VEGETATION OF INSELBERGS IN ZIMBABWE

R. SEINE*, U. BECKER†, S. POREMBSKI*, G. FOLLMANN†
& W. BARTHLOTT*

Inselbergs are rounded rock outcrops, usually of Precambrian age, with sparse vegetation cover. The vegetation of inselbergs in Zimbabwe is described for the first time, based upon data sampled from 53 localities. Inselbergs support a range of habitats whose vegetation is described. Data on species richness and floristic composition of the inselberg flora (549 vascular plant, 25 bryophyte and 136 lichen species) are presented. Phytogeography and diversity of inselberg vegetation are discussed. First records for Zimbabwe are reported in lichens and vascular plants.

Keywords. Biodiversity, inselberg, lichens, phytogeography, rock outcrop, vascular plants.

INTRODUCTION

The term 'inselberg' was introduced by the German geographer Bornhardt (1900). Inselbergs are mostly dome-shaped rock outcrops that emerge from deeply weathered plains (Fig. 1). They usually consist of Precambrian rocks (granite, gneiss), although other rock types have been recorded, and are almost devoid of soil and vegetation cover. Geomorphology of inselbergs has been studied intensively (Kayser, 1957; Bremer & Jennings, 1978). The present study refers to rounded monolithic inselbergs and excludes extremely weathered koppjes. Inselbergs occur in all climatic zones with particularly high densities in the tropics, where they are often grouped into characteristic 'inselberg landscapes'. Due to the scarce soil cover and high temperatures of the exposed rock surface, inselbergs are xeric islands, both edaphically and microclimatically (Hambler, 1964; Phillips, 1982; Porembski et al., 1996). Their vegetation contrasts sharply with that of the surrounding plains, generating a mosaic pattern resembling a marine archipelago. Unlike marine islands, however, inselbergs, even if very small, support a characteristic vegetation (Fig. 2). They are therefore extremely useful model ecosystems for the study of island biology.

The vegetation of inselbergs has mainly been studied on a local or a regional scale (e.g. Adjanohoun, 1964; Burbanck & Platt, 1964; Hambler, 1964; Scott, 1967; Ornduff, 1987; Sarthou, 1992). In Zimbabwe, inselbergs have been studied intensively by archaeologists (Summers, 1960; Rudd, 1968; Garlake, 1982) because of their cultural importance, but no study has been conducted on their vegetation. In 1990 a project was launched, with support from the Deutsche Forschungs Gemeinschaft (DFG), to study the vegetation and diversity of inselbergs on a global scale

* Botanisches Institut und Botanischer Garten der Universität, Meckenheimer Allee 170, D-53115 Bonn, Germany.
† Botanisches Institut, Universität Köln, Gyrhofstr. 15, D-50931 Köln, Germany.

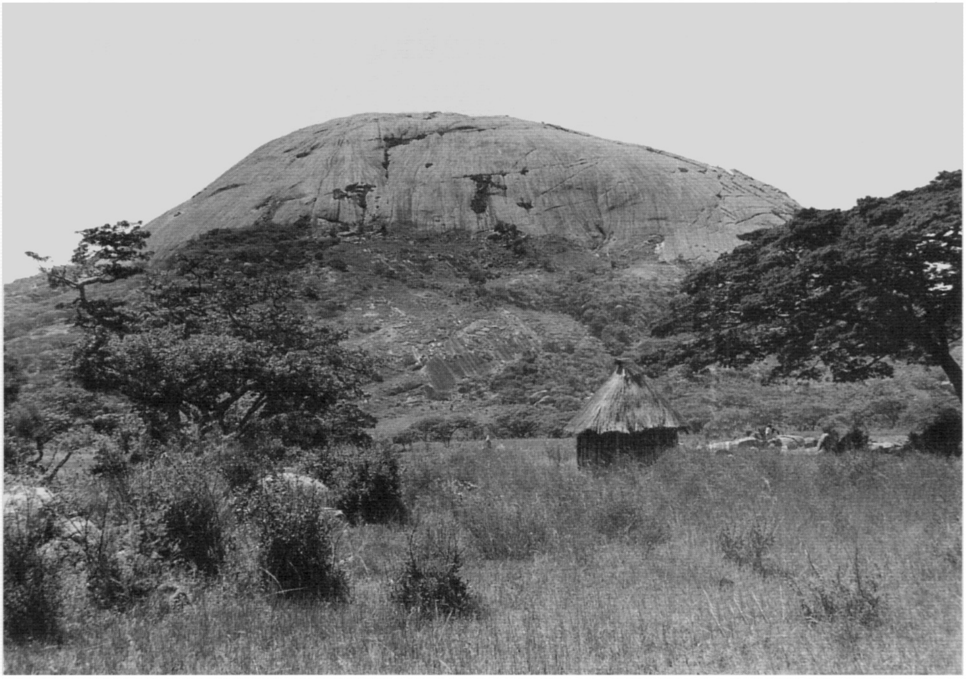

FIG. 1. Dome-shaped inselberg, Mt Dombo.

(Porembski & Barthlott, 1992; Barthlott et al.; 1993; Porembski et al., 1994; Gröger, 1995; Ibisch et al., 1995; Porembski, 1996; Porembski et al., 1996; Seine et al., 1996; Porembski et al., 1998a, b). In the global study Zimbabwe and the Ivory Coast were chosen as the major African study sites, representing different floristic regions and areas of higher and lower plant species diversity. There are large numbers of inselbergs in both countries.

The comparison of inselberg vegetation and diversity on continental and global scales is intended to contribute to our understanding of mechanisms of biodiversity maintenance in ecosystems with mosaic-like distribution patterns.

The scope of the present paper is to provide the first comprehensive survey of inselberg vegetation in Zimbabwe. Species numbers of lichens, liverworts, mosses, ferns and flowering plants are presented. The characteristic species composition and remarkable species (e.g. endemics, rare species) are described for each habitat. Notes on the ecology of inselberg vegetation are provided. New reports of species for Africa or Zimbabwe are indicated.

STUDY SITES, MATERIAL AND METHODS

The results presented here combine data from 53 inselbergs in 17 regions in Zimbabwe sampled on two field trips (May–July 1993 and November 1993–April

FIG. 2. Flat shield-inselberg, Mambo Hills.

1994). The regions are shown in Fig. 3. Inselberg size ranged from $20m^2$ to $1,500,000m^2$.

Zimbabwe is a landlocked country situated in south-eastern Africa on the Precambrian African shield between 15°35′–22°30′S and 25°10′–33°05′E. It encompasses the largest homogeneous area of granitic and gneissic rock in Africa (Kayser, 1957). Zimbabwe's landscape is classified into four natural units: Eastern Highlands (Nyanga Mts, Vumba Mts, and Chimanimani Mts on the Mozambique border), highveld (1200–1600m a.s.l.), middleveld (900–1200m a.s.l.), and lowveld (below 900m a.s.l.). Mt Inyangani (2592m a.s.l.) in the Eastern Border Mountains is the highest point in Zimbabwe. The highveld runs in a northeast–southwest direction and forms the watershed with lower ground towards the Zambesi to the north and the Limpopo to the south.

Climate is warm temperate on the highveld and the Eastern Border Mountains (Cwa[1], Cwb[2]; Köppen, 1923; Schulze & McGee, 1978), while middleveld and lowveld are subject to dry-hot savanna climate (BSh[3]; Köppen, 1923; Schulze & McGee, 1978). Occasional frosts are common during winter in the Eastern Highlands and the southern lowveld. There is a pronounced seasonal cycle with a single rainy season

[1] Warm temperate climate, winter dry season, warmest month over 22°C.

[2] Warm temperate climate, winter dry season, warmest month below 22°C, but at least four months above 10°C.

[3] Arid steppe climate, dry hot, mean annual temperature over 18°C.

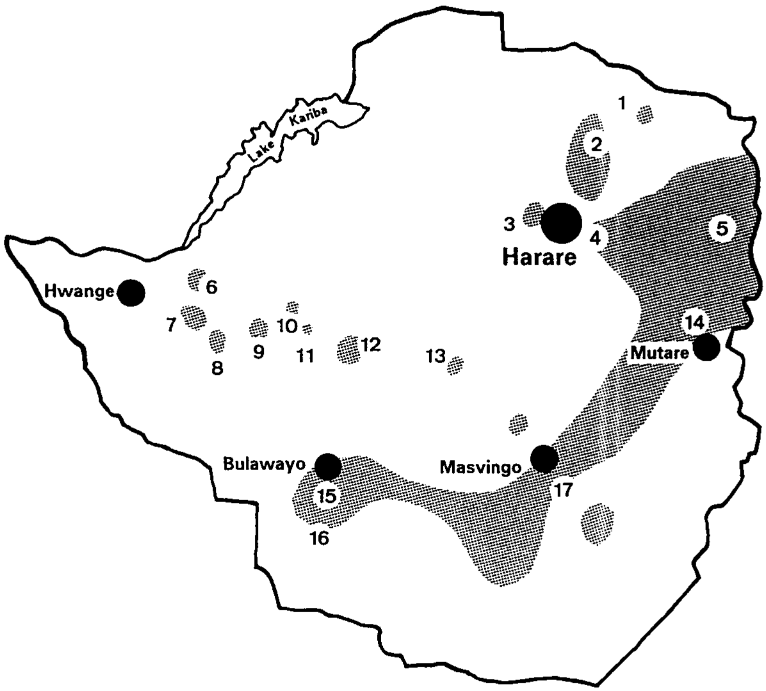

FIG. 3. Inselberg distribution and study areas (in brackets: number of inselbergs sampled): **1**, near Mt Darwin (1); **2**, Umfurudzi Safari Area (1); **3**, near Banket (3); **4**, near Harare (5); **5**, near Nyanga (8); **6**, near Hwange (1); **7**, Chibono Range (2); **8**, Dinde (1); **9**, Gwaai River Crossing (2); **10**, near St Paul's Mission (2); **11**, near Eastnor (1); **12**, Mambo Hills (6); **13**, near Gweru (1); **14**, near Mutare (1); **15**, Rhodes Matopos National Park (9); **16**, near Kezi (2); **17**, Lake Mtirikvi Recreational Park (7). Shaded areas indicate distribution of inselbergs.

of approximately six months (October to March) over most of the country. The Eastern Highlands are humid throughout the year due to orographic clouds and rain (Kreft, 1972). Annual precipitation ranges from 300mm (Beitbridge) to more than 2000mm (Eastern Highlands) and generally increases with elevation (Torrance, 1972; Department of Meteorological Services, 1984).

Floristically Zimbabwe belongs to the Zambesian subcentre of endemism (White, 1983). It harbours some 8500 vascular plant species, of which at least 5200 are present in Zimbabwe (Gibbs Russel, 1975). Brenan (1978) estimates the number of endemic vascular plant species to be 95. Due to the wide range of climatic and geological conditions, Zimbabwe supports a variety of vegetation units which have been studied and mapped by Henkel (1931), Boughey (1961), Rattray (1961), and, for the *Flora Zambesiaca*, Wild & Fernandes (1967). An excellent bibliography of vegetation survey in Zimbabwe is provided by Timberlake & Nobanda (1993). The most important vegetation types in Zimbabwe are Miombo and Mopane dry tropical forest. Savanna vegetation is found in the drier parts of the country and on the great dyke, an intrusion of ultrabasic rock. In the Eastern Highlands, submontane grassland and patches of moist montane forest are found.

The inselbergs sampled were selected to include all types of vegetation and were generally visited at least twice to include different seasonal aspects. Material collected amounts to 1600 herbarium numbers of vascular plants and 4000 specimens of lithophytic and epiphytic lichens. A set of vascular plant specimens will be deposited in the herbaria of Harare (SRGH) and Kew (K); lichen specimens are currently housed in Cologne (KOELN).

Vascular plant specimens were determined using *Flora Zambesiaca* (Exell et al., 1960–). For several groups, material was determined by the following specialists: Dr R.B. Drummond (Harare: woody specimens), Prof. Dr J.P. Frahm (Bonn: mosses), Prof. Dr P. Goetghebeur (Gent: *Cyperaceae*), Dr D.J. Goyder (Kew: *Asclepiadaceae*), Dr R. Faden (Washington: *Commelinaceae*), Priv. Doz. Dr E. Fischer (Bonn: *Scrophulariaceae*), Dr W. Luck (Leverkusen: *Asteraceae*, *Fabaceae*), Dr S. Perold (Pretoria: liverworts), Dr A. Radcliffe-Smith (Kew: *Phyllanthus*), Prof. Dr H. Scholz (Berlin: *Poaceae*), D. Supthut (Zürich: *Euphorbia*), Dr K. Vollesen (Kew: *Acanthaceae*). For determination of lichen material, Breuss (1995), Büdel (1987), Hale (1975, 1990), Purvis et al. (1992) and Swinscow & Krog (1988) were used. Dr O. Breuss (Vienna: *Catapyrenium*, *Endocarpon*), Prof. Dr B. Büdel (Kaiserslautern: checking of *Peltula*), and Dr P. Clerc (Geneva: *Usnea*) kindly assisted in the determination of specimens.

Terminology of inselberg habitats used in this paper results from the global comparison of inselberg vegetation and follows definitions in Porembski et al. (1998b). 'Rock surface' is devoid of soil and covered by cyanobacteria or lichens; 'boulders' lying on the surface and 'drainage channels' also support cryptogams. 'Wet flush' vegetation occurs where water runs continuously over inclined rock surfaces. 'Fissures' in the rock are a few millimetres to several centimetres wide and often filled with soil. 'Rock pools' are small, water-filled depressions that dry out during the rainy season. 'Rock debris' is a shallow layer (up to 5cm) of coarse rock particles that usually have a scarce vegetation cover. 'Soil-filled depressions' are more than 5cm deep and may be dominated by herbaceous or woody plants. 'Mats' are dense, usually species poor, covers of plants forming a carpet-like layer of interwoven roots and humus that can be lifted from the stone. 'Ephemeral flush' vegetation occurs where water seeps continuously through shallow soil during the rainy season; it usually consists of therophytes. Patches of woody vegetation may be found where layers of soil in excess of 50cm cover the rock.

RESULTS

Species richness and floristic composition

The inventory of the Zimbabwean inselbergs sampled includes 136 lichens, 25 bryophytes (Frahm et al., 1996), and 549 vascular plant species (Seine, 1996). A breakdown into major taxonomic groups is given in Table 1.

TABLE 1. Species numbers in major taxonomic groups.

Taxon	Families	Genera	Species
Ascolichenes	20	47	136
Bryophyta	7	14	25
Marchantiopsida	1	2	6
Bryopsida	6	12	19
Pteridophyta	9	13	26
Spermatophyta	100	295	523
Gymnospermophytina	1	1	1
Angiospermophytina	99	294	522

The ten most important lichen genera are: *Peltula* (*Peltulaceae*, 17 spp.), *Usnea* (*Parmeliaceae*, 16 spp.), *Xanthoparmelia* (*Parmeliaceae*, 15 spp.), *Buellia* (*Physciaceae*, 7 spp.), *Parmotrema* (*Parmeliaceae*, 6 spp.), *Caloplaca* (*Teloschistaceae*, 5 spp.), *Bulbothrix* (*Parmeliaceae*, 5 spp.), *Rinodina* (*Physciaceae*, 5 spp.), *Heterodermia* (*Physciaceae*, 4 spp.), *Acarospora* (*Acarosporaceae*, 4 spp.). The ten most speciose families of vascular plants are *Fabaceae* s.l. (58 spp.), *Poaceae* (53 spp.), *Cyperaceae* (40 spp.), *Asteraceae* (33 spp.), *Scrophulariaceae* (22 spp.), *Euphorbiaceae* (18 spp.), *Rubiaceae* (18 spp.), *Lamiaceae* (14 spp.), *Adiantaceae* (12 spp.), and *Acanthaceae* (10 spp.).

In the course of the study a new species, *Lindernia syncerus* Seine, Fischer & Barthlott (*Scrophulariaceae*), was discovered in ephemeral flush vegetation (Seine et al., 1995). *Peltula zahlbruckneri* (Hasse) Wetmore (*Peltulaceae*) is for the first time reported from Africa. The lichen was collected in the Mambo Hills, the Matopos, Domboshava, and near Banket (specimens: *U. Becker* 210078, 213015, 214025, 227014; all at KOELN). First records of vascular plants for Zimbabwe are *Crepidorhopalon debilis* (Skan) Fischer (*Scrophulariaceae*), *Dissotis tenuis* A. & R. Fernandes (*Melastomataceae*), and *Lindernia exilis* Philcox (*Scrophulariaceae*). In mosses and liverworts, first records have been reported elsewhere (Frahm et al., 1996). Additional first records for the lichen genus *Peltula* (*Peltulaceae*) are: *P. bolanderi* (Tuck.) Wetmore, *P. boletiformis* (Hue) Henssen & Büdel, *P. clavata* (Krempelh.) Wetmore, *P. cylindrica* Wetmore, *P. impressa* (Vain.) Swinscow & Krog, *P. lingulata* (Vain.) Swinscow & Krog, *P. marginata* Büdel, *P. obscurans* (Nyl.) Gyelnik var. *hassei* (Zahlbr.) Wetmore, *P. patellata* (Bagl.) Swinscow & Krog, *P. placodizans* (Zahlbr.) Wetmore, *P. santessonii* Swinscow & Krog, and *P. umbilicata* (Vain.) Swinscow & Krog.

Phytogeography and habitat preferences

Most lichens found on inselbergs in Zimbabwe are distributed over wide areas of the tropics and subtropics. None of the species is restricted to inselberg habitats.

Among vascular plants Zambesian distribution is most common (33%) on Zimbabwean inselbergs. Species distributed in the African savanna and dry forest belt (Sudano-Zambesian, Zambesi-Somali-Masaian, Sudano-Zambesi-Somali-Masaian) make up 20% of inselberg plants and about 15% each are tropical African and Palaeotropical species. Fifteen Zimbabwean endemic vascular plant species were recorded in inselberg vegetation. Among these, seven species are restricted to inselbergs (*Anacampseros rhodesica* N.E. Br. (*Portulacaceae*), *Delosperma steytlerae* L. Bolus (*Mesembryanthemaceae*), *Kalanchoe wildii* R. Hamet (*Crassulaceae*), *Lindernia syncerus* Seine, Fischer & Barthlott, *Portulaca rhodesiana* R.A. Dyer (*Portulacaceae*), *Rhynchosia tricuspidata* Bak.f. (*Fabaceae*), and *Rotala wildii* Fernandes (Lythraceae)).

Approximately 100 vascular plant species found on inselbergs in Zimbabwe have a strong preference for inselberg habitats or are restricted to them. Species with ecological preference for other habitats are often native to rocky places, riversides, dry forest and savanna.

Life-forms

Among the vascular plants found on inselbergs, therophytes are the most important life-form followed by phanerophytes, chamaephytes and hemicryptophytes. A slightly different picture emerges when a differentiation is made between species with their ecological preference for inselberg habitats and those with other ecological preferences (Table 2).

Inselberg vegetation according to habitat

The following comprehensive account of the vegetation of inselberg habitats gives the characteristic species composition and also some notable species. Rock surface

TABLE 2. Life-forms in inselberg vegetation. Bold type indicates strong deviations.

Life-form	Inselberg flora (total, %)	Species with preference for inselberg habitats (%)	Species with preference for other habitats (%)
Phanerophytes	22.5	**28.7**	21.6
Chamaephytes	15.3	**27.7**	12.5
Lianas	2.7	2.0	2.9
Hemicryptophytes	13.1	11.9	13.4
Geophytes	7.7	5.9	8.0
Therophytes	34.6	22.8	**37.3**
Epiphytes	0.4	0.0	0.4
Lithophytes	0.4	1.0	0.2
Hydrophytes	0.5	0.0	0.7
Uncertain	2.4	0.0	2.9

is the habitat covering the largest area on inselbergs. All other habitats are typically separated from each other by rock surface and often occur more than once on each inselberg. The number of various habitats present on an inselberg depends largely on its size and topography. Only large inselbergs feature all habitats while most inselbergs have only a subset. The descriptions below indicate how often individual habitats are found on inselbergs.

Rock surface

(a) *Cryptogamic vegetation of rock surface*
Rock surface (Fig. 4) usually accounts for more than 50% of the inselberg's surface. The brown to bright orange colour of the inselberg, as seen from some distance, is

FIG. 4. Rock surface with drainage channel, Domboshava.

due to the dense cover of cryptogams. Over lowveld, middleveld and most of the highveld the cryptogamic vegetation of the rock surface is dominated by cyanophytic lichens. They form a low carpet a few millimetres high. *Peltula* is the most important genus with approximately 20 species and is usually accompanied by *Lichinaceae* (not determined). Lichens with green algae as photobiont are restricted to small areas along drainage channels, around rock pools, or to areas of elevated microrelief. In these areas, associations of *Buellia*, *Caloplaca*, *Acarospora*, *Dermatiscum* (*Physciaceae*), *Parmelia* (*Parmeliaceae*), *Parmotrema*, *Xanthoparmelia* (*Parmeliaceae*), *Protoparmelia* (*Lecanoraceae*), and *Toninia* (*Bacidiaceae*) prevail.

Inselbergs on the highest parts of the highveld, in the Eastern Highlands, and occasionally the summits of other inselbergs are covered with green-algal (chlorophytic) lichens and a few species of *Peltula*. The former are represented by *Usnea*, *Heterodermia*, *Dimelaeana* (*Physciaceae*), *Diploschistes* (*Thelotremataceae*), *Lecanora* (*Lecanoraceae*), *Verrucaria* (*Verrucariaceae*) and the genera mentioned above. *Usnea* species sometimes form an almost continuous 'lawn' some 5cm high. *Dimelaeana* species may reach nearly 100% surface cover to the effect that the summits appear entirely green.

(b) *Cryptogamic vegetation of boulders*

Boulders are present on many inselbergs in Zimbabwe. The cryptogamic vegetation of boulders is dominated by chlorophytic lichens which may densely cover the rock surface. Many species on boulders are also found on the main rock surface (*Dermatiscum thunbergii*, *Acarospora* sp., *Buellia* sp., *Caloplaca*, *Diploschistes* sp., *Parmelia*, *Parmotrema* and *Xanthoparmelia*). Species that are restricted to boulders are found in the genera *Pertusaria* (*Pertusariaceae*), *Heterodermia* (Fig. 5) and *Pyrrhospora* (*Lecanoraceae*). Only one species of *Peltula* (*P. euploca*), the dominating genus on the rock surface, is present on boulders.

(c) *Vegetation of drainage channels*

Drainage channels are present on most larger inselbergs (Fig. 4). They are absent on flat outcrops where water runs off over the entire surface. Drainage channels are almost exclusively colonized by *Peltula* species sometimes attaining 90% cover. *Peltula cylindrica*, *P. lingulata* and *P. obscurans* grow in shaded parts of the channels. The remainder of the channels harbour *Peltula impressa*, *P. umbilicata*, *P. marginata*, *P. placodizans*, *P. umbilicata* and *P. zahlbruckneri*, i.e. species that are also found on the rock surface. The raised margins of drainage channels are inhabited by chlorophytic lichens like other areas of elevated microrelief.

Mosses sometimes colonize drainage channels and among them *Bryum arachnoideum* C. Müll. (*Bryaceae*) is relatively common. On Mt Dombo vertical drainage channels were colonized by *Rhacocarpus purpurascens* (Brid.) Par. (*Rhacocarpaceae*). Vascular plants are usually unable to grow in this habitat; only once (Mt Gwangwaza, near Banket) *Cyperus squarrosus* L. (*Cyperaceae*) was found growing in patches of *Bryum arachnoideum*.

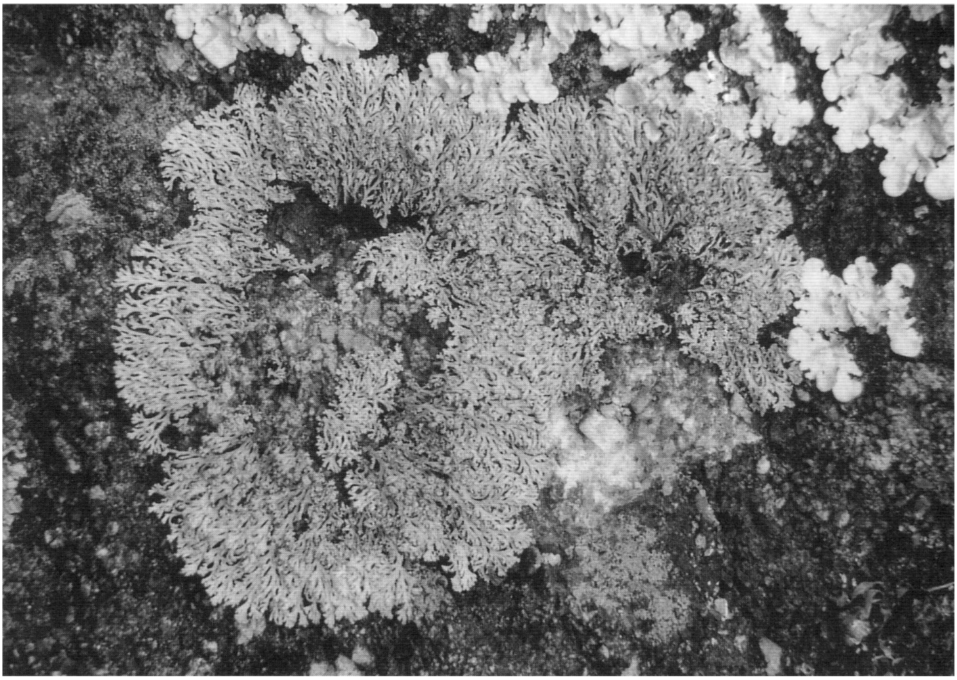

FIG. 5. *Heterodermia* sp. on boulder, near Banket.

(d) *Wet flush*

Wet flush vegetation is rather rare in Zimbabwe. A single locality has been recorded in the Rhodes Matopos National Park (Fig. 6). *Utricularia gibba* L. (*Lentibulariaceae*) was the only species of vascular plant encountered, with few scattered individuals in dense cyanobacterial and algal growth. It is, however, an almost cosmopolitan species that occupies a wide range of habitats (Taylor, 1989).

(e) *Vascular lithophytic vegetation*

Lithophytic vascular plants are rarely found in Zimbabwe. The only species recorded growing on bare rock are *Ceterach cordatum* (Thunb.) Desv. (*Aspleniaceae*), *Tridactyle tridactylites* (Lindl.) Schltr. (*Orchidaceae*) and *Angraecum* sp. (*Orchidaceae*). All of them were found in partly shaded localities where they form small groups of plants.

Fissures

(a) *Vegetation of horizontal crevices*

Horizontal crevices generated by the exfoliation of rock are a geomorphological feature found on most of the Zimbabwean inselbergs studied. The succulent *Anacampseros rhodesica* (Fig. 7) is the only vascular plant species to colonize them. Although there is an abundance of horizontal crevices, *Anacampseros rhodesica* has been recorded only on a few inselbergs.

FIG. 6. Wet flush, Rhodes Matopos National Park.

(b) *Vegetation of vertical crevices*

Vertical crevices are present on all inselbergs studied. Vegetation of vertical crevices is dominated by *Poaceae*, *Fabaceae* and *Cyperaceae* (Fig. 8). Most grasses found in crevices are common to the surroundings of the inselberg, i.e. are savanna and open woodland species, for example *Andropogon gayanus* Kunth, *Heteropogon contortus* (L.) Roem. & Schult., *Loudetia simplex* (Nees) Hubb., and *Melinis repens* (Willd.) Zizka. Of the *Fabaceae*, *Indigofera* spp. (*I. setiflora* Bak., *I. viscidissima* Bak.) and *Tephrosia* spp. (*T. decora* Bak., *T. longipes* Meisn., *T. reptans* Bak.) are characteristically found in crevices. They are often attacked by the parasitic *Striga gesnerioides* (Willd.) Vatke (*Scrophulariaceae*). *Cyperaceae* are represented by *Bulbostylis* spp. (*B. burchellii* Filcalho & Hiern, *B. hispidula* (Vahl) R. Raines) and various *Cyperus* species (e.g. *C. holostigma* Schweinfurth, *C. rupestris* Kunth). Other characteristic elements of vertical crevice vegetation are *Ceratotheca triloba* Endl. (*Pedaliaceae*), *Commelina africana* L. (*Commelinaceae*), *Gomphocarpus tenuifolius* N.E. Br. (*Asclepiadaceae*), *Hibiscus engleri* K. Schum. (*Malvaceae*), *Merremia pinnata* (Hochst. ex Choisy) Hall (*Convolvulaceae*) and *Oldenlandia herbacea* (L.) Roxb. (*Rubiaceae*). Two poikilohydric ferns, *Cheilanthes leachii* (Schelpe) Schelpe (*Adiantaceae*) and *Pellaea calomelanos* (Sw.) Link (*Adiantaceae*), are regularly found in horizontal crevices. The succulent *Sarcostemma viminale* R. Br. (*Asclepiadaceae*) spreads from crevices over the surrounding cryptogamic crust. In the Eastern

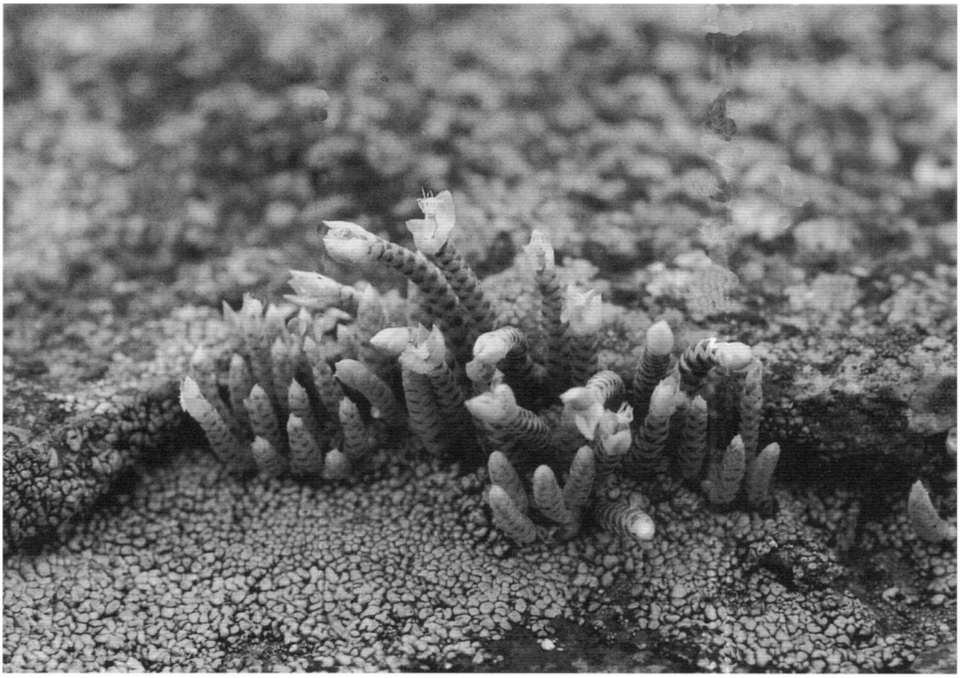

FIG. 7. *Anacampseros rhodesica* in horizontal crevice, View of the World, Rhodes Matopos National Park.

Highlands, the endemic *Aloe inyangensis* Christian (*Aloaceae*) is regularly found growing in vertical crevices.

(c) *Vegetation of clefts*

Clefts are predominantly found on larger inselbergs. The main difference between the vegetation of clefts and that of horizontal crevices is the presence of tree species. The herbaceous species of clefts are essentially the same as in horizontal crevices. Tree species such as *Brachystegia glaucescens* Burtt Davy & Hutch. (*Caesalpiniaceae*), *Bridelia mollis* Hutch. (*Euphorbiaceae*), *Commiphora marlothii* Engl. (*Burseraceae*), *Euphorbia matabelensis* Pax (*Euphorbiaceae*) and *Ficus glumosa* (Miq.) Delile (*Moraceae*) show a strong preference for the inselberg habitat. Other species are commonly found on inselbergs but are also constituents of the surrounding vegetation. Among these are *Diplorhynchus condylecarpon* (Müll. Arg.) Pichon (*Apocynaceae*), *Julbernardia globiflora* (Benth.) Troupin (*Caesalpiniaceae*), *Maytenus senegalensis* (Lam.) Exell (*Celastraceae*) and *Peltophorum africanum* Sonder. (*Caesalpiniaceae*). Most of the trees are deciduous.

(d) *Vegetation around boulder bases*

Large boulders with vegetation around the bases have been found only on large inselbergs. In accumulations of shallow soil around the base of boulders, plants that are tolerant of shade may grow. *Arthropteris orientalis* J.F. Gmel. (*Davalliaceae*) has

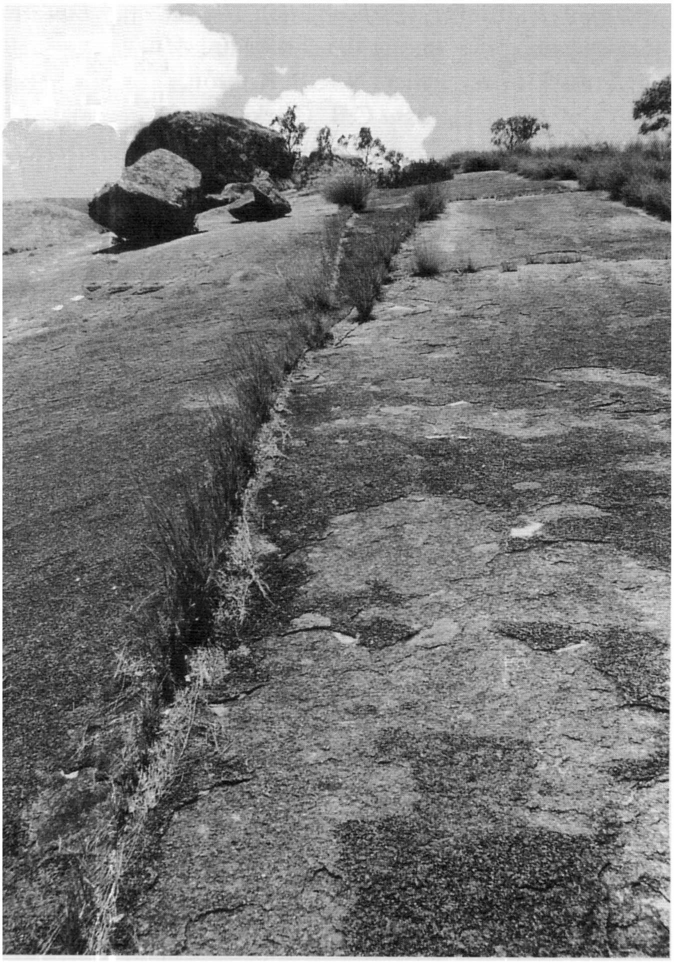

FIG. 8. Vertical crevice, Rhodes Matopos National Park.

been found only in association with boulder bases. The poikilohydric fern *Ceterach cordatum* has been recorded growing at boulder bases, but was also encountered as a lithophyte on a boulder. Other species in this habitat include *Selaginella mittenii* Baker (*Selaginellaceae*) and various mosses.

(e) *Vegetation of talus slopes*

Talus slopes support woody vegetation with a sometimes dense undergrowth. Tree constituents in this habitat include *Brachystegia glaucescens*, *Ficus abutilifolia* Miq. (*Moraceae*), *Julbernardia globiflora*, *Mimusops zeyheri* Sonder (*Sapotaceae*), *Pterocarpus angolensis* (*Caesalpiniaceae*) and *Terminalia sericea* Burch. ex DC. (*Combretaceae*). Most species occur in miombo woodland. The undergrowth is composed of lianas, shrubs and a few herbs. Lianas found in this habitat are *Cryptolepis cryptolepioides* (Schltr.) Bullock (*Asclepiadaceae*), *Gloriosa superba* L. (*Colchicaceae*), *Clerodendron glabrum* E. Meyer (*Verbenaceae*), *Tragia* sp. (*Euphorbiaceae*) and *Ipomoea* spp. (*Convolvulaceae*). Among the shrubs are *Maytenus* spp. (*Celastraceae*, e.g. *M. heterophylla* (Ecklon & Zeyher) N.K.B. Robson, *M. senegalensis*), *Poulzolzia mixta* (*Urticaceae*) and *Barleria crassa* C.B. Clarke (*Acanthaceae*). The herb layer is composed of species from savanna or dry forests, for example *Heteropogon contortus*, *Kaempferia* sp. (*Zingiberaceae*), *Loudetia simplex* and *Pavonia patens* (Andr.) Chiov. (*Malvaceae*).

Rock depressions

(a) *Vegetation of seasonal rock pools*
Rock pools are present on approximately 20% of the inselbergs sampled. Many rock pools are devoid of vegetation, whereas others are covered to various degrees. Two highly specialized species of *Scrophulariaceae* are most important in rock pool vegetation: *Lindernia monroi* (S. Moore) Fischer and *Lindernia conferta* (Hiern.) Philcox. *L. monroi* is a poikilohydric species that dries out with the pool and remains in this state until the onset of rains. It then regreens within one day and may flower a few days later. *L. conferta* produces an inflorescense of rosetted floating leaves (Fig. 9) subtending the flowers. The plant dies off in the dry season relying on seed for reproduction. *Aponogeton stuhlmannii* Engl. (*Aponogetonaceae*), *Dopatrium junceum* Buch.-Ham. (*Scrophulariaceae*), *Isoetes* sp. (*Isoetaceae*), *Ludwigia leptocarpa* (Nutt.)

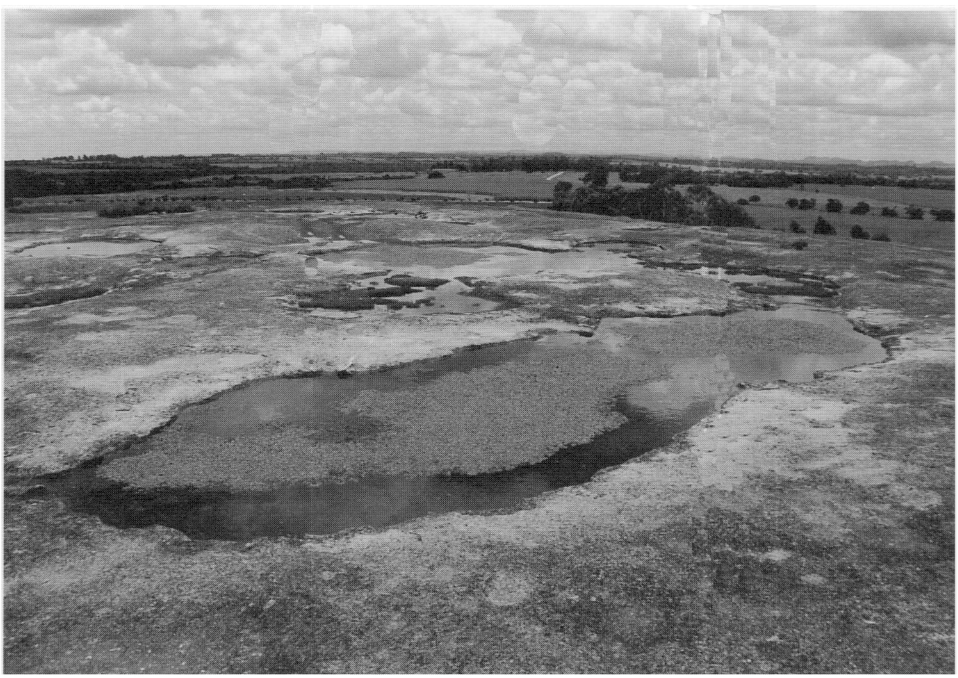

FIG. 9. Rock pool with *Lindernia conferta*, near Banket.

Hara (*Onagraceae*) and *Eriocaulaceae* may also contribute to rock pool vegetation. The margins of rock pools are sometimes colonized by lichen communities resembling those of drainage channels.

(b) *Vegetation of permanently water-filled rock pools*

Permanently water-filled rock pools are extremely rare on inselbergs. Two pools in the Umfurudzi Safari Area appeared to be water-filled throughout the year. The vegetation of these pools was very lush and dominated by perennial *Cyperus distans* L.f. (*Cyperaceae*), *Oryza barthii* A. Chev. (*Poaceae*), and *Eleocharis* cf. *acuta* (*Cyperaceae*). A floating bladderwort, *Utricularia stellaris* L.f. (*Lentibulariaceae*), *Hygrophila auriculata* (Schumach.) Heine (*Acanthaceae*) and a *Nymphaea* sp. (*Nymphaeaceae*) were also present in the pools.

(c) *Vegetation of rock debris*

Rock debris has been recorded on every inselberg studied. The habitat dries out quickly because of shallow soil and usually has a sparse vegetation cover (Fig. 10). It is predominantly inhabited by poikilohydric, succulent or annual species. The former are represented by vascular plants, liverworts and lichens. Vascular 'resurrection plants' in this habitat are *Xerophyta humilis* (Baker) Dur. & Schinz (*Velloziaceae*) and numerous *Scrophulariaceae* (i.e. *Craterostigma lanceolatum* (Engler) Skan, *Craterostigma plantagineum* Hochst., *Lindernia pulchella* (Skan) Philcox, *Lindernia*

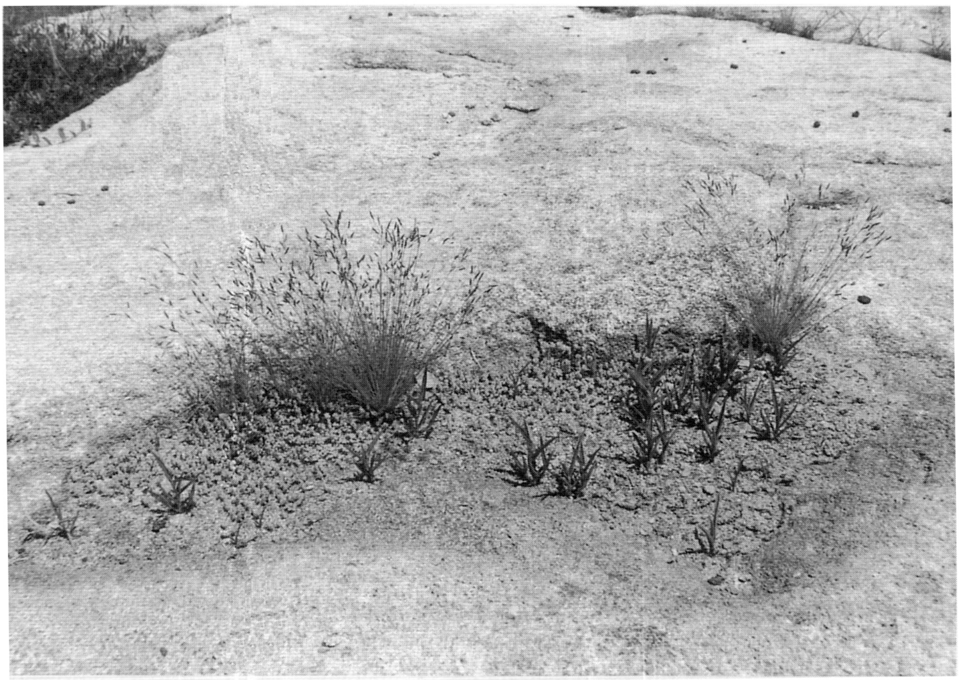

FIG. 10. Rock debris with *Cyanotis lanata*, *Bulbostylis burchellii* and *Portulaca rhodesiana*, Dinde.

wilmsii (Engler & Diels) Philcox; see Seine et al., 1995). *Craterostigma* species are vicariating: *C. plantagineum* is present over most of the country but missing in the higher elevations of the Eastern Highlands, where it is replaced by *C. lanceolatum. Selaginella dregei* (C. Presl.) Hieron. (*Selaginellaceae*) is the most frequent vascular colonizer of rock debris present on 32 of 53 inselbergs studied. Succulent plants in this habitat are *Portulaca rhodesiana*, *Crassula schimperi* Fisch. & Mey. (*Crassulaceae*) and *Cyanotis lanata* Benth. (*Commelinaceae*). *Cyanotis lanata* is widespread in tropical Africa and is regularly found on inselbergs. In Zimbabwe it has a tendency to grow in shaded localities. Annual vascular plant species regularly encountered on rock debris are *Microchloa indica* (L.f.) P. Beauv. (*Poaceae*) and the *Cyperaceae*: *Cyperus rupestris*, *Cyperus holostigma*, *Bulbostylis oligostachys* (A. Rich.) Lye and *Bulbostylis burchellii*. One geophytic species, *Eriospermum* sp. (*Eriospermaceae*), is commonly found on rock debris.

Several species of *Riccia* sometimes attain a high degree of ground cover. Occasionally lichens with cyanophytic and chlorophytic photobionts are present. Some of these species are also found on the rock surface (e.g. *Peltula patellata*) while others have been recorded only in this habitat (e.g. *Catapyrenium lacinulatum* var. *lacinulatum* and var. *latisporum*).

(d) *Herbaceous vegetation of soil-filled depressions*

This habitat is common on inselbergs in Zimbabwe. Only deep depressions (exceeding 50cm depth) are occasionally dominated by woody vegetation. Most species in this habitat are perennials usually found in savannas. The shallow rims of depressions are colonized by the species characteristic of rock debris. Herbaceous vegetation of soil-filled depressions is usually dense (Fig. 11) and dominated by *Poaceae* (*Andropogon gayanus*, *Heteropogon contortus*, *Loudetia simplex*, *Melinis repens* etc.), *Cyperaceae* (*Cyperus amauropus* Steudel, *C. cyperoides* (L.) O. Kuntze, *C. holostigma*, *C. rupestris*) and *Fabaceae* (*Indigofera* spp., *Tephrosia* spp.). Small perennial bushes regularly encountered in this habitat are *Corchorus kirkii* N.E. Br. (*Tiliaceae*), *Melhamia acuminata* Mast. (*Sterculiaceae*) and *Waltheria indica* L. (*Sterculiaceae*). Various geophytes occur in this habitat such as *Haemanthus multiflorus* Martyn (*Amaryllidaceae*), *Scilla kirkii* (*Hyacinthaceae*), *Gladiolus crassifolius* Baker (*Iridaceae*), *Dipcadi viride* (L.) Moench (*Liliaceae*) and *Ornithoglossum vulgare* B. Nordenstam. (*Colchicaceae*). Common therophytes of depressions are *Commelina africana*, *Oldenlandia herbacea*, *Hibiscus engleri* and *Ceratotheca triloba*. A few succulents, such as *Crassula schimperi*, *Aloe chabaudii* Schönland (*Aloaceae*) and *Kalanchoe sexangularis* N.E. Br. (*Crassulaceae*), are present in depressions. In larger depressions, *Euphorbia matabelensis* Pax (*Euphorbiaceae*), *E. ingens* E. Mey. ex Boiss. (*Euphorbiaceae*), *Ficus abutilifolia* and *Ficus glumosa* may establish.

(e) *Woody vegetation of soil-filled depressions*

Depressions dominated by woody vegetation are relatively rare. They usually support a subset of the surrounding forest species forming an open bush.

FIG. 11. Herbaceous vegetation of soil-filled depression, near Banket.

Mats

(a) Coleochloa-*mats*

Coleochloa-mats are present on all larger inselbergs in Zimbabwe. The dominant mat-forming species in Zimbabwe is *Coleochloa setifera* (Ridley) Gilly (*Cyperaceae*), which commonly forms extremely dense vegetation (Fig. 12). This member of the *Cyperaceae* is a resurrection plant that may form tussocks up to 50cm tall. The species usually covers 70% of mat area.

Myrothamnus flabellifolius Welw. (*Myrothamnaceae*) and two species of *Xerophyta* (*Velloziaceae*, *X. villosa* (Baker) L.B. Smith & Ayensu, *X. equisetoides* Baker) may become co-dominant. These species are also poikilohydric. *Myrothamnus* together with *Selaginella dregei* often covers the shallow margins of the mats completely. *Xerophyta* species are generally embedded in a matrix of *Coleochloa*. *Pellaea calomelanos* and *Cheilanthes viridis* (Forsk.) Sw. (*Adiantaceae*), both poikilohydric ferns, are often present in mat vegetation.

Aloe chabaudii, a stemless succulent, is the most common *Aloe* species on inselbergs and is regularly present in mats. In the Nyanga Highlands it is replaced by *Aloe cameronii* Hemsley subsp. *bondana* Reynolds (*Aloaceae*). Various other species do occur with a few individuals in *Coleochloa*-mats without being present in many mats.

FIG. 12. *Coleochloa*-mat with fringing *Myrothamnus flabellifolius*, Lake Mtirikvi Recreational Park.

(b) *Mats formed by other species*

Myrothamnus flabellifolius and *Selaginella dregei* may occasionally form dense, monospecific mats.

Ephemeral flush

Ephemeral flush is a rare habitat on Zimbabwean inselbergs; only six localities were found on the studied inselbergs. The vegetation in this habitat is commonly open, with approximately 50% ground cover. Carnivorous plants were the most conspicuous constituents of ephemeral flush vegetation with *Utricularia arenaria* A. DC. (*Lentibulariaceae*), *U. subulata* L. (*Lentibulariaceae*) and *Drosera indica* L. (*Droseraceae*, Fig. 13) being the most characteristic species. *Cyperaceae* (*Cyperus* spp., *Fimbristylis* spp., *Kyllinga* spp. and *Pycreus* spp.) dominate the vegetation. *Xyris* sp. (*Xyridaceae*) and *Polygala* spp. (*Polygalaceae*) and *Eriocaulaceae* were further important members of ephemeral flush. Two species of *Rhamphicarpa* (*Scrophulariaceae*), *R. brevipedicellata* O.J. Hansen and *R. fistulosa* (Hochst.) Benth., were found; the first is endemic to southern Africa.

FIG. 13. *Drosera indica* in ephemeral flush vegetation, Domboshava.

Woody vegetation

Woody vegetation is present on various larger inselbergs. On shallow soil (50cm depth) *Euphorbia matabelensis* may form extensive thickets. On deeper soils, woodland trees dominate. *Julbernardia globiflora*, *Brachystegia glaucescens*, *Combretum* spp. and *Terminalia sericea* were often found in this habitat. Other important species include *Kirkia acuminata* Oliver (*Simaroubaceae*), *Sclerocarya birrea* Sond. (*Anacardiaceae*), *Uapaca kirkiana* Müll. Arg. (*Euphorbiaceae*) and *Vitex payos* (Lour.) Merr. (*Verbenaceae*). Small trees and bushes of woody vegetation are *Maytenus* spp., *Ochna* spp. and *Grewia flavescens* Juss (*Tiliaceae*).

Fringing forests

Forest vegetation in the immediate vicinity of inselbergs was generally continuous with the surrounding dry woodlands. In protected places, such as valleys between inselbergs in the Rhodes Matopos National Park, forests seemed particularly lush. On the other hand, Mopane woodland extended to the very foot of inselbergs near Kezi.

DISCUSSION

Species richness and floristic composition

The number of vascular plant species found on inselbergs in Zimbabwe (549 spp.) is similar to those found in the Ivory Coast (some 600 spp., unpublished data) and reported from Venezuela (614 spp.; Gröger, 1995). Venezuela harbours a much larger plant diversity than Zimbabwe, which in turn is floristically richer than the Ivory Coast (Barthlott et al., 1995). Species numbers on tropical inselbergs do not necessarily seem to reflect general diversity of the region. The apparent limitation of species numbers on inselbergs in one area should not be interpreted in terms of niche limitation, as the life-form spectra on African inselbergs differ considerably from those on South American inselbergs. While most species on inselbergs are therophytes in Zimbabwe and the Ivory Coast, phanerophytes are the most speciose life-form in Venezuela (Porembski et al., 1998a). Another factor against niche limitation is that the number of species found in the same habitat may vary considerably between regions, for example mats are formed by only one species (*Afrotrilepis pilosa* (Boeck.) J. Raynal) in the Ivory Coast and by three species (*Coleochloa setifera*, *Myrothamnus flabellifolius* and *Xerophyta* sp.) in Zimbabwe.

Inselbergs in extratropical regions are by far less speciose, with reports of 160 spp. from Western Australia (Ornduff, 1987) and 76 spp. from the Piedmont of the USA (Burbanck & Platt, 1964). This might be attributed to the general trend of decreasing diversity towards the poles, although the studies have not been conducted using the same method nor covering the same area. However, more data from other regions are required to improve our understanding of this issue.

Inselberg vegetation (vascular plants) is quite uniform over most of the country, notwithstanding differences between the Eastern Highlands and the remainder of the country (see below). The most diverse habitat is ephemeral flush. Dörrstock et al. (1996) also found ephemeral flush to be the most diverse habitat in the Ivory Coast. High diversity in ephemeral flush is probably maintained by disturbance (dry season) impeding competitive exclusion (Dörrstock et al., 1996). Rock pools show the lowest diversity among the habitats studied. They are often colonized by just one species. In West Africa, rock pools are more diverse (Porembski et al., 1994), possibly due to higher rainfall.

Floristically, inselberg vegetation in Zimbabwe is quite similar to that found in Malawi (Porembski, 1996) and the Ivory Coast (Porembski et al., 1998a). *Fabaceae* (s.l.), *Poaceae*, *Cyperaceae*, *Scrophulariaceae*, *Euphorbiaceae* and *Rubiaceae* are among the ten most speciose families of vascular plants in Zimbabwe and the Ivory Coast. Furthermore, many genera and species are found on inselbergs in both countries. The same applies for lichens. Very close links exist between Zimbabwean and Malagasy inselbergs (e.g. *Coleochloa setifera* as the major mat-forming species). Floristic composition of inselberg vegetation in Venezuela (Gröger, 1995), the USA (Burbanck & Platt, 1964), Australia (Ornduff, 1987) and the Seychelles (Fleischmann et al., 1996) differs considerably from the one reported here.

Phytogeography and habitat preferences

White (1983) estimates that 54% of the flora of the Zambesian region is restricted to this phytochorion. Only 35% of the vascular plant species recorded from inselbergs in Zimbabwe show Zambesian distribution (Seine, 1996). The reason for this is the dominance of herbaceous plants in inselberg vegetation, because the species with Zambesian distribution are predominantly woody (White, 1983).

The majority of species are widespread in Africa or even the palaeotropics. The climatic changes of the Quaternary which led to dry corridors (Wild, 1956) may have facilitated the spread of xerotolerant species, such as many inselberg plants. On the other hand these climatic changes induced fragmentation of moist tropical forests (Maley, 1987) and, presumably, local extinction of taxa in West Africa as the Atlantic Ocean impeded southward migration of hygrophilic species. New colonization had to be from south-east and South Africa, where species losses were less severe because of the absence of barriers to migration.

In contrast to general species numbers, the number of endemic species among vascular plants on inselbergs seems to reflect the degree of endemism encountered in the region: Gröger (1995) recorded 145 endemic species on Venezuelan inselbergs while only 15 endemic species were found on Zimbabwean inselbergs and none in the Ivory Coast (Porembski et al., 1998a). Numbers of endemic vascular plant species in those countries are approximately 8000 in Venezuela (Gröger, 1995), 95 in Zimbabwe (Brenan, 1978) and 62 in the Ivory Coast (Aké Assi, 1984). The same trend is also apparent in the number of endemic species restricted to inselbergs of the region: 88 in Venezuela (Gröger, 1995), seven in Zimbabwe, and none in the Ivory Coast (Porembski et al., 1998a).

The overall impression of inselberg vegetation in Zimbabwe is quite uniform. Species composition varies from inselberg to inselberg but many species (e.g. *Coleochloa setifera*, *Lindernia pulchella*, *Selaginella dregei*) are found on a large percentage of inselbergs. Changes in the vascular plant vegetation of inselbergs were recognized between the Nyanga Mountains and the remainder of the country. These differences are partly due to the presence of many endemic species in the Nyanga Mountains (Wild, 1964). Different climatic conditions with frost and increased moisture (Lebedew, 1970) may also influence vegetation composition such as the vicariousness observed in *Aloe* (*A. chabaudii*/*A. cameronii*) and *Craterostigma* (*C. plantagineum*/*C. lanceolatum*). Differences in lichen vegetation are even more substantial (see below).

Only a minor portion (<20%) of the plants recorded from inselbergs in Zimbabwe is more or less restricted to this ecosystem. The remaining species generally prefer open habitats. There is a remarkable element of plants that are confined to rocky places. A possible reason for this may be the generally reduced frequency of fire on rocky soils (West, 1992). Many species are also found on riversides, where open ground is available for colonization, probably indicating that these plants are weak competitors in undisturbed habitats.

Life-forms

Therophytes are the most speciose life-form in the Zimbabwean inselberg flora. Germinating and fruiting within a short period of time, they are well adapted to inselberg habitats that dry out quickly after the end of the rainy season. However, among the species with a strong preference for inselberg habitats, therophytes are noticeably less important. This is due to the generally low habitat requirements of therophytes which enable them to quickly colonize open ground. Therefore many therophytes from the surrounding vegetation are able to grow on inselbergs, but also the therophytic life-form may have facilitated the spread of species from inselbergs into the surrounding areas.

The dominant role of therophytes among inselberg species is also found in West Africa (Porembski et al., 1994), Malawi (Porembski, 1996) and Western Australia (Ornduff, 1987). In the USA, the favourable adaptation of therophytes is stressed by the fact that the proportion of this life-form is higher on inselbergs than in the surrounding vegetation (Phillips, 1982). On Venezuelan inselbergs only few therophytes were recorded (Gröger, 1995), which may be due to the generally moist climate facilitating competitive exclusion by perennial species.

The second most speciose life-form are phanerophytes, which are even more important among species with a preference for inselbergs. Plants are usually small bushes and trees. These phanerogams show ecological affinities to termitaria, rocky places and riversides, i.e. open habitats that do not support a dense growth of larger trees that might outcompete them.

Phanerophytes are less important in the Ivory Coast, probably because the Zambesian region is much richer in xerotolerant tree species than the Sudanian and the Guineo-Congolian region (White, 1983). Surprisingly, almost no phanerophytes were reported from Australian inselbergs by Ornduff (1987) and Norris & Thomas (1991). However, Hopper (1992) reports that a number of *Eucalyptus* and *Proteaceae* species are found on inselbergs in Western Australia. In the south-eastern USA, with its speciose forests, Phillips (1982) recorded nearly 30% of phanerophytes. Gröger (1995) found 41% phanerophytes on Venezuelan inselbergs and attributed the dominance of this life-form to competitive advantages of trees compared with mat-forming *Bromeliaceae*. This may again be a consequence of the moist climate and water availability.

Chamaephytes show the largest difference in percentage of the total inselberg flora and of the species preferring inselberg habitats. The importance of chamaephytes among the latter indicates good adaptation of the life-form to inselbergs. This is also supported by the fact that 21 out of 28 chamaephytes which prefer inselberg habitats are poikilohydric or succulent.

Gröger (1995) reports the same tendency from inselbergs in Venezuela: chamaephytes are important among species more or less restricted to inselbergs and those species are mostly succulent or poikilohydric. In the Ivory Coast (own unpublished data), Nigeria (Hambler, 1964), the USA (Phillips, 1982) and Western Australia

(Ornduff, 1987), chamaephytes were found to be of minor importance. Obviously, chamaephytic habit is not advantageous in inselberg vegetation unless accompanied by special adaptations (i.e. poikilohydry, succulence).

Hemicryptophytes are of minor importance in Zimbabwe as well as in Venezuela (Gröger, 1995). Ornduff (1987) recorded very few hemicryptophytes in Western Australian inselbergs. By contrast, hemicryptophytes account for 23% of inselberg species in the Ivory Coast (own unpublished data) and as much as 45% in the USA (Phillips, 1982). In the Ivory Coast, the large pool of hemicryptophytic species in the Sudanian savanna may be the reason. On inselbergs in the USA, the regularly occurring frosts may favour hemicryptophytic habit.

Geophytes are quite rare on inselbergs in Zimbabwe, Australia (Ornduff, 1987) and Venezuela (Gröger, 1995). A higher percentage of geophytes is found in the Ivory Coast (own unpublished data) and the USA (Phillips, 1982). In both these countries, geophytes are well represented in the surrounding vegetation and may therefore be quite speciose on inselbergs. Generally, the scarce soil cover of inselbergs may be regarded as an obstacle for geophytes.

Lianas, epiphytes and hydrophytes are rarely found on inselbergs in general. Their habitat requirements are obviously not met on inselbergs, although lianas are more abundant on inselbergs in Venezuela (Gröger, 1995) where climbing habit is supported by the presence of many phanerophytes.

Habitat separation in lichens

Chlorophytic lichens dominate on elevated microrelief, boulders and in the Eastern Highlands, while the rock surface is usually covered by cyanophytic lichens. A similar phenomenon has also been observed in the Ivory Coast, where chlorophytic lichens are more or less restricted to elevated microrelief and boulders. This strong differentiation of habitats may be caused by specific ecophysiological characters of the two groups of lichens. Lange et al. (1993) demonstrated that lichens with cyanobacteria as photobiont require liquid water for photosynthesis while chlorophytic lichens are able to use vapour. Furthermore, they showed that chlorophytic lichens have strongly decreased photosynthesis if they are in contact with liquid water.

Water present on the rock surface of inselbergs after rains may inhibit photosynthesis of chlorophytic lichen in this habitat and restrict them to habitats that dry out quickly, i.e. elevated microrelief and boulders. Also, the rock surface heats up considerably during the day (Porembski et al., 1996), resulting in low air humidity. The relative lack of liquid water on boulders and elevated microrelief is, on the other hand, a disadvantage for the growth of cyanobacterial lichens. Exposed parts of rock have been found to be cooler than the surroundings (Wessels & Kappen, 1994), resulting in increased air humidity and even dew. This increase in air humidity should be expected to occur near elevated microrelief and boulders, thus facilitating water uptake of chlorophytic lichens from vapour.

The increasing importance of chlorophytic lichens with higher elevation in

Zimbabwe, especially in the Eastern Highlands, may also be due to increasing air humidity. The Eastern Highlands and the highest parts of the highveld are quite regularly subject to fog (Kreft, 1972). With respect to the dominating cryptogams of the rock surface, a distinction within 'lichen-inselbergs' (Porembski & Barthlott, 1992) should be made between cyanophytic lichen-inselbergs and chlorophytic lichen-inselbergs.

Special adaptations

Resurrection plants are very speciose in Zimbabwe. Species numbers are much higher than in West Africa (Porembski et al., 1994) and Venezuela (Gröger, 1995). South-east Africa is thought to be a centre of diversity of poikilohydric vascular plants (Seine et al., 1996). There is also a higher number of succulents than on inselbergs in West Africa (Porembski et al., 1994). This may be due to the close proximity to the arid regions of South Africa and therefore to a species pool that could colonize inselbergs as 'xeric islands'. Venezuelan inselbergs, with an even larger pool of succulents available for colonization, harbour more succulent plants than Zimbabwean inselbergs. Quaternary climatic oscillations resulted in moist pluvials and dry non-pluvials in Africa (Zinderen Bakker, 1976). In south-east Africa, vegetation zones were free to move with these climatic changes (Wild, 1968), while in West Africa migration of species was impeded by the Atlantic Ocean. The dry corridors repeatedly opened by non-pluvials may have contributed to the high species numbers of succulents and resurrection plants in Zimbabwe.

Carnivorous plants are found on inselbergs throughout the world (Seine et al., 1996). Carnivory is advantageous because of the low nutrient conditions on inselbergs (Dörrstock et al., 1996). The number of carnivorous species recorded for inselbergs in Zimbabwe is relatively low and the genus *Genlisea*, which could be expected in ephemeral flush vegetation, could not be located. This may be due to the special climatic conditions in the years preceding the study which were extremely dry. The severe drought may have caused local extinction in ephemeral flush, a vegetation type that is entirely dependent on rainfall.

ACKNOWLEDGEMENTS

We would like to thank the Deutsche Forschungs Gemeinschaft (DFG, Schwerpunktprogramm: Mechanismen der Aufrechterhaltung tropischer Diversität) for funding the Inselberg Project. Scholarships granted to R. Seine by the Studienstiftung des deutschen Volkes and to U. Becker by the Graduiertenförderung des Landes Nordrhein-Westfalen and Richard-Winter-Stiftung are gratefully acknowledged. The Research Council of Zimbabwe kindly granted permission to conduct research in Zimbabwe. Our thanks are extended to R.B. Drummond, S. Kativu, T. Müller and N. Nobanda (all National Herbarium and Botanic Gardens, Harare) for their invaluable cooperation during research. B. Büdel (Kaiserslautern),

P. Clerc (Geneva) and G. Pope (Kew) are thanked for valuable discussions. The German Embassy (Harare), T. Piesch (Harare) and I. Nägel (Tshotsholo) provided support during fieldwork. L. Siklossy kindly checked the manuscript.

REFERENCES

ADJANOHOUN, E. (1964). Végétation des savanes et des rochers découverts en Côte d'Ivoire centrale. *Memoirs ORSTOM* 7.

AKÉ ASSI, L. (1984). *Flore de la Côte d'Ivoire: Étude descriptive et biogeographique, avec quelques note ethnobotaniques*. Abidjan: Thesis.

BARTHLOTT, W., GRÖGER, A. & POREMBSKI, S. (1993). Some remarks on the vegetation of tropical inselbergs: Diversity and ecological differentiation. *Biogéographica* 69(3): 17–36.

BARTHLOTT, W., POREMBSKI, S. & NIEDER, J. (1995). Biodiversität im Fokus der Forschung: Tropische Inselberge und Epiphyten. *Akademie Journal* 2: 50–55.

BORNHARDT, W. (1900). Zur Oberflächengestaltung und Geologie Deutsch-Ostafrikas. In: *Deutsch-Ostafrika. Wissenschaftliche Forschungsresultate über Land und Leute unseres ostafrikanischen Schutzgebietes und der angrenzenden Länder*. Bd. VII. Berlin: Reimer.

BOUGHEY, A. S. (1961). The vegetation types of Southern Rhodesia. *Proc. Rhodesia Sci. Assoc.* 49: 54–98.

BREMER, H. & JENNINGS, J. (eds) (1978). Inselbergs/Inselberge. *Zeitschr. f. Geomorph.*, Supplement 31.

BRENAN, J. P. M. (1978). Some aspects of the phytogeography of tropical Africa. *Ann. Missouri Bot. Gard.* 65: 437–478.

BREUSS, O. (1995). The genus *Catapyrenium* (Verucariales) in Southern Hemisphere. *Crypt. Bot.* 5: 177–183.

BÜDEL, B. (1987). Zur Biologie und Systematik der Flechtengattungen *Heppia* und *Peltula* im südlichen Afrika. *Biblioth. Lichenol.* 23: 1–115.

BURBANCK, M. I. & PLATT, R. B. (1964). Granite outcrop communities of the Piedmont Plateau in Georgia. *Ecology* 45: 292–306.

DEPARTMENT OF METEOROLOGICAL SERVICES (1984). *Mean Annual Rainfall.* Ed. 2. Harare: Government Printer.

DÖRRSTOCK, S., POREMBSKI, S. & BARTHLOTT, W. (1996). Ephemeral flush vegetation on inselbergs in the Ivory Coast (West Africa). *Candollea* 51: 407–419.

EXELL, A. W. et al. (eds for Flora Zambesiaca Committee) (1960–). *Flora Zambesiaca.* London: Crown Agents.

FLEISCHMANN, K., POREMBSKI, S., BIEDINGER, N. & BARTHLOTT, W. (1996). Inselbergs in the sea: vegetation of granite outcrops on the islands of Mahé, Praslin and Silhouette (Seychelles). *Bull. Geobot. Inst. ETH Zürich* 62: 61–74.

FRAHM, J.-P., POREMBSKI, S., SEINE, R. & BARTHLOTT, W. (1996). Moose von Inselbergen aus Elfenbeinküste und Zimbabwe. *Nova Hedwigia* 62: 177–189.

GARLAKE, P. (1982). *Life at Great Zimbabwe.* Gweru: Mambo.

GIBBS RUSSEL, G. E. (1975). Comparison of the size of various African floras. *Kirkia* 10: 123–130.

GRÖGER, A. (1995). *Die Vegetation der Granit-Inselberge Südvenezuelas: Ökologische und biogeographische Untersuchungen.* Bonn: Thesis.

HALE, M. E. (1975). A revision of the lichen genus *Hypotrachyna* (Parmeliaceae) in tropical America. *Smithsonian Contr. Bot.* 25: 1–73.

HALE, M. E. (1990). A synopsis of the lichen genus *Xanthoparmelia* (Vainio) Hale (Ascomycotina, Parmeliaceae). *Smithsonian Contr. Bot.* 25: 74–250.
HAMBLER, D. J. (1964). The vegetation of granitic outcrops in Western Nigeria. *J. Ecol.* 52: 573–594.
HENKEL, J. S. (1931). Provisional map of the types of vegetation in southern Rhodesia. *Proc. Rhodesian Sci. Assoc.* 30: 1–23.
HOPPER, S. D. (1992). Pattern of plant diversity at the population and species levels in south-west Australian mediterranean ecosystems. In: HOBBS, R. J. (ed.) *Biodiversity of Mediterranean Ecosystems in Australia*, pp. 27–46. Chipping Norton, New South Wales: Surrey Beatty & Sons.
IBISCH, P. L., RAUER, G., RUDOLPH, D. & BARTHLOTT, W. (1995). Floristic, biogeographical, and vegetational aspects of Pre-Cambrian rock outcrops (inselbergs) in eastern Bolivia. *Flora* 190: 299–314.
KAYSER, K. (1957). Zur Flächenbildung, Stufen- und Inselberg-Entwicklung in den wechselfeuchten Tropen auf der Ostseite Süd-Rhodesiens. *Deutscher Geographentag* 1957: 165–172.
KÖPPEN, W. (1923). *Die Klimate der Erde*. Berlin, Leipzig.
KREFT, J. (1972). Fog in Rhodesia. *Climate Information Sheet* 41. Salisbury: Department of Meteorological Services.
LANGE, O. L., BÜDEL, B., MEYER, A. & KILIAN, E. (1993). Further evidence that activation of net photosynthesis by cyanobacterial lichens requires liquid water. *Lichenologist* 25: 175–189.
LEBEDEW, A. N. (ed.) (1970). *The Climate of Africa.* Vol. I. Jerusalem.
MALEY, J. (1987). Fragmentation de la forêt dense humide africaine et extension des biotopes montagnards au Quaternaire récent: nouvelles données polliniques et chronologiques. Implications paléoclimatiques et biogéographiques. *Palaeoecol. Africa* 18: 307–334.
NORRIS, E. H. & THOMAS, J. (1991). Vegetation on rocky outcrops and ranges in central and southeastern New South Wales. *Cunninghamia* 2: 411–441.
ORNDUFF, P. (1987). *Islands on Islands: Plant Life on the Granite Outcrops of Western Australia.* Honolulu: University of Hawaii Press.
PHILLIPS, D. L. (1982). Life-forms of granite outcrop plants. *Amer. Midl. Naturalist* 107: 206–208.
POREMBSKI, S. (1996). Notes on the vegetation of inselbergs in Malawi. *Flora* 191: 1–8.
POREMBSKI, S. & BARTHLOTT, W. (1992). Struktur und Diversität der Vegetation westafrikanischer Inselberge. *Geobot. Kolloquien* 8: 69–80.
POREMBSKI, S., BARTHLOTT, W., DÖRRSTOCK, S. & BIEDINGER, N. (1994). Vegetation of rock outcrops in Guinea: granite inselbergs, sandstone table mountains and ferricrete: remarks on species numbers and endemism. *Flora* 189: 315–326.
POREMBSKI, S., BECKER, U. & SEINE, R. (1998b). Islands on islands: Habitats on inselbergs. In: POREMBSKI, S. & BARTHLOTT, W. (eds) *Vegetation of Inselbergs.* Ecological Studies. Berlin, Heidelberg: Springer, (in press).
POREMBSKI, S., GRÖGER, A., SEINE, R., IBISCH, P. & BARTHLOTT, W. (1998a). Vegetation neotropischer und paläotropischer Inselberge – ein Vergleich. *Mitt. Bundesforschungsanst. Forst- Holzw. Reinbek.*, (in press).
POREMBSKI, S., SZARZYNSKI, J., MUND, J.-P. & BARTHLOTT, W. (1996). Biodiversity and vegetation of small-sized inselbergs in a West African rain forest (Tai, Ivory Coast). *J. Biogeogr.* 23: 47–55.

PURVIS, O. W., COPPINS, B. J., HAWKSWORTH, D. L., JAMES, P. W. & MOORE, D. M. (1992). *The Lichen Flora of Great Britain and Ireland.* London: Natural History Museum Publications.

RATTRAY, J. M. (1961). Vegetation types of Southern Rhodesia. *Kirkia* 2: 68–93.

RUDD, S. (1968). Lekkerwater ruins, Tsindi Hill, Theydon, Rhodesia. *Proc. Rhodesia Sci. Assoc.* 52: 38–50.

SARTHOU, C. (1992). *Dynamique de la végétation pionniere sur un inselberg en Guyane Francais.* Paris: Thesis.

SCHULZE, R. E. & McGEE, O. S. (1978). Climatic indices and classifications in relation to the biogeography of southern Africa. In: WERGER, M. J. A. (ed.) *Biogeography and Ecology of southern Africa*, pp. 19–54. The Hague: W. Junk.

SCOTT, E. D. (1967). Studies of the lichen symbiosis: 3. The water relations of lichens on granite kopjes in Central Africa. *Lichenologist* 3: 368–385.

SEINE, R. (1996). Vegetation von Inselbergen in Zimbabwe. *Archiv naturwissenschaftlicher Dissertationen* 2. Wiehl: Martina Galunder Verlag.

SEINE, R., FISCHER, E. & BARTHLOTT, W. (1995). Notes on the Scrophulariaceae of Zimbabwean inselbergs, with the description of *Lindernia syncerus* sp. nov. *Feddes Repert.* 106: 7–12.

SEINE, R., POREMBSKI, S. & BARTHLOTT, W. (1996). A neglected habitat of carnivorous plants: inselbergs. *Feddes Repert.* 106: 555–562.

SUMMERS, R. (1960). Environment and culture in Southern Rhodesia. *Proc. Amer. Philos. Soc.* 104: 266–292.

SWINSCOW, T. D. V. & KROG, H. (1988). *Macrolichens of East Africa.* London: British Museum (Natural History).

TAYLOR, P. (1989). The genus *Utricularia. Kew Bulletin Additional Series* XIV. London: HMSO.

TIMBERLAKE, J. & NOBANDA, N. (1993). Vegetation survey in Zimbabwe. *Kirkia* 14: 24–48.

TORRANCE, J. D. (1972). *Malawi, Rhodesia and Zambia.* In: GRIFFITHS, J. F. (ed.) *Climates of Africa*, pp. 409–460. World Survey of Climatology Vol. 10. Amsterdam.

WESSELS, D. C. J. & KAPPEN, L. (1994). Aspect, microclimate and photosynthetic activity of lichens in the Northern Transvaal and Karoo, South Africa. *Crypt. Bot.* 4: 242–253.

WEST, O. (1992). *Aloes in Zimbabwe.* Ed. 2. Harare: Longman.

WHITE, F. (1983). The vegetation of Africa. *Natural Resources Research* 20. Paris: UNESCO.

WILD, H. (1956). The principal phytogeographic elements of the Southern Rhodesian flora. *Proc. Rhodesia Sci. Assoc.* 44: 53–62.

WILD, H. (1964). The endemic species of Chimanimani Mountains and their significance. *Kirkia* 4: 125–157.

WILD, H. (1968). Phytogeography in South Central Africa. *Kirkia* 6: 197–222.

WILD, H. & FERNANDES, A. (1967). Vegetation Map of the Flora Zambesiaca area. *Flora Zambesiaca Supplement.* Salisbury: Collins.

ZINDEREN BAKKER, E. M. VAN (1976). The evolution of late-quaternary palaeoclimates of Southern Africa. In: ZINDEREN BAKKER, E. M. VAN (ed.) *Palaeoecology of Africa* 9, pp. 160–202. Cape Town, Rotterdam: Balkema.

Received 10 September 1996; accepted with revision 24 January 1997