 m^2 for forest fringes and 95 m^2 for shrubby fringes). The Braun-Blanquet scale (Barkman et al. 1964) was used to estimate the cover and abundance of each species. For part of the relevés, soil depth and vegetation height were measured. Soil depth corresponded to the average of three measurements at different places. Taxa were identified to species and morphospecies and at least one voucher specimen of each taxon was deposited in the Herbarium of the Université Libre de Bruxelles, Belgium (BRLU). We followed Lebrun & Stork (1991, 1992, 1995, 1997, 2003) and Kramer & Green (1990) for taxonomic names, but latest nomenclature has been checked on the IPNI (http://www.ipni.org/) and Missouri Botanical Garden websites (http://www.mobot.org/).

Data processing

A cluster analysis (abundance data) was run on the 191 relevés and 1103 species (UPGMA, Bray-Curtis distance) with the MVSP 3.1 software (Kovach Computing Services 2004). The resulting hierarchical tree was analyzed in the light of our field observations and adapted to reach a final classification of the plots. To determine the diagnostic species for each level of this hierarchical classification, we used the indicator method of Dufrêne & Legendre (1997). This method (IndVal) calculates an indicator value (IV) for each species in relation to a given pre-defined group of relevés. It is an integrated measure for the relative mean abundance and the relative frequency of the species in each group. Only species that have both a high mean abundance and are present in the majority of the relevés in a group will score a high IV for that particular group. To test whether the observed IV of a species in a group was higher than it could be expected based on a random distribution of individuals over the locations, the observed IV was compared with 999 randomly generated IVs. Species present with one individual and in one plot only were not entered into this analysis. A synoptic table was produced and the plant communities were compared with the existing phytosociological literature. Relevés were ordinated to characterize the main floristic gradients (DCA). The DCA was run with CANOCO for Windows 4.0 (ter Braak & Šmilauer 2002). Information about the distribution and ecology of character species was extracted from the Flora of West Africa (Hutchinson & Dalziel 1954–1972), Flora of Cameroon (Aubréville et al. 1961–1999), Flora of Gabon (Aubréville et al. 1963–1998), Flora of Senegal (Bérhaut 1971–1988), Lebrun & Stork (2003, 2006), the Missouri Botanical Garden website, and Senterre (2005), the latter based on extensive field work in the area.

RESULTS

A total of 709 vascular plant species have been identified. Additionally, 394 morpho-species were recognized (see appendix 1). Fifty percent of the species and morpho-species were found in more than one relevé, the others are considered occasional. Within the 709 identified species, 455 are non occasional. The first floristic gradient in the DCA, which also corresponds to the three ecogeographical groups (fig. 2), is negatively correlated to rainfall and altitude. The second ordination axis is correlated to the plant formation (shrubby fringe or forest fringe), i.e. to the position along the inselberg - rainforest ecotone. The low percentage of the floristic variance represented by the two first axes (4%) is due to the large number of relevés and species.

In the cluster analysis, the most important divisions divided the data set in groups of relevés according to the three ecogeographical groups and to the plant formation (appendix 2). We subdivided ecogeographical group 2 into plots belonging mostly to forest fringes or mostly to shrubby fringes. We did not consider further subdivisions within the relevés from ecogeographical groups 1 and 3 to avoid the description of communities from a low number of plots. Taking into account statistical results and our knowledge of the field, the plots could be assigned to a hierarchical system of plant communities. A synoptic table of these plant communities and their characteristic species is presented in table 2. The full table is available in the appendix 1.

Relevés from shrubby fringes (*sf*) and from forest fringes (*ff*) differ significantly (ANOVA $p < 0.001$) in their mean vegetation height (*sf* 5.0 m, N = 101; *ff* 12.9 m, N = 64) and in their mean soil depth (*sf* 7.5 cm, N = 84; *ff* 15.9 cm, N = 59).

Ecogeographical groups 1 and 2

Ten character species are common ecogeographical groups 1 and 2 (table 2, col. 1 to 6).

Table 2 − Synoptic table of the plant communities of shrubby and forest fringes in inselbergs of Atlantic Central Africa.
Indicator value of the species (IV) and value of the test, frequency classes (I to X, each 10% wide), mean cover (MC). Only character species are given.

column n°			1	2	3	4	5	6	7	8
community			**A**		**B1**		**B2**		**C**	
total number of relevés			19		73		82		17	
total number of identified species			280		437		327		152	
mean number of species and morphospecies per plot			50		37		26		29	
mean plot size (m2)			360		264		74		75	
	IV	**test**	**fr.**	**MC**	**fr.**	**MC**	**fr.**	**MC**	**fr.**	**MC**
Ecogeographical groups 1 and 2										
Nephrolepis biserrata (Sw.) Schott	59	**	VI	2.03	V	7.71	VII	16.11		
Memecylon collinum Jacq.-Fél.	44	**	VI	4.37	I	9.03	IV	6.38		
Lannea nigritana (Scott-Elliot) Keay	38	**	I	0.79	IV	1.93	I	2.97		
Schefflera barteri (Seem.) Harms	28	*	VII	1.26	IV	2.12	I	1.57		
Rhaphidophora africana N.E.Br.	27	*	IV	0.84	V	4.10	I	0.76		
Calvoa pulcherrima Gilg ex Engl.	45	**	II	0.39	IV	2.51	VI	5.89		
Asplenium africanum Desv.	19	NS	III	0.53	IV	1.57	I	0.16		
Jasminum dichotomum Vahl	18	NS	II	0.32	I	0.70	III	2.50		
Calvoa monticola A.Chev. ex Hutch. & Dalziel	17	NS	III	1.84	III	1.37	I	0.73		
Emilia lisowskiana C.Jeffrey	16	NS	II	0.32	II	0.45	II	0.71		
Ecogeographical group 1										
Rauvolfia vomitoria Afzel.	87	**	IX	3.66	I	0.08	I	0.01		
Costus dinklagei K.Schum.	73	**	VIII	7.26	I	0.05				
Asplenium dregeanum Kunze	62	**	VII	4.13	I	0.07				
Kinghamia nigritana (Benth.) C.Jeffrey	60	**	VII	6.84	I	0.82	I	1.83		
Dissotis thollonii Cogn. var. *thollonii*	58	**	VI	22.24						
Oncoba glauca (P.Beauv.) Planch.	58	**	VII	7.08	I	0.06			II	0.18
Megaphrynium macrostachyum (Benth. & Hook.f.) Milne-Redh.	53	**	VII	2.95	I	0.35	I	0.22	II	0.29
Hypselodelphys violacea (Ridl.) Milne-Redh.	52	**	VII	4.66	II	1.24	I	0.44		
Mikania chenopodifolia Willd.	49	**	VI	1.24	I	0.12	I	0.07		
Costus letestui Pellegr.	47	**	VI	8.74	I	0.89	I	1.23		
Ecogeographical group 2										
Sterculia tragacantha Lindl.	40	**			VII	5.66	IV	1.46	II	0.18
Costus lucanusianus J.Braun & K.Schum. var. *major* K.Schum.	26	**			III	0.97	III	2.41		
Euphorbia letestui J.Raynal	25	**			II	2.99	I	9.22		
Cissus aralioides (Welw. ex Baker) Planch.	19	*			III	0.49	I	0.37		
Forest fringes in ecogeographical group 2										
Garcinia punctata Oliv.	24	**	I	0.13	IV	2.34	I	0.45		
Julbernardia letouzeyi J.F.Villiers	23	**			III	9.62	I	0.02		
Palisota ambigua (P. Beauv.) C.B.Clarke	22	**	I	0.26	IV	0.76	I	0.13		
Phyllanthus odontadenius Müll. Arg.	19	**			III	0.51	I	0.14		
Cremaspora triflora (Thonn.) K.Schum.	18	**			III	4.26	I	0.68		
Allophylus welwitschii Gilg	18	**	I	0.05	III	0.92	I	0.37		
Brillantaisia debilis Burkill	18	**	I	0.13	III	0.88	I	0.46		
Shrubby fringes in ecogeographical group 2										
Clappertonia polyandra Bech.	49	**			IV	2.90	VIII	19.01	II	5.44
Pellaea holstii Hiern	30	**					IV	3.46	I	0.15
Virectaria herbacoursi N.Hallé var. *petrophila* N.Hallé	23	**					III	2.07		
Hymenodictyon biafranum Hiern	21	**			I	1.11	III	4.99		

Table 2 (continued) − Synoptic table of the plant communities of shrubby and forest fringes in inselbergs of Atlantic Central Africa.

column n°			1	2	3	4	5	6	7	8
community			**A**		**B1**		**B2**		**C**	
total number of relevés			19		73		82		17	
total number of identified species			280		437		327		152	
mean number of species and morphospecies per plot			50		37		26		29	
mean plot size (m2)			360		264		74		75	
	IV	**test**	**fr.**	**MC**	**fr.**	**MC**	**fr.**	**MC**	**fr.**	**MC**
Ecogeographical group 3										
Erythroxylum emarginatum Thonn.	77	**			I	3.18	I	0.50	IX	23.68
Anchomanes difformis (Blume) Engl.	60	**	I	0.05	II	0.18	I	0.08	VII	5.79
Pellaea doniana Hook.f.	60	**			IV	1.45	II	1.16	IX	6.32
Costus lucanusianus J.Braun et K.Schum.	55	**			I	1.03	I	0.46	VII	7.79
Markhamia tomentosa (Benth.) K.Schum. ex Engl.	53	**							VI	5.41
Urena lobata L.	53	**							VI	5.65
Streptogyne crinita P.Beauv.	51	**			I	0.07	I	0.03	VI	2.79
Cissus dinklagei Gilg & M.Brandt	38	**	I	0.05	I	0.08	I	0.46	V	0.94
Costus afer Ker Gawl.	36	**			I	0.75	I	0.21	V	1.68
Other grasslands and herbaceous fringes of inselberg										
Habenaria procera (Afzel. ex Sw.) Lindl.			III	0.29	II	0.51	V	3.63	III	0.50
Scleria melanotricha Hochst. & A.Rich.			II	0.39			I	0.73		
Utricularia andongensis Hiern			I	0.26						
Torenia dinklagei Engl.			V	7.24						
Justicia amanda Hedrén subsp. *saxatilis* Champl. & I.Parm.			I	0.26						
Ischaemum indicum (Houtt.) Merr.			II	5.39						
Lipocarpha chinensis (Osbeck) Kern			I	0.26						
Rubus pinnatus Willd.			III	0.53	I	0.01				
Virectaria belingana N.Hallé					I	0.79	II	1.77		
Solenangis scandens (Schltr.) Schltr.			I	0.13	III	1.31	IV	3.12	II	1.18
Plectranthus occidentalis B.J.Pollard					III	2.22	IV	5.10		
Tricarpelema africanum Faden					I	0.31	III	0.84		
Phymatosorus scolopendria (Burm.f.) Pic.Serm.			II	0.39	VI	4.64	VI	7.07	I	0.15
Loudetiopsis glabrata (K.Schum.) Conert							I	0.66		
Antherotoma irvingiana (Hook.) Jacq.-Fél.					I	0.01	I	0.29		
Actinoschoenus filiformis (Thwaites) Benth.							I	0.70		
Justicia insularis T.Anders.			II	0.32	I	0.84	I	3.98		
Epistemma rupestre H.Huber					I	0.07	I	0.58		
Plectranthus inselbergi B.J.Pollard & A.J.Paton			II	0.39			III	1.85		
*Afrotrilepis pilos*a (Boeckeler) J.Raynal							I	3.47		
Oreonesion testui A.Raynal							II	0.71		

Plant communities in this group are distributed in Equatorial Guinea, in North Gabon and in the Ebolowa region in Cameroon. Mean vegetation height of the stands is 8 m and mean soil depth is 11 cm. *Memecylon collinum* and *Calvoa pulcherrima* are restricted to the inselberg habitat and to the Lower Guinea region (Parmentier 2005). *M. collinum* is a small tree with small coriaceous leaves. *C. pulcherrima* is a chamaephyte up to 1 m high with slightly succulent stems and leaves. *C. monticola* is also almost restricted to the inselberg habitat but can also be found on other types of rocks in the forest. It can either live on the ground or as an epiphyte. *Schefflera barteri* is typical for the submontane and montane belts. *Nephrolepis biserrata* is a pantropical species common in fallows and secondary forest. Its presence in some inselberg plant communities may be related to fire events (Mutch 1970). It can be an epiphyte or grow directly on shallow soils on the rock.

Ecogeographical group 1, Community A – (table 2, col. 1 to 2). Ten character species are identified in ecogeographical group 1. This is the community of shrubby and forest fringes on rock outcrops in the Niefang Mountain range. It is so far documented with relevés from the rock outcrops of Monte

Alèn and Engong at an altitude around 1100 m with mean annual rainfall of around 2350 mm. Mean vegetation height is 10 m and mean soil depth is 8 cm. *Rauvolfia vomitoria* and *Asplenium dregeanum* are distributed in the Guineo-Congolian region. *R. vomitoria* is a small pioneer tree. *A. dregeanum* is an epiphyte also occurring in cloud forests of the submontane and montane belts. *Costus dinklagei* is a geophyte distributed in Lower Guinea in swamp forest. *Dissotis thollonii* var. *thollonii* is known from humid grasslands in the Guineo-Congolian region. The habitat of this plant community is characterized by a high degree of atmospheric and soil humidity and epiphytes are numerous (field observations).

Ecogeographical group 2, Community B – (table 2, col. 3 to 6). This group of relevés assembles the shrubby and forest fringes on inselbergs in ecogeographical group 2 (rainfall 1750–2200 mm, altitude 570–800 m) and counts four character species. *Sterculia tragacantha* has a large distribution in tropical Africa. It is a medium size tree commonly found in secondary forests and at forest edges. It generally sheds its leaves during the dry season. *Euphorbia letestui* is restricted to the inselberg habitat and is only known from Cameroon, Equatorial Guinea and Gabon. It is a succulent euphorbia that can reach 4 m height. This group has been further subdivided in two sub-communities: one corresponding mostly to forest fringes and the other mostly to shrubby fringes (appendix 3).

Community B1: Forest fringes in ecogeographical group 2 (table 2, col. 3 to 4). This community is so far documented from inselbergs and rock outcrops below 800 m altitude in Equatorial Guinea, North Gabon and in the Ebolowa region in Cameroon. Mean vegetation height is 11 m, mean soil depth is 16 cm. It counts seven character species. *Julbernardia letouzeyi* is a medium size tree only known from the inselberg - rainforest fringes in Gabon, Equatorial Guinea and Cameroon. It can be locally dominant in the forest fringe.

Community B2: Shrubby fringes in ecogeographical group 2 (table 2, col. 5 to 6). It counts four character species. Mean vegetation height is 8 m and mean soil depth 13 cm. *Clappertonia polyandra* can be found in riverine and swamp forest, fallows and at the edges of woods. It is common on inselbergs where it can form dense stands in the shrubby fringe. It is able to survive fire events. Indeed, we observed a large number of seedlings growing through the ashes of burned vegetation. *Pellaea holstii* is a xerophytic species growing on different types of rocks exposed to the sunlight. *Virectaria herbacoursi* var. *petrophila* is endemic from inselbergs in Gabon and Equatorial Guinea. *Hymenodictyon biafranum* is a small tree typical for inselbergs and rock outcrops in Lower Guinea. It can also be found on cliffs in submontane forests and can occasionally be an epiphyte.

Ecogeographical group 3

Ecogeographical group 3, Community C: Shrubby and forest fringes – (table 2, col. 7 to 8). This community is known from the rock outcrops of the Dja Fauna reserve in south Cameroon. Rainfall is around 1630 mm and altitude 600–750 m.

Its nine character species are widespread in tropical Africa or more generally in the tropics, except *Pellaea doniana* that is distributed in the Guineo-Congolian region and is always found on shaded rocks. Mean vegetation height is 6 m and mean soil depth is 8 cm.

Note that table 2 also includes species typical for the grasslands and herbaceous fringes that are often present in the ground layer of the shrubby and forest fringes.

DISCUSSION

Floristic affinities with other plant communities in Central and West Africa

Only few species considered as character species for the shrubby fringes and forest fringes in ACA appear in described plant communities of West Africa: *Schefflera barteri*, *Asplenium dregeanum*, *Markhamia tomentosa*, *Sterculia tragacantha*, and *Costus lucanusianus* var. *major*. *Markhamia tomentosa* is described as a pioneer forest species on granitic outcrops in W. Nigeria (Hambler 1964) and as common on inselbergs in the Taï National Park in S. Côte d'Ivoire (Porembski et al. 1996). *Schefflera barteri* is cited from low-growing mountain forests in the Fon and Fouta Djallon mountain chains in Guinea by Schnell (1952). This author also names the epiphytic fern *Asplenium dregeanum* a character species for the mountain forests in West Africa, but *Parinari excelsa*, the dominating tree species in these West African mountain forests, is missing in our relevés. Although there are some structural similarities between these forests and the forest fringes described in this paper (such as the presence of epiphytic orchids, ferns, and mosses), there are practically no floristic parallels on the species level between West African mountain forests and our relevés from ACA. Looking at the genus level, several genera like *Gaertnera* (Rubiaceae), *Memecylon* (Melastomataceae), *Habenaria* (Orchidaceae), *Peperomia* (Piperaceae) and *Garcinia* (Clusiaceae) can be named as common to West and Central Africa. An interesting vicariance is that of succulent euphorbia species that have also been described from other areas, e.g. from Nigeria (Richards 1957), the Ethiopian Simen mountains (*Euphorbia abyssinica*) (Puff & Nemomissa 2001), Rwanda (*Euphorbia dawei*) and Cameroon (*Euphorbia kamerunica*) (Noumi & Akoa 2003). In his PhD thesis about the Nkoltsia inselberg in S. W. Cameroon, Villiers (1981) described a plant community with *Euphorbia letestui*, *Eugenia afzelii* (not present in our data set) and *Hymenodictyon floribundum*. The two most common and prevailing herbaceous species in the ground layer in this unit are *Loudetiopsis glabrata* and *Afrotrilepis pilosa*. Both species are characteristic for herbaceous plant communities of inselbergs in ACA (Parmentier & Müller 2006, Parmentier et al. 2006). Villiers (1981) also described a two layered saxicolous forest community ("Forêt basse claire") dominated by *Julbernardia letouzeyi*. He described *Schefflera barteri* as a characteristic species of this community. Ngok Banak (2006) studied the vegetation of the Milobo inselberg in northern Gabon with a particular attention to the saxicolous forests on shallow soils on the inselberg slopes and on the summit plateau. In the tree canopy and the second tree layer, *Julbernardia letouzeyi* turned out to be the most frequent and aspect-forming species and *Memecylon collinum* was abundant in the forest fringe.

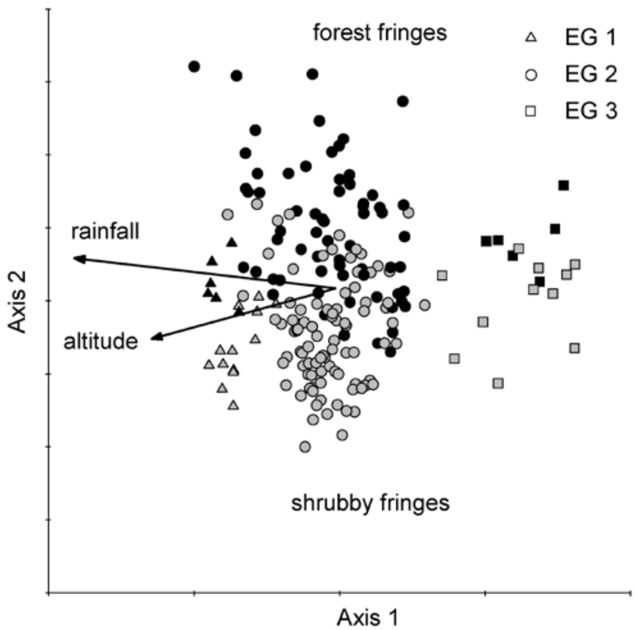

Figure 2 – DCA of 191 vegetation plots and 1103 species and morphospecies in shrubby fringes and forest fringes of the inselberg - rainforest - grassland ecotone. Axes 1 and 2 represent respectively 2.3% and 1.7% of total variability. Altitude and rainfall are passive variables in the analysis. Black symbols are forest fringes and grey symbols are shrubby fringes. Symbol shapes vary according to the three ecogeographical group (EG).

Factors differentiating the plant communities at the local and regional scale

At the regional scale, the main floristic gradient is correlated to spatial variables, to altitude and to annual rainfall; differentiating the three ecogeographical groups previously defined in Parmentier & Müller (2006) (see figs 1 & 2). With a limited number of families, when comparing plots belonging to the same plant formation, Parmentier et al. (2005) showed that floristic similarity between plots decreased with increasing spatial distance. The origin of this pattern as a result of limited species dispersal (cf. neutral theory, Hubbell 2001) or as a result of spatial autocorrelation of environmental conditions among inselbergs was difficult to assess. Indeed, the geographical scale of variation of environmental variables and species data were similar. However, following the analysis of the evolution of the phylogenetic structure of inselberg plant communities according to ecological and spatial distance, Parmentier & Hardy (2009) were able to demonstrate that dispersal limitation is probably responsible for that pattern rather than regional ecological gradients.

Within an ecogeographical group, the position along the inselberg - rainforest ecotone is the main determinant of plant communities (axis 2 in fig. 2): shrubby fringes and forest fringes differ in their floristic composition. The floristic difference is accompanied by a physiognomic difference: the mean vegetation height of shrubby fringes is less than half of that of forest fringes. This is reflecting the ecological gradients along the inselberg - rainforest ecotone, particularly the variation of soil depth, which is lower in the shrubby fringes than in the forest fringes. Soil depth has been recognized as the main factor controlling the variability of inselberg vegetation in several tropical regions (i.e. Richards 1957, Reitsma et al. 1992, Sarthou 2001, Oumorou & Lejoly 2003). Although the two plant formations can be distinguished in the field from their physiognomy, the transition from the shrubby fringe to the forest fringe is progressive (fig. 2) and there are plots that cannot be attributed to the one or to the other plant formation. Note also that it is possible to distinguish the plant communities from the shrubby fringes from those of the forest fringes in ecogeographical groups 1 and 3 but that we decided not describe these separately because of the low number of plots available.

Ecology, conservation value and distribution of the component species

Most of the species present in the inselberg forest and shrubby fringes are also cited from different ecological contexts. However, there are species limited to the inselberg habitat, some of which are also endemic to ACA, including for example *Euphorbia letestui*, *Polyscias aequatoguineensis*, *Memecylon collinum*, *Julbernardia letouzey* and *Calvoa pulcherrima*... These endemics are estimated to represent less than 10% of the number of species in the inselberg flora but can be very abundant locally and structure the inselberg plant communities (Reitsma et al. 1992, Parmentier 2005). Precise numbers of endemics are difficult to assess because the knowledge of the flora of our research area is incomplete. To establish the ecology and geographical distribution of all species, searches in the literature and in herbaria are needed. Reitsma et al. (1992) estimated that 6% of the species were endemic to inselbergs and rock outcrops in the Cameroon-Gabon region. In a study limited to Melastomataceae species, Parmentier (2005) found three species (out of 37) limited to rocky outcrops in the Lower Guinea subcenter of endemism. In a study focusing on Rubiaceae, Degreef et al. (2006) found two species and one variety restricted to inselbergs and rock outcrops in Lower Guinea. Note that the shrubby fringes share many herbaceous species and lianas with the inselberg herbaceous fringes and grasslands, some of which are also restricted to the inselberg habitat and to ACA (for more details see Parmentier & Müller 2006).

Several species have a larger distribution and ecology or are typical for other biotopes, but characterize inselbergs in our study area. As an example, *Hymenodictyon floribundum* can be found from 500 to 1850 m a.s.l. in savanna, woodland, moist evergreen forest and mountain forest in the whole Sudano-Zambezian area. However, in the African rainforests, this species characterizes rock outcrops and inselbergs. *Schefflera barteri*, *Asplenium dregeanum*, *Polyscias fulva* and *Olea capensis* subsp. *hochstetteri* are characteristic for the submontane and lower montane belts of African rainforests. The presence of these submountain and mountain hygrophilous species at a lower altitude in the inselberg fringes might be explained by the fact that rock faces or steep slopes are locally responsible for air humidity saturation at lower elevation than expected (Vesey-Fitzgerald 1940, Senterre 2005). Many light demanding species of open forest habitats and river borders like *Lannea nigritana*, or secondary forest species like *Musanga cecropioides*, *Alstonia boonei*, *Bridelia* *micrantha* or *Sterculia tragacantha* are abundant in shrubby and forest fringes. Species from dense, humid, semi-deciduous lowland forests are also present, i.e. *Piptadeniastrium africanum*, *Celtis zenkeri*, *Tabernaemontana crassa*, or *Turraeanthus africanus*. Epiphytes or facultative epiphytes are abundant in the inselberg fringes. It is not rare to find trunks or branches still carrying epiphytes that have fallen from the adjacent shrubby and forest fringes into the herbaceous fringes. It is one of the ways by which facultative epiphytes colonize the herbaceous fringes (Stévart 2003). Ecologically, this phenomenon is explained by the similarity of environmental conditions on the rock and on the inselberg rainforest ecocline with environmental conditions encountered by epiphytes in the upper part of the forest canopy (shallow organic substrate, high insulation, see Reitsma et al. 1992 for more details).

There is no doubt that inselberg shrubby and forest fringes have a high conservation value. They contribute to the regional biodiversity through (i) the presence of species endemic to ACA or restricted to the inselberg habitat, (ii) the presence of species that inside the rainforest zone, can only be found on inselbergs, their main distribution being in the savannas or in mountains at higher elevations and (iii) the unique inselberg shrubby and forest fringes plant communities described in this paper. Inselberg fringes are particularly vulnerable to the cultivation of fields at the inselberg foot. The fringe might be completely destroyed (slash and burn cultivation), be indirectly affected by the introduction of weeds and invasive plants or be submitted to an increased frequency of fires. Similar dangers arise from the presence of artisanal stone quarries. Industrial quarries can even completely destroy an inselberg. An efficient conservation strategy of the inselberg ecosystem in ACA should include the preservation of at least three inselbergs groups, one in each of the identified ecogeographical group. The rainforest surrounding these inselbergs should also be preserved to avoid the destruction or alteration of the inselberg rainforest fringes and to keep the insular character of the rainforest inselberg habitat.

SUPPLEMENTARY DATA

Supplementary data are available at *Plant Ecology and evolution*, Supplementary Data Site (http://www.ingentaconnect.com/content/botbel/plecevo/supp-data), and consist of the following: (1) the full synoptic table with 1103 species and morphospecies (pdf format); (2) the result of the cluster analysis of all 191 plots and 1103 species and morphospecies (pdf format); (3) the DCA of the 155 vegetation plots and 844 species and morphospecies in ecogeographical group 2 (pdf format).

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