

**Zeitschrift:** Bulletin of the Geobotanical Institute ETH  
**Herausgeber:** Geobotanisches Institut, ETH Zürich, Stiftung Rübel  
**Band:** 62 (1996)

**Artikel:** Inselbergs in the sea : vegetation of granite outcrops on the islands of Mahé, Praslin and Silhouette (Seychelles)  
**Autor:** Fleischmann, Karl / Porembski, Stefan / Biedinger, Nadia  
**DOI:** <https://doi.org/10.5169/seals-377797>

### **Nutzungsbedingungen**

Die ETH-Bibliothek ist die Anbieterin der digitalisierten Zeitschriften auf E-Periodica. Sie besitzt keine Urheberrechte an den Zeitschriften und ist nicht verantwortlich für deren Inhalte. Die Rechte liegen in der Regel bei den Herausgebern beziehungsweise den externen Rechteinhabern. Das Veröffentlichen von Bildern in Print- und Online-Publikationen sowie auf Social Media-Kanälen oder Webseiten ist nur mit vorheriger Genehmigung der Rechteinhaber erlaubt. [Mehr erfahren](#)

### **Conditions d'utilisation**

L'ETH Library est le fournisseur des revues numérisées. Elle ne détient aucun droit d'auteur sur les revues et n'est pas responsable de leur contenu. En règle générale, les droits sont détenus par les éditeurs ou les détenteurs de droits externes. La reproduction d'images dans des publications imprimées ou en ligne ainsi que sur des canaux de médias sociaux ou des sites web n'est autorisée qu'avec l'accord préalable des détenteurs des droits. [En savoir plus](#)

### **Terms of use**

The ETH Library is the provider of the digitised journals. It does not own any copyrights to the journals and is not responsible for their content. The rights usually lie with the publishers or the external rights holders. Publishing images in print and online publications, as well as on social media channels or websites, is only permitted with the prior consent of the rights holders. [Find out more](#)

**Download PDF:** 05.07.2025

**ETH-Bibliothek Zürich, E-Periodica, <https://www.e-periodica.ch>**

## Inselbergs in the sea: vegetation of granite outcrops on the islands of Mahé, Praslin and Silhouette (Seychelles)

KARL FLEISCHMANN\*, STEFAN POREMBSKI\*\*,  
NADIA BIEDINGER\*\* & WILHELM BARTHLOTT\*\*

\* *Geobotanisches Institut ETH, Zürichbergstrasse 38, 8044 Zürich, Switzerland, corresponding author*

\*\* *Botanisches Institut der Universität Bonn, Meckenheimer Allee 170, 53115 Bonn, Germany*

### Summary

**1** The flora and vegetation of rock outcrops (inselbergs) of granitic islands of the Seychelles are briefly described, and the ecological status of four inselbergs on Mahé and Silhouette is quantitatively investigated and compared with the status of habitats in their immediate vicinity.

**2** Most habitat types which are also characteristic of inselbergs in other tropical regions occur. Only monocotyledonous mats and ephemeral flush vegetation are absent.

**3** Species richness of Seychelles inselbergs is considerably lower compared to the vegetation of rock outcrops in tropical mainland areas. Differences in the species inventories of the inselbergs investigated are not significant, i.e.  $\beta$ -diversity is low. Phytogeographical affinities of the rock outcrop flora are more directed to south-east Asia than towards Africa or Madagascar.

**4** Though relatively poor in species the Seychelles rock outcrops harbour a considerable number of palaeoendemics (e.g. *Medusagyne oppositifolia*, *Nepenthes pervillei*). Quantitative investigations showed that indigenous and endemic species are the most prominent components of the rock outcrop vegetation, whereas alien species, such as *Cinnamomum zeylanicum* play only a minor role.

**5** In terms of conservation all sites investigated reveal outstanding floristic and ecological values. The still high regeneration rates of native species suggest that rock outcrops are not yet seriously endangered by invasion of alien plants.

**Keywords:** conservation, diversity, ecological status matrix, glaxis, prominence value, protection value

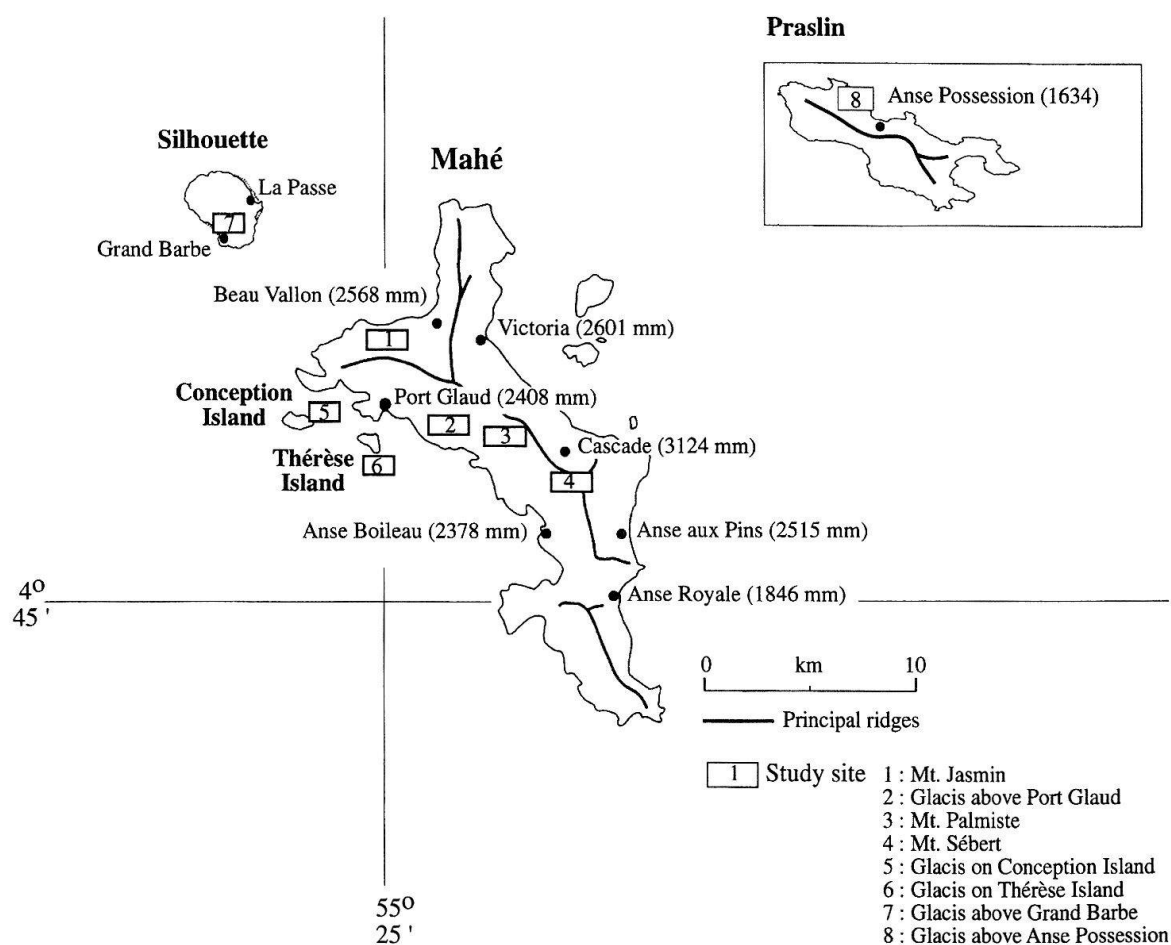
**Nomenclature:** S.A. Robertson (1989)

*Bulletin of the Geobotanical Institute ETH* (1996), **62**, 61–74

### Introduction

The Seychelles archipelago consists of about 115 islands, of which some are coralline and others granitic (Fig. 1). The latter are the oldest oceanic islands in the world and represent

fragments of the original land-mass of Gondwanaland (Baker & Miller 1963). Located in the Western Indian Ocean their geographical position is very isolated (Stoddart 1968).



**Fig. 1.** The location of the eight study areas on five islands of the Seychelles (mean annual rainfall is given in brackets).

Of all oceanic islands, those of the Seychelles may have had the longest time for vegetation to develop by purely natural immigration and evolutionary processes (Dalziel 1995). These islands must have been continuously available for plant colonization for millions of years before the first human settlers arrived in 1768 (Lionnet 1984). This rare situation and the geographically isolated position gave rise to the formation of relictual vegetation elements of considerable botanical interest and a high level of endemism (High 1982). More than half of the native plant species are endemics, including many famous rarities like *Lodoicea maldivica* and *Medusagyne oppositifolia*.

Several accounts (e.g. Vesey-Fitz-Gerald 1940; Bailey 1971; Procter 1984a) provide general descriptions of the vegetation of the granitic islands. With the studies of Robertson (1989) and Friedmann (1991) updated reports on their floristics are available. There is a large variety of vegetation types with coastal formations including mangroves and different forest types. In the inner islands, particularly Mahé, the ecosystems can be divided into four categories (Jeffrey 1962; Procter 1984b): vegetation of the coastal plateau, lowland forest (coastal plateau – 300 m), intermediate forest (300–550 m), mountain mist forest (550–910 m).

There is a fifth vegetation element which cannot be related to altitude. This vegetation type, comprising vegetation growing on solitary, often monolithic rocks or parts of mountain systems which rise abruptly from their surroundings, is locally called “glacis-type” vegetation (Fig. 2). The term “glacis” is French and means “steep, rocky slope”. Glacis are exposed Precambrian rock outcrops which are known to geomorphologists as inselbergs (cf. Bremer & Jennings 1978). They occur on the old crystalline shields throughout the tropics and differ strongly from the surrounding areas, thus emphasizing their insular character (“xeric islands”). Temperatures on the exposed rocks can be high (they regularly exceed 50 °C), while relative air humidity may drop below 30 % even under a rainforest climate. They can thus be considered as “micro-environmental deserts” (Phillips 1982). Several regional descriptions of the vegetation of inselbergs are available (e.g. Richards 1957; Adjanohoun 1964; Hambler 1964; Porembski *et al.* 1994, 1995; Ibisch *et al.* 1995). However, the vegetation of Seychelles rock outcrops has not been

dealt with hitherto, apart from Fleischmann (in press) who emphasized their unique plant cover, with special reference to problems of invasive alien plants and conservation.

Granitic and gneissic inselbergs offer a range of different habitats which can be classified according to their physiognomy. The most important habitats are (after Barthlott *et al.* 1993): (1) cryptogamic crusts on open rock surfaces (consisting of lichens and cyanobacteria), (2) drainage channels, (3) rock crevices and boulder falls, (4) seasonal rock pools, (5) shallow depressions, (6) monocotyledonous mats, (7) ephemeral flush vegetation, and (8) wet flush vegetation. Despite fundamental floristic differences, the physiognomy of habitats on inselbergs remains remarkably similar irrespective of geographical location: in tropical Africa and Madagascar monocotyledonous mats are dominated by Cyperaceae (*Afrotrilepis* in West Africa; *Coleochloa* in East Africa and Madagascar) and Velloziaceae, whereas Bromeliaceae dominate on neotropical inselbergs as mat-forming elements. Concerning species richness and number of endemics, the



Fig. 2. Inselberg (glacis) on Mahé Island.



vegetation of inselbergs in a particular region is influenced by climate, degree of isolation and historical effects. Being terrestrial islands which occur in many climatic and vegetational zones of the tropics, inselbergs provide opportunities for comparative analyses.

## Objectives

The aim of the present study is to provide an account of the rock outcrop vegetation of the largest granitic islands in the Seychelles (Mahé, Silhouette, Praslin), and to compare the results with those from other tropical regions (in particular Africa) in terms of species composition, biogeography and species richness.

This study also attempts to evaluate the ecological status of inselberg vegetation in terms of diversity, singularity, regeneration and prominence value of alien and native plants in the Seychelles. We have the following specific objectives: (1) to establish a database for monitoring of habitat changes; (2) to compare the ecological status of inselbergs with that of adjacent habitats; (3) to assess the threat from the most prominent and potentially dangerous invaders within Seychelles inselberg vegetation, and (4) to identify potentially important biodiversity sites which deserve to become strictly protected areas.

## Study sites

The investigations were conducted on Mahé (the largest granitic island of the Seychelles, 154 km<sup>2</sup>), on Praslin (37 km<sup>2</sup>) and on Silhouette (19 km<sup>2</sup>); Fig. 1 shows the location of the rock outcrops studied.

Precambrian alkali granite containing microperthite dominates on Mahé (Baker & Miller 1963). In western Mahé at Port Glaud and on the offshore islands of Thérèse and Conception a porphyritic granodiorite occurs

(Braithwaite 1984), whereas on the geologically much younger Silhouette syenitic rock is prevailing.

The climate is tropical with an average annual rainfall of 2200 mm. Mean monthly rainfall exceeds 100 mm except in June, July and August. Mean annual temperatures at sea level are around 27 °C at Victoria. Seasonal and diurnal temperature ranges are very small. Humidity also varies little with season; in Victoria monthly means of relative air humidity vary only from 75 % in April to a maximum of 80 % in January (at the height of the rainy season). For a detailed description of the climatic situation we refer to Walsh (1984).

## Methods

In July/August 1994 and March/April 1995 twelve rock outcrops were surveyed and in four instances also their surrounding habitats were studied for comparison. On four sites (27 sampling units) quantitative vegetation surveys were conducted (see Fig. 1 sites 1, 3, 4 and 7). Each of these sites comprise both: inselberg vegetation (14 sampling units) and surrounding habitats belonging mainly to moist intermediate forest types (13 sampling units). All vascular plant species were recorded and life-form spectra compiled using the Raunkiaer (1934) classification.

For the assessment of the ecological status of inselbergs a new evaluation scheme which allows a quantitative ecological validation was introduced. The method to accomplish this objective of the study follows closely that used by Fleischmann (in press) on a survey defining conservation values of potentially important biodiversity sites on the islands of Silhouette and Mahé. The presence and abundance of all naturalized alien and native plants were recorded for eight habitats within the locations 1, 3, 4 and 7 (see Fig. 1).

Recordings were made while walking along trails within the survey area. The nearest plant with a height >2 m to every third step was recorded. A series of 100 successive plants within a trail-transect was defined as one sampling unit (subtransect). Most of the selected trails were completely overgrown and in many cases had almost vanished.

Abundance estimates (Henderson & Musil 1984) were based on frequency of encounter within transects of 666–888 m. In this study recordings were made along a total trail length of approximately 5994 m. Since all trail-transects were plotted on maps, this part of the survey is easily repeatable despite the use of variable transect lengths.

#### FREQUENCY

The percentage frequency  $f_{ij}$  of occurrence of a species  $i$  within an individual transect  $j$  was calculated as follows, where  $n_{ij}$  is the number of sampling units in transect  $j$  having species  $i$  and  $n_j$  the number of sampling units in transect  $j$ .

$$f_{ij} = \frac{n_{ij}}{n_j} 100$$

#### PROMINENCE VALUE

Prominence (in terms of frequency and abundance) was used here in preference to the term importance (Mueller-Dombois & Ellenberg 1974). The prominence value  $PV_{ij}$  for a species  $i$  in transect  $j$  was calculated as follows, where  $f_{ij}$  is the frequency of species  $i$  in transect  $j$  and  $a_{ijk}$  denotes the abundance class value of species  $i$  in sampling unit  $k$  of transect  $j$ .

$$PV_{ij} = \frac{f_{ij}}{\sum_i f_{ij}} 100 + \frac{\sum_k a_{ijk}}{\sum_i \sum_k a_{ijk}} 100$$

M 1	DIVERSITY NATIVES		
	3	2	1
SINGULARITY	3	3	3
	2	3	2
	1	2	1

M 2	ABUNDANCE INVADERS		
	3	2	1
ABUNDANCE NATIVES	3	3	3
	2	3	2
	1	2	1

M 3	REGENE- RATION		
	3	2	1
M 2	3	3	3
	2	3	2
	1	2	1

M 4	M 3		
	3	2	1
M 1	3	5	4
	2	4	3
	1	3	2

**Fig. 3.** The form of ecological status matrices: data of five ecological criteria are entered into matrices M1 to M3, following the validation given in Table 1. The three matrices are then compiled to a single end-matrix (M4). Values in matrices: 1 = low; 2 = medium; 3 = high. Values in matrix 4 (protection values): 1 = very low; 2 = low; 3 = medium; 4 = high; 5 = very high.

#### THE USE OF ECOLOGICAL STATUS MATRICES

Ecological status matrices (Schulte & Marks 1985) proved useful for the evaluation of conservation values of potentially important habitats. In this survey the use of ecological status matrices involves the study of several parameters such as “abundance” of native and invasive woody plants, “diversity”, “singularity” and “regeneration”. To estimate the conservation value of a particular sampling unit (i.e. 100 subsequent plants >2 m) within an individual transect, values for the above parameters are entered into matrices M1 to M3 (Fig. 3), following the validation given in Table 1. The three matrices are then compiled to a single end-matrix (M4); values of this matrix are the so-called protection values which, in terms of conservation, indicate the protection priority of a particular site.

**Table 1.** Ecological criteria used in the evaluation of the status of the inselberg vegetation investigated (SU, sampling unit)

Criteria (in SU)	Category (in SU)	Value
Diversity of natives	<8 species	1
	8–16 species	2
	>16 species	3
Singularity (acc. red list status 1–4)	<5 species	1
	5–10 species	2
	>10 species	3
Total abundance of invaders	<30 species	3
	30–60 species	2
	>60 species	1
Total abundance of natives	<30 species	1
	30–60 species	2
	>60 species	3
Regeneration (indigenous and endemic saplings 0.5–2.0 m heigh)	< 34%	1
	34–66%	2
	>66%	3

In this survey singularity refers to unique and rare species based on the Red Book status of Seychelles endemic plants. The proposed status-rating for IUCN Red Book of endangered species has been assessed by Procter (1974). Regeneration is the percentage of native saplings of 0.5–2.0 m within each subunit of an individual transect.

Ecological status matrices make the process of assessment of a particular vegetation easily comprehensible and a re-evaluation of a particular habitat possible. They do not follow rigid standards and therefore are a flexible approach in assessing vegetation structures. It is important to note that quality depends not only on species richness. If a particular site shows a low diversity of native species (which gives a low value in matrix 1, Fig. 3), but harbours several rare and endangered plants, matrix 1 shows that it is assigned to give a fairly high aggregated value.

In reflection of conservation priorities of the selected inselbergs based on habitat potential in the future, the above criteria regeneration, singularity and diversity have been given a slightly higher weighting than other criteria.

## Results and discussion

### DESCRIPTION OF HABITAT TYPES

In the Seychelles, inselbergs occur from the sea-shore to mountain-tops. Extreme edaphic and climatic conditions (high degree of insolation combined with high evaporation rates and poor soil water storage) exert selective pressures resulting in a vegetation that completely differs from that of the surroundings. On inselbergs exposure is severe. Soil which accumulates in pockets and fissures consists largely of coarse quartz sand with variable amounts of peaty organic matter. If the peat cover is destroyed by clearings or fire and subsequent erosion, bare rock is exposed. The thin soil and scarce vegetation cover of glacia habitats can retain only a small percentage of the precipitation. The erosive power of the run-off water has produced picturesque drainage channels which cut into the rock.

In accordance with Barthlott *et al.* (1993) the following habitat types were found: (1) exposed rock surfaces, (2) drainage channels, (3) rock crevices, (4) rock pools and (5) shallow depressions filled with debris. Certain habitat types, such as monocotyledonous mats formed by dense stands of Cyperaceae (e.g. *Afrotrilepis pilosa*; Porembski 1996) which are usually present in tropical Africa and Madagascar, were absent. Though *Lophoschoenus hornei* forms dense monospecific stands, they cannot be classified as monocotyledonous mats since their cover does not form carpet-like structures. Small

depressions and crevices are typical sites for *Lophoschoenus*. Also missing is ephemeral flush vegetation which develops where water seeps continuously during the rainy season, and wet flush vegetation that occurs on steeply inclined bare rocky slopes, where often vascular plants such as *Utricularia* spp. are attached to cryptogamic crusts.

In the following account the most important features of the five habitat types are briefly discussed: Exposed rock surfaces are devoided of phanerogams, but are almost completely covered by dense crusts of cyanobacteria which are responsible for the dark brownish colour of the rock outcrops. For this reason the inselbergs investigated can be classified as "cyanobacteria-inselbergs" in contrast to "lichen-inselbergs" where the rock surfaces are covered by lichens. The latter type occurs under drier climatic conditions (Porembski & Barthlott 1992). Occasionally lichen covered boulders could be found, but more often lichens were restricted to the lower, less exposed surfaces of overhanging rock. On all sites investigated inselbergs rising directly from the sea are characterized by a 3–5 m wide cyanobacteria-free strip of bare rock due to the influence of salt spray.

Drainage channels are formed by run-off water and are totally covered by cyanobacteria; the taxa are probably different to those on the flat rocky slopes. Frequently these channels are bordered by small zones (mostly 3–5 cm in width) of bare rock which are not covered by cyanobacteria.

Rock crevices occur in large numbers and different dimensions, from small fissures to broad clefts. They are dominated mostly by native woody plants (e.g. *Canthium bibracteatum*, *Dracaena reflexa*, *Erythroxylum sechellarum*, *Euphorbia pyrifolia*, *Lophoschoenus hornei*, *Memecylon eleagni*, *Pandanus multispicatus*, *Pandanus sechellarum*

and *Pandanus balfourii*). Annuals are only sparsely represented (e. g. *Kyllinga* spp.). Occasionally alien plants such as *Cinnamomum zeylanicum* and *Chrysobalanus icaco* occur.

Rock pools are present in only small numbers. Mostly irregularly shaped, only a few are circular in outline. The bottom of such pools is usually covered by a thin sandy substrate. No higher plants grew in these sites.

Shallow depressions of different size filled with quarzitic and organic debris, occur in large numbers. The substrate is usually less than 5 cm in depth. Frequently *Memecylon eleagni*, *Lophoschoenus hornei*, *Pandanus* spp. and *Dianella ensifolia* show high percentage cover values. Another prominent feature of this habitat type is the occurrence of xeromorphic trees. Annuals such as *Bulbostylis barbata* and *Fimbristylis dichotoma* were recorded in small numbers. Characteristically, the mosses *Campylopus brevirameus* and *C. robillardae* occur.

#### FLORISTIC COMPOSITION AND PHYTOGEOGRAPHICAL ASPECTS

We found 56 species in 53 genera and 37 families of vascular plants on the inselbergs studied. Families with the most species were Apocynaceae (4), Arecaceae (4), Cyperaceae (4), Euphorbiaceae (4), Rubiaceae (4), Orchidaceae (3), Pandanaceae (3), Poaceae (3), Cactaceae (2), Melastomataceae (2), Mimosaceae (2) and Sapotaceae (2). Dicots (59%) outnumber the monocots (35%), with ferns accounting for 6% of the total number of species recorded. Only a single genus (*Pandanus*, three species) was represented by more than one species.

Life-form spectra were dominated by phanerophytes (nearly 50% of all species recorded). They are followed by therophytes accounting for 15% and chamaephytes (c. 3%); Cryptophytes and hemicryptophytes were lacking in this study area.

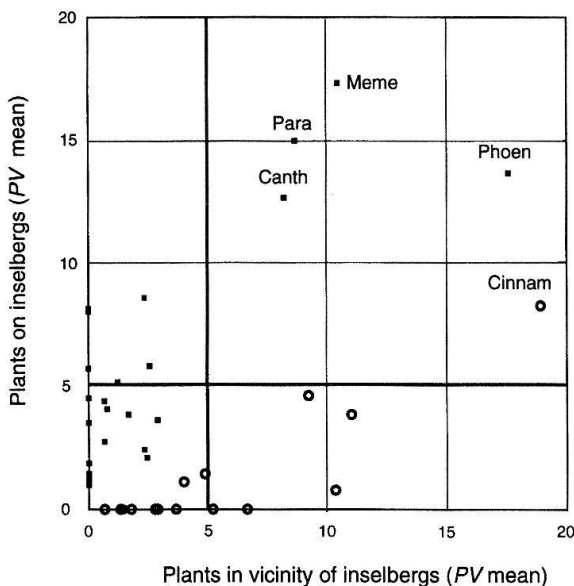
A first survey of the phytogeographical relationships of the Seychelles rock outcrop flora reveals the following patterns: (1) Endemic species (i.e. confined to the granitic islands of the Seychelles), such as *Medusagyne oppositifolia*, *Pandanus multispicatus*, *Memecylon eleagni*, *Erythroxylum sechellarum* and *Lophoschoeneus hornei*. (2) Indigenous species with restricted distribution, e.g. *Euphorbia pyrifolia* (Seychelles, Mauritius, Madagascar), *Dianella ensifolia*, (Seychelles, Madagascar). Endemics and indigenous species with restricted distribution make up the largest portion of the Seychelles inselberg vegetation. (3) Indigenous species with widespread distribution, such as *Canthium bibracteatum* (Seychelles, Madagas-

car, East Africa), *Cerbera manghas* (Seychelles to South East Asia and Polynesia), *Rhipsalis baccifera* (Seychelles, tropical America, tropical Africa, Madagascar, Sri Lanka). (4) Naturalized species, e.g. *Ananas comosus*, *Chrysobalanus icaco*, *Psidium littorale* (tropical America), *Cinnamomum zeylanicum* (Sri Lanka). (5) Status uncertain, e.g. *Bulbostylis barbata* (Old World Tropics) and *Fimbristylis dichotoma* (pantropic).

#### THE ECOLOGICAL STATUS OF INSELBERG VEGETATION ON MAHÉ AND SILHOUETTE

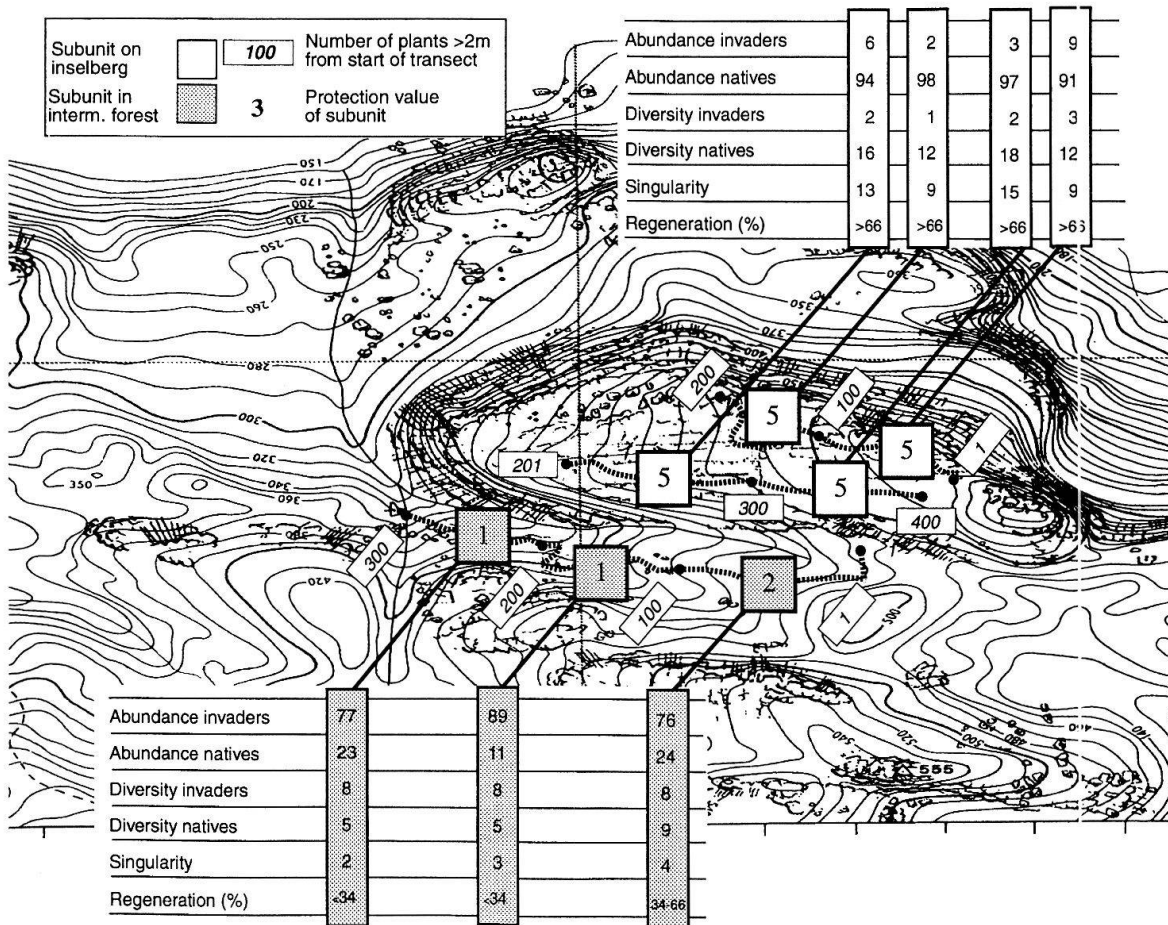
This part of the study refers to quantitative investigations within the sites 1, 3, 4 and 7 (see Fig. 1). For a total transect length of almost 6 km the number of species sampled is small in comparison with other mountainous, humid equatorial environments (Whitmore 1993).

Up to 23 species were recorded per sampling unit (100 individuals). The most prominent species (prominence values >8.0, see Fig. 4) were (in decreasing order): *Memecylon eleagni*, *Paragenipa lancifolia*, *Phoenixophorium borsigianum*, *Canthium bibracteatum*, *Nephrosperma vanhoutteana*, *Cinnamomum zeylanicum*, *Dillenia ferruginea* and *Pandanus multispicatus*. Out of these, *Cinnamomum zeylanicum* is the only alien species, and five taxa are endemic to the Seychelles. Within the immediate vicinity of inselbergs (surrounding habitats) the most prominent species were (in decreasing order): *Cinnamomum zeylanicum*, *Phoenixophorium borsigianum*, *Adenanthera pavonina*, *Chrysobalanus icaco*, *Memecylon eleagni*, *Nephrosperma vanhoutteana*, *Tabebuia pallida*, *Paragenipa lancifolia*, *Canthium bibracteatum*. Four of these species (*Adenanthera*, *Cinnamomum*, *Chrysobalanus*, *Tabebuia*) are among the most important alien invaders in Seychelles. The endemic palm, *Phoenixophorium*, is established in both



**Fig. 4.** Comparison of the prominence values (PV) of plants >2.0 m in height between inselbergs and adjacent habitats. On inselbergs the prominence values of the most serious alien invaders are small (i.e. PV<5.0) or even missing. Endemic and indigenous species are mostly confined to inselbergs. The five most prominent plants are: Meme = *Memecylon eleagni*; Para = *Paragenipa lancifolia*; Phoen = *Phoenixophorium borsigianum*; Canth = *Canthium bibracteatum*; Cinnam = *Cinnamomum zeylanicum* (■ = indigenous and endemic plants; ○ = alien (often invasive) plants).





**Fig. 5.** The ecological status of the vegetation on Mont Sébert, Mahé. The sudden and spatially abrupt change in ecological habitat qualities (i.e. decreasing protection values) between this particular inselberg and the habitats in its immediate vicinity is striking (protection values: 1, very low; 2, low; 3, medium; 4, high; 5, very high).

**Table 2.** Seychelles inselbergs show an outstanding ecological status compared with habitats in their immediate surroundings (PV = prominence value of natives; DI = diversity of natives; SI = singularity; PTV = protection value). The sum of the relative means of each criteria mentioned above is 100%

	INSELBERGS (7 SU within 2 sites) extremely isolated (Mt. Sébert, Mt. Palmiste)				INSELBERGS (7 SU within 2 sites) medium isolated (Gr. Barbe, Mt. Jasmin)				SURROUNDING HABITATS (13 SU within 4 sites) mainly moist intermediate forest			
	PV	DI	SI	PTV	PV	DI	SI	PTV	PV	DI	SI	PTV
Sub-totals in	179.2	58.0	46.0	20.0	163.8	42.0	14.0	19.0	83.1	19.0	9.0	4.0
Sampling units	176.2	47.0	30.0	15.0	166.6	42.0	17.0	15.0	89.2	26.0	7.0	6.0
									71.2	34.0	13.0	13.0
									124.4	26.0	5.0	7.0
<b>Absolute mean</b>	<b>50.8</b>	<b>15.0</b>	<b>10.9</b>	<b>5.0</b>	<b>47.2</b>	<b>12.0</b>	<b>4.4</b>	<b>4.9</b>	<b>28.3</b>	<b>8.1</b>	<b>2.6</b>	<b>2.3</b>
<b>Relative mean</b>	<b>40.2</b>	<b>42.7</b>	<b>60.7</b>	<b>41.1</b>	<b>37.4</b>	<b>34.2</b>	<b>24.7</b>	<b>39.9</b>	<b>22.4</b>	<b>23.1</b>	<b>14.6</b>	<b>19.0</b>



habitat types. This palm is not only adapted to xeric conditions, it has also the potential of taking over in many places of secondary forest, gradually replacing the alien species mentioned above.

The ecological status of one site (typical of the whole study area) is shown in Fig. 5. Extremely high rates of diversity and abundance of natives together with a regeneration rate of native saplings >66% are responsible for the very high protection values of this particular site. Fig. 5 shows one of the four locations in the Seychelles where the very rare *Medusagynne oppositifolia* still survives.

The two inselbergs Mont Sébert and Montagne Palmiste are geographically isolated and much exposed to exceptional climatic and edaphic factors. These habitats score a relative mean protection value of 41% (Table 2). Though the less isolated inselbergs above Grand Barbe (Silhouette) and Mont Jasmin (Mahé), have a slightly smaller relative mean protection value (40%), they still show clearly higher protection values than the habitats in their immediate surroundings (relative mean protection value = 19%). The same is true for the relative mean of singularity which is 61% for isolated inselbergs, 25% for medium isolated inselbergs and 15% for habitats in the vicinity of the inselbergs investigated. Within individual inselbergs the highest mean protection values were found on isolated sites where climatic and edaphic factors are extreme. On Mont Sébert and Montagne Palmiste singularity and diversity, together with the abundance of native species, decrease as soon as one moves towards the less exposed centre of the plateau.

The highest average degree of endemism per sampling unit has been found on Mont Sébert with 85%, while in the surrounding habitats the average value was only 5%. The ecological status in terms of protection values is exceptionally high for extremely iso-

lated inselberg formations. Prominence values of alien and native plant species between inselbergs and adjacent habitats (mainly moist intermediate forests) are significant (Mann-Whitney *U*-test,  $P < 0.005$  for native plants).

The following alien invaders were found in the adjacent habitats but were absent on the inselbergs investigated: *Artocarpus heterophyllus*, *Bambusa vulgaris*, *Angiopteris madagascariensis*, *Eugenia jambos*, *Flacourtia ramontchi*, *Mangifera indica*, *Merremia peltata*, *Pentadesma butyracea*, *Pterocarpus indicus*, *Sandoricum indicum* and *Swietenia macrophylla*. Native species not found in the surrounding forests but present on inselbergs were: *Erythroxylum sechellarum*, *Eugenia wrightii*, *Euphorbia pyrifolia*, *Intsia bijuga*, *Lophoschoenus hornei*, *Medusagynne oppositifolia*, *Mimusops sechellarum*, *Pandanus multispicatus* and *Pittosporum wrightii*. At higher elevations with higher humidity there are several species restricted to this habitat (e.g. *Nepenthes pervillei*, *Glionetia sericea* and *Pandanus sechellarum*).

The endemic palm *Phoenicophorium bor-sigianum* had surprisingly high prominence values and percentage frequencies, both on inselbergs and in closed forests. In fact this species showed, apart from *Cinnamomum zeylanicum*, the second highest prominence value in the study area. With mean prominence values of 14 on inselbergs and 18 in the surrounding habitat types, it showed an outstanding potential to maintain and establish itself in areas which have suffered serious forest destruction and topsoil erosion.

Like *Phoenicophorium* most woody species found showed special properties which might help to withstand the environmental extremes characteristic for exposed rock outcrops. Widespread are xeromorphic (e.g. *Memecylon eleagni*) or slightly succulent leaves (e.g. *Euphorbia pyrifolia*).

Poikilohydry among higher plants has not been reported yet from the Seychelles. However, we suspect that the stem producing Cyperaceae *Lophoschoenus hornei* may be poikilohydric. This assumption is supported by a striking parallel in habit with the poikilohydric Cyperaceae *Afrotrilepis pilosa*, a character species of West African inselbergs (Porembski *et al.* in press).

Composition and species diversity of the inselberg vegetation seem to be surprisingly constant and the vegetation dynamics less pronounced than in the surrounding habitats, which are more affected by fire and logging. The lack of distinct climatic changes in the course of the year may explain why annuals are extremely rare, compared with West African inselbergs where annuals are the dominant life-form (Porembski & Brown 1995). Differences in the species inventories of the inselbergs investigated are not significant, i.e.  $\beta$ -diversity is low. Low  $\beta$ -diversity suggests that deterministic processes must have been important in the past. This is shown by the high percentage of highly adapted specialists (e.g. *Canthium bibracteatum*, *Euphorbia pyrifolia*, *Lophoschoenus hornei*, *Medusagyne oppositifolia*, *Memecylon eleagni*, *Nepenthes pervillei*, *Sarcostemma viminale*) which are strictly confined to rock outcrops and which, with the exception of *Medusagyne*, occurred on almost every outcrop investigated.

#### BIOGEOGRAPHICAL ASPECTS

The diversity of Seychelles inselberg vegetation is low, especially when compared with inselbergs similar in size to those studied in mainland areas. They therefore provide an interesting example which illustrates the relationship between regional and local species diversity.

Inselbergs bear a considerable number of endemics, both in the Seychelles and in other

tropical and temperate regions (Ornduff 1987; Baskin & Baskin 1988; Alves & Kolbeck 1994). West African inselbergs differ in this respect, with an almost complete absence of endemics, which may have historical reasons (e.g. climatic perturbations, see Porembski *et al.* in press). The high proportion of endemic plants on Seychelles inselbergs is probably the consequence of long and relatively stable conditions which resulted in a considerable number of woody palaeoendemics (e.g. *Medusagyne oppositifolia*, of which only 15 trees exist!). The present-day inselberg flora of the Seychelles seems to be the product of long isolation. This is in strong contrast to the situation on inselbergs in the southeast of the USA, where ecotypic differentiation caused a large number of neoendemics, mainly among herbaceous taxa (Quarterman *et al.* 1993).

It is remarkable that almost no phylogeographic links exist between Seychelles inselbergs and those of Madagascar and Africa. Thus characteristic elements of African and Madagascan inselbergs, like carnivorous plants (*Utricularia* spp., *Drosera* spp.), succulents (*Aloe* spp., *Kalanchoe* spp.) and mat-forming Cyperaceae are absent. Due to the lack of data it is not yet clear whether there exist more pronounced affinities to the inselberg flora of the east, e.g. of Sri Lanka and India. However, at the generic level (e.g. *Nepenthes*, *Lophoschoenus*, *Pandanus*) it is evident that phylogeographic relationships tend towards Asia rather than to Africa or Madagascar.

#### Conclusion

This survey has shown that the aboriginal vegetation of the mountains and interior lowlands of the Seychelles is highly vulnerable to human disturbance. With exception of a few intact plant communities of the mountain mist forest, the few relics which still survive

are strongly associated with inselbergs. This unique vegetation is dominated by endemic and indigenous species. There are steep gradients of diversity, prominence values of native plants, singularity and protection values between inselbergs and adjacent habitat types.

Though moderately isolated inselbergs show the potential of being colonized by invasive plants which may gradually replace native species, these plants are clearly less abundant or even missing on the inselbergs investigated. The aggressively invasive species *Cinnamomum zeylanicum* and *Alstonia macrophylla* are able to colonize inselbergs, but extremely high degrees of native regeneration suggest that these habitats are not yet seriously endangered by invasive alien plants. It seems that inselbergs are inhospitable to more mesic invaders. The greater degree of invasion in the surrounding forests can mainly be attributed to the more favourable growth conditions and the accessibility for invasive plants.

The study suggests that several factors limit the number of alien species on inselbergs. The aridity of the habitat is probably of paramount importance, while low fertility of soils together with accumulation of leaf litter (mainly of *Pandanus multispicatus* and *Memecylon eleagni*) act as a mechanical barrier against seed establishment.

So far the famous *Medusagyne oppositifolia* has been found only on Mont Sébert, Montagne Palmiste, Mont Copolia and Mont Jasmin, Mahé. These sites are exclusively parts of inselbergs. Not only because of that but for reasons of their exceptional ecological status and their extremely high degree of endemism, Mont Sébert and Montagne Palmiste should be given high priority for community conservation planning. These sites should become strictly protected areas as soon as possible.

## Acknowledgements

We would like to thank Dr. M. Kirkpatrick for her participation in the fieldwork. We are grateful to U. Fleischmann and Dr. J. Kollmann for corrections and valuable comments on earlier drafts of the manuscript. Furthermore thanks go to the following people: the biology students of the Seychelles Polytechnic for their help in collecting data on Silhouette, our guides on Silhouette, A. Paul and F. Malbrook, and the authorities of I.D.C. for transport to the island of Silhouette. Fieldwork of S. Porembski and W. Barthlott was supported by the Deutsche Forschungsgemeinschaft (Ba 605/4–2).

## References

- Adjanohoun, E. (1964) Végétation des savanes et des rochers découverts en Côte d'Ivoire centrale. Mémoires *ORSTOM*, **7**, 1–178.
- Alves, R. J. V. & Kolbeck, J. (1994) Plant species endemism in savanna vegetation on table mountains (Campo Rupestre) in Brazil. *Vegetatio*, **113**, 125–139.
- Bailey, J. P. (1971) *Flowering Plants and Ferns of Seychelles*. Government printer, Seychelles.
- Baker, B. H. & Miller, J. A. (1963) Geology and geochronology of the Seychelles islands and structure of the floor of the Arabian sea. *Nature*, **199**, 346–348.
- Barthlott, W., Gröger, A. & Porembski, S. (1993) Some remarks on the vegetation of tropical Inselbergs: diversity and ecological differentiation. *Biogéographica*, **69**, 105–124.
- Baskin, J. M. & Baskin, C. C. (1988) Endemism in rock outcrop plant communities of unglaciated eastern United States: an evaluation of the roles of the edaphic, genetic and light factors. *Journal of Biogeography*, **15**, 829–840.
- Braithwaite, C. J. R. (1984) Geology of the Seychelles. Stoddart, D. R. (ed.) *Biogeography and Ecology of the Seychelles Islands*, pp. 17–33. Dr. W. Junk Publishers, Boston.
- Bremer, H. & Jennings, J. (1978) Inselbergs/ Inselberge. *Geomorphology* N.F., Suppl. **31**, 103–127.

- Dalziel, I.W.D. (1995) Earth before pangea. *Scientific American*, **272**, 30–37.
- Fleischmann, K. (in press) Invasion of alien woody plants on the Islands of Mahé and Silhouette, Seychelles. *Journal of Vegetation Science*.
- Friedmann, F. (1987) *Flowers and Trees of Seychelles*. OSTROM, Paris.
- Friedmann, F. (1991) *The Threatened Species of the Flora of the Seychelles and their Conservation*. OSTROM, Paris.
- Hambler, D.J. (1964) The vegetation of granitic outcrops in Western Nigeria. *Journal of Ecology*, **52**, 573–594.
- Henderson, L. & Musil, K.J. (1984) Exotic woody plant invaders of the Transvaal. *Bothalia*, **15**, 297–313.
- High, J. (1982) *The Natural History of the Seychelles*. Phillips, London.
- 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.
- Jeffrey, C. (1962) *Report on the Forests of the Granitic Islands of the Seychelles*. Department of Technical Co-operation, London.
- Lionnet, G. (1984) Observations d'histoire naturelle faites aux Seychelles en 1768 par l'expédition Marion-Dufresne. *Mauritius Institute Bulletin*, **10**, 15–73.
- Mueller-Dombois, D. & Ellenberg, H. (1974) *Aims and Methods of Vegetation Ecology*. Wiley, New York.
- Ornduff, R. (1987) *Islands on Islands: Plant life on the granite outcrops of Western Australia*. University Press of Hawaii, Honolulu.
- Phillips, D. L. (1982) Life forms of granite outcrop plants. *American Naturalist*, **106**, 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. *Geobotanisches Kolloquium*, **8**, 69–80.
- Porembski, S., Barthlott, W., Dörrstock, S. & Biedinger, N. (1994) Vegetation of rock outcrops in Guinea: granite inselbergs, sandstone table mountains, and ferricretes – remarks on species numbers and endemism. *Flora*, **189**, 315–326.
- Porembski, S. & Brown, G. (1995) The vegetation of inselbergs in the Comoé-National Park (Ivory Coast). *Candollea*, **50**, 351–365.
- Porembski, S., Brown, G. & Barthlott, W. (1995) An inverted latitudinal gradient of plant diversity in shallow depressions on Ivorian inselbergs. *Vegetatio*, **117**, 151–163.
- Porembski, S., Szarzynski, J. & Mund, J.-P. & Barthlott, W. (in press) Biodiversity and vegetation of miniature inselbergs in the West African tropical Taï rain forest (Ivory Coast). *Journal of Biogeography*.
- Procter, J. (1974) The endemic flowering plants of the Seychelles: an annotated list. *Candollea*, **29**, 345–387.
- Procter, J. (1984a) Floristics of the granitic islands of the Seychelles. Stoddart, D.R. (ed.) *Biogeography and Ecology of the Seychelles Islands*, pp. 209–219. Junk, Boston.
- Procter, J. (1984b). Vegetation of the granitic islands of the Seychelles. Stoddart, D.R. (ed.) *Biogeography and Ecology of the Seychelles Islands*, pp. 195–207. Junk, Boston.
- Quartermann, E., Burbanck, M. P. & Shure, D. J. (1993) Rock outcrop communities: Limestone, sandstone, and granite. pp. 35–85. Martins, W. H., Boyce, S. G. & Echternach, A. C. (eds.), *Biodiversity of the Southeastern United States*. Wiley, New York.
- Raunkiaer, C. (1934) *The Life-Forms of Plants and Statistical Plant Geography*. Oxford University Press, Oxford.
- Richards, P.W. (1957) Ecological notes on West African vegetation. *Journal of Ecology*, **45**, 563–577.
- Robertson, S. A. (1989) *Flowering Plants of Seychelles*. Royal Botanic Gardens, Kew.
- Schulte, W. & Marks, R. (1985) Die bioökologische Bewertung von Grünflächen als Begründung für ein naturnah gestaltetes Grünflächen-Schutzgebietssystem. *Natur und Landschaft*, **60**, 302–305.
- Stoddart, D.R. (1968) Isolated island communities. *Scientific Journal*, **4**, 37–44.
- Vesey-Fitzgerald, D. (1940) On the vegetation of Seychelles. *Journal of Ecology*, **28**, 465–483.
- Walsh, R. (1984) Climate of the Seychelles. Stoddart, D.R. (ed.) *Biogeography and Ecology of the Seychelles Islands*, pp. 39–62. Junk, Boston.

Whitmore, T.C. (1993) *An Introduction to Tropical Rain Forests*. Clarendon, Oxford.

*Received 15 March 1996*

*revised version accepted 17 April 1996*