

# Vegetation and vegetation-environment relationships at Grootbos Nature Reserve, Western Cape, South Africa

M. MERGILI\* and S. PRIVETT\*\*

**Keywords:** Afromontane Forest, Agulhas Plain, biodiversity, CCA, fynbos, GIS, Milkwood Scrub Forest, numerical vegetation analysis, TWINSpan, Western Cape

## ABSTRACT

The private Grootbos Nature Reserve is located at the Western edge of the Agulhas Plain in the Cape Floristic Region of South Africa, an area characterized by high habitat and floristic diversity. The Reserve is covered in near-natural fynbos shrublands with a few patches of forest and wetland. The main objective of this study was to classify the vegetation into discrete units and relate them to the prevailing environmental conditions. The vegetation was analysed by numerical means (TWINSpan, DCA, CCA) and mapped on GIS. At the vegetation type level, Forest & Thicket and Fynbos formed distinctive clusters, whereas the wetland relevés were intermixed, but without relationships to one of these units. Fire incidence served as the major determinant of the forest-fynbos boundary. The Forest & Thicket grouping was separated into Thicket (as transitional to fynbos), Afromontane Forest and Milkwood Scrub Forest. Two broad complexes were distinguished within the Fynbos grouping, the Alkaline Sand Fynbos Complex corresponding to Coastal Fynbos, and the Acid Sand Fynbos Complex corresponding to Mountain Fynbos. They discriminated along gradients of pH, soil depth and rock cover. The complexes were further subdivided into formations by using one or a few subjectively chosen dominant species as indicators. The transitions between these formations were rather continuous than discrete. The vegetation type and complex levels correspond well to existing fynbos-wide classifications. Comparing the formations to the results of other vegetation studies is problematic even on the scale of the Agulhas Plain, due to the high regional plant diversity in the Fynbos Biome.

## INTRODUCTION

An important, and well-established aspect of the species-rich Cape flora is the difficulty in resolving regional vegetation associations into meaningful, easily identifiable floristic groupings (Campbell 1986). Various authors have tried to classify the habitat types and the plant communities of the Fynbos Biome in the previous decades, some looking at broad descriptions of major vegetation types (Taylor 1978; Moll *et al.* 1984; Campbell 1985; Cowling & Hejnis 2001) and others at detailed descriptions of communities (McKenzie *et al.* 1977; Boucher 1978; Taylor 1983; Richards *et al.* 1995; Cowling *et al.* 1996; McDonald *et al.* 1996; Taylor 1996). The Agulhas Plain, covering an area of 270 000 hectares of semi-arid lowland fynbos and renosterveld, has been prioritized as an area of high irreplaceability and high vulnerability, with exceptionally rich coastal lowland ecosystems (Cowling *et al.* 1999). Cowling *et al.* (1988) applied the mountain vegetation classification approach of Campbell (1985) to the Agulhas Plain. This classification was produced using the Braun-Blanquet method of table sorting and was based on structural and higher taxon characteristics of the vegetation. Nine zonal communities, at various hierarchical levels, were recognized and mapped. This phytosociological approach provided a qualitative description of community environmental characteristics on the Agulhas Plain. The only study on the Agulhas Plain to provide a quantitative assessment of the importance of environmental factors was Richards *et al.* (1995) who explored vegetation-environment rela-

tionships in a 30 ha study area, the Soetanyenberg,  $\pm 15$  km west of Cape Agulhas ( $34^{\circ}45' S$ ;  $19^{\circ}50' E$ ). However, no comparable studies have been undertaken on the west side of the Agulhas Plain.

The major objective of this study was to fill this gap through a detailed mapping and numerical analysis of the vegetation of Grootbos Nature Reserve (GNR), which is located at the western edge of the Agulhas Plain, between the villages of Stanford and Gansbaai (Figure 1A). The geographic coordinates are  $34^{\circ}32'30'' S$  and  $19^{\circ}24'50'' E$ . The privately owned reserve consists of seven formerly separate farms covering an area of 1 700 ha. It is run as an upmarket ecotourism lodge. The landscape is sloping, with a maximum elevation of  $\pm 475$  m along the slopes of the Swartkransberg (Figure 1B). The underlying rock type of the more elevated hills is quartzitic Table Mountain Sandstone. On the lower slopes, deposits of sandy aeolian material overlay the bedrock. Outcrops of the Bredasdorp Limestone are exposed in some places.

The climate, which can be characterized as maritime mediterranean, shows a strong seasonality in precipitation. May to August are the wettest months (most precipitation is carried by northwesterly winds), whereas the southeasterly winds prevailing in the summer months are dry. There has been no long-term precipitation record at GNR. The mean annual rainfall from 1996–1998 was 730 mm. The mean maximum daily temperatures fluctuate between  $25^{\circ}C$  in February and  $14^{\circ}C$  in July. The GNR is frost-free.

Since 1995 the property has been managed for conservation and ecotourism. Over the last decade a team of botanists has been actively sampling and collecting plant specimens over the entire reserve. At the latest count, 660 species of indigenous plants have been recorded on the property, with still more being found

\* Corresponding author: Institute of Geography, University of Innsbruck, Innrain 52, 6020 Innsbruck, Austria and Mountain Research: Man and Environment, Austrian Academy of Sciences, Technikerstrasse 21a, 6020 Innsbruck, Austria. E-mail: martin.mergili@uibk.ac.at.

\*\* Grootbos Private Nature Reserve, P.O. Box 148, 7220 Gansbaai, South Africa. E-mail: sean@greenfutures.co.za.

MS. received: 2005-12-15.

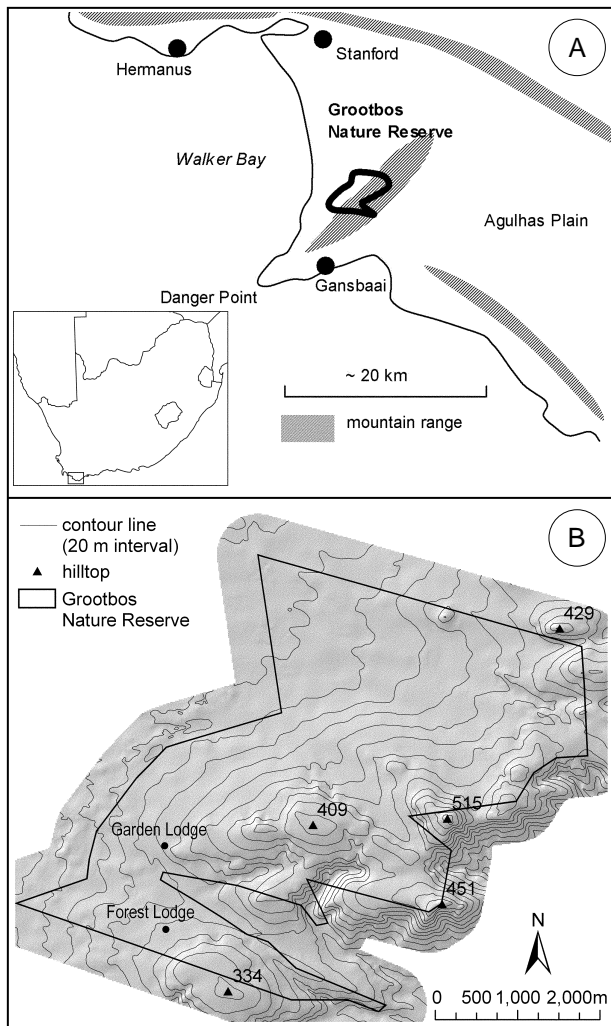


FIGURE 1.—A, study area located between Cape Town and Cape Agulhas, 5 km east of Walker Bay seashore; B, western part of Grootbos Nature Reserve gently sloping towards Walker Bay, eastern part hilly with maximum elevation slightly below 500 m.

each year (Privett & Lutzeyer in press). Fifty-one species are included in the Red Data List of threatened species (Hilton-Taylor 1996), and three species (*Erica magnisylvae*, *Cliffortia anthospermoides*, *Lachenalia lutzeyerii*) were recently discovered and are considered endemic to the Reserve. The vegetation of GNR, largely fynbos shrubland with some patches of forest and wetland, is amongst the best surveyed in the Cape Floristic Region and lends itself to a detailed quantitative analysis of vegetation-environment relationships.

## METHODS

### Data collection

Vegetation sampling at GNR was carried out in winter 1997 and in spring 2004. Seventy-one 50 m<sup>2</sup> (10 × 5 m) rectangular relevés were analysed for their floristic composition and their major environmental features. They were subjectively chosen in order to represent homogeneous patches of vegetation and divided into 10 cells, 2.0 × 2.5 m each. The floristic composition was investigated for each cell, including all identifiable species. All

taxonomy followed Goldblatt & Manning (2000). The cover was recorded as a percentage. Soil samples were taken at random localities within each relevé, in depths of 5–30 cm depending on soil depth. Environmental data were recorded for each relevé: topographic parameters (slope, elevation, aspect), vegetation age, soil depth, rock cover, pH, resistance and nutrient levels of the soil. Flow accumulation (wetness index), solar radiation and the exposure to the fire-bearing southeasterly winds were computed from a digital elevation model (DEM). All relevés were used for analysis, including those located in transitional vegetation. The GPS coordinates of each relevé were stored and the southwestern corner was marked with a concrete lintil or an iron peg to enable further monitoring.

In addition to the regular relevés (core dataset), 127 sites were analysed to a lesser extent (these and the core dataset together are referred to as the extended dataset). This was done without setting up a formal plot and only the dominant and easily identifiable species were recorded. The coordinates were located with a GPS and stored for mapping. No environmental data were taken directly for these additional relevés, but the parameters extracted from the DEM were stored.

### Numerical vegetation analysis

A classification and certain ordinations were applied to the sampled dataset. The classification was performed using TWINSpan (Hill 1994). For the classification of the core dataset, the pseudospecies cut levels were set to 0, 5, 10, 20 and 50, for the extended dataset to 0, 2, 5, 10, 20, 50. The first pseudospecies of the extended dataset was excluded from the classification. Splitting was allowed down to two species (default: five) for both datasets. An indirect ordination (Detrended Correspondence Analysis, DCA) was performed for the extended dataset. A direct ordination (Canonical Correspondence Analysis, CCA) was applied to the core dataset (due to the availability of environmental data). Both ordinations were run with the whole dataset and then repeated only including relevés classified as Fynbos. The default parameters suggested by the programs (DECORANA for the DCA and MVSP for the CCA) were applied to the analyses.

### Vegetation mapping

A set of colour orthophotos (spatial resolution: 0.75 m) as well as a GIS dataset representing preliminary vegetation units mapped in 1997 were available. Attempts to extract vegetation units from the imagery by numerical means failed as the different fynbos types showed very similar reflection properties, while the reflection properties varied very much within each type. Consequently, GNR was explored during several excursions and assessed according to the subjective impression of the authors, supported by the relevé information. In addition, a large number of localities were recorded by GPS in order to locate the transitions between vegetation units. All the point data were transferred to a GIS and mapped onto the composite orthophoto. The information provided by the orthophotos was combined with the point data, the results of the numerical vegetation analysis and the existing GIS dataset to generate a comprehensive map of meaningful vegetation units.

## RESULTS

*Numerical vegetation analysis*

The TWINSPAN classification clearly supported the presence of two major vegetation types on GNR: one fynbos (Cape Fynbos Shrublands) and the other non-fynbos (Forest & Thicket). The wetland relevés were not clearly assigned to any of these groups, and as a result were considered as an independent vegetation type. The Fynbos grouping was further split into an Acid Sand Fynbos Complex and Alkaline Sand Fynbos Complex, the Forest & Thicket grouping in Milkwood Scrub Forest, Afromontane Forest and Thicket. No further significant splitting was possible in the wetland grouping.

The level of vegetation complexes was the maximum of detail supported by the classification. However, for the fynbos, some smaller units were clearly recognizable in the field, mostly dominated by a few or even only one species and with the bulk of the species shared among all the units of the corresponding complex. These detailed units were conceptualized as formations, which are summarized in Table 1.

The ordination results corresponded well to the classification results. In the DCA for the extended dataset, Afromontane Forest, Milkwood Scrub Forest and Fynbos were clearly separated along the first axis (eigenvalue = 0.91), with the Thicket and the Wetland relevés intermediate between Milkwood Scrub Forest and Fynbos (Figure 2A). The two fynbos complexes were discriminated along the second axis (eigenvalue = 0.65). The DCA only including the relevés classified as fynbos (Figure 2B; eigenvalues: 0.68 for the first axis and 0.62 for the second axis) showed a clear clustering of some formations established in the classification (*Thamnochortus fraternus* Restioid Fynbos, *Erica sessiliflora* Ericaceous Fynbos) and the post-fire relevés of *Protea repens* Proteoid Fynbos. The transitions between the remaining formations appeared to be highly continuous.

The CCA (Figure 3A) illustrated the clear and discrete discrimination of Fynbos and Forest depending on vegetation age, which was almost coincident with the first axis (for eigenvalues and canonical coefficients compare Table 2). The forest complexes were discriminated by elevation, slope, aspect and certain soil characteristics. The fynbos relevés were aligned continuously along the second axis, discriminated by gradients of elevation, slope, pH, soil depth and rock cover. The Alkaline Sand Fynbos Complex and the Acid Sand Fynbos Complex were clearly recognizable, but closely together. The exclusion of all non-fynbos relevés from the CCA (Figure 3B) did not lead to a clearer distinction of these clusters. No clear structure was recognizable within the two subclusters either. Only the *Thamnochortus fraternus* Restioid Fynbos and the *Protea repens* Proteoid Fynbos formed  $\pm$  proper clusters. A number of environmental variables showed similar explanatory value. In addition to the site scores, the scores of selected species were plotted (Figure 4). The species were grouped in the same manner as the relevés they dominate. The red data species appear to be associated with rather extreme conditions as they occupy the edges of the plot.

*Vegetation units*

## Afromontane Forest

Five patches of Afromontane Forest are present at the GNR, all of them situated in the forest valley (Figure 5A). The CCA suggested an association with shallow, neutral to slightly acid soils rich in K and Mg. The relief is characterized by steep slopes protected from the southeasterly winds. Afromontane Forests form tall canopies with heights of more than 10 m. The canopy is frequently dominated by *Rapanea melanophloeos*. The well-developed subcanopy is 3–10 m high, comprising *Celtis africana*, *Chionanthus foveolatus*, *Diospyros whyteana*, *Kiggelaria africana* and *Sideroxylon inerme*. Most of these species have the potential to grow to canopy height. Due to the dark interior of the forest, the ground layer is usually sparse with *Asplenium adiantum-nigrum*, *Droguetia iners* and *Ehrharta erecta* as the most common species. Climbers are present (*Asparagus aethiopicus*, *A. scandens* and *Cynanchum obtusifolium*). The species diversity is low at the 50 m<sup>2</sup> level, averaging 13.2 identifiable species per relevé.

The range of temperate forest ecosystems referred to as Afromontane Forest includes the mountains of the southern Cape but stretches far into tropical Africa where they occur at higher altitudes (Midgley *et al.* 1997). The Afromontane Forests of the Agulhas Plain are ecologically similar but floristically distinct from those considered by Campbell (1985). Instead they show affinities to the dune forests of the Tongaland-Pondoland Forest (Moll & White 1978). These forests, and also the Afromontane Forest along the south coast (Knysna, Tsitsikamma), have significantly higher species diversities than the forests on the GNR. They host taxa not present on GNR, such as Podocarpaceae and Cyatheaceae. One reason for the declining diversity towards the southwest may be that more and more species disappear as the climatic conditions become harsher and the forest patches smaller.

## Milkwood Scrub Forest

Four patches of Milkwood Scrub Forest are present at low elevations, associated with deep, slightly acid to alkaline, sandy, colluvial soils with high contents of Ca and P. In contrast to the Afromontane Forest, the CCA did not indicate a negative spatial coincidence with the southeasterly winds. The high levels of mineral components appear to be a distinctive feature of this type of ecosystem. Ca in particular is considerably richer in the forest than anywhere else on the GNR. In addition, the soils are very fertile due to plant-induced organic enrichment (Thwaites & Cowling 1988), which makes them suitable for agriculture and thus susceptible to anthropogenic disturbance.

A single tree layer, usually dominated by *Sideroxylon inerme*, attains a height of 6 m and a very dense cover. *Euclea racemosa* does form part of the canopy in some places, whereas *Chionanthus foveolatus*, *Gymnosporia buxifolia* and the winter-deciduous *Celtis africana* occur as single trees or small groups. The soil is covered by a 50–300 mm high, sparse to dense (where sufficient light is available) herb layer dominated by *Droguetia iners* and *Ehrharta erecta*. The only shrub species in the full

TABLE 1.—Summary of vegetation units recognized in this study. Average species numbers of complexes on 50 m<sup>2</sup> level in brackets

Vegetation unit	Diagnostic spp.	Common species	Average value		
			a	b	c
<b>Milkwood Scrub Forest (11.0)</b>		<i>Sideroxylon inerme</i> , <i>Euclea racemosa</i> , <i>Myrsine africana</i> , <i>Cynanchum obtusifolium</i> , <i>Asparagus aethiopicus</i> , <i>Droguetia iners</i> , <i>Ehrharta erecta</i>	<b>246</b>	<b>91</b>	<b>7.2</b>
<b>Afromontane Forest (13.2)</b>		<i>Rapanea melanophloeos</i> , <i>Kiggelaria africana</i> , <i>Diospyros whyteana</i> , <i>Celtis africana</i> , <i>Chionanthus foveolatus</i> , <i>Droguetia iners</i> , <i>Asparagus scandens</i> , <i>Asplenium adiantum-nigrum</i>	<b>308</b>	<b>34</b>	<b>6.7</b>
<b>Thicket Complex (ND)</b>			<b>ND</b>	<b>ND</b>	<b>ND</b>
True Thicket	< 3: <i>Pteris dentata</i>	<i>Euclea racemosa</i> , <i>Salvia africana-lutea</i> , <i>Myrsine africana</i> , <i>Nylandtia spinosa</i> , <i>Gymnosporia buxifolia</i> , <i>Leucadendron coniferum</i> , <i>Thamnochortus erectus</i> , <i>Sideroxylon inerme</i>	ND	ND	ND
<i>Pteris dentata</i> Shrubland	> 2: <i>Pteris dentata</i>	<i>Pteris dentata</i> , <i>Leucadendron coniferum</i> , <i>Myrsine africana</i> , <i>Diospyros whyteana</i>	ND	ND	ND
<b>Wetland Complex (9.3)</b>			<b>272</b>	<b>100</b>	<b>6.8</b>
TWINSPAN indicator: <i>Mariscus thunbergii</i>					
True Wetland	< 3: <i>Pteris dentata</i>	<i>Mariscus thunbergii</i> , <i>Artemisia afra</i> , <i>Cliffortia ferruginea</i> , <i>Psoralea arborea</i> , <i>Senecio halimifolius</i> , <i>Zantedeschia aethiopica</i> , <i>Gunnera perpensa</i> , <i>Hippia frutescens</i> , <i>Helichrysum cymosum</i> subsp. <i>cymosum</i> , <i>Leonotis leonurus</i>	291	100	7.1
<i>Pteris dentata</i> Fernland	> 2: <i>Pteris dentata</i>	<i>Pteris dentata</i> , <i>Mariscus thunbergii</i> , <i>Kiggelaria africana</i> , <i>Zantedeschia aethiopica</i> , <i>Diospyros whyteana</i> , <i>Gunnera perpensa</i>	236	100	6.1
<b>Alkaline Sand Fynbos Complex (24.9)</b>			<b>286</b>	<b>62</b>	<b>7.3</b>
Dune Asteraceous Fynbos	< 2: <i>Leucadendron coniferum</i> , <i>Leucospermum patersonii</i> , <i>Protea obtusifolia</i> , <i>P. repens</i> , <i>Thamnochortus fraternus</i> ; < 3: <i>Erica coccinea</i> (yellow-flowered variant)	<i>Metalasia muricata</i> , <i>Passerina vulgaris</i> , <i>Euclea racemosa</i> , <i>Erica irregularis</i> , <i>Ischyrolepis eleocharis</i> , <i>Thamnochortus erectus</i> , <i>Otholobium bracteolatum</i> , <i>Anthospermum aethiopicum</i>	255	77	7.7
Neutral Sand Proteoid Fynbos	> 1: <i>Leucadendron coniferum</i> or <i>Leucospermum patersonii</i> ; < 3: <i>Erica coccinea</i> (yellow-flowered variant); < 2: <i>Protea obtusifolia</i> , <i>P. repens</i> , <i>Thamnochortus fraternus</i>	<i>Leucadendron coniferum</i> , <i>Leucospermum patersonii</i>	335	59	6.5
<i>Protea repens</i> Proteoid Fynbos	> 1: <i>Protea repens</i> ; <i>P. obtusifolia</i> < <i>P. repens</i>	<i>Protea repens</i> , <i>Cliffortia ilicifolia</i> , <i>Willdenowia teres</i> , <i>Phylica disticha</i> , <i>Diosma subulata</i> var. <i>subulata</i> , <i>Passerina vulgaris</i>	326	100	6.0
<i>Protea obtusifolia</i> Proteoid Fynbos	> 1: <i>Protea obtusifolia</i> ; < 2: <i>Thamnochortus fraternus</i> ; <i>P. obtusifolia</i> => <i>Erica coccinea</i> (yellow-flowered variant)	<i>Protea obtusifolia</i> , <i>Erica coccinea</i> (yellow-flowered variant), <i>Leucadendron coniferum</i> , <i>Leucospermum patersonii</i>	258	82	7.7
<i>Erica coccinea</i> Ericaceous Fynbos	> 2: <i>Erica coccinea</i> (yellow-flowered variant); < 2: <i>Thamnochortus fraternus</i> ; <i>E. coccinea</i> (yellow-flowered variant) < <i>Protea obtusifolia</i> , <i>Leucadendron coniferum</i> and <i>Leucospermum patersonii</i>	<i>Erica coccinea</i> (yellow-flowered variant), <i>Erica irregularis</i> , <i>Cullumia squarrosa</i> , <i>Oedera capensis</i> , <i>Indigofera brachystachya</i>	209	30	8.0
<i>Thamnochortus fraternus</i> Restioid Fynbos	> 1: <i>Thamnochortus fraternus</i>	<i>Thamnochortus fraternus</i> , <i>Erica coccinea</i> (yellow-flowered variant), <i>Protea obtusifolia</i> , <i>Leucadendron coniferum</i> , <i>Indigofera brachystachya</i>	323	2	7.3
<b>Acid Sand Fynbos Complex (35.0)</b>			<b>376</b>	<b>28</b>	<b>5.5</b>
TWINSPAN indicators: <i>Mimetes cucullatus</i> , <i>Leucadendron salignum</i> , <i>Erica glabella</i>					
Acid Sand Proteoid Fynbos	< 2: <i>Leucadendron coniferum</i> , <i>Leucospermum patersonii</i> , <i>Protea obtusifolia</i> ; < 3: <i>Erica sessiliflora</i> , <i>Elegia thyrsoifera</i>	<i>Mimetes cucullatus</i> , <i>Leucadendron salignum</i> , <i>Aulax umbellata</i> , <i>Protea cynaroides</i> , <i>L. xanthoconus</i> , <i>Protea longifolia</i> , <i>Penaea mucronata</i> , <i>Morella quercifolia</i> , <i>Indigofera brachystachya</i> , <i>Elegia juncea</i> , <i>Pseudopentameris macrantha</i> , <i>Bobartia indica</i> , <i>Erica glabella</i> , <i>Trichocephalus stipularis</i>	386	26	5.4
Transitional Proteoid Fynbos	> 1: <i>Leucadendron coniferum</i> or <i>Leucospermum patersonii</i> ; <i>Erica sessiliflora</i> , <i>Elegia thyrsoifera</i> < <i>L. coniferum</i> , <i>L. patersonii</i>	<i>Leucadendron coniferum</i> , <i>Leucospermum patersonii</i> , <i>Protea obtusifolia</i> , <i>Mimetes cucullatus</i> , <i>Leucadendron tinctorum</i> , <i>L. salignum</i> , <i>Erica glabella</i>	376	40	5.6
<i>Erica sessiliflora</i> Ericaceous Fynbos	> 2: <i>Erica sessiliflora</i> ; <i>E. thyrsoifera</i> , <i>Leucadendron coniferum</i> , <i>Leucospermum patersonii</i> < = <i>E. sessiliflora</i>	<i>Erica sessiliflora</i> , <i>E. glabella</i> , <i>Leucadendron coniferum</i> , <i>Mimetes cucullatus</i> , <i>Leucospermum patersonii</i> , <i>Drosera capensis</i> , <i>Cliffortia ferruginea</i> , <i>Psoralea arborea</i> , <i>Berzelia lanuginosa</i> , <i>Staavia radiata</i>	297	55	5.6
<i>Elegia thyrsoifera</i> Restioid Fynbos	> 2: <i>Elegia thyrsoifera</i> ; <i>E. thyrsoifera</i> => <i>Leucadendron coniferum</i> , <i>Leucospermum patersonii</i> ; <i>E. thyrsoifera</i> > <i>Erica sessiliflora</i>	<i>Elegia thyrsoifera</i> , <i>Helichrysum patulum</i> , <i>Thamnochortus erectus</i> , <i>Morella quercifolia</i> , <i>Leucospermum patersonii</i> , <i>Leucadendron coniferum</i> , <i>Erica sessiliflora</i>	ND	ND	ND

a, elevation (m); b, soil depth (cm); c, pH; ND, no data.

Numbers close to diagnostic species: pseudospecies levels of TWINSPAN-classification for extended dataset.

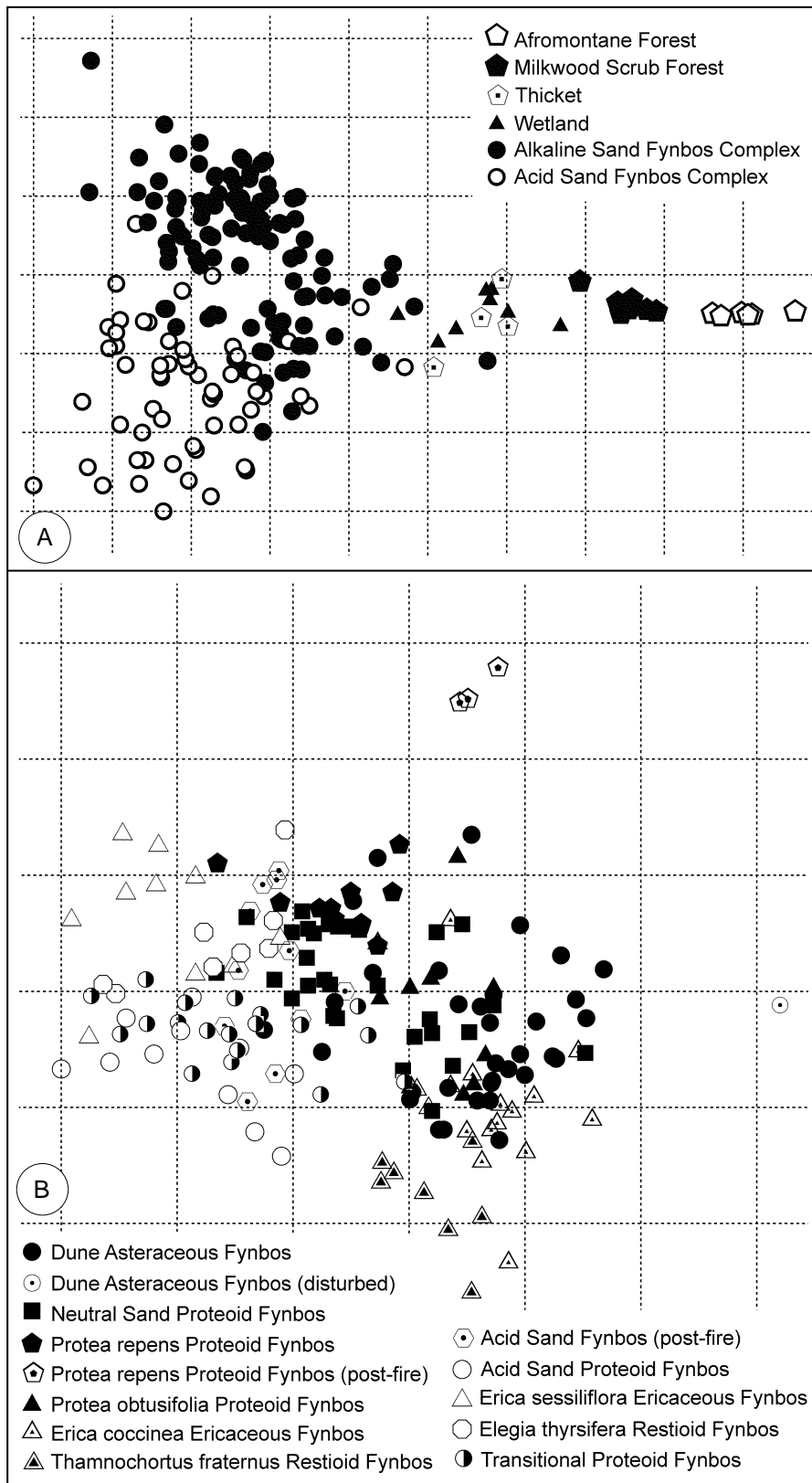


FIGURE 2.—A, Detrended Correspondence Analysis (DCA) for complete extended dataset resulted in clusters of Afromontane Forest, Milkwood Scrub Forest, Alkaline Sand Fynbos Complex and Acid Sand Fynbos Complex; B, DCA for fynbos relevés of extended dataset resulted in discrimination of two fynbos complexes.

shade of the forest is *Myrsine africana*, which may grow higher than 1 m. The abundance of lianas (*Asparagus aethiopicus*, *Cynanchum obtusifolium*) and epiphytes (mainly cryptogams) is considerable. Dead vertical branches of the spiny *A. aethiopicus* are particularly responsible for parts of the forest having a thicket-like character (Figure 5B). The species diversity is low at the 50 m<sup>2</sup> level, averaging only 11 identifiable species.

Thicket

The fynbos-forest boundary is rarely sharply defined, but is often made up of a thicket of varying height and density. This vegetation unit does not necessarily correspond to the Subtropical Thicket described by Midgley *et al.* (1997), although it may share certain characteristics with it. Thickets are characterized by a mixture of forest and fynbos elements. They occur at sites where

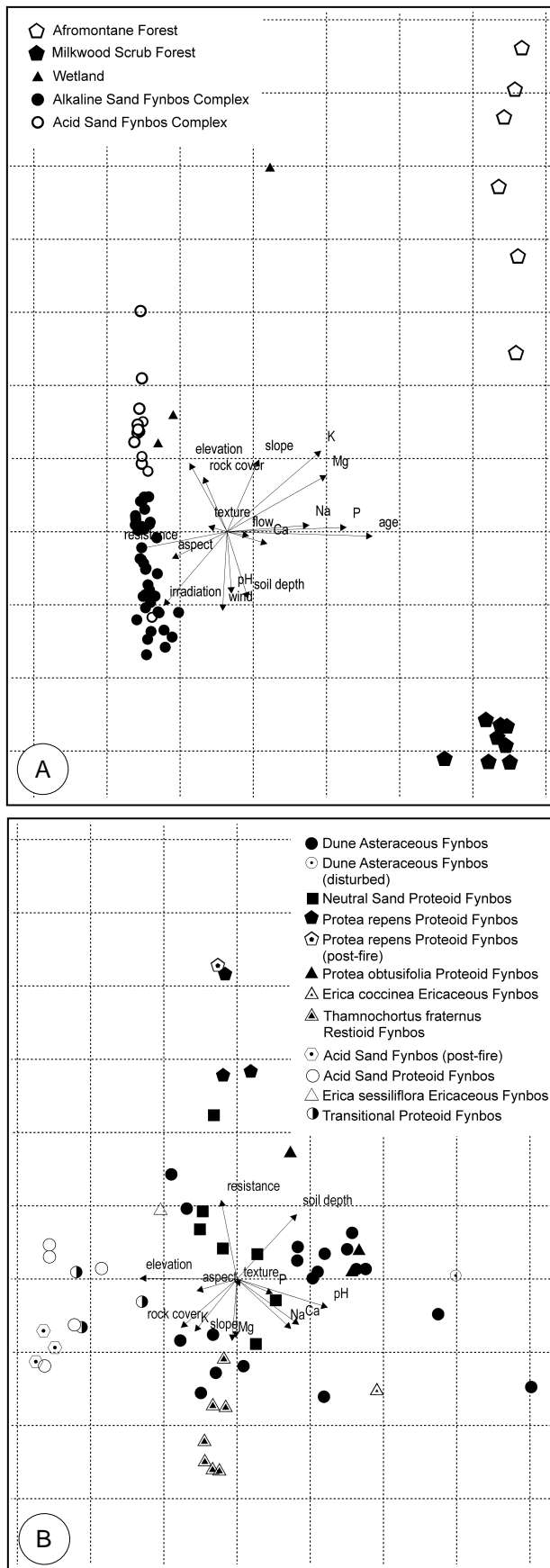


FIGURE 3.—A, results of Canonical Correspondence Analysis (CCA) for entire core dataset indicate clear separation between Fynbos complexes, Afromontane Forest and Milkwood Scrub Forest, whereas Wetland relevés are intermixed; B, results of CCA for fynbos relevés of core dataset show continuous transition between formations.

fire frequency or intensity have been reduced over a certain period, but not sufficiently to support forest: in the buffer zones between fynbos and the Milkwood Scrub Forest, in protected ravines as a successional stage from fynbos to Afromontane Forest and on some south-facing slopes of the forest valley. The latter (adjacent to the Afromontane Forest) is dominated by the fern *Pteris dentata*, which attains a very high cover in these places. These ecosystems are therefore considered as separate formations (*Pteris dentata* Shrubland, compare Figure 8). Forest edge thickets and valley thickets, in contrast, are floristically similar so that a separation into two formations is not supported. The broad-leaved subtropical shrub species (Cowling *et al.* 1997), mainly *Euclea racemosa*, *Olea capensis*, *O. exasperata* and various species of *Searsia* (Moffett 2007) frequently dominate thickets on GNR together with *Salvia africana-lutea*. Among the fynbos elements, large individuals of *Leucadendron confiferum* and *Thamnochortus erectus* are most common. Certain forest elements, most commonly *Sideroxylon inerme*, may join the thicket but some thicket species may also occur as trees in the Milkwood Scrub Forest.

Wetlands

The catchment areas supplying the GNR are not large enough to support permanent streams under the prevailing precipitation regime. In winter, some springs can develop and small rivers may persist until the end of October. As a result, the distribution of true wetlands is extremely limited at the GNR and is confined to a few suitable habitats. Nevertheless the diversity of different wetland habitats is considerable and it is difficult to point out one type of wetland characteristic of the GNR. As the different types are located adjacently along several environmental gradients, they will be treated as one entity. Wetlands are related to soils with a high content of organic matter, indicated by the dark colour. The ordinations placed the wetland relevés in between for-

TABLE 2.—Eigenvalues and canonical coefficients of Canonical Correspondence Analyses (CCA) for complete core dataset and fynbos relevés of core dataset

	Complete core dataset		Core dataset—fynbos	
	axis 1	axis 2	axis 1	axis 2
Eigenvalues	0.95	0.63	0.57	0.47
Environmental variables: canonical coefficients				
elevation	-0.10	0.38	-0.39	-0.11
slope	-0.01	-0.19	0.21	-0.26
aspect	-0.01	0.02	0.10	0.12
flow acc.	0.03	0.09	*	*
irradiation	-0.01	-0.78	*	*
SE wind	-0.02	-0.37	*	*
veg. age	0.91	-0.23	*	*
soil depth	0.03	-0.05	0.12	0.39
rock cover	0.01	0.10	-0.23	0.13
texture	-0.03	-0.15	0.01	0.18
pH	-0.11	0.12	0.04	-0.09
resistance	-0.03	-0.16	-0.03	0.36
Na	-0.08	-0.39	0.30	-0.02
P	0.01	-0.40	-0.04	0.20
K	0.01	0.23	-0.05	0.16
Ca	0.08	-0.11	0.12	-0.13
Mg	0.08	0.50	-0.25	-0.16

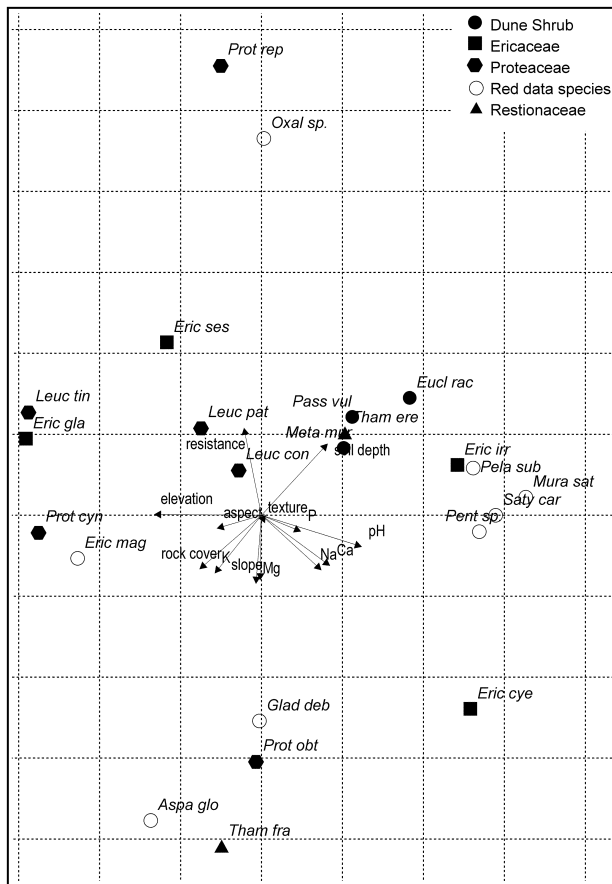


FIGURE 4.—Canonical Correspondence Analysis (CCA) biplot score for some selected species. *Aspa glo*, *Aspalathus globulosa*; *Eric cye*, *Erica coccinea* (yellow-flowered variant); *Eric gla*, *Erica glabella*; *Eric irr*, *Erica irregularis*; *Eric mag*, *Erica magnisylvae*; *Eucl rac*, *Euclaea racemosa*; *Glad deb*, *Gladiolus debilis*; *Leuc con*, *Leucadendron coniferum*; *Leuc pat*, *Leucospermum patersonii*; *Leuc tin*, *Leucadendron tinctum*; *Eric ses*, *Erica sessiliflora*; *Meta mur*, *Metalasia muricata*; *Mura sat*, *Muraltia satureioides*; *Oxal sp.*, *Oxalis sp.*; *Pass vul*, *Passerina vulgaris*; *Pela sub*, *Pelargonium suburbanum*; *Pent sp.*, *Pentaschistis sp.*; *Prot cyn*, *Protea cynaroides*; *Prot obt*, *Protea obtusifolia*; *Prot rep*, *Protea repens*; *Saty car*, *Satyrium carneum*; *Tham ere*, *Thamnochortus erectus*; *Tham fra*, *Thamnochortus fraternus*.

est and fynbos without clear relationships to any of the measured variables. The pH ranges from 6.1–7.9 but the relevé with the highest value is situated below a slope that may have an alkaline character. The largest patch is located at the bottom of the forest valley. South-facing slopes are covered in a dense, 1.5 m high canopy of *Pteris dentata*, (recognized as formation *Pteris dentata* Fernland), whereas slightly north-facing slopes support mats of *Cliffortia ferruginea* and dispersed stands of *Artemisia afra*, *Leonotis leonurus* and some thicket species. *Gunnera perpensa* and *Senecio halimifolius* are dominant directly in the temporary stream. Species such as *Mariscus thunbergii*, *Hippia frutescens* and *Zantedeschia aethiopica* are present in all types. Transitions to Thicket are common. One characteristic feature of the wetlands is their low alpha-diversity with an average of only 9.3 species per relevé.

#### Alkaline Sand Fynbos Complex

The Alkaline Sand Fynbos Complex covers most of the lower parts of the GNR. Two hundred species were

recorded in 42 relevés, averaging at 24.9 species per relevé. The substrate is mainly wind-blown, colluvial sand of varying depth, pH and nutrient levels. Dune Asteraceous Fynbos, Neutral Sand Proteoid Fynbos and *Protea repens* Proteoid Fynbos are associated with these habitats. Some limestone outcrops show a different vegetation but they are too small to house many of the rare limestone endemics found a few kilometres to the east on larger patches. Three different limestone formations, which are frequently intermixed, have been recorded: *Protea obtusifolia* Proteoid Fynbos, *Erica coccinea* Ericaceous Fynbos and *Thamnochortus fraternus* Restioid Fynbos.

Dune Asteraceous Fynbos covers the entire western part of the GNR. It forms an extensive matrix of low ericoid/restioid fynbos, higher ericoid fynbos and thicket dominated by broad-leaved shrubs (Figure 6A). The formation is characterized by low elevation, alkaline, deep soils (> 100 cm) and low rock cover. It corresponds well with the Dune Asteraceous Fynbos described by Cowling *et al.* (1988) for the Agulhas Plain and with the Eastern Type of Coastal Fynbos (Kruger 1979). Large ericoids (*Metalasia muricata* and *Passerina vulgaris*) and non-proteoid broad-leaved shrubs (*Chrysanthemoides monnifera*) are the structural dominants, in some places joined or replaced by fabaceous shrubs, *Otholobium bracteolatum*, *Aspalathus forbesii*. *Erica irregularis* and certain non-ericaceous ericoids (*Anthospermum aethiopicum*, *Phylla ericoides*) are widespread. *Thamnochortus erectus* is the most conspicuous restioid but the lower *Ischyrolepis eleocharis* has a very high cover in some sites. Lower individuals of the subtropical shrub species are very common all over the Dune Asteraceous Fynbos (*Euclaea racemosa*, *Olea capensis* subsp. *capensis*, *O. exasperata* and *Searsia laevigata*). One characteristic feature of the Dune Asteraceous Fynbos is the lack of proteoids. If they occur, especially *Leucadendron coniferum* and *Protea obtusifolia*, they indicate a transition to other formations.

Neutral Sand Proteoid Fynbos is associated with intermediate, but varying environmental variables. The pH ranges from 4.8–7.8. The soils are usually shallower than those supporting Dune Asteraceous Fynbos, but the depths range from 0 to > 100 cm. Wind-blown alkaline sands lying over the acidic Table Mountain Sandstone provide intermediate habitats between the Dune Asteraceous Fynbos and the Acid Sand Fynbos Complex. The formation shows some association with the *Protea susannae*–*Leucadendron coniferum* Proteoid Fynbos described by Cowling *et al.* (1988) and Richards *et al.* (1995), and the Neutral Sand Proteoid Fynbos described by Mustart *et al.* (2003). These units prefer rather deep, colluvial neutral sands at least partly derived from Bredasdorp Limestone. *Protea susannae*, however, does not occur on the GNR. Instead, *Leucadendron coniferum* and *Leucospermum patersonii* are dominant with shifting composition. Relatively old, almost monospecific stands of *L. coniferum* resemble low forests with canopy heights of up to 5 m (Figure 6B), but with an extremely high density of thin stems, making them almost impenetrable. In young stands (up to 10 years after fire), the two proteoids are approximately equally abundant. An ericoid layer with variable density is present. As in the

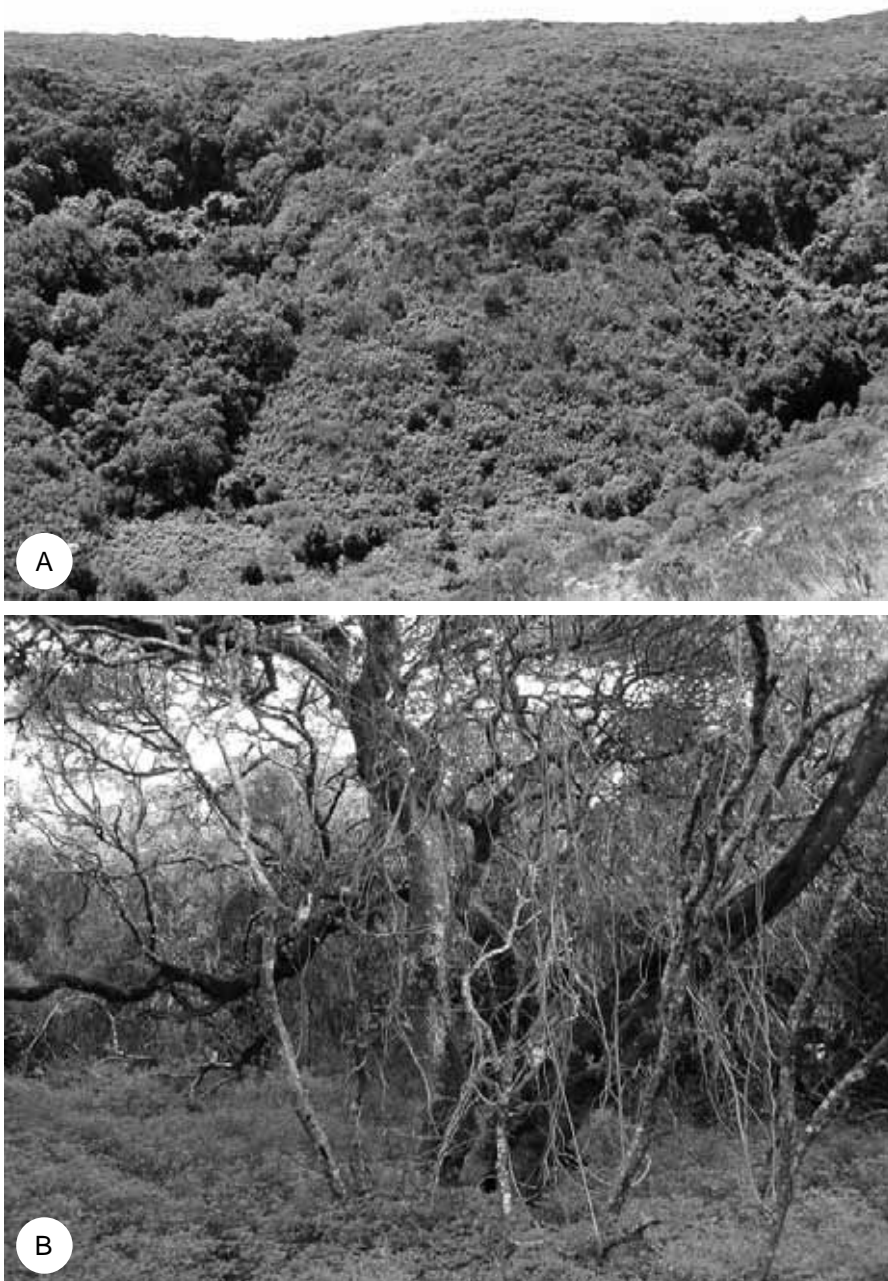


FIGURE 5.—A, patches of Afro-montane Forest concentrated in south-facing ravines (left and right); *Pteris dentata* Shrubland in centre; B, interior of Milkwood Scrub Forest. Dense undergrowth of *Droguetia iners* can only develop in light places, e.g. after anthropogenic disturbance. Photographs: M. Mergili.

Dune Asteraceous Fynbos, *Thamnochortus erectus* is the most conspicuous restioid element, whereas low restioids occur in the ground layer, together with various species of the sedge *Ficinia*. North- and east-exposed slopes of the forest valley are covered in a different vegetation unit. Owing to the high frequency of *Leucadendron coniferum* and *Leucospermum patersonii* and the scarcity of species indicating a different unit, it has been assigned to the Neutral Sand Proteoid Fynbos, but as a different unit in Figure 7.

*Protea repens* Proteoid Fynbos occupies the lower slopes of the Swartkransberg heading northwards towards the broad Steynsbos Valley, as well as large parts of the Steynsbos Valley itself. It forms 2.5 m high, medium-dense to dense stands of Proteoid Fynbos, associated with extraordinarily high values for electrical resistance

of the deep (> 1 m), slightly acid soils. The pH ranges from 6.4–6.7 and at the transition to the Acid Sand Fynbos Complex it is 5.6. It is inappropriate to compare this formation to the *Protea repens* Proteoid Fynbos described by Cowling *et al.* (1988) for the Agulhas Plain as it differs structurally and floristically. The formation is clearly dominated by *Protea repens*, but it shares most of its species with the Dune Asteraceous Fynbos and the Neutral Sand Proteoid Fynbos. *Leucadendron coniferum* is frequently intermixed. The ericoids *Cliffortia ilicifolia* and *Passerina vulgaris* are very frequent, growing up to more than 1.5 m, as does the restioid *Thamnochortus erectus*. A sparse to medium-dense undergrowth attains heights of some tens of centimetres. Parts of the formation were in an early post-fire stage at the time of the survey, showing a high cover of *Aspalathus microphylla* and lacking visible individuals of *Protea repens*.





FIGURE 6.—A, Dune Asteraceous Fynbos: in foreground *Otholobium bracteolatum*, the large shrub at left, *Metalasia muricata*. Note thicket element *Olea capensis* subsp. *capensis* in centre; B, fourteen-year-old stand of *Leucadendron coniferum* (Neutral Sand Proteoid Fynbos). Photographs: M. Mergili.

*Protea obtusifolia* Proteoid Fynbos grows on limestone outcrops and is associated with shallow to moderately deep, alkaline soils and with low rock cover. The pH ranges from 6.9–8.1. The formation is characterized by 2 m high, sparse to medium-dense stands of *P. obtusifolia* often intermixed with *Leucadendron coniferum* and sometimes with *Leucospermum patersonii*. The bulk of the species occurs throughout the Alkaline Sand Fynbos. The formation is frequently intermixed with other formations of the Alkaline and even the Acid Sand Fynbos, sometimes on a very fine scale. Despite floristic differences, it shows affinities to the *Protea obtusifolia*–*Leucadendron meridianum* Proteoid Fynbos of the Agulhas Plain (Cowling *et al.* 1988) and to the *Leucadendron meridianum*–*Protea obtusifolia* Proteoid Fynbos of the Soetanyberg (Richards *et al.* 1995).

*Erica coccinea* Ericaceous Fynbos is associated with alkaline soils rich in Na and Ca. It is not related to the

Ericaceous Fynbos of Campbell (1985) and Cowling (1988) and has its centre of distribution on rather steep limestone outcrops. It is characterized by a high cover of *E. coccinea* (yellow-flowered variant), which is frequently joined by *Indigofera brachystachya* and *Cullumia squarrosa*. Transitions to other formations of the Alkaline Sand Fynbos are common.

*Thamnochortus fraternus* Restioid Fynbos (Figure 8A) grows on steep limestone slopes supporting shallow, rocky, Mg-rich soils with low resistance and a pH between 7.6 and 8.0. It is structurally dominated by < 1 m high stands of the limestone endemic *T. fraternus*. The usually sparse ground cover is made up of shrubs such as *Indigofera brachystachya* or *Cullumia squarrosa*, and also *Erica coccinea* (yellow-flowered variant), the latter indicating a transition to the *E. coccinea* Ericaceous Fynbos. *Protea obtusifolia* and small individuals of *Leucadendron coniferum* may appear

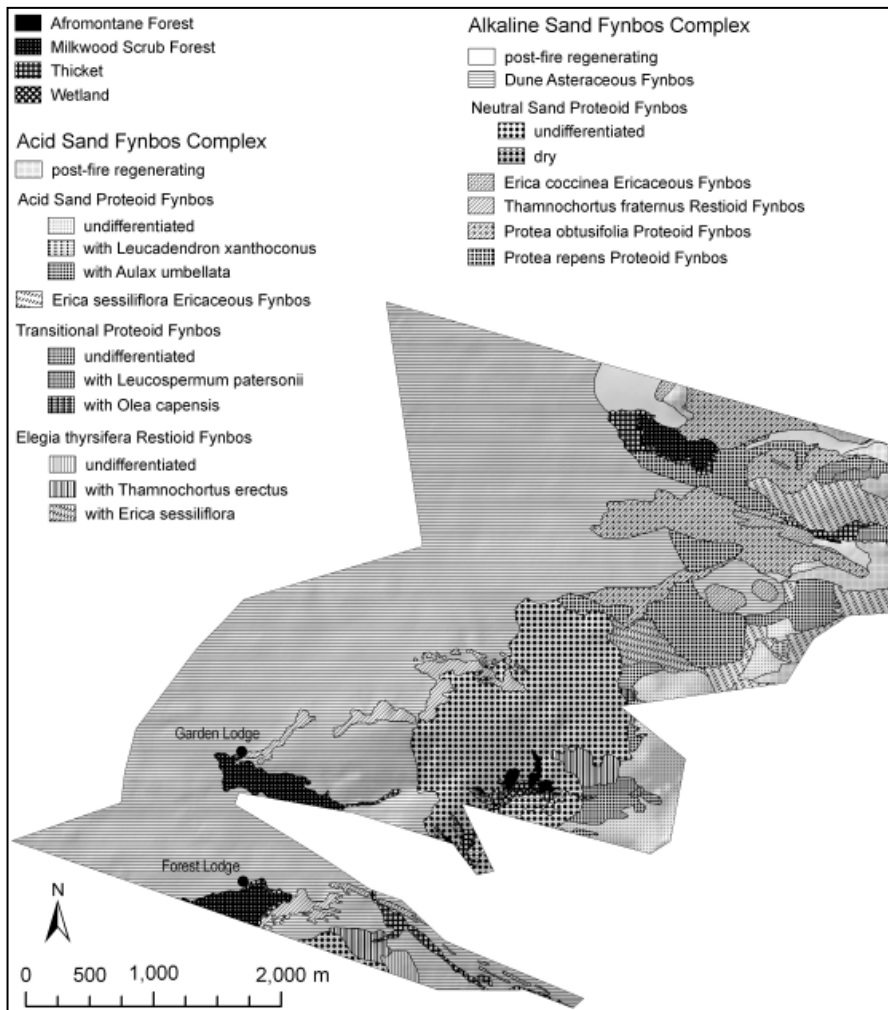


FIGURE 7.—Vegetation map of Grootbos Nature Reserve, based on orthophotos and field studies.

as well. The formation is associated to Kruger's (1979) limestone fynbos.

#### Acid Sand Fynbos Complex

The Acid Sand Fynbos Complex is indicated by the presence of one or more Proteaceae species associated with shallow, acidic soils derived from Table Mountain Sandstone (*Mimetes cucullatus* and *Leucadendron salignum* are the most frequent). The higher hills of the GNR are entirely covered in this complex (Figure 8B). Acid Sand Fynbos has the highest species diversity among the vegetation complexes of Grootbos, averaging at 35 species per relevé with a maximum of 48 species. One hundred and forty-nine species were recorded in the 12 relevés of the core dataset altogether. Four formations of Acid Sand Fynbos were separated in this study. Part of the complex was in an early post-fire stage at the time of the survey and was dominated by *Aspalathus ciliaris*, *Pseudopentameris macrantha*, *Thesium strictum* and *Othonna quinquedentata*.

Acid Sand Proteoid Fynbos grows predominantly on hilltops and steeper slopes, with its largest patch on the Swartkranseberg. It is associated with high elevation, shallow, rocky and acidic (pH 5.2–5.6) soils with low levels of all nutrients except K, and north-facing slopes. The formation shows environmental and structural affinities to both the *Leucadendron xanthoconus*–*Leucospermum cordifolium* Ericaceous Fynbos and the

*Aulax umbellata*–*Protea compacta* Proteoid Fynbos of the Soetanyenberg (Richards *et al.* 1995). It is floristically and structurally characterized by the absence of species that have their centre of distribution in the Alkaline Sand Fynbos Complex and by a low to medium-dense proteoid layer usually less than 1.5 m tall, including several acidophilous Proteaceae with a changing composition and without clear dominance of one species. *Mimetes cucullatus* and *Leucadendron salignum* are the most common, joined by *Aulax umbellata*, *Leucadendron tinctum*, *L. spissifolium*, *L. xanthoconus*, *Protea acaulos*, *P. cynaroides*, *P. longifolia* and *P. speciosa*. Several smaller species of *Erica* and further ericoid shrubs form a sparse to medium, low-height ground layer. The restioid component is variable but *Elegia juncea* in particular is abundant in some places, as is the large 'graminoid' Iridaceae *Bobartia indica*. Some of the non-sprouting Proteaceae, in particular *Aulax umbellata* and *Leucadendron xanthoconus*, may gain dominance in some places as well. According to Campbell (1986) and Cowling *et al.* (1988), part of the Acid Sand Proteoid Fynbos distinguished in this study should instead be recognized as Asteraceous Fynbos as those authors only recognize a community as Proteoid Fynbos if it contains more than 10% cover of reseeded proteoids. The resprouting *Mimetes cucullatus* and *Leucadendron salignum*, in contrast, do not fulfil this requirement.

*Erica sessiliflora* Ericaceous Fynbos grows on damp, south-facing slopes and in valleys. The Acid Sand



FIGURE 8.—A, *Thamnochortus fraternus* Restioid Fynbos on limestone ridge; B, Acid Sand Fynbos on southwestern slope of Swartkransberg; Acid Sand Proteoid Fynbos with *Mimetes cucullatus* and *Aulax umbellata* in foreground; Transitional Proteoid Fynbos with high cover of *Leucadendron coniferum* in background. Photographs: M. Mergili.

Fynbos elements are joined by several moisture indicators, such as *Berzelia lanuginosa*, *Cliffortia ferruginea*, *Drosera capensis* and *Psoralea arborea*. Structurally dominant is *Erica sessiliflora*, which can be up to 1.5 m high and can attain cover values of more than 75%. *Mimetes cucullatus*, *Leucadendron coniferum* and *E. glabella* are common. The largest patch occurs on the southern slope of a mountain on the Steynsbos property, but extended canopies of *E. sessiliflora* also occur on the northern slope of the Swartkransberg, indicating that the species can also cope with less moist conditions. Transitions to other fynbos formations are manifold. The formation corresponds well to the Wet Ericaceous Fynbos described by Campbell (1986) and Cowling *et al.* (1988).

*Elegia thyrsoifera* Restioid Fynbos occupies three patches of fynbos on GNR. It is structurally domi-

nated by *Elegia thyrsoifera* and *Thamnochortus erectus* which can both exceed a height of 2 m. Proteoids (*Leucadendron coniferum*, *Leucospermum patersonii* and partly *Mimetes cucullatus*) are abundant but not dominant. *Helichrysum patulum* and *Morella quercifolia* show high cover values in some places. The formation is associated with north-facing slopes and corresponds to Campbell's (1986) Restioid Fynbos although it is difficult to be assigned to one of the subseries. The sites on the GNR may represent a gradient from Mesic Restioid Fynbos with a higher share of ericaceous Ericaceae (mainly *E. sessiliflora*) to Dry Restioid Fynbos. Floristically it does not correspond to the Dry Restioid Fynbos of the Agulhas Plain (Cowling *et al.* 1988).

Transitional Proteoid Fynbos constitutes a mixture of species centred in the Alkaline Sand Fynbos, and species centred in the Acid Sand Fynbos. The transitional

character is well indicated by the CCA. The pH, however, does not exceed 6. Various subtypes of this formation are present on GNR. Some patches are structurally similar to the Neutral Sand Fynbos but acidophilous proteoids, usually *Mimetes cucullatus*, indicate the more acidic conditions. Damp ravines on the southern slope of the Swartkransberg support a thicket-like vegetation with a high cover of *Olea capensis*, but still with fynbos character. Another transition zone exists between *Protea obtusifolia* Proteoid Fynbos and Acid Sand Fynbos, leading to very complex situations with *P. obtusifolia* and *Aulax umbellata* growing almost together, but representing completely different soil nutrient regimes. The major difference to the transition described above is that it is not based on a gradual decrease of soil depth and pH-value, but on a fine-grained mosaic of young wind-blown, shallow, calcareous soils, older limestone ridges and underlying Table Mountain Sandstone. Extremely complex situations prevail at the western slope of a mountain at Steynsbos, where *Leucadendron coniferum*, *Leucospermum patersonii* and *P. obtusifolia* coexist with some of the acid sand proteoids.

#### Vegetation mapping

The vegetation units illustrated in the map (Figure 7) largely correspond to the units established in the analysis. Only a few changes were made (e.g. patches of fynbos in early post-fire stages). An additional level of detail was introduced in some cases. Most of GNR is covered in Fynbos (1 620 ha or 95.3%). Forest & Thicket account for 78 ha or 4.6% (Afromontane Forest 4.1 ha or 0.2%, Milkwood Scrub Forest for 43 ha or 2.5% and Thicket for 30.9 ha or 1.8%), whereas only 1.4 ha (0.1%) are covered in Wetland. Dune Asteraceous Fynbos covers more than half of GNR (914 ha or 53.8%), and the whole Alkaline Sand Fynbos Complex occupies 1 385 ha or 81.5%. Even the second largest formation of this complex, the Neutral Sand Proteoid Fynbos (191 ha or 11.3%), approaches the same amount of cover as the whole Acid Sand Fynbos Complex (235 ha or 13.8%).

Figure 7 also gives an idea of the fragmentation of the vegetation units. The interpretation of this information has to be approached with caution because the fragmentation may be caused by different factors, including the shape of GNR. Dune Asteraceous Fynbos and Neutral Sand Proteoid Fynbos cover continuous, hardly fragmented areas with average patch sizes of 305 and 96 ha, respectively. *Protea repens* Proteoid Fynbos and *Erica sessiliflora* Ericaceous Fynbos also exceed average patch sizes of 25 ha. In contrast, the distribution of Limestone Fynbos is rather patchy, with 27 patches ranging from tens of hectares of *Protea obtusifolia* Proteoid Fynbos to tiny limestone outcrops covered with *Thamnochortus fraternus* Restioid Fynbos. The average patch size (6 ha) is not representative in this case. In the Forest the patch size of the highly fragmented Afromontane Forests remains below 1 ha (0.81), whereas the patches of Milkwood Scrub Forest occupy slightly more than 10 ha on average.

#### DISCUSSION

Three levels of vegetation units were established on the GNR: the vegetation type level and the vegetation

complex level were based on environmental conditions and species groupings (TWINSPAN), and the formation level on dominant species.

The units of the vegetation type level largely correspond to the biome level of the Broad Habitat Units established by Cowling & Heijnis (2001), based on environmental variables. The Fynbos and Forest Biomes occur on GNR, the Thicket Complex identified in this study does not correspond to the Thicket Biome of Cowling & Heijnis. The complexes of this study correspond partly to the primary units. Campbell (1985) considered Forest and Thicket as one group, as in this study. Wetlands are neither considered by Campbell (1985) nor by Cowling & Heijnis (2001). Cowling *et al.* (1988) classified them as azonal vegetation.

The separation of the fynbos on GNR into an Alkaline and an Acid Sand Fynbos Complex seems sufficiently supported by the classification and the ordinations. The two complexes correspond to the Coastal Fynbos (or Lowland Fynbos) and Mountain Fynbos, respectively (Acocks 1953; Taylor 1978; Kruger 1979; Moll *et al.* 1984). According to Cowling *et al.* (1988), a separation of fynbos in this way has to be rejected because none of the structural units (Campbell 1985) are restricted to one of those groups, and because the floristic changes within the Mountain Fynbos are as significant as between Mountain Fynbos and Lowland Fynbos. However, this study shows that it appears to be highly relevant on a local scale, where the gamma-diversity does not play the role it does on a broader scale while the beta-diversity is still high.

The division of the complexes into proper communities presents problems. Most subcomplex vegetation units are based on one or a maximum of two dominant species which give the landscape a very characteristic appearance. Nevertheless, the classic concept of plant communities as an association of several characteristic species which differentiates it from other communities should not be applied to these entities. The structural component in such a classification is evident, and the groups (here called formations) show a fairly strong correlation to the classification systems of Campbell (1985) and Cowling *et al.* (1988) where structural features of the vegetation were included more systematically. The difficulty of purely floristic classification systems in the Fynbos Biome, due to high gamma-diversity, is illustrated by comparing the findings of this study to the vegetation study of Richards *et al.* (1995) for the Soetansberg. Despite environmentally comparable conditions and a distance of < 50 km, substantial floristic differences, also among the dominant species, are evident.

The expected dependence of fynbos vegetation on certain environmental factors was confirmed by the study. The major explanatory variables in the CCA of Richards *et al.* (1995) in their vegetation study of the Soetansberg were pH, rock cover, soil depth and soil texture. Apart from soil texture, which was investigated in more detail than in this study, the explanatory variables are the same as for GNR. Elevation, which plays a major role here but not in the Soetansberg, is probably mainly a surrogate for the aeolian sediment accumula-

tion budget, wind speed and the distribution of different substrate types, as the correlation values (e.g. 0.78 with pH) indicate.

The clustering of the relevés in the DCA and the CCA was rather poor (compare Figures 2B; 3B) and the transitions between the fynbos units many. Only the Acid Sand Proteoid Fynbos formed a clear cluster, together with some relevés of Transitional Proteoid Fynbos. This finding is partly in line with the study of Richards *et al.* (1995): the relevés connected to low pH (sandstone) were poorly clustered in the CCA biplot, but they were clearly separated from the relevés on limestone. On GNR, the transition between the limestone formations and the remaining formations was continuous with the Neutral Sand Proteoid Fynbos as intermediate formation, but rather with affinities to the limestone formations. In contrast, the *Protea susannae*–*Leucadendron coniferum* Proteoid Fynbos of Richards *et al.* (1995), a formation that is associated with neutral sands according to Cowling *et al.* (1988), did not differ substantially in pH from the sandstone formations, but was clearly discriminated from the limestone formation (*Protea obtusifolia*–*Leucadendron meridianum* Proteoid Fynbos).

The poor clustering in the fynbos of the GNR may be explained by a variety of factors. The location of the relevés (some of them were placed in transitional zones) and the high level of detail in the study (leading to a considerable amount of noise) may serve as one explanation, the topographic and geological patterns on GNR as another; alkaline sands cover the entire western part of the GNR, and limestone ridges of varying shape and size are widely dispersed. This leads to wind-blown alkaline sands of variable depth over large parts of acid substrate and to an extremely fine-scaled pattern of different physical and chemical substrate properties. This is especially true for the foothills and the lower slopes of the higher hills of GNR, leading to very complex vegetation patterns; in some places *Aulax umbellata*, a strong indicator of acidic conditions, and *Protea obtusifolia*, a strong indicator of alkaline conditions, grow immediately adjacent to each other. Only the highest parts of the GNR, the Acid Sand Fynbos Complex, remain untouched and do not contain calcareophilous species. In such a fine mosaic of different environmental conditions, the vegetation is sensitive to influences other than topographic and substrate variables. The problems with grouping fynbos ecosystems based on reseeded proteoids (Richardson & Van Wilgen 1992; Privett *et al.* 2001) are well established, as these organisms are susceptible to local extinction ('drifting clouds of species abundance'). Therefore the structural dominants of the vegetation of a certain place may shift from fire interval to fire interval, as Privett *et al.* (2001) have shown for the Cape Peninsula. However, this phenomenon only occurs at a subcomplex level. The boundaries of the fynbos complexes are not affected as steep environmental gradients prevent mixing of the species pools (high beta-diversity).

Figure 9 represents the floristic diversity of the vegetation of GNR at the complex level. Fynbos and Forest constitute completely different species pools. Less than ten taxa occur in both vegetation types, whereas Acid Sand Fynbos and Afromontane Forest share no taxa at all. In contrast the complexes within each vegetation

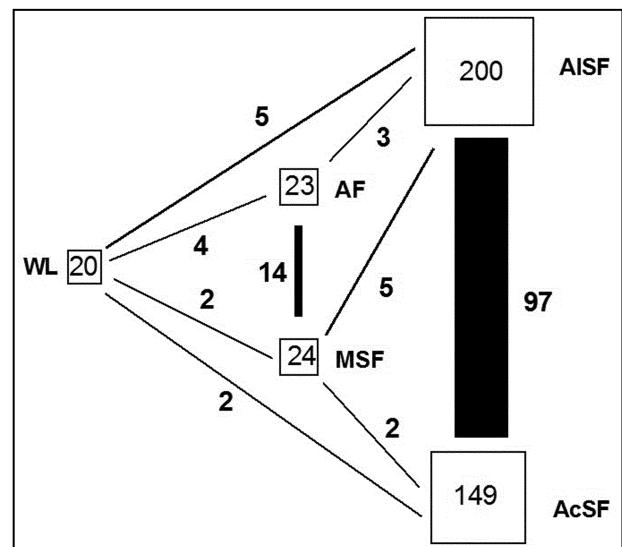


FIGURE 9.—Species diversity of vegetation complexes of Grootbos Nature Reserve. Size of each box and number inside indicate total species number of complex, whereas width of lines and adjacent numbers indicate number of species shared by two complexes. AcSF, Acid Sand Fynbos Complex; AISF, Alkaline Sand Fynbos Complex; MSF, Milkwood Scrub Forest; AF, Afromontane Forest; WL, Wetland.

type share a considerable number of their taxa. Wetland shares only a few taxa with the other groupings, but the low diversity of the wetland may contribute to this phenomenon. Although the Alkaline Sand Fynbos hosts more taxa (200) than the Acid Sand Fynbos (149), the diversity of the latter is more than four times higher if normalized to the area (0.63 and 0.14 taxa per hectare respectively). Even though this ratio may be of limited value, it confirms the general patterns obtained from the relevé data.

As a conclusion, it can be stated that the vegetation patterns of GNR were investigated in great detail, leading to a differentiated picture of the spatial distribution of the vegetation units and the vegetation-environment relationships. The major implications for further management is the potential impact of fire on vegetation structure, in particular the vegetation units dominated by reseeded proteoids. Careful planning to mimic natural fire frequencies and conditions will be necessary in order to prevent local extinction. In order to protect Red Data species, particular care has to be taken when undertaking controlled burns of extreme habitats, such as steep limestone ridges and sandstone slopes.

#### SHORT NOTE

In February 2006, after the submission of this paper, the fynbos ecosystems of the entire GNR were burnt by a fire. Since then, the number of species recorded has increased from 660 to 732 (Privett & Lutzeyer in press) and two further new species (*Capnophyllum* sp. nov. and *Pterygodium* sp. nov.) were recorded.

#### ACKNOWLEDGEMENTS

Thanks to the Lutzeyer family and the staff of Grootbos Nature Reserve for their support during the

field work. Special mention of G. Siebrits who undertook the original vegetation survey on Grootbos in 1997. Grateful thanks also to the Dean's Office of the Faculty for Natural Sciences of the University of Innsbruck and to the Office for International Relations, University of Innsbruck, for their grants enabling the field work in spring 2004, as well as to B. Erschbamer of the Department of Botany, University of Innsbruck for her valuable comments and to A. Erhard<sup>†</sup> (Institute of Geography, University of Innsbruck), P. De Necker (Department of Geography, University of Stellenbosch) and S. Smuts (Department of Botany, University of Cape Town) for their support.

## REFERENCES

- ACOCKS, J.P.H. 1953. Veld types of South Africa. *Memoirs of the Botanical Survey of South Africa* No. 28: 1–128.
- BOUCHER, C. 1978. Cape Hangklip Area II. The vegetation. *Bothalia* 12: 455–497.
- CAMPBELL, B.M. 1985. A classification of the mountain vegetation of the fynbos biome. *Memoirs of the Botanical Survey of South Africa* No. 50: 1–121.
- CAMPBELL, B.M. 1986. Montane Plant Communities of the Fynbos Biome. *Vegetatio* 66: 3–16.
- COWLING, R.M., CAMPBELL, B.M., MUSTART, P., MCDONALD, D.J., JARMAN, M.L. & MOLL, E.J. 1988. Vegetation classification in a floristically complex area: the Agulhas Plain. *South African Journal of Botany* 54: 290–300.
- COWLING, R.M. & HEIJNIS, C.E. 2001. The identification of Broad Habitat Units as biodiversity entities for systematic conservation planning in the Cape Floristic Region. *South African Journal of Botany* 67: 15–38.
- COWLING, R.M., MACDONALD, I.A.W. & SIMMONS, M.T. 1996. The Cape Peninsula, South Africa; physiographical, biological and historical background to an extraordinary hot-spot of biodiversity. *Biodiversity and Conservation* 5: 527–550.
- COWLING, R.M., RICHARDSON, D.M. & MUSTART, P.J. 1997. Fynbos. In R.M. Cowling, D.M. Richardson & S.M. Pierce, *Vegetation of southern Africa*: 99–130. Cambridge University Press, Cambridge.
- COWLING, R.M., PRESSEY, R.L., LOMBARD, A.T., HEIJNIS, C.E., RICHARDSON, D.M. & COLE, N. 1999. *Framework for a conservation plan for the Cape Floristic Region*. A report for the Cape Project for World Wide Fund, South Africa.
- GOLDBLATT, P. & MANNING, J.C. 2000. Cape Plants. A conspectus of the Cape flora of South Africa. *Strelitzia* 9. National Botanical Institute, Cape Town & Missouri Botanical Gardens, St. Louis.
- HILL, M.O. 1994. *DECORANA and TWINSPLAN, for ordination and classification of multivariate species data; a new edition, together with supporting programs, in FORTRAN 77*. Institute of Terrestrial Ecology, Huntingdon.
- HILTON-TAYLOR, C. 1996. Red Data List of southern African plants. *Strelitzia* 4. National Botanical Institute, Pretoria.
- KRUGER, F.J. 1979. South African heathlands. In R.L. Specht, *Heathlands and related shrublands—descriptive studies. Ecosystems of the World* 9A: 19–53. Elsevier, Amsterdam.
- MCDONALD, D.J., COWLING, R.M. & BOUCHER, C. 1996. Vegetation-environment relationships on a species-rich coastal mountain range in the fynbos biome (South Africa). *Vegetatio* 123: 165–182.
- MCKENZIE, B., MOLL, E.J. & CAMPBELL, B.M. 1977. A phytosociological study of Orange Kloof, Table Mountain, South Africa. *Vegetatio* 34: 41–53.
- MIDDLEY, J.J., COWLING, R.M., SEYDACK, A.H.W. & VAN WYK, G.F. 1997. Forest. In R.M. Cowling, D.M. Richardson & S.M. Pierce, *Vegetation of southern Africa*: 278–299. Cambridge University Press, Cambridge.
- MOFFET, R.O. 2007. Name changes in the Old World *Rhus* and recognition of *Searsia* (Anacardiaceae). *Bothalia* 37: 165–175.
- MOLL, E.J., CAMPBELL, B.M., COWLING, R.M., BOSSI, L., JARMAN, M.L. & BOUCHER, C. 1984. *A description of major vegetation categories in and adjacent to the Fynbos Biome*. South African National Scientific Programmes Report No. 83.
- MOLL, E.J. & WHITE, F. 1978. The Indian Ocean Coastal Belt. In M.J.A. Werger, *Biogeography and ecology of southern Africa*. Junk, The Hague.
- MUSTART, P., COWLING, R.M. & ALBERTYN, J. 2003. *Southern Overberg*. South African Wild Flower Guide 8. Botanical Society of South Africa, Cape Town.
- PRIVETT, S.D.J., COWLING, R.M. & TAYLOR, H.C. 2001. Thirty years of change in the fynbos vegetation of the Cape of Good Hope Nature Reserve, South Africa. *Bothalia* 31: 99–115.
- PRIVETT, S.D.J. & LUTZEYER, H.H.M. in press. *The flora of Grootbos Nature Reserve, Western Cape, South Africa*.
- RICHARDS, M.B., COWLING, R.M. & STOCK, W.D. 1995. Fynbos plant communities and vegetation-environment relationships in the Soetanyberg hills, Western Cape. *South African Journal of Botany* 61: 298–305.
- RICHARDSON, D.M. & VAN WILGEN, B.W. 1992. Ecosystem, community and species response to fire in Mountain Fynbos. Conclusions from the Swartboskloof Experiment. In B.W. Van Wilgen, D.M. Richardson, F.J. Kruger & H.J. Van Hensbergen, *Fire in South African Mountain Fynbos*: 273–284. Springer, Berlin.
- TAYLOR, H.C. 1978. Capensis. In M.J.A. Werger, *Biogeography and ecology of southern Africa*. Junk, The Hague.
- TAYLOR, H.C. 1983. The vegetation of the Cape of Good Hope Nature Reserve. *Bothalia* 14: 779–784.
- TAYLOR, H.C. 1996. Cederberg vegetation and flora. *Strelitzia* 3. National Botanical Institute, Pretoria.
- THWAITES, R.N. & COWLING, R.M. 1988. Landscape-vegetation relationships on the Agulhas Plain, South Africa. *Catena* 15: 333–345.



2006-12-12

### NOTICE ON CHANGE OF POLICY FOR REPRINTS OF *BOTHALIA*

As from the 12 December 2006, the policy on reprints of *Bothalia* articles has been amended as follows:

The author receives 20 reprints free. If there is more than one author, this number will have to be shared between them. The author will also receive a pdf file free on request (via the email or a CD included with the reprints): if there is more than one author, the co-author(s) should contact the first author for a copy.

The pdf file may only be used by the author in a private capacity as SANBI retains the copyright of the article and it may not be reproduced in another publication.

G. Germishuizen and Mrs B.A. Momberg: Editors, *Bothalia*  
for Director: Research