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Vegetation of high-altitude fens and restio marshlands of the Hottentots Holland Mountains, Western Cape, South Africa

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ABSTRACT

Seepages occurring at high altitudes in the Hottentots Holland Mountains (HHM) (Western Cape Province, South Africa) were subject to a phytosociological survey. Relevé sampling method and classification procedures of the floristic-sociological (Braun-Blanquet) approach as well as numerical data analyses (numerical classification and ordination) were used to reveal syntaxonomic patterns and characterize the position of the syntaxa along major environmental gradients. Nine plant communities were recognized, three of which were classified as associations, following formal syntaxonomic and nomenclatural rules of the floristic-sociological approach. Most of the studied mire communities were dominated by low-growing clonal restios (Restionaceae), whereas some consisted of other types of graminoids. The most important species determining the structure (and function) of the mire communities on sandstones of the HHM include restios *Anthochortus crinalis, Chondropetalum deustum, C. mucronatum, Elegia intermedia, E. thyrsifera, Restio subtilis, R. purpurascens*, cyperoids *Epischoenus villosus, Ficinia argyropa*, grasses *Ehrharta setacea* subsp. *setacea, Pentameris hirtiglumis* as well as shrubs *Berzelia squarrosa, Cliffortia tricuspidata, Erica intervallaris* and *Grubbia rosmarinifolia. Protea lacticolor* and *Restio perplexus* dominate a rare shale band seepage community. There are two major groups of communities—the fens (dominated by carpets of *Anthochortus crinalis* and other low-growing species) and the restio marshlands (mosaics of low tussocks of *Restio subtilis* and tall *Chondropetalum mucronatum*). The degree of soil (and water) minerotrophy was found to be the most important differentiating feature between the mire (fen and restio marshland) communities studied. The soils in the centre of mires were found to have high contents of peat and showed very little influence from the underlying sandstone. The soils along the mire margins had a greater admixture of mineral soil derived from the sandstone or shale bedrock.

INTRODUCTION

The Cape mountain ranges are important catchments for high-quality drinking water. A vast quantity of this water is stored in the basement rocks before it is released into river systems via seepages (Hewlett 1982). Seepage is a very general term for an area where water percolates through the upper soil layers (mostly lying over a layer of impenetrable rock) and usually forms the source of rivers. It includes the majority of wet slopes as well as many mires of the Cape mountains. The quality of water is largely determined by the soil conditions that percolating water encounters prior to its emergence at the surface and on its way to a river, hence seepages are of great importance to river ecosystems (Bosch *et al.* 1986). However, the total surface area of seepages that influence the water quality of rivers is variable and many seepages can be out of touch with the river system for a long time. This was called the Variable Source Area Concept by Hewlett (1961). After heavy rains the Source Area of a river expands and much water, that was stored in basement rocks or in fens for a long time, moves into the river. During its storage in the seepage areas, water is stained by tannins leached from decaying plant litter. This explains the brown colour that is characteristic of many of Western Cape rivers, particularly after heavy rains (King & Day 1979; Dallas & Day 1993).

Some seepages located in high-altitude areas supporting fynbos vegetation have soils rich in peat—accumulated organic material (Gore 1983)—they can be classified as mires. These are defined as wet, swampy habitats characterized by peaty soils, regardless of the chemico-physical properties of the peat and water captured in the peaty soils. Concepts such as bogs and fens refer to specific types of mires (Gore 1983). The term bog refers to the strictly ombrotrophic (rain-fed) and usually oligotrophic mires found in places with high precipitation, whereas fens are the mires (minerotrophic or transitional) that are fed to a larger extent by water that has percolated through the mineral substrate. The Cape high-altitude mires generally qualify as fens; true bogs are rare in the southern hemisphere, although they do occur on some steep south-facing slopes in Western Cape mountains. In the mountains, mires are found at the sources of the rivers and in watersheds. Riparian mires can be formed in places where the floodplain is very wide and the area remains inundated long after a flood has receded.

There are four types of seepages linked to the drainage network of riverine systems recorded in the Cape mountain ranges, namely:

1, well-drained *slope seepages* supporting soils of the Fernwood form (Fry 1987); this type shows a high level of variability and can be characterized by the increased presence of Bruniaceae; Campbell (1986) in his structural classification of the Fynbos Biome, classified the vegetation of these seepages as Wet Ericaceous Fynbos;

2, low-altitude *valley seepages* characterized by high soil water levels and peaty Champagne soils (Fry 1987); Boucher (1978) described the *Erica–Osmitopsis* Seepage Fynbos in this habitat in the Kogelberg Biosphere Reserve. A subtype of the low-altitude valley seepages occurs on temporarily wet sandy soils. It is dominated by *Elegia filacea* (Taylor 1978);

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3, the high-altitude *fens*, situated at the sources of rivers: Campbell (1986) has classified the vegetation of this habitat as Sneeukop Azonal Restioid Fynbos and Otterford Wet Proteoid Fynbos;

4, in order to distinguish between the different degrees of minerotrophy in the mires described in this study, we want to introduce the term *restio marshlands* for the better-drained sites at the edges of mires of the Fynbos Biome, in contrast to the 'fens' being situated in the centre of the mire. The restio marshland supports a vegetation structural type called Sneeukop Azonal Restioid Fynbos (Campbell 1986).

Most of the African swamps (including mires and other types of marshlands) are dominated by grasses and sedges (Van Zinderen Bakker & Werger 1974; Weisser & Howard-Williams 1982; Thompson & Hamilton 1983; Rogers 1995, 1997). The fens and restio marshlands of the Fynbos Biome are conspicuously different due to the dominance of (often endemic) Restionaceae (Campbell 1986). Despite their peculiarity, the wetland ecosystems of the Cape mountain ranges have received little attention (Boucher 1988; Rogers 1997) and hence deserve a closer look.

This study describes vegetation types found in the rare and poorly studied high-altitude fens and restio marshlands located in the region of richest precipitation in Western Cape—the Hottentots Holland Mountains (HHM). The floristic composition of these vegetation types and their relationship to major ecological factors are the main foci of this paper.

MATERIAL AND METHODS

Study area: location, climate, geology and soils

The majority of vegetation samples used for this paper were recorded from the HHM (between 33° 56' S and 34° 03' S latitude and 18° 57' E and 19° 09' E longitude). This area is situated between the towns of Stellenbosch, Franschhoek and Grabouw in Western Cape, South Africa—the region with the highest rainfall in Western Cape and possibly also in the entire South Africa. There are many peaks reaching above 1 000 m altitude, where numerous and extensive mires have developed. We have added some additional vegetation samples from the Du Toitskloof Mountains, which are located to the north of the HHM and some from the Groenland Mountains, southeast of the HHM.

Most of the fens in the HHM are found in the Palmiet River catchment, although the Riviersonderend and Eerste Rivers are fed by water from fairly extensive mire systems. Two other rivers originating in the area, the Berg River and the Lourens River, barely receive water from mires as they originate on very steep mountain headwalls.

The climate of the Fynbos Biome in the southwestern Cape is classified as mediterranean, with hot, dry summers and mild, wet winters. In the Köppen (1931) system the climate of the area is classified as Csb—having mesothermal (C) climate with a warm, dry summer and average temperatures above 22°C and relatively wet winters (sb). Most mountains of the Fynbos Biome have a rainfall between 1 000 and 2 000 mm mean annual precipitation (MAP), but in the wettest areas (such as the HHM) it might exceed 3 000 mm (Schulze 1965). Most low-lying localities receive much less—up to 750 mm near the coast, and mostly less than 400 mm MAP in the intermontane valleys (Fuggle & Ashton 1979). The mountains in the Fynbos Biome play a major role in influencing precipitation and evaporation. Extremely high regional variation in precipitation (Figure 1) occurs due to the windward-leeward geomorphological dichotomy in the mountains and the fact that winds can sweep unhindered over the coastal plains (Deacon *et al.* 1992). Schulze (1965) described a strong gradient in rainfall with increasing altitude—50 mm of precipitation increase per 300 m increase in altitude. The regional rainfall pattern in the mountains is variable, depending on aspect of slope as well as frequency and strength of northwesterly and southwesterly winds. Mountains can

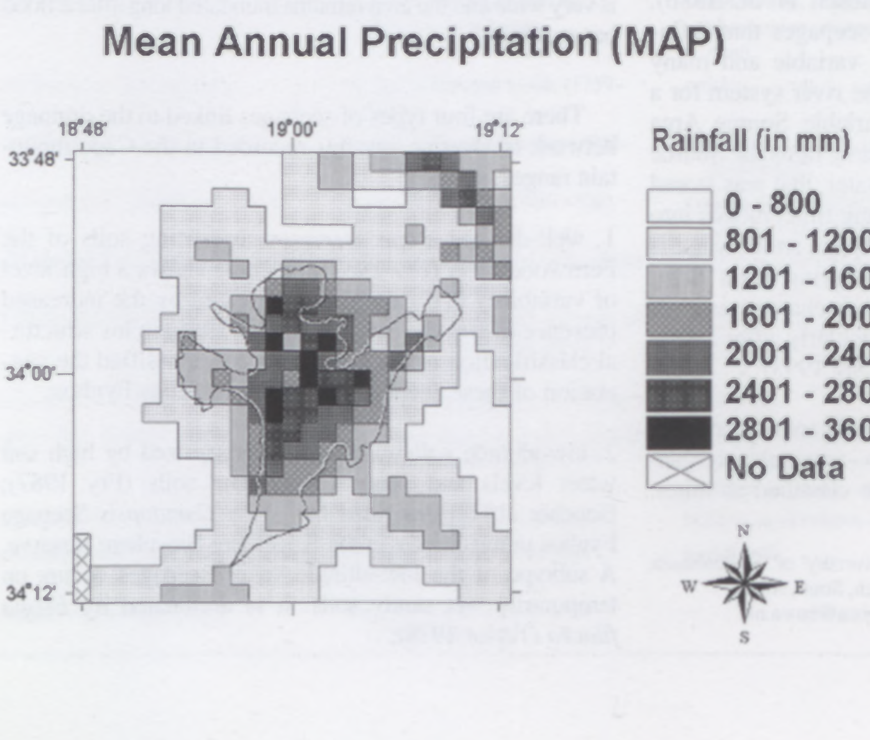

FIGURE 1.—Grid with Mean Annual Precipitation in Hottentots Holland Mountains (Source: Computing Centre for Water Research; grid data computed from weather data from nine official weather stations in vicinity, extrapolated using methodology of Dent *et al.* 1987).

also receive much precipitation (not registered in the rain gauges) from mist (Kerfoot 1968; Fuggle & Ashton 1979) associated with the summer trade winds, locally known as 'southeasters'.

Sixty per cent of the precipitation falls in the wettest four months spanning June to September. This precipitation is mostly in the form of rain, but snow regularly occurs in winter on the mountain peaks (Fuggle & Ashton 1979). Wind speeds are the highest in winter on the mountain tops (Fuggle 1981). This is in contrast with the wind patterns in the surrounding lowlands, showing the highest speed in summer.

The geology of the HHM is dominated by sandstones and shales of the Table Mountain Group, especially at the higher altitudes. Some of the valleys are underlain by Achaean Cape Granite and Malmesbury Group shales, but no mires were recorded on these latter substrates. The Table Mountain Group sandstones (TMS) are mainly from the Nardouw Formation (De Villiers *et al.* 1964). High-altitude shale bands of the Cederberg Formation accompanied by tillites of the Pakhuis Formation occur throughout the area. The shale bands are situated at higher altitudes than most of the seepage areas and virtually all the vegetation types (with one exception) described in this study, are reported from sandstone.

Soils of the mires are classified as belonging to the Champagne Form (Soil Classification Working Group 1991). The amount of peat is variable; towards the outer edges of seepages, the soil contains a greater portion of minerotrophic material (mainly sand) originated from sandstone. Here the prevailing soil form is the Fernwood Form. In this study, we have used soils as a major criterion for the location and delimitation of the fens.

Methods of data collection

Vegetation was studied by means of plot sampling. The plots were laid out in selected fen and marshland habitats in a representative way (Westhoff & Van der Maarel 1978). The size of most of the plots was 10 × 10 m (sometimes less in the case of small vegetation stands), as this was considered to be sufficient to record the species richness. In each plot, each plant species was recorded and the cover-abundance of each was estimated using the modified Braun-Blanquet sampling scale (Barkman *et al.* 1964). Thirty-three plots were recorded in the HHM. We also added a further two samples from the Du Toitskloof Mountains merely to point out that similar communities also occur in the neighbouring mountain ranges (Appendix 2). Soil samples were only collected from the topsoil (A-horizon). The particle size distribution of the soils is determined for the fractions finer than 2 mm Ø. After drying and grinding the soil to break up any coagulation, the soils were shaken through a set of sieves. The sieves of the following raster size were used: 500 μm (to separate coarse sand), 106 μm (to separate medium sand) and 63 μm (to separate fine sand). The fraction that passes through all the sieves is composed of silt and clay. Acidity and resistance were measured in water-saturated soils using a pH meter (Orion 420A) and a conductivity meter (YSI 3200). The fraction of organic matter was measured by titration according to the Walkley-Black method (Walkley 1935; Non-Affiliated Soil Analysis Work Committee 1990).

A list of environmental variables and other relevant information is presented in Table 1.

TABLE 1.—Explanatory variables used in the canonical ordination. Data type: I: interval scale; R: ratio-scale variables, N: nominal-scale variable

Name of variable	Data type	Methods of measurement/estimation, scales, and identity of states for the nominal variables
Soil reaction (pH)	I	Measured in H_2O using pH-meter ORION 420A.
Organic matter (ORGANIC)	R	Percentage calculated by titration using the Walkley-Black method (Walkley 1935).
Slope (SLOPE)	R	Angle measured by slope-meter in degrees.
Geology	N	Determined using geological map (SACS) and by field observations. States: Sandstone (San), Tillite (Til), Shale (Sha), Granite (Gra), Alluvium (Qua).
Soil type	N	Determined after Fry (1987) and Soil Classification Working Group (1991) and on basis of field observations (character of top soil layer and soil depth). States (Soil Forms): Mispah, Magwa, Oakleaf, Fernwood, Glenrosa, Champagne.
Aspect	N	Measured by compass and classified into quadrants. States: N, W, S & E.
Altitude (ALTITUDE)	R	Determined from orthophotographic maps (scale 1:10 000); expressed in m.
Resistance (RESISTAN)	R	Resistance to an electrical current (Ω) measured using a YSI model 3200 conductivity meter.
Gravel (GRAVEL)	R	% of coarse material (>2 mm) in soil sample.
Coarse sand (CSAND)	R	% of coarse sand (0.5–2 mm) in soil sample.
Medium sand (MSAND)	R	% of medium sand (106–500 μm) in soil sample.
Fine sand (FSAND)	R	% of fine sand (63–106 μm) in soil sample.
Silt (SILT)	R	% of silt (< 63 μm) in soil sample.
Soil depth (SOILDEPT)	R	Depth of soil until bedrock; estimated average expressed in cm.
Bedrock cover (BEDROCK)	R	Estimate of cover (%) of bedrock.
Large cobbles (LG_COBB)	R	Estimate of cover (%) of large cobbles (13–25 cm Ø).
Small cobbles (SM_COBB)	R	Estimate of cover (%) small cobbles (6–13 cm Ø).
Pebbles (PEBB)	R	Estimate of cover (%) pebbles (2–6 cm Ø).

Methods of data handling and presentation

The vegetation samples were stored in a database in the format of the National Vegetation Database (Mucina *et al.* 2000) and using the database-management software Turboveg (Hennekens 1996b; Hennekens & Schaminée 2001). The original cover-abundance data was transformed into percentage format using Turboveg. The data were classified using Two-way Indicator Species Analysis (TWINSPAN) (Hill 1979) followed by manual table-sorting using MEGATAB 2.0 (Hennekens 1996a), aimed at improvement of coincidence between the groups of relevés and groups of species. Differential species for communities and their groups were identified on the basis of fidelity. The differential species, constant companions and the dominant species are identified in each case. A differential species is a species that can be used to differentiate between one community or a group of communities and the rest at the same syntaxonomic level (Westhoff & Van der Maarel 1978; Mucina 1993). The difference in the frequency of more than two presence classes (40%) was taken as sufficient for a species to be considered to be differential for one of the communities under comparison. However, a species can also be ranked as differential on the basis of distribution of cover values (dominant versus non-dominant) among relevés of the communities under comparison. A dominant species is a species that is constant and has an average cover of more than 25% (Westhoff & Van der Maarel 1973). A constant companion is a species that occurs in more than 60% of all the samples in a community and is not considered differential at the same time. Less frequent species recorded in plots are listed in Appendix 1. The communities are described here at the level of association or rankless vegetation type comparable to the level of association. We refrained from defining units of the higher syntaxonomic ranks due to limited extent of the data and local character of the study. We have used only two informal groups of the communities based on the habitat characteristics (fens vs. restio marshlands).

The relationship between the environmental data and the vegetation data was determined using multivariate techniques. We follow Økland (1996), who made a case for validity of use of both ordination and constrained ordination as complementary approaches, both direct and indirect gradient analyses were performed. The four variables, coarse sand, medium sand, fine sand and silt, together comprise 100% in every soil sample so they are not independent from each other. According to the recommendations of Ter Braak & Šmilauer (1998) this sort of (compositional) data, has to be log-transformed prior to analysis. Correspondence Analysis (CA) was adopted as the indirect gradient analysis technique, while Canonical Correspondence Analysis (CCA) was used to perform the direct gradient analysis (see Ter Braak 1986; Jongman *et al.* 1987 for details on the techniques). The Canoco 4 program suite (Ter Braak & Šmilauer 1998) was used to perform CA and CCA.

Nomenclature of taxa and plant communities

The nomenclature of plant species follows Germishuizen & Meyer (2003). Three of the well-sampled plant communities were named according to the rules for syntaxomic nomenclature (Weber *et al.* 2000). Vernacular names, using a combination of important taxa and vegetation structure (Edwards 1983), were coined for all plant communities as well.

RESULTS

The fens (and most of the restio marshlands) of the region have a high cover of Restionaceae. Only a few seepage types are dominated by grasses or sedges, such as *Carpha glomerata*, *Epischoenus* spp., *Isolepis prolifer* and *Pennisetum macrourum*. Some Restionaceae typically occurring in the seepages are *Anthochortus crinalis*, *Chondropetalum mucronatum*, *Elegia thyrsifera* and *Restio subtilis*. Two graminoids such as *Ehrharta setacea* subsp. *setacea* and *Epischoenus villosus* are also common.

The following Community Groups and Communities have been revealed in our data:

Community Group A: Fens

Fens form the wettest parts of the seepages—they are poorly drained and contain much peat. The low-grown restio *Anthochortus crinalis* is usually dominant and forms dense mats in between the tussocks of cyperoid *Epischoenus villosus*. Five fen communities were distinguished: the Communities A1 and A2 occur on steep slopes and experience somewhat better drainage than the flat-habitat fen communities (Communities A3, A4 and A5).

Community A1: *Protea lacticolor–Hippia pilosa* Tall Shrubland

(Table 2, relevés 1, 2)

The Community A1 is peculiar due to its link to shale bands. *Protea lacticolor* is the dominant species and forms a dense shrubbery 2–4 m tall. This is the only form of proteoid fynbos recorded on the slope seepages in HHM. The herb layer covers over 80% and is dominated by tussocks of *Epischoenus villosus* and mats of *Restio perplexus*. Other important species include *Senecio umbellatus*, *Seriphium plumosum* (= *Stoebe plumosa*), *Hippia pilosa* and *Oxalis truncatula*. The stands of this community were recorded on the eastern slopes of Somerset Sneeukop at a very high altitude (about 1 400 m). The habitat receives a very high annual rainfall (more than 3 300 mm), some of it in the form of snow, which might persist longer on the southern than on the northern slopes of the mountain. A dense mist blanket covers the mountain especially in summer. It is purported to contribute a considerable additional amount of ambient precipitation (Marloth 1903). Campbell (1986) refers to this vegetation (in structural terms) as Otterford Wet Proteoid Fynbos.

Community A2: *Elegia thyrsifera–Centella eriantha* Short Closed Herbland

(Table 2, relevés 3, 4)

This community is found near the sources of the Lourens River on the western slopes of Somerset Sneeukop (1 100 m) at high altitudes and receives a high precipitation. The upper herb layer is formed by the dominating *Elegia thyrsifera*, whereas the lower herb layer is formed by a multitude of species, such as *Senecio umbellatus*, *Hippia pilosa* and *Erica curviflora*. This community, like the *Protea lacticolor–Hippia pilosa* Tall Shrubland, is quite atypical for the seepages of the studied area. The differential species, *Carpacoce spermacocea*, *Centella eriantha*, *Othonna quinquedentata* and *Ursinia eckloniana*, are all more common in typical ericaceous fynbos (Sieben 2003). The *Elegia thyrsifera–Centella eriantha* Community occurs on steep slopes on sandstone.

Community A3: *Anthochortus crinalis–Elegia intermedia* Tall Closed Restioland

(Table 2, relevés 5–8)

Scientific name: *Anthochorto crinalis–Elegietum intermediate ass. nova hoc loco*

Holotypus: Table 2, relevé 7

This is an extremely species-poor seepage community, which is limited to the Dwarsberg Mountains in the Berg River catchment. The dominant vegetation stratum is a dense layer of *Elegia intermedia*, which grows 1.2 to 1.5 m tall. Linder (1987) has not recorded this species outside the Cape Peninsula, but Kruger (1978) found it on the Dwarsberg. In this study, it was recorded in several other locaties in the HHM. The lower herb layer of the community is dominated by *Anthochortus crinalis* and is less dense. Dwarsberg receives more than 3 000 mm rainfall per annum and the community is found in the wettest, extremely peaty habitats, surrounded by stands of the *Ficinio argyropae–Epischoenetum villosi* and *Tetrario capillaceae–Restietum subtilis*. *Epischoenus villosus*, *Senecio crispus* and the moss *Campylopus stenopelma* as well as the species mentioned above are the only species present in the vegetation.

Community A4: *Ficinia argyropa–Epischoenus villosus* Short Closed Restioland

(Table 2, relevés 9–14)

Scientific name: *Ficinio argyropae–Epischoenetum villosi ass. nova hoc loco*

Holotypus: Table 2, relevé 9

This is one of several seepage communities dominated by the restio *Anthochortus crinalis*. This clonal species forms dense mats and is often found intertwined with *Ehrharta setacea* subsp. *setacea*, *Cliffortia tricuspidata* and *Senecio crispus*. The vegetation is much shorter than in the previous communities. The tallest restio present is *Elegia grandis*, which grows taller than 0.5 m together with the tussocks of *Epischoenus villosus*. In the limited open spaces, low-grown *Ficinia argyropa* and *Anthoxantum tongo* can be found. This community as well as the Community A5, resemble similar vegetation described from the Table Mountain (Glyphis *et al.* 1978: *Erica mollis* Fynbos Community; Laidler *et al.* 1978: *Restio–Hypolaena* Subcommunity). Both communities are associated with peaty soils that are waterlogged for most of the time. *Ficinia argyropa–Epischoenus villosus* community also represents a typical form of what is described by Campbell (1986) as Sneeukop Azonal Restioid Fynbos. In one relevé, *Carpha glomerata* was recorded as the dominant species—a situation usually encountered in wet habitats at lower altitudes.

Community A5: *Restio bifurcus–Anthochortus crinalis* Short Closed Restioland

(Table 2, relevés 15–18)

A further seepage type is also dominated by *Anthochortus crinalis*. Floristically and structurally this community resembles the previous one closely and it might also be considered as a subassociation of the *Ficinio argyropae–Epischoenetum villosi*. The main difference is in the absence of *Senecio grandiflorus* and *Ficinia argyropa*, but this community also has some differential species of its own, such as *Gladiolus carneus*, *Restio bifurcus*, *Restio corneolus*, *Tetraria capillacea* and *Chondropetalum mucronatum* (the last-named reaches far above the dominant herb layer). Notable is the occurrence of *Prionium serratum*—a typical shrub in Cape mountain streams (Sieben 2003).

Community Group B: Restio Marshlands

The habitats supporting all four communities of Community Group B are better drained than those of Community Group A. The soils are largely of minerotrophic origin and the peat content is low. They are often found on the edges of the mires and the water drains into the fens. The restio marshlands are richer in species than the fens. The Communities B1 and B2 show transitional features between restio marshlands and fens, through occurrence of species such as *Senecio crispus*.

Community B1: *Platycaulos depauperatus* Short Closed Restioland

(Table 2, relevés 19–21)

This is the only seepage type dominated by restio *Platycaulos depauperatus*, which forms dense green mats and is the most conspicuous differential species of this community. The tussock-forming *Restio subtilis* is the co-dominating element. Together they form the lower herb stratum. One emergent 1.5 m tall restio, *Chondropetalum mucronatum*, forms its own stratum. *Epischoenus villosus*, *Elegia neesii* and *Tetraria capillacea* are significantly shorter. Apart from the eponymous, the only other differential species of this community are the grass *Pentameris hirtiglumis* and the geophyte *Kniphofia tabularis*, flowering after a fire. We believe that this community, although only recorded in our study in three samples, due to being visible after a recent fire, is quite common in the Palmiet River catchment. It seems to occupy an intermediate ecological position between the *Ficinio argyropae–Epischoenetum villosi* Association (from peaty soils) and the *Tetrario capillaceae–Restietum subtilis* Association (from more minerotrophic soils). The localities of this community receive less rainfall than other seepage types, with a MAP of just over 2 000 mm.

TABLE 2.—Classification of the high-altitude mires of Hottentots Holland and Du Toitskloof Mountains. Mountain range: H, Hottentots Holland; D, Du Toitskloof Mountains. River basin: B, Berg River; E, Eerste River; L, Lourens River; P, Palmiet River; R, Riversonderend River; W, Wit River (in Du Toitskloof Mtns). Geomorphology: S, steep; F, flat. Geology: S, shale; T, Table Mountain sandstone. Rare species are listed in Appendix 1

Community Group A (Fens)
Community A1: *Protea lacticolor–Hippia pilosa* Tall Shrubland
Community A2: *Elegia thyrsifera–Centella eriantha* Short Closed Herbland
Community A3: *Anthochorto crinalis–Elegietum intermediae*
Community A4: *Ficinio argyropae–Epischoenetum villosi*
Community A5: *Restio bifurcus–Anthochortus crinalis* Short Closed Restioland

Community Group B (Restio marshlands)
Community B1: *Platycaulos depauperatus* Short Closed Restioland
Community B2: *Erica autumnalis–Restio purpurascens* Tall Closed Restioland
Community B3: *Grubbia rosmarinifolia–Restio* aff. *versatilis* Medium Closed Shrubland
Community B4: *Tetrario capillaceae–Restietum subtilis* Short to Tall Closed Restioland

Relevé no.			1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35
Field code			1	2	2	2	2	2	2	2	2	2	2	2	2	2	1	2	2	2	1	1	1	1	1	1	1	1	8	8	1	1	1	1	1	2	2
			1	3	4	4	2	2	2	3	2	3	3	4	4	5	8	0	0	0	3	3	6	3	3	2	2	2	6	7	2	2	6	6	8	3	6
			1	3	1	2	7	8	9	0	6	1	2	3	4	9	8	1	2	3	5	6	5	1	4	4	7	8			3	9	3	4	9	4	2
Transect no.			3	1	1	1	1	1	1	1	9	1	1	1	1	1	7	8	8	8	4	4	6	4	4	4	4	4	2	2	4	4	6	6	7	1	1
			4	0	1	1	0	0	0	0	9	0	0	1	1	2	7	7	8	9	8	9	4	6	7	2	4	4	4	5	2	5	2	3	8	0	2
				6	0	1	0	1	2	3		4	5	2	3	5																				7	8
Mountain range			H	H	H	H	H	H	H	H	H	H	H	H	H	D	H	H	H	H	H	H	H	H	H	H	H	H	H	H	H	H	H	H	H	H	D
River basin			R	R	L	L	B	B	B	B	B	R	R	E	E	W	R	E	E	E	P	P	P	P	P	P	P	P	P	P	P	P	P	P	R	P	W
Geomorphology			S	S	S	S	F	F	F	F	F	F	F	F	F	F	F	F	F	F	F	F	F	F	F	F	F	F	F	F	F	F	F	F	F	F	F
Geology			S	S	T	T	T	T	T	T	T	T	T	T	T	T	T	T	T	T	T	T	T	T	T	T	T	T	T	T	T	T	T	T	T	T	T
Community group			A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B
Community			1	1	2	2	3	3	3	3	4	4	4	4	4	4	5	5	5	5	1	1	1	2	2	3	3	3	4	4	4	4	4	4	4	4	4
Protea lacticolor	A1	sl	3	5																																	
Restio perplexus	A1	hl	a	3																																	
Ursinia ecklonia	A2	hl			1	a																															
Centella eriantha	A2	hl			a	4																1															
Othonna quinquedentata	A2	hl			1	+																															
Carpacoce spermacocea	A2	hl		1	1	1																															
Elegia intermedia	A3	hl					5	5	5	5	1	a	a									a															
Ficinia argyropa	A4	hl									1	1	3	1	a	1																					
Carpha glomerata	A4	hl										4																									
Senecio umbellatus	A1,A4	hl	1	a	b	a					a	1	a	r	+																						
Anthoxanthum tongo	A1,A4	hl	1	+							1					a																					
Restio bifurcus	A5	hl																1	+	1																	
Prionium serratum	A5	hl																1	+	+																	
Gladiolus carneus	A5	hl									+						+	+	+															r			
Anthochortus cf. *graminifolius*	A5	hl																		4																	
Stoebe plumosa	A	hl	3	b							1		+			+		+	1			+								+							
Cliffortia tricuspidata	A	hl								+		a	a		+	b			b	4	a																
Elegia grandis	A	hl												1	a			+	+																		

Platycaulos depauperatus	B1	hl																			b	5	3														
Pentameris hirtiglumis	B1	hl																			m	+		b													
Kniphofia tabularis	B1	hl	1																		+	1															
Erica autumnalis	B2	hl		+																		1		3	1												
Cliffortia ovalis	B2	hl				b																		1	1												
Aristea bakeri	B2	hl																						1	1												
Elegia racemosa	B2	hl																			a			1	+												
Asteraceae species	B2	hl																						+	+												
Hippia pilosa	A1-2, B2	hl	m	3	b	+																		1	r												
Elegia thyrsifera	A1-2, B2	hl	4		5	4																		1	b			1							a		
Tetraria cuspidata	A1-2, B2	hl	1		a	a																		m													
Senecio crispus	A, B1-2	hl	+				+		+	+	a	1	1			1	+	+	a	a	1	1	m	1	1												+
Restio bifidus	B3	hl																						1		1	1	m						+			
Brunia alopecuroides	B3	hl																								1	+	+				1					
Erica lutea	B3	hl																								+	1										
Erica sitiens	B3	hl																								1		+									
Adenandra acuta	B3	hl																								1		1									
Erica coccinea	B3	hl																						r		+		+									
Gnidia galpinii	B3	hl																								1		1									
Stoebe cinerea	B3	hl																								+		+									
Clutia polygonoides	B3	hl,jl				r																		r		1		+									
Chrysithrix dodii	B4	hl																						+					m						1		1
Berzelia squarrosa	B3,B4	hl			+																					1	+	5			+	1				+	+
Erica fastigiata	B3,B4	hl															1									+	r	+				1				+	
Restio burchellii	B3,B4	hl														+										+			1			1			1	a	
Erica curviflora	B3,B4	s2																										a					1	+			
Restio aff. *versatilis*	B	hl																			m					m	a	a	m		1		1			a	
Erica hispidula	B	hl																				1		b	a	1		+		+		+					1
Chrysithrix junciformis	B	hl																			m								m			1			m	+	
Elegia neesii	B	hl	a																		m		1	1		m		m						b			
Grubbia rosmarinifolia	B	hl																					a			4	+	a	4		+	4	b	+	+	r	
Restio ejuncidus	B	hl																				+			+		a				m						
Sphagnum capense	B	ml																			m	m											m		m		
Chondropetalum mucronatum	B,A5	hl														+	4				3		4	1		a	1	+	b	m		3	3	a	a	3	
Restio subtilis	B,A5	hl														4					4	a	b			3			5	5	m	3	m	4	4	5	
Restio purpurascens	B,A5	hl																a			+	3	+	4	5	4	1	3		3	1		+	1			
Chondropetalum deustum	B,A5	hl															1							m	1	1		m				1	+	a	m		
Tetraria capillacea	B,A5	hl											b			+	1				m		1	m		1			m	+	1	a	a		1	m	
Restio corneolus	B,A5	hl														+	1		1							1		1	1	m		+		1	1		

TABLE 2.—Classification of the high-altitude mires of Hottentots Holland and Du Toitskloof Mountains. Mountain range: H, Hottentots Holland; D, Du Toitskloof Mountains. River basin: B, Berg River; E, Eerste River; L, Lourens River; P, Palmiet River; R, Riversonderend River; W, Wit River (in Du Toitskloof Mtns). Geomorphology: S, steep; F, flat. Geology: S, shale; T, Table Mountain sandstone. Rare species are listed in Appendix 1 (cont.)

Community Group A (Fens)
Community A1: *Protea lacticolor–Hippia pilosa* Tall Shrubland
Community A2: *Elegia thyrsifera–Centella eriantha* Short Closed Herbland
Community A3: *Anthochorto crinalis–Elegietum intermediae*
Community A4: *Ficinio argyropae–Epischoenetum villosi*
Community A5: *Restio bifurcus–Anthochortus crinalis* Short Closed Restioland

Community Group B (Restio marshlands)
Community B1: *Platycaulos depauperatus* Short Closed Restioland
Community B2: *Erica autumnalis–Restio purpurascens* Tall Closed Restioland
Community B3: *Grubbia rosmarinifolia–Restio* aff. *versatilis* Medium Closed Shrubland
Community B4: *Tetrario capillaceae–Restietum subtilis* Short to Tall Closed Restioland

Relevé no.		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35
Field code		111	233	241	242	227	228	229	230	226	231	232	243	244	259	188	201	202	203	135	136	165	131	134	124	127	128	86	87	123	129	163	164	189	234	262
Transect no.		34	106	110	111	100	101	102	103	99	104	105	112	113	125	77	87	88	89	48	49	64	46	47	42	44	44	24	25	42	45	62	63	78	107	128
Mountain range		H	H	H	H	H	H	H	H	H	H	H	H	H	D	H	H	H	H	H	H	H	H	H	H	H	H	H	H	H	H	H	H	H	H	D
River basin		R	R	L	L	B	B	B	B	B	R	R	E	E	W	R	E	E	E	P	P	P	P	P	P	P	P	P	P	P	P	P	P	R	P	W
Geomorphology		S	S	S	S	F	F	F	F	F	F	F	F	F	F	F	F	F	F	F	F	F	F	F	F	F	F	F	F	F	F	F	F	F	F	F
Geology		S	S	T	T	T	T	T	T	T	T	T	T	T	T	T	T	T	T	T	T	T	T	T	T	T	T	T	T	T	T	T	T	T	T	T
Community group		A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B
Community		1	1	2	2	3	3	3	3	4	4	4	4	4	4	5	5	5	5	1	1	1	2	2	3	3	3	4	4	4	4	4	4	4	4	4
Epischoenus villosus	hl	+	a			m	m	1	1	3	4	3	4	4	m	a	m	4	b	m	1	m			m			a	m		+	a	m	a		
Anthochortus crinalis	hl				1	a	3	b	b	5	m	a	3	3	4	4	3	3	4				a	a	m			m	m	m		4		3		5
Ehrharta setacea s. *setacea*	hl		+							m	1	3	m		b	m	a	b	a	m	a	m	a	+	m			m	1		+		1	m		1
Erica intervallaris	hl												b	1	1		b			a	+	a	a			+		a			a	a	3	1	a	1
Ursinia caledonica	hl												b	4		+	a				1		m	+	1			b	3		a			1	1	
Ehrharta rehmannii	hl	1	1		1										+						+		a		1	1									1	
Drosera aliciae	hl												+		+					+					+	1						+	+			
Gnidia oppositifolia	hl			1	+										+						1		1										+			1
Oxalis truncatula	hl	1	+		+								+										r	+	r		1									
Erica curviflora	hl			+	a																		1			+										
Restio echinatus	hl									a							1			m			m													m
Erica calycina	hl																+		+			1			r											
Campylopus stenopelma	ml					1		m																		m		a	m							
Elegia spathacea	hl														m																			1		+
Nebelia fragarioides	hl																r								1						+					
Erica triflora	hl														+						a														+	

Community B2: *Erica autumnalis–Restio purpurascens* Tall Closed Restioland

(Table 2, relevés 22, 23)

This is one of the two communities described from riparian mires. From the point of view of hydrology and species composition these communities are closely related to the Restio Marshlands, hence they are classified as such in this study. These communities occur along the highest reaches of the rivers (in this study all were sampled in the Palmiet River catchment) and have a mixture of seepage and riparian elements making up very species-rich communities, both in comparison with other seepage types as well as with riparian communities. The *Erica autumnalis–Restio purpurascens* community has a more prominent tall herb layer than most of the seepage communities. The dominant species is *Restio purpurascens*, but *Elegia racemosa* and *E. thyrsifera* are also abundant. In the lower stratum, *Anthochortus crinalis* is conspicuous. Some species such as *Hippia pilosa* and *Senecio crispus* are shared with Community Group A. This type can best be described as a Restioland, because small and big restio species are its most important structural constituents. It is difficult to determine the differential species in a situation where relevés are few, but *Aristea bakeri*, *Cliffortia ovalis*, *Elegia racemosa*, *Hippia pilosa* and an unidentified species of Asteraceae, might serve as possible candidates. Eponymous *Erica autumnalis* is endemic to the HHM. The community occurs in the highest reaches of the Wesselsgat River, where riverbanks are steep and rocky.

Community B3: *Grubbia rosmarinifolia–Restio* aff. *versatilis* Medium Closed Shrubland

(Table 2, relevés 24–26)

This is the other type of riparian mire found along high altitude streams. The main difference from the previous type is the shape of the banks, which are flatter and less rocky in this vegetation. The dominant small restio here is *Restio* aff. *versatilis*, compared with *Anthochortus crinalis* in community B2.

This community has a tall herb stratum (reaching 1.0–1.5 m), dominated by the shrubs *Berzelia squarrosa*, *Brunia alopecuroides* and *Grubbia rosmarinifolia* and restioids *Restio purpurascens* and *Chondropetalum mucronatum*. The most closely related riparian community is the *Erico–Tetrarietum crassae* (Sieben 2003), which shares many *Erica* species with the *Grubbia rosmarinifolia–Restio* aff. *versatilis* Closed Shrubland. The most closely related seepage community is the *Tetrario capillaceae–Restietum subtilis*. A species that is shared with this community is *Restio* aff. *versatilis*, which is the dominating element of the ground layer. The *Grubbia rosmarinifolia–Restio* aff. *versatilis* Community is typical of situations where river banks are not steep and there is a lot of lateral seepage. It can be described as a shrubland because of the high cover of shrubs of Ericaceae and Bruniaceae. There are many differential species, most of which are shared with ericaceous fynbos and the *Erico–Tetrarietum crassae* in particular. These are, amongst others, *Brunia alopecuroides*, *Berzelia squarrosa*, *Erica fastigiata*, *Grubbia rosmarinifolia* and *Restio bifidus*.

Community B4: *Tetraria capillacea–Restio subtilis* Short to Tall Closed Restioland

(Table 2, relevés 27–35)

Scientific name: *Tetrario capillaceae–Restietum subtilis ass. nova hoc loco*

Holotypus: Table 2, relevé 27

This is the most common type of seepage community in the area, which can be characterized by the absence of *Senecio crispus*. The dominant restio is *Restio subtilis*, with *Anthochortus crinalis* and *Restio* aff. *versatilis* as co-dominants. A typical characteristic is the mosaic formed by patches of low vegetation of small restios and sedges (*Restio subtilis*, *R.* aff. *versatilis*, *Tetraria capillacea* and *Epischoenus villosus*) and patches of tall vegetation consisting only of *Chondropetalum mucronatum*. This species does not resprout after fires, like many other seepage species, but regenerates from seed. It tends to dominate the community, because the old plants form a thick litter layer on the soil beneath it, which seems to prohibit other (aggressively spreading) clonal species from growing there.

Differential species of this community are few, because most species are shared with the *Grubbia rosmarinifolia–Restio* aff. *versatilis* Closed Shrubland. Diagnostic features are mostly the dominance of *Restio subtilis* and the occurrence of *Chrysithrix* species. As in the case of the riparian seepage types, this community contains numerous shrub species, such as the differential species *Grubbia rosmarinifolia* and *Berzelia squarrosa*, but they do not grow very tall.

This community occurs on more minerotrophic soils than the former communities. Nevertheless, the soils are very acidic and highly organic. In one case it was found in a riparian zone and it is closely related to the riparian seepage types described above. The community described by Boucher (1978) as *Chondropetalum–Restio* Tussock Marsh seems to be quite similar, but the dominant small restio in the Kogelberg is not *Restio subtilis* but *R. ambiguus* and many other species are absent in the Kogelberg community.

Gradient analyses

The most important environmental factors that come out of the CCA (Figure 2) are slope and altitude. This is mainly due to the outlier communities of A1 and A2, which are located at a higher altitude and on steeper slopes than any other of the mire communities. They also have, together with the riparian mire communities B2 and B3, the highest values for rockiness. It is interesting to see that there is a sharp contrast in the fraction of soil particle sizes: the fraction of coarse sand is an important environmental variable and the communities with a high fraction of coarse sand are the riparian mires (B2 and B3)

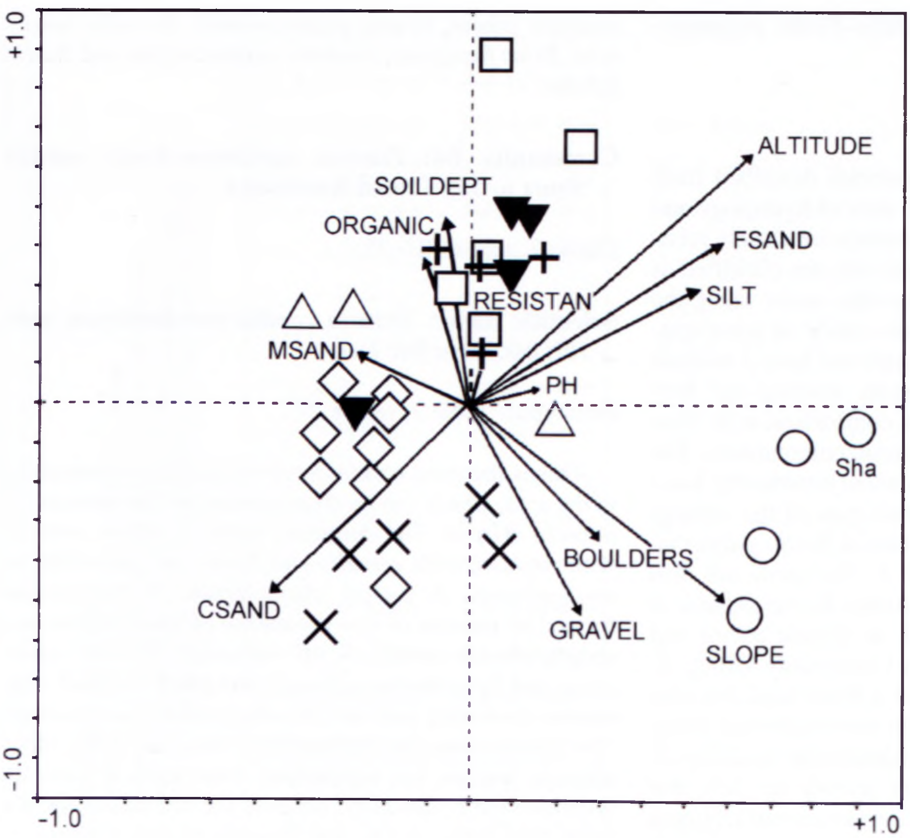

FIGURE 2.—Biplot of constrained ordination (CCA) of mire vegetation of Hottentots Holland Mountains, featuring Axes 1 and 2 with position of community samples and selected environmental variables. Comm. A1 and Comm. A2, O; Comm. A3, +; Comm. A4, □; Comm. A5, ▼; Comm. B2 and Comm. B3, ×; Comm. B3, Δ; Comm. B4, ◊.

and restio marshlands (B4) which are the most minerotrophic mires in the mire system. On the other hand, there are the communities which have a high fraction of fine sand and silt, which represent the fens in the middle of the mire system where peat formation occurs (especially A3, but also A4 and A5). The axis that is formed by the variable of coarse sand, fine sand and silt reflects a gradient in minerotrophy or in waterlogging. The fens (A3, A4 and A5) have the highest values for organic matter contents and soil depth. They are also mainly found at the higher altitudes because this is where the highest rainfall occurs.

DISCUSSION

One of the most important questions that is raised from the results of this study is where the high-altitude mires of the Fynbos Biome fit into the world-wide typology of fens and mires. Although the mires regularly form the sources of the rivers, they are clearly very different from the European spring ecosystems (Zechmeister & Mucina 1994). Swamps and bogs with a high graminoid cover are found extensively in the boreal zone of the northern hemisphere (Sjörs 1983) and the vegetation cover of swamps and bogs in Africa is also mostly dominated by graminoids (Thompson & Hamilton 1983).

Gore (1983) distinguishes between ombrotrophic and minerotrophic mires, based on the origin of the water. In ombrotrophic seepage, a thick layer of peat has developed and there is no more contact with the mineral substrate. The water originates exclusively from rain, which results in very oligotrophic conditions. The water from minerotrophic mires seeps through the mineral substrate into the mire, so it is richer in nutrients than the ombrotrophic mire. Ombrotrophic mires can only exist in very humid climates such as the blanket bogs of the British Isles and the elevated bogs of northern Europe; they are quite rare in the southern hemisphere. Actually, the distinction between ombrotrophic and minerotrophic mires is more like a gradient, an idea expressed by Sjörs (1983). Ombrotrophic mires are on the one extreme of this gradient and all mires that do not feed exclusively on rainwater make up the rest of this gradient.

Sjörs (1983) also gives a more detailed subdivision of European mires: topogenous mires (influenced by stagnant water), soligenous mires (influenced by seepage), limnogenous mires (influenced by floodwaters) and ombrogenous mires (influenced by rainwater). Soligenous and limnogenous mires are both associated with rivers. Soligenous mires form around springs and limnogenous mires occur in the floodplains along the lower reaches of rivers. The mires described in this study are all of the soligenous type. The different communities described in this study are situated along a gradient from dry to moist. In the *Ficinio argyropae–Epischoenetum villosi* Association, occurring in the centre of the mire, water stagnates more because the drainage is slow. On the edges, the *Tetrario capillaceae-Restietum subtilis* Association, which has a faster drainage, will prevail. Further towards the margins, communities dominated by *Chondropetalum deustum* can occur, but these were not recorded during this study. Two communities can occur towards the centre of very wet mires, namely the *Anthochorto crinalis–Elegietum intermediae* Association or the *Isolepis prolifer–Bulbinella nutans* Tall Closed Sedgeland described from the Du Toitskloof Mountains. Both communities are extremely poor in species, because of the specific stresses that occur under waterlogged conditions. It is clear that this gradient, from well-drained to poorly drained or from the edge to the centre of the mire, is also very prominent in the ordination diagrams. This gradient was also found by Bragazza & Gerdol (1999) in some mires in the southeastern Alps. The other distinguishing feature that shows clearly in the ordination diagrams is the importance of the substrate, as can be seen from the *Protea mundii–Hippia pilosa* Tall Shrubland from the shale band.

A conspicuous thing about the vegetation of mires of the Fynbos Biome is that they are dominated by the clonal restios *A. crinalis*, *P. depauperatus* and *R. subtilis* (Linder 1985). Because these species tend to cover everything, the vegetation is relatively poor in species. Clonal reproduction is often coupled to environmental plasticity, so the species can tolerate slight differences in the environment. The diversity of microsites is much bigger than the species richness suggests (Price & Marshall 1999). The tall restio *C. mucronatum* only regenerates from seed after fires and usually occurs in large, dense monotypic stands when mature. It does not support much vegetation underneath it. The dead material from previous generations can form dense accumulations of debris and this creates a very unfavourable substrate for other species.

In marshes elsewhere in the world, clonal sedges and grasses take the place of the clonal Restionaceae recorded in this study. It is generally accepted that the clonal growth form is an adaptation to the stress of waterlogging. This is confirmed by the investigations by Soukupová (1994) of three clonal graminoids. After waterlogging there is an increase in clonal modules. Specht (1981) reviews many of the problems that sclerophyllous plants have to overcome in seasonally waterlogged areas.

It has become clear from this study that the mires in South Africa are very different from those in the northern hemisphere. Although they are vulnerable to predicted climate change (Rutherford *et al.* 1999), there is very little knowledge about the fens and mires of the southern hemisphere. In order to be able to make general statements about mire ecosystems, more attention should be paid to the mire ecosystems in countries like South Africa.

REFERENCES

BARKMAN, J.J., DOING, H. & SEGAL, S. 1964. Kritische Bemerkungen und Vorschläge zur quantitativen Vegetationsanalyse. *Acta Botanica Neerlandica* 13: 394–419.

BOSCH, J.M., ALLETSON, D.J., JACOT GUILLARMOD, A.F.M.G., KING, J.M. & MOORE, C.A. 1986. River response to catchment conditions. In J.H. O'Keeffe, *The conservation of South African rivers*. South African National Scientific Programmes Report No. 131.

BOUCHER, C. 1978. Cape Hangklip area. II. The vegetation. *Bothalia* 12: 455–497.

BOUCHER, C. 1988. Wetland vegetation of the Fynbos Biome. In J.M.King, *Hydrology and hydrobiology in the Fynbos Biome*: 34–40. Ecosystems Programmes Occasional Report No. 26, CSIR, Pretoria.

BRAGAZZA, L. & GERDOL, R. 1999. Hydrology, groundwater chemistry and peat chemistry in relation to habitat conditions in a mire on the southeastern Alps of Italy. *Plant Ecology* 144: 243–256.

CAMPBELL, B.M. 1986. A classification of the mountain vegetation of the Fynbos Biome. *Memoirs of the Botanical Survey of South Africa* No. 50: 1–121.

DALLAS, H.F. & DAY, J.A. 1993. *The effect of water quality variables on riverine ecosystems: a review*. Water Research Commission Report TT 61/93, Pretoria.

DEACON, H.J., JURY, M.R. & ELLIS, F. 1992. Selective regime and time. In R.M. Cowling, *The ecology of fynbos: nutrients, fire and diversity*: 6–22. Oxford University Press, Cape Town.

DENT, M.C., LYNCH, S.D. & SCHULZE, R.E. 1987. *Mapping mean annual precipitation and other rainfall statistics over southern Africa*. Agricultural Catchments Research Unit Report No. 27. Water Research Commission Report No. 109/1/89.

DE VILLIERS, J., JANSEN, H. & MULDER, M.P. 1964. *Die geologie van die gebied tussen Worcester en Hermanus*. Geological Survey, Pretoria.

EDWARDS, D. 1983. A broad-scale structural classification of vegetation for practical purposes. *Bothalia* 14: 705–712.

FRY, M. ST. L. 1987. *A detailed characterization of soils under different fynbos-climate-geology combinations in the southwestern Cape*. M.Sc. thesis, University of Stellenbosch.

FUGGLE, R.F. 1981. *Macro-climatic patterns within the Fynbos Biome. Final Report*. National Programme for Environmental Sciences, Fynbos Biome Project, Cape Town.

FUGGLE, R.F. & ASHTON, E.R. 1979. Climate. In J. Day, W.R. Siegfried, G.N. Louw & M.L. Jarman, *Fynbos ecology: a preliminary synthesis*. South African National Scientific Programmes Report No. 40: 7–15.

GERMISHUIZEN, G. & MEYER, N.L. (eds). 2003. Plants of southern Africa: an annotated checklist. *Strelitzia* 14. National Botanical Institute, Pretoria.

GLYPHIS, J., MOLL, E.J. & CAMPBELL, B.M. 1978. Phytosociological studies on Table Mountain, South Africa. 1. The Back Table. *Journal of South African Botany* 44: 281–289.

GORE, A.J.P. (ed.). 1983. *Ecosystems of the World 4. Mires: swamp, bog, fen and moor. A. General studies*. Elsevier, Amsterdam.

HENNEKENS, S.M. 1996a. *MEGATAB—a visual editor for phytosociological tables*. Version 1.0. User's Guide, Giesen & Geurts, Ulft.

HENNEKENS, S.M. 1996b. *TURBOVEG: software package for input, processing, and presentation of phytosociological data*. Version July 1996. User's guide. IBN-DLO & Lancaster University, Wageningen & Lancaster.

HENNEKENS, S.M. & SCHAMINÉE, J.H.J. 2001. TURBOVEG, a comprehensive data base management system for vegetation data. *Journal of Vegetation Science* 12: 589–591.

HEWLETT, J.D. 1961. *Soil moisture as a source of base flow from steep mountain watersheds*. Southeastern Experimental Station, USDA Forest Service Paper 132.

HEWLETT, J.D. 1982. *Principles of forest hydrology*. University of Georgia Press, Athens, Georgia.

HILL, M.O. 1974. Correspondence analysis: a neglected multivariate method. *Applied Statistics* 23: 340–354.

HILL, M.O. 1979. *TWINSPAN—a FORTRAN program for arranging multivariate data in an ordered two way table by classification of individuals and attributes*. Cornell University, Ithaca, New York.

JONGMAN, R.H.G., TER BRAAK, C.J.F. & VAN TONGEREN, O.F.R. 1987. *Data analysis in community and landscape ecology*. Pudoc, Wageningen.

KERFOOT, O. 1968. Mist precipitation on vegetation. *Forestry Abstracts* 29: 8–20.

KING, J.M. & DAY, J.A. 1979. Hydrology and hydrobiology. In J. Day, W.R. Siegfried, G.N. Louw & M.L. Jarman, *Fynbos ecology: a preliminary synthesis*. South African National Scientific Programmes Report No. 40: 27–42.

KÖPPEN, W. 1931. *Grundriß der Klimakunde*. De Gruyter, Berlin.

KRUGER, F.J. 1978. South African heathlands. In R.L. Specht, *Ecosystems of the World 9. Heathlands and related shrublands. B. Analytical studies*: 19–80. Elsevier, Amsterdam.

LAIDLER, D., MOLL, E.J., CAMPBELL, B.M. & GLYPHIS, J. 1978. Phytosociological studies on Table Mountain, South Africa. 2. The Front Table. *Journal of South African Botany* 44: 291–295.

LINDER, H.P. 1985. Conspectus of the African species of Restionaceae. *Bothalia* 15: 387–503.

LINDER, H.P. 1987. The evolutionary history of the Poales/Restionales—a hypothesis. *Kew Bulletin* 42: 297–318.

MARLOTH, R. 1903. Results of experiments on Table Mountain for ascertaining the amount of moisture deposited from the southeast clouds. *Transactions of the Royal Philosophical Society of South Africa* 14: 403–408.

MUCINA, L. 1993. Nomenklatorische und syntaxonomishe Definitionen, Konzepte und Methoden. In L. Mucina, G.

Grabherr & T. Ellmauer, *Die Pflanzengesellschaften Österreichs. Teil I. Anthropogene Vegetation:* 19–28. Gustav Fischer, Jena.

MUCINA, L., BREDENKAMP, G.J., HOARE, D.B. & MCDONALD, D.J. 2000. A national vegetation database for South Africa. *South African Journal of Science* 96: 497, 498.

NON-AFFILIATED SOIL ANALYSIS WORK COMMITTEE. 1990. *Handbook of standard soil testing methods for advisory purposes.* Soil Science Society of South Africa, Pretoria.

ØKLAND, R.H. 1996. Are ordination and constrained ordination alternative or complementary strategies in general studies? *Journal of Vegetation Science* 7: 289–292.

PRICE, E.A.C. & MARSHALL, C. 1999. Clonal plants and environmental heterogeneity. *Plant Ecology* 141: 3–7.

ROGERS, K.H. 1995. Riparian wetlands. In G.I. Cowan, *Wetlands of South Africa*: 41–52. Department of Environmental Affairs and Tourism, Pretoria.

ROGERS, K.H. 1997. Freshwater wetlands. In R.M. Cowling, D.M. Richardson & S.M. Pierce, *Vegetation of southern Africa*: 322–347. Cambridge University Press, Cambridge.

RUTHERFORD, M.C., POWRIE, L.W. & SCHULZE, R.E. 1999. Climate change in conservation areas of South Africa and its potential impact on floristic composition: a first assessment. *Diversity and Distribution* 5: 253–262.

SCHULZE, B.R. 1965. *Climate of South Africa. Part 8. General survey.* Government Printer, Pretoria.

SIEBEN, E.J.J. 2003. *The riparian vegetation of the Hottentots Holland Mountains, Western Cape, South Africa.* Ph.D. thesis, University of Stellenbosch.

SJÖRS, H. 1983. Mires of Sweden. In A.J.P. Gore, *Ecosystems of the World 4. Mires: swamp, bog, fen and moor. B. Regional studies*: 69–94. Elsevier, Amsterdam.

SOIL CLASSIFICATION WORKING GROUP 1991. *Grondklassifikasie. Een taksonomiese sisteem vir Suid-Afrika.* Department of Agriculture Affairs, Pretoria.

SOUKUPOVÁ, L. 1994. Allocation plasticity and modular structure in clonal graminoids in response to waterlogging. *Folia Geobotanica & Phytotaxonomica* 29: 227–236.

SPECHT, R.L. (ed.). 1981. *Ecosystems of the World 9. Heathlands and related shrublands. B. Analytical studies.* Elsevier, Amsterdam.

TAYLOR, H.C. 1978. Capensis. In M.J.A. Werger, *Biogeography and ecology of southern Africa*: 171–229. Junk, The Hague.

TER BRAAK, C.J.F. 1986. Canonical Correspondence Analysis: a new eigenvector technique for multivariate direct gradient analysis. *Ecology* 67: 1167–1179.

TER BRAAK, C.J.F. & ŠMILAUER, P. 1998. *CANOCO Reference Manual and User's Guide to Canoco for Windows. Software for Canonical Community Ordination (version 4).* Microcomputer Power , Ithaca, New York.

THOMPSON, K. & HAMILTON, A.C. 1983. Peatlands and swamps of the African continent. In A.J.P. Gore, *Ecosystems of the World 4. Mires: swamp, bog, fen and moor. B. Regional studies*: 331–373. Elsevier, Amsterdam.

VAN ZINDEREN BAKKER, E.M. & WERGER, M.J.A. 1974. Environment, vegetation and phytogeography of the high-altitude bogs of Lesotho. *Vegetatio* 29: 37–49.

WALKLEY, A. 1935. An examination of methods for determining organic carbon and nitrogen in soils. *Journal of Agricultural Science* 25: 598–609.

WEBER, H.E., THEURILLAT, J.-P. & MORAVEC, J. 2000. International Code of Phytosociological Nomenclature, edn 3. *Journal of Vegetation Science* 11: 739–768.

WEISSER, P. J. & HOWARD-WILLIAMS, C. 1982. The vegetation of the Wilderness Lakes system and the macrophyte encroachment problem. *Bontebok* 2: 19–40.

WESTHOFF, V. & VAN DER MAAREL, E. 1978. The Braun-Blanquet approach. In R.H. Whittaker, *Classification of plant communities*: 287–399. Junk, The Hague.

ZECHMEISTER, H. & MUCINA, L. 1994. Vegetation of European springs: high-rank syntaxa of the Montio-Cardaminetea. *Journal of Vegetation Science* 5: 385–399.

APPENDIX 1.—List of less frequent species having one or two occurrences in the relevé table. Sequence: name of species, the field code of the relevé(s) and cover-abundance (in brackets)

Agathosma pentachotoma 262 (2a)
Askidiosperma chartaceum 262 (2a)
Askidiosperma esterhuyseniae 164 (2b), 202 (+)
Berzelia lanuginosa 262 (+)
Blechnum tabulare 131 (+)
Bobartia gladiata 259 (+)
Chironia decumbens 262 (r)
Cliffortia graminea 165 (1)
Cliffortia ruscifolia 233 (2a)
Corymbium congestum 131 (1)
Corymbium cymosum 131 (+)
Dicranoloma billardieri 123 (2a)
Disa tripetaloides 123 (2m), 127 (2a)
Edmondia pinifolia 131 (+)
Ehrharta ramosa 259 (1)
Ehrharta setacea subsp. *uniflora* 111 (2m)
Epischoenus complanatus 131 (1), 201 (+)
Epischoenus gracilis 262 (2a)
Erica longifolia 262 (r)
Euchaetis glabra 201 (1)
Euryops abrotanifolius 232 (2m), 233 (1)
Felicia cymbalariae 111 (1)
Ficinia cf. *involuta* 259 (3)
Ficinia sp. 233 (1)
Fissidens plumosus 111 (2m)
Geissorhiza umbrosa 131 (+)
Helichrysum cymosum 233 (2a)
Hymenophyllum peltatum 131 (2m)
Hypochaeris radicata 259 (+)
Ischyrolepis triflora 262 (1)
Isolepis digitata 135 (2m)
Kogelbergia verticillata 127 (+)
Lobelia jasionoides 134 (+)
Lycopodiella caroliniana 123 (+)
Osmitopsis afra 241 (+)
Oxalis nidulans 202 (+)
Pentameris thuarii 233 (2b)
Pentaschistis pallida 135 (+)
Protea cynaroides 128 (+), 233 (r)
Psoralea aculeata 241 (2a)
Raspalia virgata 136 (2a)
Restio bifarius 131 (+)
Restio intermedius 128 (3)
Restio obscurus 262 (1)
Restio pedicellatus 259 (+), 262 (3)
Schizaea tenella 127 (1)
Senecio coleophyllus 134 (2a)
Senecio pubigerus 233 (1)
Senecio rigidus 131 (+)
Sonchus oleraceus 259 (+)
Staberoha cernua 234 (1)
Staberoha vaginata 124 (+), 189 (+)
Seriphium plumosum (juvenile) 188 (r)
Tetraria pillansii 201 (1), 259 (2a)
Tetraria thermalis 124 (r)
Todea barbara 111 (1), 259 (2a)
Ursinia dentata 233 (1), 241 (+)
Utricularia bisquamata 163 (+)
Villarsia capensis 163 (1), 164 (+)
Wahlenbergia procumbens 201 (1), 241 (2b)
Watsonia borbonica 241 (r).

APPENDIX 2.—Selected data on sampled vegetation properties and geographical location of two relevés in Du Toitskloof Mtns and relevés in Hottentots Holland Mtns. No., relevé number; Com., community; FC, field code; As., aspect; Sl., slope in degrees; Area, sampled area (m^2); CE2, cover of shrub layer (%); CE1, cover of herb layer (%); CE0, cover of moss layer (%); HE2, height of shrub layer (m); HE1, average height of herb layer (m); SR, species richness

No.	Com.	FC	As.	Sl.	Area	CE2	CE1	CE0	HE2	HE1	SR	Locality	Latitude	Longitude	Altitude	Date
1	A1	111	E	20	100	30	100	0	3.0-4.0	0.5–1.0	20	Hottentots Holland Mtns: Somerset Sneeukop, Eastern Slope	34°02'18"	18°59'18"	1365	1998/10/07
2	A1	233	E	32	100	80	80	0	2.0-3.0	0.1–0.5	20	Hottentots Holland Mtns: Somerset Sneeukop, Eastern Slope	34°02'05"	18°59'24"	1460	1999/05/01
3	A2	241	W	24	100	0	100	0		0.2–1.0	16	Hottentots Holland Mtns: top of Lourens River Catchment	34°00'56"	18°58'42"	1100	1999/05/12
4	A2	242	W	24	100	0	90	0		0.2–1.0	15	Hottentots Holland Mtns: top of Lourens River Catchment	34°00'56"	18°58'42"	1100	1999/05/12
5	A3	227	-	0	100	0	95	0		0.3–1.5	5	Hottentots Holland Mtns: Dwarsberg, Berg River Catchment	33°59'57"	19°00'54"	1200	1999/03/25
6	A3	228	-	0	100	0	100	0		0.3–1.0	3	Hottentots Holland Mtns: Dwarsberg, Berg River Catchment	33°59'57"	19°00'54"	1200	1999/03/25
7	A3	229	-	0	100	0	95	0		0.3–1.5	5	Hottentots Holland Mtns: Dwarsberg, Berg River Catchment	33°59'57"	19°00'54"	1200	1999/03/25
8	A3	230	-	0	100	0	100	0		0.3–1.0	5	Hottentots Holland Mtns: Dwarsberg, Berg River Catchment	33°59'57"	19°00'54"	1200	1999/03/25
9	A4	226	-	0	100	0	95	0		0.2–0.5	11	Hottentots Holland Mtns: Dwarsberg, Berg River Catchment	33°59'57"	19°00'54"	1200	1999/03/25
10	A4	231	-	0	100	0	90	0		0.3–0.6	9	Hottentots Holland Mtns: between Somerset Sneeukop and the Triplets	34°01'25"	18°59'02"	1370	1999/05/01
11	A4	232	-	0	100	0	90	0		0.3–0.6	10	Hottentots Holland Mtns: between Somerset Sneeukop and the Triplets	34°01'25"	18°59'02"	1370	1999/05/01
12	A4	243	-	0	100	0	90	0		0.2–0.5	11	Hottentots Holland Mtns: top of Eerste Waterval Catchment	34°00'57"	18°58'15"	1125	1999/05/12
13	A4	244	-	0	100	0	90	0		0.2–0.5	8	Hottentots Holland Mtns: top of Eerste Waterval Catchment	34°00'57"	18°58'15"	1125	1999/05/12
14	A4	259	NE	7	100	0	100	0		0.1–0.4	22	Du Toitskloof Mtns: Wit River Catchment	33°40'35"	19°05'36"	unknown	1999/11/02
15	A5	188	NE	6	100	0	100	0		0.1–0.4	12	Hottentots Holland Mtns: Landdroskop, Riviersonderend Catchment	34°02'50"	19°00'06"	1070	1999/02/17
16	A5	201	S	7	100	0	95	0		0.3–1.0	23	Hottentots Holland Mtns: Dwarsberg, Eerste River Catchment	34°00'24"	19°01'03"	1280	1999/03/07
17	A5	202	S	7	100	0	100	0		0.1–0.3	13	Hottentots Holland Mtns: Dwarsberg, Eerste River Catchment	34°00'24"	19°01'03"	1280	1999/03/07
18	A5	203	S	7	100	0	100	0		0.1–0.3	10	Hottentots Holland Mtns: Dwarsberg, Eerste River Catchment	34°00'24"	19°01'03"	1270	1999/03/07
19	B1	135		0	100	0	90	10		0.2–0.5	21	Hottentots Holland Mtns: Landdroskop, Western Slope	34°03'34"	18°59'05"	1180	1998/11/10
20	B1	136	W	10	100	0	100	5		0.5–1.0	22	Hottentots Holland Mtns: Landdroskop, Western Slope	34°03'34"	18°59'45"	1175	1998/11/10
21	B1	165	-	-	100	0	100	0		0.3–1.5	13	Hottentots Holland Mtns: Landdroskop, Western Slope	34°04'00"	19°00'21"	1170	1999/01/28
22	B1	131	SE	18	30	0	100	0		0.3–1.5	39	Hottentots Holland Mtns: top of Wesselsgat Catchment	34°03'36"	18°59'07"	1160	1998/11/10
23	B2	134	SE	40	20	0	80	0		0.2–1.0	18	Hottentots Holland Mtns: top of Wesselsgat Catchment	34°03'36"	18°59'07"	1145	1998/11/10
24	B3	124	E	12	30	0	100	0		0.2–0.8	33	Hottentots Holland Mtns: top of Palmiet River Catchment	34°03'35"	19°00'39"	1000	1998/11/09
25	B3	127	E	10	100	0	30	0		0.3–1.0	18	Hottentots Holland Mtns: top of Palmiet River Catchment	34°03'43"	19°00'50"	980	1998/11/09
26	B3	128	E	10	10	90	80	0	1.0-1.5	0.1–0.3	23	Hottentots Holland Mtns: top of Palmiet River Catchment	34°03'43"	19°00'50"	980	1998/11/09
27	B4	86	-	0	100	0	95	10		0.1–0.5	15	Hottentots Holland Mtns: around Landdroskop Hut	34°02'58"	19°00'18"	1075	1998/09/10
28	B4	87	-	0	100	0	95	5		0.1–0.5	12	Hottentots Holland Mtns: around Landdroskop Hut	34°02'58"	19°00'18"	1060	1998/09/10
29	B4	123	E	12	100	0	90	0		0.1–0.3	11	Hottentots Holland Mtns: around Landdroskop Hut	34°03'35"	19°00'39"	1000	1998/11/09
30	B4	129	-	0	100	0	95	0		0.2–0.5	17	Hottentots Holland Mtns: around Landdroskop Hut	34°02'56"	19°00'34"	1060	1998/11/10
31	B4	163	-	-	100	20	90	0	1.5-2.0	0.1–0.3	15	Hottentots Holland Mtns: around Landdroskop Hut	34°03'31"	19°00'15"	1075	1999/01/27
32	B4	164	-	-	100	0	100	0		0.3–1.2	17	Hottentots Holland Mtns: around Landdroskop Hut	34°03'31"	19°00'15"	1075	1999/01/27
33	B4	189	-	0	100	0	90	10		0.3–0.5	18	Hottentots Holland Mtns: around Landdroskop Hut	34°02'50"	19°00'06"	1075	1999/02/17
34	B4	234	-	0	100	0	100	0		0.2–1.2	14	Hottentots Holland Mtns: around Landdroskop Hut	34°02'56"	19°00'34"	1060	1999/05/01
35	B4	262	SW	5	100	0	100	0		0.5–1.0	19	Du Toitskloof Mtns: Wit River Catchment	33°41'08"	19°06'08"	unknown	1999/11/02