Anales Inst. Biol. Univ. Nac. Autón. México, Ser. Bot. 67(1): 73-86. 1996

DIVERSITY, LIFE STRATEGIES, ORIGINS AND DISTRIBUTION OF TROPICAL INSELBERG BRYOPHYTES

JAN-PETER FRAHM*

RESUMEN

La brioflora de los "inselbergs" de Costa de Marfil y de Zimbabwe contiene 31 y 25 especies, respectivamente. Ocho especies, siete géneros y tres familias son comunes en los inselbergs de ambos países. El número de briofitas no está correlacionado con el tamaño o elevación de los inselbergs. En Costa de Marfil hay más briofitas sobre los inselbergs de las sabanas que en los de bosques lluviosos. En ambos países cerca del 30% de las briofitas son de distribución pantropical, africano-tropical y sudanés-zambesiana; el 12-13% son especies cosmopolitas. La falta aparente de reproducción sexual y de propagación vegetativa es conspicua entre los musgos de los inselbergs; también es notable el pequeño porcentaje de especies con adaptaciones morfológicas o anatómicas a este hábitat extremo. En comparación con las angiospermas, las briofitas de los inselbergs pertenecen a elementos fitogeográficos grandes y no incluyen especies endémicas. En los dos grupos la mayoría de las especies pertenecen a unas cuantas familias; los inselbergs de las sabanas son más ricos en especies que los bosques lluviosos. Las fanerógamas de los inselbergs son principalmente anemócoras o zoócoras; en cambio, los musgos son "ácoros", sin predominio de métodos sexuales o vegetativos de propagación.

Palabras clave: inselberg, África tropical, diversidad, conservación, brioflora.

ABSTRACT

The bryophyte flora of inselbergs in Ivory Coast and Zimbabwe consists of 31 and 25 species, respectively. Eight species, seven genera and three families are common on inselbergs in both countries. The number of species of bryophytes on inselbergs is not correlated with their size or their elevation. In Ivory Coast, more bryophyte species are found on inselbergs in savanna regions than in rain forest regions. In Ivory Coast and Zimbabwe, roughly 30% of the bryophytes are

* Botanisches Institut der Rheinischen Friedrich-Wilhelms-Universität, Meckenheimer Allee 170, D 53115 Bonn, Germany.

pantropical, tropical African and Sudano-Zambesian in distribution; 12-13% are cosmopolitan species. The apparent lack of sexual and vegetative propagation is conspicuous in inselberg mosses as is the small percentage of species that show specialized anatomical or morphological adaptations to this extreme habitat. Compared to flowering plants, inselberg bryophytes belong to larger phytogeographical elements and have no endemic species. In flowering plants and in bryophytes most species belong to a few families and inselbergs in savanna regions are richer in species than those in rain forest regions. Whereas inselberg phanerogams are mostly anemo- or zoochorous, inselberg mosses are "achor" showing predominantly neither sexual nor vegetative means of propagation.

Key words: inselberg, tropical Africa, diversity, conservation, bryophyte flora.

INTRODUCTION

Inselbergs are isolated monolithic mountains or rocks that rise abruptly from surrounding plains. They exist in all climates but their origin is connected with tropical or subtropical, semiarid or humid conditions, especially in semiarid regions where they are in sharp contrast with the surrounding plains. Inselbergs originate when rocky outcrops with a slow erosion are situated in plains with a strong denudation. Inselbergs may consist of various rocks but mainly of granite or gneiss that erode to dome-shaped forms. Therefore inselbergs are mainly distributed in the Paleozoic shields of the Old and New Worlds. The age of individual inselbergs can be several million years and some are pre-Tertiary in age. Their size, the distance to the next inselberg and also their elevation is variable. Inselbergs can be as high as 100 m or only a few meters above the surroundings (shield-inselbergs). Because of their genesis by slow erosion and the rapid denudation of the surroundings, their age is correlated with the elevation: the older the inselberg the higher. More important is that inselberg vegetation is very different from that of the surroundings. Thus inselbergs are models for island ecology. Their isolated occurrence raises questions concerning the dispersal of species and the age and origin of the species; the extreme ecological conditions provide interesting insights on the structural adaptations and their old age provides stable ecological conditions over long periods.

Inselbergs bear numerous habitats such as forests, open rocks, wet flush areas, fissures, rock pools and swamps. Inselbergs located in savannas are usually unaffected by savanna fires. Because of their open rocky surface, inselbergs are relatively rich in cryptogams, with lichens dominanting the presumably drier inselbergs, cyanobacteria in the wetter ones. The latter probably have a strong impact on the nutrient supply of the nutrient poor rocks.

The vegetation of tropical inselbergs is being studied at the Botanical Institute of the University of Bonn within the framework of a research project on tropical ecology supported by the German Research Foundation. Inselberg studies have

been performed in Venezuela, French Guiana, Brazil, Ivory Coast, Senegal, Guinea, Madagascar and Zimbabwe (Barthlott, Gröger and Porembski, 1993; Porembski and Barthlott, 1992a, 1992b; Porembski *et al.*, 1994)

Within this project, bryophytes were collected in Ivory Coast, Senegal and Guinea (Frahm and Porembski, 1994). The floristic account revealed 43 new records of species for these countries. Since that report, additional collections of bryophytes were made in Ivory Coast, Zimbabwe, the Seychelles and, to a smaller extent, in Venezuela. Although the main goal of the project was devoted to phanerogams, these collections give a first idea of the diversity, life strategies, structural adaptations, fertility, dispersal, origin and distribution of bryophytes from inselbergs. They also allow interesting comparisons with the results of the phanerogamic studies.

The following study is based on an evaluation of the bryophyte collections from inselbergs in Ivory Coast and Zimbabwe.

Part of the floristic data from Ivory Coast were already published (Frahm and Porembski, 1994); additional records included here are based on collections from Ivory Coast made by S. Porembski and N. Biedinger in September 1993. The inselbergs in Ivory Coast are situated in part in the rain forest belt, in part in the savanna belt. The length of rainy season and the precipitation decrease from S to N. The annual precipitation in the south is 2300 mm, the dry season is 2-4 months; in the north precipitation is only 900-1600 mm and the dry season lasts up to 8 months (Anhut, 1994; Eldin, 1971). The inselbergs are formed by pre-Cambrian rocks (Wilson, 1968) and are situated in elevations between 100 and 400 m.

The inselberg specimens from Zimbabwe were collected from April to July 1993 and November to April 1994 by R. Seine. The rainy season lasts between three and seven months and the precipitation between 300 and 1700 mm (Wilson, 1968). The vegetation consists of dry deciduous forests; in the mountains of the east there are also evergreen forests (Wild and Fernandes, 1967). Zimbabwe is situated on the pre-Cambrian shield consisting of granite and gneiss, like in Ivory Coast, with elevations between 400 m and 2500 m.

The results of the study of collections from Ivory Coast as well as the collections from Zimbabwe are being published separately (Frahm *et al.*, in prep.).

The species of inselberg forests, especially the epiphytic species, are not considered, since they are not always present and are presumably of less interest because of their lack of inselberg characteristics.

The general remarks on the ecology of inselbergs as well as on the phanerogamic flora are taken from Barthlott, Porembski *et al.* (1993).

FLORISTIC DIVERSITY

The bryophyte species of the surroundings were not studied during the inselberg projects. Therefore the floristic contrast between the inselbergs and the surround-

ing savannas could not be determined. In Ivory Coast, 36 bryophyte species (two hornworts, seven liverworts and 27 mosses) were obtained on inselbergs according to records by Frahm and Porembski (1994) and other unpublished records. These species are:

Anthoceros sp., *Notothylas* aff. *javanica* (Sande Lac.) Gott., *Riccia discolor* L. & L., *R. cf. fluitans* L., *R. lanceolata* Steph., *R. moenkemeyeri* Steph., *R. cf. radicosa* Pears., *Caudalejeunea hanningtonii* (Mitt.) Schiffner, *Lejeunea caespitosa* Lindenb., *Archidium globiferum* (Brid.) Frahm, *Garckea moenkemeyeri* C. Müll., *Campylopus savannarum* (C. Müll.) Mitt., *Octoblepharum albidum* Hedw., *Calymperes erosum* C. Müll., *C. palisotii* Schwaegr., *Syrrhopodon planifolius* P. Varde, *Anoectangium aestivum* (Hedw.) Mitt., *Hyophila involuta* (Hook.) Jaeg., *Trichostomum brachydontium* Bruch, *Funaria calvescens* Schwaegr., *Brachymenium acuminatum* Harv., *B. exile* (Dozy & Molk.) Bosch & Lac., *Bryum arachnoideum* C. Müll., *B. depressum* C. Müll. ex Broth., *Haplodontium cf. ovale* (Mitt.) Broth., *Plagiobryum zierii* Lindb., *Philonotis cf. mniobryoides* Broth., *P. hastata* Duby, *P. strictula* Card., *Erythrodontium squarrosum* (Hampe) Par., *Trachyphyllum dusenii* (Broth.) Broth., *Entodontopsis tenuinervis* (Broth. & Par.) Buck & Irel., *Stereophyllum radiculosum* (Hook.) Mitt., *Sematophyllum fulvifolium* Mitt. and *Vesicularia* sp.

In Zimbabwe, 25 bryophyte species were found on inselbergs (six hepatics and 19 mosses):

Exormotheca holstii Steph., *Riccia atropurpurea* Sim, *R. congoana* Steph., *R. microciliata* Volk & Perold, *R. okahandjana* S.W. Arnell, *R. rosea* Volk & Perold, *Campylopus decaryi* Thér., *C. flaccidus* Ren. & Card., *C. nanophyllus* C. Müll. ex Broth., *C. pilifer* Brid., *Leucobryum madagassum* Besch., *Octoblepharum albidum* Hedw., *Trichostomum brachydontium* Bruch, *Brachymenium acuminatum* Harv. in Hook., *Brachymenium dicranoides* Hornsch., *Brachymenium exile* (Dozy & Molk.) Bosch & Lac., *B. philonotula* Broth., *Bryum arachnoideum* C. Müll., *Plagiobryum zierii* Lindb., *Pohlia cf. elongata* Hedw., *Hedwigia ciliata* (Hedw.) P. Beauv., *Braunia arbuscula* (Welw. & Duby) Gepp, *Rhacocarpus purpurascens* (Brid.) Par., *Polytrichum piliferum* Hedw. and *Polytrichum subpilosum* P. Beauv.

Amongst the hepatics, there are mainly (in Zimbabwe exclusively) thalloid species, especially dry adapted species of *Riccia.*

The low number of species corresponds with a low number of families. The 31 species of mosses from Ivory Coast belong to 13 families; the 19 species of mosses from Zimbabwe to only 6 families (Table 1, 2). Species of Archidiaceae, Ditrichaceae, Calymperaceae, Funariaceae and Bartramiaceae as well as all pleurocarpous mosses were only found in Ivory Coast, whereas Hedwigiaceae, Rhacocarpaceae and Polytrichaceae were only present on inselbergs in Zimbabwe. Thus, there are significant differences in the inselberg bryoflora of both countries. The reason is presumably the different elevation of the study areas. The lack of *Philonotis* (represented in Ivory Coast by four species) and of pleurocarpous species is conspicuous in Zimbabwe.

Common to both study areas are only representatives of three families (Dicranaceae, Pottiaceae and Bryaceae). Within these families, there are 7 genera in

Table 1. Species numbers of bryophytes from inselbergs in Ivory Coast and Zimbabwe

	Ivory Coast	Zimbabwe
Thallose hepatics	7	6
Foliose hepatics	2	-
Bryophytes in total	27	19
Arocarpous mosses		
Fissidentaceae	*	*
Archidiaceae	1	-
Ditrichaceae	1	-
Dicranaceae (with Leucobryaceae)	4	6
Calymperaceae	2	-
Pottiaceeae	4	1
Funariaceae	1	-
Bryaceae	6	7
Bartramiaceae	4	-
Hedwigiaceae	-	2
Rhacocarpaceae	-	1
Polytrichaceae	-	2
Pleurocarpous mosses		
Entodontaceae	2	-
Plagiotheciaceae	2	-
Sematophyllaceae	1	-
Hypnaceae	1	-

* unidentified

Table 2. Floristic diversity of bryophytes from inselbergs in Ivory Coast and Zimbabwe

	Ivory Coast	Zimbabwe	common
Family level	13	6	3
Genus level			7
Species level	31	19	8

common, and even species identical in Ivory Coast and Zimbabwe, *e.g.*, *Campylopus nanophyllus* and *Octoblepharum albidum* amongst the Dicranaceae, *Trichostomum brachydontium* amongst the Pottiaceae and 5 of 9 species of Bryaceae (*Brachymenium exile, B. philonotula, B. acuminatum, Bryum arachnoideum, Plagiobryum zierii*).

Table 3. Floristic composition of inselbergs in Ivory Coast related to their size, location in different vegetation belts and elevation

Inselberg	Aben-gourou	Tai Park	Dué-koué	Séguéla	Bouaké	Nassian	Boun-diali	Kakpin
Size (ha)	0.2	0.3	0.064	0.5	0.3	0.3	0.2	0.015
Elevation (m)	45	75	8	60	70	50	160	2. May
Veg.belt (Rain forest/Savanna)	R	R	R	R/S	R/S	S	S	S
Riccia discolor				x		x		x
Riccia fluitans				x				
Riccia lanceolata	x			x		x		x
Riccia moenkemeyeri		x	x	x		x		x
Garckea moenkemeyeri				x			x	
Campylopus savannarum						x		
Octoblepharum albidum			x	x				
Calymperes erosum		x						
Syrrhopodon planifolius				x		x		
Anoectangium aestivum				x				
Brachymenium acuminatum			x	x	x		x	x
Brachymenium exile	x		x		x	x	x	x
Bryum arachnoideum				x	x		x	x
Bryum depressum		x	x		x	x	x	

The floristic diversity of inselbergs in Ivory Coast was studied in correlation with their elevation, their size and their location in different vegetation belts (rain forest, rain forest-savanna transition and savanna; *cf.* Table 3). Species numbers are not correlated with the elevation or size of the inselbergs. Part of the inselberg species occur only in rain forest regions (*Calymperes erosum, Octoblepharum albidum*), part only in savanna regions (*Riccia discolor, R. fluitans, Campylopus savannarum, Syrrhopodon planifolius, Bryum arachnoideum*). All other species are found in rain forest as well as savanna regions. The highest number of species was found in the transition zone, where species from both vegetation types are found. These are species occurring in half or more of the inselbergs (*Riccia lanceolata, R. moenkemeyeri, Brachymenium acuminatum, B. exile, Bryum depressum*).

Generally, the β-diversity of inselberg bryophytes is relatively low, but this is not surprising, since extreme ecological conditions reduce the species number. Furthermore, it is evident from Table 3, that inselbergs from rain forest regions have less species; it seems paradoxical that inselbergs in rain forest regions with an annual precipitation of 1500-2000 mm are less species rich than inselbergs in savanna regions with a precipitation of 1100-1500 mm.

Table 4. Soerensen coefficient of similarity between the bryophyte flora of the inselbergs from Ivory Coast

	Aben-gourou	Tai Park	Doué-koué	Séguéla	Bouaké	Nassian	Boun-diali	Kakpin
Abengourou								
Tai	0							
Douékoué	.14	.75						
Séguéla	.16	.15	.4					
Bouaké	.33	.28	.66	.28				
Nassian	.44	.4	.5	.47	.36			
Boundiali	.33	.28	.44	.42	.75	.18		
Kakpin	.44	.4	.66	.58	.72	.71	.54	

A basic question is then, how the floristic composition on single inselbergs is determined? There are two models: First, species composition can be determined by the available ecological niches, and second, as determined by chance of spore dispersal or disturbance of habitats. Generally, the low species diversity can be used as indicator of deterministic processes. To determine which factors are responsible, the floristic affinities between the inselbergs in Ivory Coast were calculated; high correlation between the bryofloras of different inselbergs would suggest deterministic processes in the composition of species.

For the calculation of the similarity of the bryophytic inselberg flora, the Sörensen coefficient was used (Table 4). A low similarity coefficent indicates strong stochastic processes while a high similarity coefficient indicates deterministic processes in the composition of bryophytes.

The β-diversity between the bryophyte floras of the inselbergs is relatively low; the index is mostly < 0.5. This concerns comparisons of inselbergs from rain forest regions, the transition zone and savanna regions as well as comparisons between the inselbergs from different regions. The similarity is higher in some cases, but this cannot be correlated with any factor. It seems, therefore, at the present state of knowledge, that stochastic factors are responsible for the composition of the bryoflora on inselbergs.

It has to be kept in mind that inselbergs in rain forest regions are (1) less numerous than in savanna regions, and (2) the ecological conditions surrounding the inselbergs differ much more than in savanna regions. Thus, stochastic processes play here a more important role whereas the colonization of inselbergs in savanna regions is determined less by chance but by the available ecological niches.

A differentiation of the Sörensen index according to different habitats on inselbergs could not be made because of the relatively few data. It seems, however, that the thalloid species of shallow depressions (*Riccia* spp.) and also all the

Table 5. Phytogeographic composition of bryophytes from inselbergs in Ivory Coast and Zimbabwe

	Ivory Coast	Zimbabwe
Cosmopolitan	13%	12%
Pantropical or almost (disjunct between trop. Africa and America or SE-Asia)	35%	28%
Tropical African	32%	16%
South- and East African	-	12%
Sambezian	-	20%
Sudanian	6%	-
Sudano-Sambezian	9%	4%
Holarctic -African	3%	8%

Bryaceae with a presence of more than 50% on all inselbergs, occupy distinct ecological niches and belong to the inventory of inselbergs, whereas all other species with a presence of 50% on inselbergs are dispersed to this habitat by chance.

It may be assumed that the distance between single inselbergs could also be a factor for the species richness and isolated inselbergs harbour fewer species, because the chance of recolonization after extinction is lower in isolated inselbergs.

DISTRIBUTION PATTERNS

The distribution patterns of inselberg bryophytes from Ivory Coast and Zimbabwe (Table 5) are conspicuously similar. The largest group with 35 species or 28% is that of pantropical species followed by the cosmopolitan species with 12, *i.e.*, 13%. If, in the case of Zimbabwe, the tropical African species are added to the east African species (28%), a similar percentage is reached as the tropical African species in Ivory Coast (32%). Of Sambezian, *i.e.*, Sudano-Sambezian distribution type are especially the species of *Riccia*. The *Riccia* species from Ivory Coast (*Riccia discolor, R. fluitans, R. lanceolata, R. moenkemeyeri, R. cf. radicosa*) are, with the exception of the worldwide distributed *R. fluitans*, Sudano-Sambian elements. In contrast, all species of *Riccia* from Zimbabwe (with the exception of *R. atropurpurea* with Sudano-Sambezian distribution) are of Sambian distribution. Since all species of *Riccia* from Ivory Coast are according to their Sudano-Sambezian distribution pattern also present in Zimbabwe, the lack of these species in the inselbergs studied may be explained by the different elevation of the inselbergs which are situated in Ivory Coast between 200 and 500 m, but in Zimbabwe between 1000 and 2000 m altitude. Conspicuous is the high percentage of species with cosmopolitan or pantropical distribution. This may be explained by either good means of propagation

or the age of the taxa. Since most of the inselberg bryophytes are found in sterile condition, at least under the present climatic conditions as mentioned later, age of the taxa seems to be more probable.

Inselbergs are relatively old habitats. Geomorphologically, larger inselbergs are 40-120 million years old. They are thus of importance as very old and stable habitats. The habitats are therefore older than the evolutionary age of most flowering plants growing on inselbergs. Only cryptogams (cyanobacteria, lichens and bryophytes) have an evolutionary age that resembles the geological age of the inselbergs. With regard to the relatively stable habitat, inselbergs may be relict habitats for cryptogams. This is supported by the presumably old age of bryophytes indicated by their large ranges. Wide ranges and lack of fertility or high spore production seems to support the relict character of inselberg bryophytes. The stability of habitats plays an important role with regard to climatic changes, especially during the Pleistocene. Thus, inselbergs may have functioned as refugia during humid climatic phases where dry adapted species could have survived in humid climatic phases and allowed a recolonization of savannas in dry climatic phases. Climatic fluctuations could have caused restriction of bryophytes to inselberg and subsequent extension.

HABITAT SPECIFICITY

The main habitat types on inselbergs are open rocks, phanerogam mats, ephemeral wet flushes and rock pools. Bryophytes are not very characteristic of open rocks, where lichens seem to be more competitive. Rather, typical bryophyte habitats are mats of phanerogams, episodic water flushes and shallow depressions. *Riccia* species are most characteristic of shallow depressions. In Ivory Coast, many bryophyte species are found at the margins of mats of (also poikilohydric) *Afrotrilepis pilosa* (Cyperaceae) where they are frequently supplied by dripping water. Since collections from the surroundings of inselbergs were not made, it is not known whether the inselberg species are all, or in what percentage, confined to this kind of habitat and which species are perhaps typical of inselbergs.

Inselbergs are extremely dry habitats. Rainfall runs off rapidly leaving bare rocks exposed to insolation and cryptogams to fast desiccation. The only exception are the shallow depressions in which water remains. These depressions, especially when dried up, are characterized by an accumulation of rock debris. They dry up seasonally and may fill fast with water, thus providing a changing habitat and thus typical for annual therophytic species and species that can tolerate extremely dry and extremely wet phases. Longer dry phases (dry seasons) are survived as spores; short ones by good desiccation tolerance.

LIFE FORMS

The life form system developed by Raunkiaer is based on the place of perennating organs. Adaptations for bryophytes were made by Düll (1969), who included other aspects into the life form system as epiphytism and hygrophytism, which do not relate to life forms. Life forms according to Mägdefrau (1969) are growth forms. Thus, only a differentiation between annual and perennial bryophytes remains for bryophytes.

All species of *Riccia* are annual, and these represent most of the hepatics. Their annual life form is an adaptation to the habitat of shallow depressions which dries up seasonally. Amongst mosses, a few exceptions (*Archidium globiferum*) are annual, the majority of species is perennial.

PROPAGATION

A peculiarity of most inselberg mosses is their apparent sterility. From all mosses collected in Zimbabwe, only *Polytrichum piliferum* and *Bryum arachnoideum* were found with sporophytes. The first was collected only once, the second more frequently but only once with sporophytes. All mosses collected in Ivory Coast were sterile. The reasons for the predominant sterility of inselberg bryophytes, especially of mosses, are difficult to determine. Dioecy may be one of them, since all species of the families represented such as Dicanaceae or Bryaceae, are dioicous. However, this could only cause a rare production of sporophytes, but not a lack of sporophytes. The mosses reported from inselbergs also lack any specialized methods of vegetative propagation. An exception is *Brachymenium exile* in which rhizoidal gemmae were encountered for the first time. This raises the question as to how these species are distributed. Predominant lack of spores or other means of vegetative propagation can be explained by two hypothesis. The species are either "achor" under present climatic conditions and are not enabled to reach other habitats. This would suggest that these species are trapped on inselbergs where their only chance for direct propagation is by stem fragments. Their occurrence must be interpreted as a relict; dispersal by air would only be possible by hurricanes. The other possibility would be that they are zoochorous, *e.g.*, fragments may be transported by birds.

Amongst the liverworts, *Exormotheca pustulosa* produces spores very rarely; *Riccia rosea* is dioicous and is also found rarely with sporophytes. The other species of *Riccia* are monoicous and produce spores more frequently, but possess spores of 60-90µm in diameter which are not very suitable for aerial transport. The spore production in the thalli of liverworts are generally apparently not dispersed by wind but by water or birds. The occurrence of *Riccia* species in dried up shallow depressions would suggest zoochory for their dispersal.

Lack of effective dispersal mechanisms may be the reason for the floristic differences between inselbergs. If bryophytes dispersed effectively, the inselberg flora

would probably be much more homogenous. Thus, chance seems to be the factor determining the composition of bryophytes on inselbergs except for availability of habitats. On the other hand, fertility or unisexuality of bryophytes need not necessarily lead to extinctions. There are many examples of species that have survived in small ecological niches apparently for thousands of years, *e.g.* relicts from the Tertiary in the southern Alps of Europe or the hyperatlantic parts of the British Isles.

ECOLOGICAL ADAPTATIONS

Inselbergs are harsh environments. Ecological conditions there are characterized by high temperatures, high insolation, poor nutrients and poor water supply only from rainfalls and, to a smaller extent (not at lower elevations), dew. Poikilohydric plants have apparently advantages in such an environment; some flowering plants also use this strategy. *Afrotrilepis pilosa* (Cyperaceae) and *Tripogon minimus* (Poaceae) are poikilohydric species of flowering plants in the Ivory Coast, the former being very abundant; *Coleochloa setifera* (Poaceae), *Myrothamnus flabellifolius* (Myrothamnaceae) and *Xerophyta* spp. (Veloziaceae) in Zimbabwe. Poikilohydric plants avoid water stress; they can react directly to water supply. It is conspicuous that most of the bryophytes found on inselbergs have no special morphological adaptations. It would be expected that bryophytes from such a habitat had papillose leaf surfaces, dense foliation or tomentum as adaptations to the ecological conditions. However, the species of Ditrichaceae, Dicranaceae and most Bryaceae lack any special adaptations. Papillose leaf surfaces are only found in one (!) species (*Trichostomum brachydontium*) of the 27 species of mosses from inselbergs in Ivory Coast, and in 4 (*Trichostomum brachydontium, Hedwigia ciliata, Braunia arbuscula, Rhacocarpus purpurascens*, the latter with a reticulate leaf surface) of the 19 moss species from Zimbabwe. Special adaptations for storing water are present in two species from Ivory Coast (*Octoblepharum albidum, Calymperes erosum*) and 4 from Zimbabwe (*Leucobryum magadassum, Octoblepharum albidum, Polytrichum piliferum, P. subpilosum*). Vermiculate foliation and silvery leaves are shown in *Bryum arachnoideum* and *Plagiobryum zierii* in Ivory Coast as well as Zimbabwe. It is interesting that more inselberg mosses from Zimbabwe are adapted against desiccation, although the inselbergs in Zimbabwe are situated at a higher elevation and probably tolerate less ecological stress than the mosses from Ivory Coast.

LIFE STRATEGIES

Models of life strategies in bryophytes were proposed by During (1979). These models are based primarily on the cycles of sexual and asexual reproduction. As mentioned above, inselberg bryophytes are characteristically sterile and generally

show no special means of asexual reproduction. This cannot mean that inselberg bryophytes do not exhibit life strategies. Two possibilities can be considered: (a) Sterile bryophytes are dispersed as spores from other habitats than inselbergs, where they are able to produce sporophytes. On inselbergs, they do not produce sporophytes but remain sterile. The populations are continuously renewed by spores. An argument against this hypothesis may be that the bryophytic inselberg flora is relatively poor in species and that occasionally spore dispersal to inselbergs would result in a higher number of less constant species. (b) Inselberg bryophytes produce spores irregularly and were not found with sporophytes during the field studies. The irregularity of fertilization may be a result of the microclimatic conditions on inselbergs. Only the species of *Riccia* growing in shallow depressions are found regularly with sporophytes, however, under moist conditions.

COMPARISON WITH FLOWERING PLANTS

Bryophytes and flowering plants have different life strategies (although the poikilohydric life strategy is common to some flowering plants on inselbergs). Therefore it is interesting to see in which regard the two groups of plants show similar or different effects in inselbergs. An evaluation of the (more numerous and more comprehensive) data for flowering plants (Barthlott, Porembski *et al.*, 1993) reveals the following:

- More than 30% of the flowering plants from inselbergs in Ivory Coast are Guinean in origin, 17% Sundano-Sambian, 17% are tropical African, 12% pantropical. In contrast, the highest percentage of bryophytes is pantropical (35%), followed by tropical African species (32%); Sudanian or Sudano-Sambezian species count only with 6 or 9%. Thus, the distribution types with the largest extension have the highest percentages in bryophytes, which is just opposite in flowering plants.

- About 24 of the flowering plant species are endemic on inselbergs of the Guinean inselbergs, but none of the bryophytes. Low endemism is also typical for bryophytes of other parts of the world and other habitats, although unrevised old records from the last century from some tropical regions such as tropical islands seem to be different.

- Inselbergs from savanna regions have a richer phanerogamic flora than those from rain forest regions. This effect is also found in bryophytes.

- In flowering plants, more than half of the species from inselbergs in Ivory Coast belongs to 3 families (Poaceae, Cyperaceae, Fabaceae). A similar effect is observed in bryophytes. Most of the species are from a few families (Ricciaceae, Dicranaceae, Pottiaceae, Bryaceae, Bartramiaceae).

- 40% of the species of flowering plants are endozoochorous, 25% anemochorous, 10% epizoochorous. Those species confined to inselbergs have a maximum (40%) of anemochorous species while the most widespread, most common

and most frequent species elsewhere are anemochorous. Curiously, most of the bryophytes produce neither spores nor means of vegetative propagation.

- The phanerogamic flora "of inselbergs is highly influenced by deterministic processes as indicated by the dominance of highly adapted specialists. The influence of stochastic processes is of fundamental importance for the colonization of rock pools" (Porembski and Barthlott, 1992a). Bryophytes seem to react just opposite; the bryophyte flora of shallow depressions with *Riccia* species as the only bryophytes determined, whereas the bryophyte flora of rocks consists in part of steady species, in part of accidental species.

- An average of 30-40 species of flowering plants grow exclusively and are characteristic of inselbergs in contrast to only 6 bryophytes, part of which may be more widespread.

- The flora of flowering plants is absolutely different in South America and tropical Africa, but apparently not that of bryophytes. Thus bryophytes could have persisted in inselbergs after the separation of both continents, illustrating their higher age as compared with flowering plants.

- The dominance of the therophytic life form amongst bryophytes of shallow depressions is in accordance with that of flowering plants; 82% of the flowering plants of shallow depressions from inselbergs in Ivory Coast are therophytes.

ACKNOWLEDGMENTS

I would like to thank B.J. O'Shea, who provided a checklist of the mosses from Zimbabwe from his database of the mosses of tropical Africa. Dr. S. Perold kindly identified the thalloid liverworts and provided information concerning their fertility and ranges. The bryophyte material used for this study was collected by Dr. S. Porembski and R. Seine (Botanical Institute, University of Bonn). Both provided additional information and stimulation.The inselberg project was supported by the German Research Foundation (DFG) within the program "mechanisms and maintenance of tropical diversity".

LITERATURE CITED

ANHUF, D. 1994. Zeitlicher Vegetations- und Klimawandel in Côte d'Ivoire. *In:* W. Lauer (ed.), *Erdwissenschaftliche Forschung* 30: 7-299, Stuttgart.

BARTHLOTT, W., S. POREMBSKI, *et al.* 1993. *Vegetation von Inselbergen: Struktur, Diversität und ökogeographische Differenzierung einer tropischen Lebensgemeinschaft.* Interner Zwischenbericht, Botanisches Institut der Universität Bonn.

BARTHLOTT, W., A. GRÖGER AND S. POREMBSKI. 1993. Some remarks on the vegetation of tropical inselbergs: Diversity and ecological differentiation. *Biogeographica 69*: 105-124.

DÜLL, R. 1969. Moosflora von Südwestdeutschland. Mitt. Bad. Landesver. *Naturkunde Naturschutz N.F. 10*: 39-128.

DURING, H.J. 1979. Life strategies of bryophytes: a preliminary review. *Lindbergia 5*: 2-18.

ELDIN, M. 1971. Le Climat. *In:* Le milieu naturel de la Côte d'Ivoire. *Mémoires ORSTMO 50*: 73-108.

FRAHM, J.-P. AND S. POREMBSKI. 1994. Moose von Inselbergen aus Westafrika. *Trop. Bryol. 9*: 59-68.

MÄGDEFRAU, K. 1969. Die Lebensformen der Laubmoose. *Vegetatio 16*: 285-297.

POREMBSKI, S. AND W. BARTHLOTT. 1992a. Struktur und Diversität der Vegetation westafrikanischer Inselberge. *Geobot. Koll. 8*: 69-80.

POREMBSKI, S., AND W. BARTHLOTT. 1992b. Ökogeographische Differenzierung und Diversität der Vegetation von Inselbergen in der Elfenbeinküste. *In:* W. Bartlott *et al.*, *Animal-plant interactions in tropical environments. Results of the Annual Meeting of the German Society for Tropical Ecology held at Bonn*, February 13-16, 1992, pp. 149-158

POREMBSKI, S., W. BARTHLOTT, S. DÖRRSTOCK AND N. BIEDINGER. 1994. Vegetation on rock outcrops in Guinea: granite inselbergs, sandstone table mountains and ferricretes - remarks on species numbers and endemism. *Flora 189*: 315-326.

WILD, H. AND A. FERNANDES (eds.) 1967. Vegetation map of the Flora Zambesiaca area. *Flora Zambesiaca Supplement*, Salisbury.

WILSON, A.F. 1968. Geological report on granites in West Africa. *In: Proceedings of the Symposium on the Granites of West Africa*, Paris. pp. 123-147.