The high altitude flora and vegetation of the Cape Floristic Region, South Africa

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Although the rich flora of the south-western Cape Province, South Africa, has recently received much attention, the possibility of an altitudinal zonation, and in particular the presence of a distinct high-altitude flora and vegetation, has been ignored. Using the results of a survey of the flora and vegetation above 1 800 m in the Klein Swartberg, the highest mountain in the region, we show that there are differences in the vegetation structure and composition at high altitudes from that found on the middle and lower slopes. We also show that the floristic composition of the flora deviates from that of the Cape Floristic Region as a whole. Although most species found above 1 800 m are also found at lower altitudes, there is a set of species which is restricted to these high-altitude areas, and consequently it may be possible to regard this set of species as constituting a distinct high-altitude flora. However, there do not appear to be sharp altitudinal disjunctions, similar to those documented for the Central African mountains in the classical studies of Hedberg.

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Introduction

Despite the incredibly speciose flora of the south-western Cape Province (the Cape Flora, found in the Cape Floristic Region of Goldblatt 1978 and White 1983, the South African Kingdom – Cape Region of Good 1974, Cape Floristic Kingdom of Takhtajan 1986, Capensis of Taylor 1978), and the fact that the flora occurs in a mountainous region with an altitudinal range of 2 300 m, the effects of altitudinal zonation in this area have not yet been investigated. In fact, the two current classifications of the vegetation appear to depend more on rainfall and edaphic factors than on altitude (Moll et al. 1984; Moll & Bossi 1984; Campbell 1985; Cowling et al. 1988; Cowling & Holmes 1992), and do not comment on the effects of altitude on the flora or vegetation. This is despite the comments by Marloth (1902) that there is a distinct change in the spectrum of growth-forms of the typical fynbos plants above 1800 m. Although his data were very inadequate, he also suspected that there is a floristic change with increasing altitude, as he collected 14 new species on one of the high summits in one day. Taylor (1978) relied heavily on Marloth's observations, but was not able to add much new information on the distinctness of the upper mountain zone.

Hedberg (1951) developed a model of altitudinal zonation for the high mountains of central Africa. Simplistically, this model recognises a lower zone of evergreen forest, a middle belt of heath or ericoid forest or scrub forest, and an upper belt of a peculiar tropic-alpine vegetation. These zones are evident from both structural and floristic data. Linder (1990) showed that with increasing seasonality of the rainfall, the ericoid belt is transformed into a montane grassland. Grassland penetrates into the forest vegetation as well. Linder (1990) also attempted to equate the 'fynbos', the heathy macchia that dominates the vegetation on sandstone derived soils in the south-western and southern Cape Province, with the ericoid belt, showing that it interpenetrates the forest belt, and extends above the forest zone.

This lack of attention to the altitudinal zonation, and particularly the biology of the upper regions of the mountains, in the Cape Floristic Region may be due to several factors. The first must be the limited extent of the areas above 1800 m, and their inaccessibility. This is reflected by the small number of botanists that have collected above this altitude. The first was Dr Marloth, and the large number of new species he was able to collect on these summits is a good indication how poorly known these peaks were by the end of the last century. From 1920 to 1950 T. P. Stokoe, R. Primos and H. K. C. Andreae collected on various mountains, and in 1928

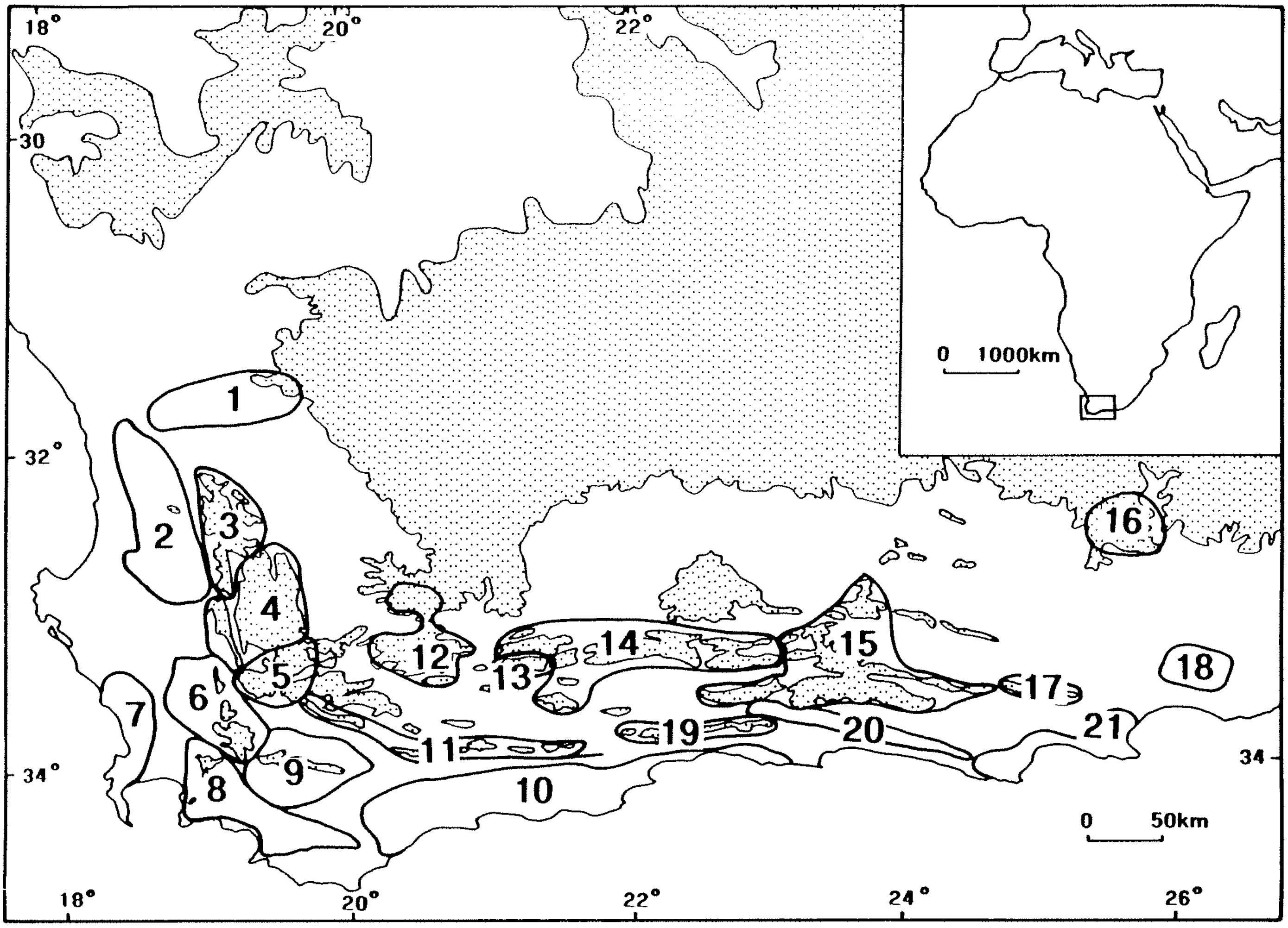


Fig. 1. Map of the south-western Cape Province, indicating the areas used for the analysis of the phytogeographical relationships of the Klein Swartberg flora. The 1000 m altitude contour is indicated.

they made the first high altitude collections in the cold and high mountains of the Klein Swartberg. From 1940 to 1990 many of the higher peaks were thoroughly explored by Elsie Esterhuysen, whose rich collections reflect the distribution ranges of most high-altitude species, and indeed many of the species were described and documented from her collections. The second factor must be that there is no dramatic change in the vegetation, equivalent to the tree-lines, vegetable hedgehog zones, ericoid scrub-forests or bamboo forests that are so typical of the zonation on other mountains (Hedberg 1951; Walter 1974). This striking lack of obvious zonation, and constancy in the vegetation and plant structure was commented on by Adamson (1958) and Linder et al. (1992). Marloth (1902) speculated that this may be due to the possibility that the heathy vegetation of the Cape Floristic Region was generally drought adapted, and consequently preadaptated to the alpine environment.

Consequently, no data are published on what happens to the floristic component of the vegetation above 1800 m. This paper describes the results of a first analysis of the flora and vegetation above 1800 m in this area, and presents some initial hypotheses on the phytogeography and ecology of this zone.

Physiography of the Cape Mountains

The southern and south-western Cape Province (Fig. 1), South Africa (more or less the area delimited as the 'Cape Floristic Region' by Goldblatt 1978) is the region which effectively lies between the southern margin of the 'Great Escarpment' (Partridge & Maud 1987) and the sea. This plain is traversed by the Cape Fold Mountains. These complexly folded mountains have two dominant directional trends. In the western sector the folds trend northwards, running parallel to the Atlantic coastline on the west side of southern Africa. This ridge abutts onto the Great Escarpment in the Nieuwoudtville area. The higher mountain blocks found in this megafold are the Cedarberg and Bokkeveld mountains in the north-west, the Hex River mountains at the inland syntaxis with the eastern set of megafolds, and the Du Toits Kloof mountains at the

Tab. 1. Temperature data for the Swartberg and Kammanassie mountains.

		Minimum		Maximum	
		Absolute	Mean	Absolute	Mean
Besemfontein	July	−3.5°C	−2.7°C	18.0°C	13.3°C
(1 920 m)	January	−1.0°C	3.4°C	34.0°C	29.2°C
Kammanassie	July	−8.0°C	−4.6°C	21.0°C	17.6°C
(1 500 m)	January	−2.0°C	1.6°C	41.0°C	32.1°C

south-eastern end of the northern megafold. Of these mountains, although there are many peaks in excess of 1800 m, only the Hex River mountains present a substantial area above this altitude, with the Matroosberg massif reaching 2249 m.

In the southern sector two distinct megafolds trend eastwards to Port Elizabeth, again running parallel to the coast. The coastal megafold forms the Langeberg, Outeniqua and Tsitsikamma mountains. These are very deeply dissected, and present no peaks above 1800 m. However, at the western end of this range is the Keeromsberg mountain, which has a large area above 1800 m, with the peaks rising to 2073 m. This is only a few kilometers from the Hex River mountains. The inland range is much taller than the coastal range, forming the Swartberg mountain and its outliers. In this block the Klein Swartberg mountain lies almost entirely above 1800 m, and also contains the highest peaks in the Cape fold belt, including Seweweekspoort peak at 2 325 m and six other peaks exceeding 2000 m.

These mountains were uplifted during the Cape orogeny, which occurred during the Permian and Triassic Periods (Deacon et al. 1992). They are built of sediments of the Cape Supergroup deposited during the Late Ordovician and the Carboniferous Periods. These sediments consist of medium to coarse sands, with thinner interpolated layers of shales (Campbell 1983). Since the original uplift, which probably ceased more than 200 my ago, the mountains have been substantially eroded, leaving only the hard quartzitic layers. Consequently, many of the highest peaks, such as the upper ridge of the Klein Swartberg, are orthoquartzitic sandstones of the Nardouw Subgroup (SACS 1980), and form rugged ridges and peaks (Fig. 3A, B). Where shale lenses or bands occur, domed peaks are formed (such as Victoria Peak), but these are absent from the Klein Swartberg and are generally rare. This long history has resulted in deeply dissected, rugged mountains with very steep slopes and extensive boulder fields (Campbell 1983) (Fig. 3B, D).

The quartzitic bedrock of the mountains has resulted in thin, highly leached lithosols, which are deficient in nutrients (Deacon et al. 1992), and in particular in phosphates and bases (Campbell 1983; Stock & Allsopp 1992). This is in sharp contrast to the intermontane valleys, which have soils derived from shales, mudstones and tillites, and although still nutrient deficient, are much less so than the lithosols on the mountains.

Climate of the south-western Cape Province

The south-western and southern Cape Province has a mediterranean type climate, but the true winter-rainfall area is restricted to the north-western corner of the area, around the Cedarberg (Cs in the Koeppen system, Campbell 1983). Further east an increasing quantity of the rain falls in the summer months, and would be classified as Bsk (Campbell 1983). In the north-west the summers are dry, with 80% of the rain falling in the three winter months, while in the east only 35% falls in the winter, with some areas effectively having all-year-round rainfall. Along the plains the precipitation ranges from 250 to 1000 mm per annum, while the mountains may receive up to 2.5 m of rain. Rainfall gradients can vary from 400 mm to over 2000 mm over a few kilometers (Fuggle & Ashton 1979; Campbell & Werger 1988).

The mountains often have a cloud cover in summer, resulting in condensation (Marloth 1904; Schulze & McGee 1978) and in transpiration reduction, thus ameliorating the effects of the summer drought. However, no data are available on the frequency of the cloud cover on the inland, more isolated, and higher mountains.

There are some rainfall data available for the southern Cape Province mountains, and these suggest that the highest rainfall may be on the middle slopes, at ca. 1600 m (Swartberg Pass, at 1600 m, has a mean annual rainfall of 1011 mm for 1980 to 1990) while the rainfall appears to be lower at higher altitudes (Blesberg peak received a mean annual rainfall of 563 mm p.a. for 1984 to 1989, at 2030 m; and Besemfontein in the Klein Swartberg, at 1920 m, only 292 mm p.a. between 1980 and 1990). Personal observation by one of the authors (J.H. Vlok) suggests that the higher peaks often emerge above the rain-bearing clouds, indicating that the higher-altitude areas may be substantially drier than the mid-slopes.

The effects of local topographic variation on rainfall cannot be completely discounted. The Swartberg Pass station, which received by far the highest rainfall, is on a windy col, while the Besemfontein station is on a north-facing slope and the Blesberg station is on a mountain summit. However, more data are needed to understand the patterns of variation in the rainfall, and to disentangle the effects of local topography and altitude. It is clear that the situation may not be as simple as suggested by Fuggle & Ashton (1979).

The mean annual temperature across the whole south-western Cape Province is about 17°C, but the range varies from less than 8°C at the coast to more than 14°C along the inland margins of the area. The temperature lapse rate for these mountains is not known. Fuggle & Ashton (1979) suggest a figure of 0.55°C per 100 m, while Scharf has documented 0.6°C for the Great Winterhoek mountains (Cowling 1984). There are limited temperature data available for the middle altitudes (Tab. 1). The temperature data were collected weekly, not daily,

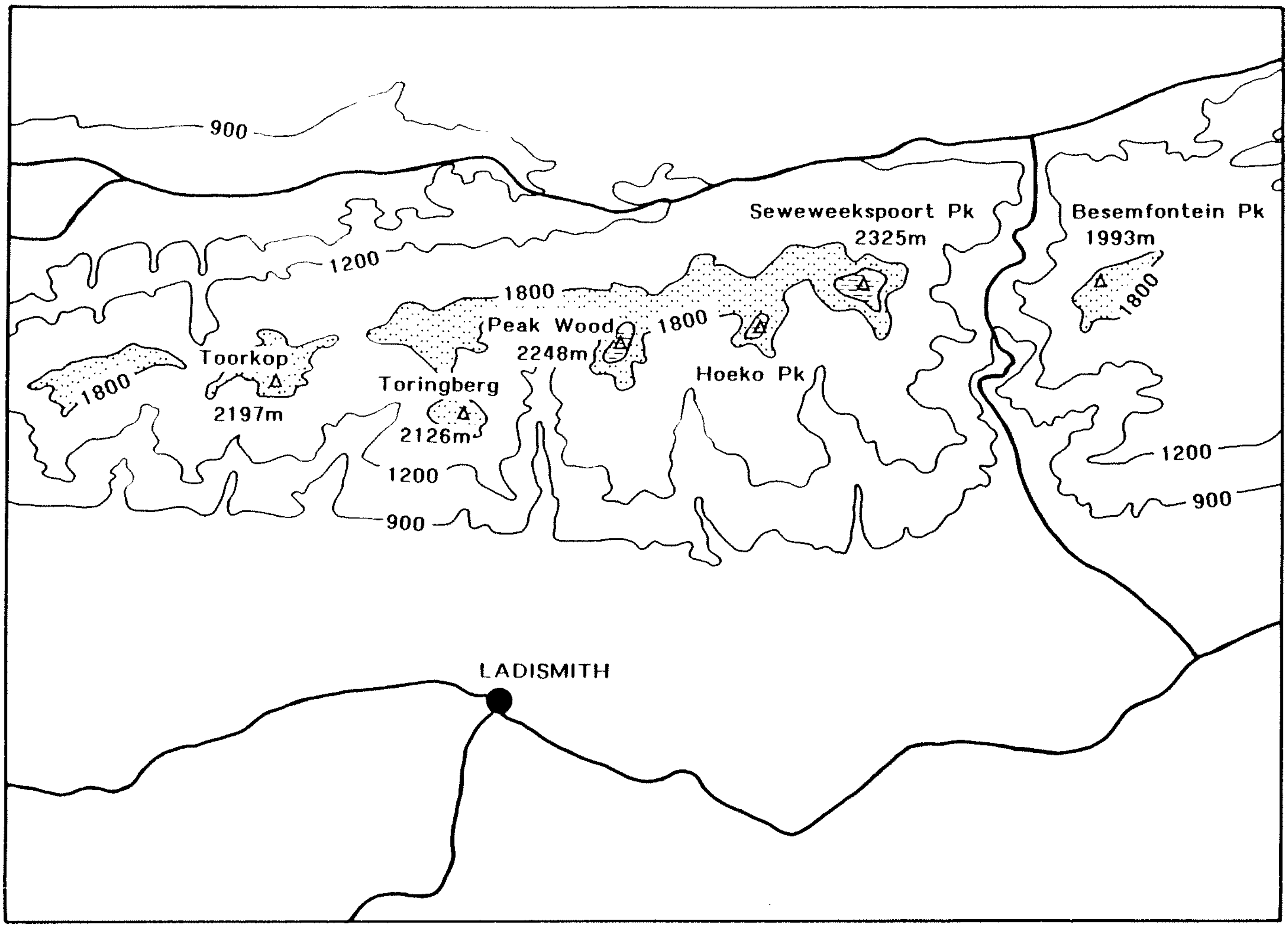


Fig. 2. Detailed map of the Klein Swartberg and surrounding features, indicating the names of the peaks along the range. Alternative names are Towerkop for Toorkop, Elandsberg for Toringberg and Steenslang Peak for Hoeko Peak. The highest contour line is 2000 m.

and results for a ten-year period are available. These results suggest that the temperatures are often below freezing, but also that the variation can be extreme. For example, at the Besemfontein station, both the absolute minimum (-7.5°C) and the maximum (35.0°C) occurred in September 1987.

The frequency of snow in the mountains of the south-western Cape is about 5.4 snow-falls per year, of which 3.2 occur between June to August (Schulze & McGee 1978). No direct observations for the higher peaks are available.

During the Pleistocene the glacials were probably ca. 5°C cooler in the south-western Cape than the interglacials (Deacon et al. 1992), but even under the coldest conditions of the Pleistocene the higher peaks still lay below the permanent snow line (Deacon et al. 1992), and there is no evidence of glaciation. However, extensive boulder screes below cliffs, and at times quite a distance from the nearest cliffs, have been interpreted as the result of the freezing and thawing cycle that would indicate conditions colder than at present (Deacon & Lancaster 1988).

Vegetation

The vegetation on the mountains of the Cape is essentially heathy, and is associated with soils derived from quartzites, which are nutrient poor, sandy, shallow and acidic (mean pH of 4.0, Campbell & Werger 1988). This vegetation formation appears to be more a consequence of edaphic factors than of climatic determinants, and although some earlier systems used to recognise Montane and Coastal Fynbos (Kruger 1979), as well as various variants of Coastal Fynbos (Taylor 1978; Kruger 1979; Moll et al. 1984), Cowling et al. (1988) and Rebelo et al. (1991) have shown the two types to be structurally and floristically similar and best referred to in the general term of fynbos.

According to Taylor (1978) three vegetation strata can be recognised:

a. An upper, 2–3 m tall, proteoid layer with medium to large coriaceous leaves. This is restricted to the lower and middle slopes, and seldom reaches above 1500 m.

Tab. 2. Braun-Blanquet (B-B) table of the plant communities at high altitude on the Klein Swartberg. The cover-abundance values are: R = rare; + = sparse, cover low; 1 = cover <5%; M = cover 5%, abundance high; A = cover 5–12%; B = 12–25%; 3 = cover 25–50%; 4 = cover 50–75%; 5 = cover 75–100%; O = within 1.5 m outside the plot boundary.

Releve number	2	7	6	1	4	5	8	3
Soil depth in		3		0	2	1	2	2
cm		0	5	5	0	0	5	0
Rock cover %	2	?	9	6	4	6		
	0		8	5	0	5	5	3
Vegetation	8	?	0	3	5	3	8	8
cover %	0	?	2	5	5	5	5	5
Number of	0	0	2	2	2	2	1	1
species	8	9	0	2	9	3	7	4
A. Acmadenia teretifolia shrubland								
Acmadenia teretifolia	4	2		0				
Restio papyraceus	3							
Erica esteriana var. *swartbergensis*	+							
Erica nubigena	+							
Restio sejunctus	+							
Senecio sp.	+							
Erica vlokii	R							
B. Bryomorphe lycopodioides herbland								
Bryomorphe lycopodioides			+					
Castalis sp.			+					
Pentaschistis eriostoma			+					
Species common to communities A and B								
Pentaschistis densifolia		+	+					
Pentaschistis rigidissima		+	+					
Ornithogalum sp.		R	+					
C. Erica toringbergensis shrubland								
Erica toringbergensis				+	A	O		
Elegia filacea					A	+		
Erica humifusa					R	R		
Thesium cf. *carinatum*				+	R	R		
Erica esterhuyseniae				+	A			
Erica strigifolia				A		R		
Pentaschistis pungens					+	+		
Cyclopia aurescens					1			
Spatalla confusa					A			
Staberoha aemula					A			
Erica ostiaria					1			
Senecio hastatus					R			
Diosma sp.				R				
Erica oresigena var. *mollipila*				R				
Ficinia sp.						R		
Gladiolus caryophyllaceus						R		
Theilera guthriei						R		
Lightfootia fasciculata					R			
Muraltia cf. *meyeri*					R			
Centella affinis var. *richardiana*					R			
Lobelia sp.					R			
Argyrolobium sp.					R			
Chenopodium sp.					R			
D. Ischyrolepis distracta restioland								
Ischyrolepis distracta							4	
Pentaschistis pyrophila							1	
Dianthus laingsburgensis							R	
Helichrysum zwartbergensis							R	
Species common to communities B, C and D								
Tetraria crassa				R	R	R	+	
Felicia filifolia ssp. *bodkinii*			+	+	R	+		
Cliffortia setifolia			+			1	A	
Cannomois nitida				1		+	A	
Cliffortia crassinervis			+	A		1		
Stoebe plumosa			+	1				
Pentameris distichyophylla			+	1				
Passerina comosa			+			+		
Pentaschistis malouinensis			+			+		
Helichrysum sp.					R		+	
Ursinia sericea					R		+	
Species common to communities A, B, C and D								
Selago ramulosa		R	+	R	R		R	
Ischyrolepis schoenoides		5		+	1	1		
Watsonia marlothii		R		A		M		
Athanasia pachycephala		+	+		R		O	
Ruschia stenophylla		+	+	R				
Ficinia nigrescens	R		+	R				
E. Willdenowia stokoei restioland								
Willdenowia stokoei								3
Anthospermum spathulatum ssp. *spathulatum*			+					2
Lachnaea penicillata								+
Cullumia bisulca								R
Thamnochortus petrophylla								R
Species common to communities B, C, D and E								
Ischyrolepis laniger			B	B	+	1	2	4
Cliffortia eriocephalina			+		+	+	+	+
Anomalanthus scoparius				+	1	1		+
Thamnochortus papyraceus				1		B	O	O
Pentameris macrocalycina				+		1		A
Rhodocoma alpina						1	+	A
Protea scolopendrifolia					1		1	+
Rafnia cf. *retroflexa* (swartbergensis)					R			R

b.
A middle layer of ericoids and composites, generally with leptophyllous leaves.

c. A lower layer of Restionaceae. This is often difficult to distinguish from the middle layer, and the two layers are often completely integrated.

Trees and annuals are largely absent from this vegetation.

Campbell (1985) used this structural variation to construct a classification system, which recognises four major structural types in fynbos: Asteraceous Fynbos on drier, lower slopes, Grassy Fynbos at the eastern end of the distribution of the fynbos, Restioid Fynbos where environmental conditions prevent the development of taller vegetation and Proteoid fynbos where conditions allow the development of taller proteoid vegetation. Although there is some congruency between a floristic and a structural classification, much of the subtlety of a floristic classification may be lost in this system. However, it does give a broad framework with which to interpret the variation in fynbos.

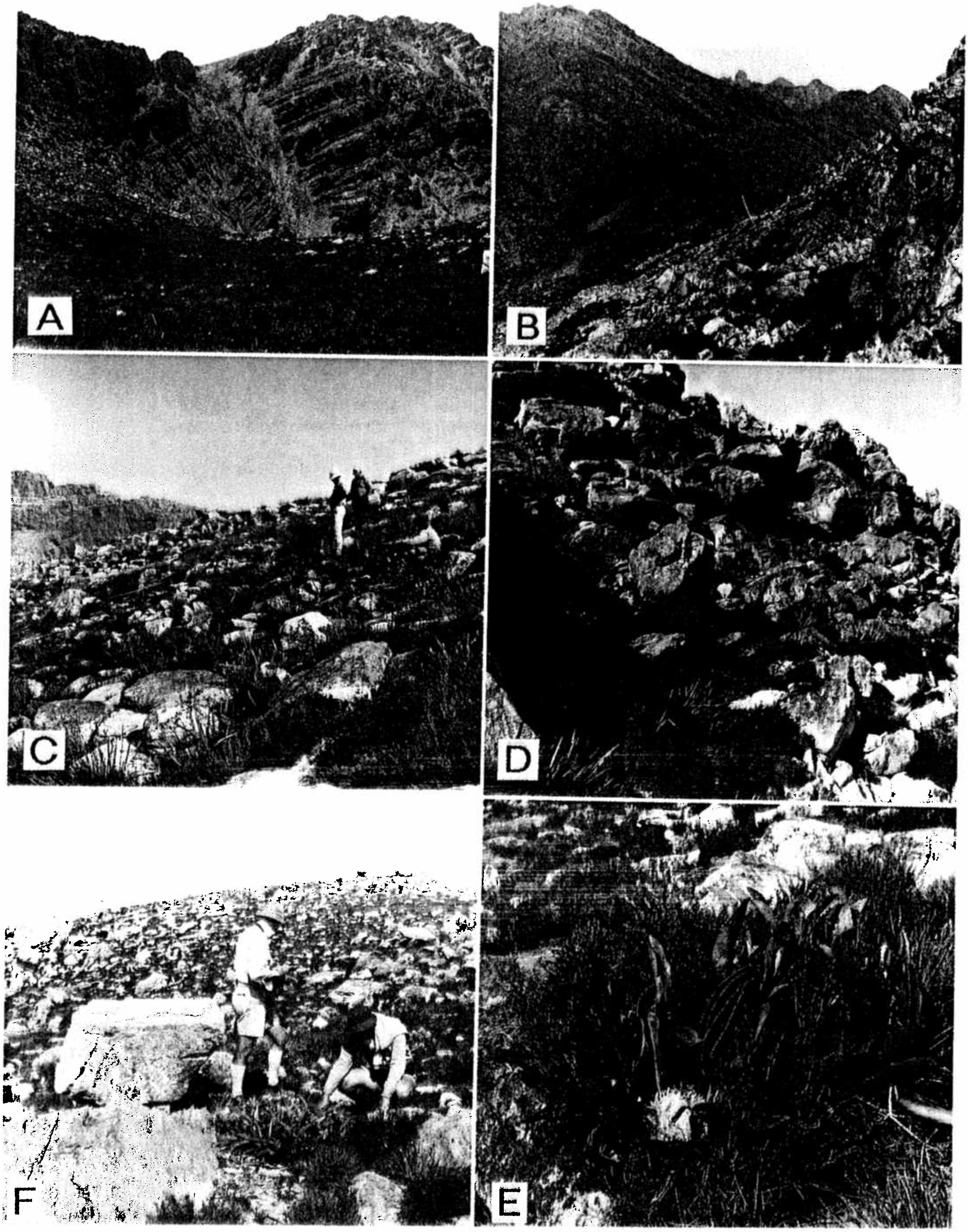


Fig. 3. Eastern end of the Klein Swartberg, at ca. 2000 m. – A. View towards Seweweekspoort peak, showing the steep south-facing cliffs, and the *Willdenowia stokoei* restioland in the foreground. – B. View northwards, past Hoeko peak, with Toorkop in the distance, showing boulder screes, with the *Acmadenia teretifolia* shrubland in the foreground. – C. *Erica toringbergensis* shrubland on a rocky slope. – D. Boulder scree with *Acmadenia teretifolia* shrubland. – E. *Protea pruinosa* in the *Erica toringbergensis* shrubland. – F. *Protea pruinosa* showing decumbend habit and a large inflorescence, growing in a tussock of *Ischyrolepis distracta* (Restionaceae)

Klein Swartberg high-altitude fynbos

The phytosociological variation in the vegetation is described both from informal observations during a traverse along the ridge to Toorkop, and from seven formal Braun-Blanquet type relevés of 5 × 10 m and one informal 'plot list' made at the eastern end of the Klein Swartberg range (Fig. 2). Attributes of the vegetation assessed include percentage litter cover, standing vegetation cover, disturbances and vegetation maturity. Definitions used are the same as those used by Boucher (1987) and McDonald (1988). The number of species found in each relevé was noted, and any species occurring within 1.5 m surroundings of the plot boundary were recorded. Structural terms used are based on Campbell et al. (1981). The dimensions of "average" plants of each species found in the sampling sites were recorded in an attempt to convey the overall appearance of the vegetation. Environmental factors including land facets, altitude, aspect, slope, geology, soil forms, substrate type, soil depth (mean of four sites in each relevé), rock cover and moisture regime were assessed and recorded. The relevés were ordinated using detrended correspondence analysis (DCA) (Hill 1979) to examine which environmental factors accounted for most of the observed variation between the communities.

The five vegetation communities which were identified from the formal releves, their characteristics and species compositions are summarised in Tab. 2.

A. Acmadenia teretifolia shrubland

The *Acmadenia teretifolia* shrubland is characteristic of the cooler, moister south-facing slopes where it forms dense stands in between boulders and on rock ledges where deeper soil has accumulated (Fig. 3B, D). This community has the lowest number of species recorded in the survey. Crustose lichens cover 80% of the exposed rocks. Structurally this community is a low closed restioid shrubland which has a single stratum 1.00 m tall. It is dominated by the leptophyllous, evergreen woody shrub *Acmadenia teretifolia* and the leafless tussock-forming hemicryptophytes *Ischyrolepis schoenoides* and the endemic *Restio papyraceus*. This is the tallest community encountered at this altitude probably because the large boulders offer protection from strong winds and support when covered with snow. A form of this community is conspicuous among the rocks and boulders around the summit zone of the Seweweekspoort peak, but here *I. schoenoides* is totally dominant. The dicotyledonous shrubby element is more prominent in the community at lower altitudes, between 1800 and 2000 m.

B. Bryomorphe lycopodioides herbland

The north-facing *Bryomorphe lycopodioides* community is found where rock cover is 98%. Plants occur in shallow soil between the rocks. The habitat is the most arid of those encountered, and this is reflected by nature of the vegetation. This sparse restioland is dominated by the 0.30 m tall tussock-forming hemicryptophyte, *Ischyrolepis laniger*. Lichens cover 75% of the rocks. Some of the rocksheets facing north have dense stands of the widespread grass *Pentaschistis eriostoma*, which generally grows in crevices and on small ledges. Due to the general orientation of the strata, the ridge forms sloping rocksheets to the north where this community is found, and ledges and cliffs to the south, where the *Acmadenia teretifolia* shrubland is found.

C. Erica toringbergensis shrubland

This low open to mid-dense restioid shrubland is dominated by the following species: *Cliffortia crassinervis, Elegia filacea, Erica esterhuysenìae, E. toringbergensis, E. strigilifolia, Ischyrolepis laniger, Spatalla confusa, Staberoha aemula, Thamnochortus papyraceus* and *Watsonia marlothii*. Two strata generally occur in which the upper stratum (0.2–0.50 m) is dominated by leptophyllous ericoid-leaved shrubs and the lower stratum (0–0.20 m) by tussock-forming leafless hemicryptophytes, interspersed with ericoid-leaved shrubs (Fig. 3C, F). The *Erica toringbergensis* community is the richest sampled. It is also reminiscent of communities expected at lower altitudes on coarse sand amongst sandstone rocks. It is frequent along the ridge, occurring wherever there are gravelly or stony slopes, without too much boulder cover. The species composition of this community appears to vary somewhat along the ridge.

D. Ischyrolepis distracta restioland

The flatter basal convexo-concave slopes support the *Ischryolepis distracta* restioland. Both this community and the *Willdenowia stokoei* community are dominated by dense tussocks of Restionaceae and an intermediate number of species was recorded in these communities during the survey. This community was recorded on a north-western aspect, on sandy soil, with a perched water table. This low closed restioland (0.45 m) is dominated by leafless tussock-forming hemicryptophytes such as *Cannomois nitida, Ischyrolepis distracta* and *I. laniger* and leptophyllous shrubs such as *Cliffortia setifolia*. The exposed environment without rock protection and relatively deep soil is probably the reason that low wiry restioids are dominant in this community and in the next (the *Willdenowia stokoei* restioland). This is a relatively rare community along the ridge.

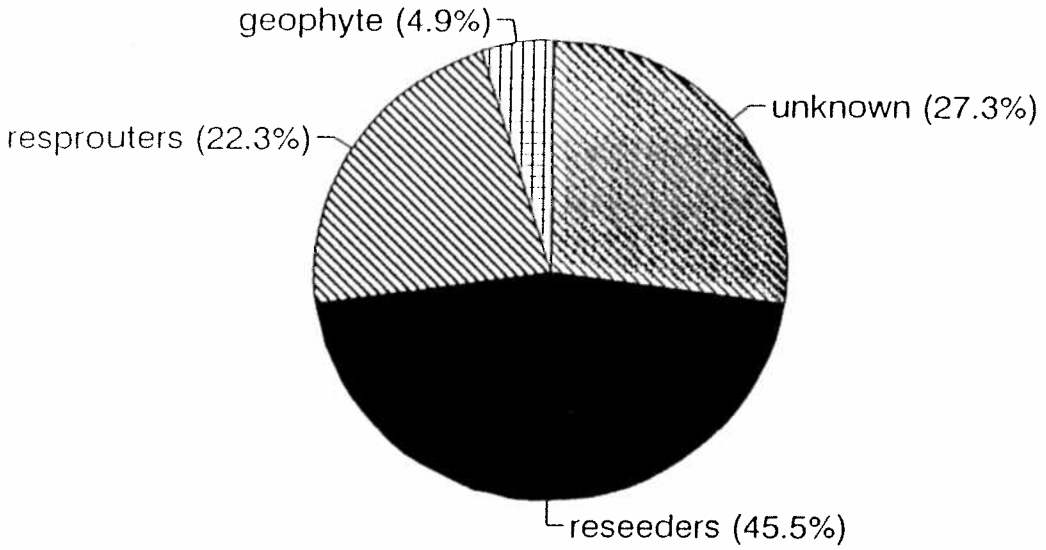


Fig. 4. Pie diagram showing the percentages of the different fire-survival mechanisms in the high-altitude flora of the Klein Swartberg. Of the species of which the fire-survival mechanisms are known, some 67 reseed after fire.

E. Willdenowia stokoei restioland

The *Willdenowia stokoei* restioland occurs on east-facing detrital or upper pediment slopes (Fig. 3A). The community is a low closed restioland and is dominated by 0.40 m tall tussock-forming species which include the following: *Anthospermum spathulatum*, *Ischyrolepis laniger*, *Pentameris macrocalycina*, *Rhodocoma alpina* and *Willdenowia stokoei*.

F. Pentameris swartbergensis grassland

This community was not sampled, but occurs sporadically along the ridge where it is restricted to gullies in the steep south-facing cliffs which are generally cool, damp habitats and receive little sun. They would presumably retain snow cover for the longest period. Typical species of this community are *Pentameris swartbergensis*, *P. glacialis* and *Ehrharta rupestris*.

Discussion of the vegetation

Rockiness or rock cover appears to be the major determinant of the variation in the vegetation, as the DCA Axis I, which represents rockiness or rock cover, accounts for 91% of the variation in the data set. This is not surprising, as there are no seepages, streambanks, or great altitudinal variation within the area studied. This lack of environmental variation in factors other than rockiness may be a general feature of the zone above 1800 m in the Cape Mountains, due to the steep topography, which leads to rapid run-off, and the absence of deeply formed valleys or permanent water.

Marloth (1902) recorded alpine growth forms from about 1800 m on the Groot and Klein Winterhoek Ranges, on the Matroosberg, Hex River Range and on the Swartberg Range and characterized alpine vegetation by the absence of trees, tall shrubs and high herbaceous plants. Many shrubs produce no central stems but a large number of very short stems packed closely together to form an almost solid cushion, whereas others have rosettes of leaves close to the ground. Almost all have large root systems. Marloth also mentioned that the typical hairy or leathery leaves are for protection against heat, not cold, i.e. to protect them against loss of too much water during dry periods. No critical comparative study of the plant growth-forms has yet been undertaken to test Marloth's statements on plant form, although casual observations and comments in various taxonomic studies (Rourke 1969; Williams 1982) tend to confirm his observations.

Comparison of high-altitude and montane fynbos

This vegetation type would probably be classified under Campbell's (1985) Azonal Restioid Fynbos, in particular his Trident Azonal Restioid Fynbos and Langberg Azonal Restioid Fynbos. This structural type occurs wherever conditions prevent the development of taller dicotyledon-dominated vegetation. These conditions include both the climatic effects of high altitudes, and water-logging conditions. The only differential between these two types of conditions is in the species composition, with *Ischyrolepis laniger* and *Cannomois nitida* being characteristic of the climatically controlled types, and *Anthochortus crinalis* and *A. ecklonii* dominating the edaphically controlled types. No communities floristically equivalent to those described here are known from the southern Langeberg. This is probably because the latter range is not as high and there is an ameliorating coastal influence. However, similar communities have been observed on the Keeromsberg (2073 m) at the north western end of the Langeberg range, on the Hex River mountains, as well as other peaks exceeding 1800 m.

Tab. 3. Numbers of species and genera per family for the Klein Swartberg high-altitude flora, and the relative importance of each family.

Rank in Cape flora[1]	Families	Genera: Number	Species: Number	Percent	Cumulative
2	Ericaceae	3	29	23.2	
8	Restionaceae	9	16	12.8	36.0
1	Asteraceae	11	15	12.0	48.0
14	Poaceae	5	13	10.4	58.4
5	Fabaceae	4	7	5.6	64.0
7	Proteaceae	3	5	4.0	68.0
4	Iridaceae	4	4	3.2	71.2
9	Rutaceae	3	4	3.2	74.4
20	Rosaceae	1	4	3.2	77.6
13	Scrophulariaceae	3	4	3.2	80.8
10	Campanulaceae	3	3	2.4	83.2
	Thymelaeaceae	2	2	1.6	84.8
	Rhamnaceae	1	2	1.6	86.4
3	Mesembryanthemaceae	2	2	1.6	88.0
	Caryophyllaceae	1	2	1.6	89.6
	Apiaceae	2	2	1.6	91.2
	Cyperaceae	2	2	1.6	92.8
	Rubiaceae	1	1	0.8	93.6
	Santalaceae	1	1	0.8	94.4
	Brassicaceae	1	1	0.8	95.2
	Dipsacaceae	1	1	0.8	96.0
	Gentianaceae	1	1	0.8	96.8
	Geraniaceae	1	1	0.8	97.6
	Orchidaceae	1	1	0.8	98.4
	Polygalaceae	1	1	0.8	99.2
6	Liliaceae	1	1	0.8	100.0
Totals:	27	67	123		

1. From Goldblatt (1978).

High-altitude plant biology

The main flowering season at high altitudes seems to be much later than at lower altitudes, and some 80% of the species were in flower in February, compared to the main flowering season at the coast, which is in August-September. Some species, like *Erica nervata*, flower in November. However, precise phenological data are not yet available, and it is not clear how long the various species stay in flower. The length of the flowering season would obviously effect the pollinator spectrum. This would be fruitful area for further research.

A profound environmental factor in the Cape Floristic Region is fire, so that the fynbos can be described as pyrophytic. Generally, the frequency of the fires varies from five to 50 years (van Wilgen 1987), and fires can have dramatic effects on the structure and composition of the vegetation (van Wilgen 1981). Generally, perennial plants have three broad strategies for surviving fires: they may be killed by the fire, and rely on reseeding themselves into the habitat (reseeders), they may have special organs or structures that allow the plants to survive fires (resprouters, although many other mechanisms may be used), or they are generally dormant underground during the fire season (usually geophytes). The ratio of reseeders to resprouters may be informative on the fire frequency, intensity and predictability (Le Maitre & Midgley 1992). However, there are several competing theories, and it is not clear which one is correct. Nonetheless, we collected data on the fire-survival mode of the plants in the high-altitude zone of the Klein Swartberg (Fig. 4). This shows that there are about twice as many species which reseed after fire, than species which survive fire: of the species for which data are available, some 67% are killed by fire, and re-establish from seed. Data collected by one of the authors (J. H. Vlok) suggests that for the southern Cape mountains as a whole 56% of the species are killed by fire, indicating that the high-altitude region may have relatively more species which re-establish from seed after fire.

The high-altitude areas, with their shorter, more open vegetation, and rockier, more dissected terrain, probably have less frequent and less intense fires than are found on the lower mountain slopes. In addition, the summit regions are much more rocky, thus increasing the possibility that small patches of vegetation may survive wildfires. This decreased fire-intensity and frequency may result in the greater dominance of reseeders. This may also contribute to the enormous effect which rockiness has on the different vegetation types.

Phytogeography

The general phytogeographical patterns in the Cape Floristic Region were analysed by Weimarck (1941), Oliver et al. (1983) and Cowling et al. (1992). The influence of the high-altitude areas in these studies is lost in the large numbers of mid- or low-altitude species. Several centres and gross patterns of species richness in the Cape Floristic Region are recognised. The only study that investigated the possible effects on species richness is by Linder (1991), but this also used a 1/16 degree scale which is too coarse to detect the unmitigated effect of high altitudes, which generally occupy smaller areas.

Analysis of the Klein Swartberg flora

A checklist of the species above 1800 m on the Klein Swartberg was compiled during a field-trip in February, 1992. This list was further extended from records in various herbaria and from published revisions. The larger families (Ericaceae, Fabaceae, Restionaceae, Proteaceae and Poaceae) were all checked by specialists, but many of the smaller families may still be problematic. In many cases, particularly in the Ericaceae, there are taxonomic problems, which would effect the details of the list, and ephemeral geophytes could have been missed. The distributions of the Klein Swartberg species were plotted from herbarium material held in the Bolus Herbarium. As the higher peaks in the Cape Floristic Region have been extensively collected by Elsie Esterhuysen, whose collections are held in the Bolus Herbarium, this record is probably fairly complete. In fact, the Klein Swartberg is probably the poorest collected high altitude range in the Cape Floristic Region. The distributions were checked against published information, and for the Ericaceae against the lists of herbarium specimens produced by one of the authors (E. G. H. Oliver).

Analysis of the composition of the flora

A total of 123 species in 67 genera and 27 families have been recorded. Of the 27 families, only ten have more than three species, and these ten families contain 80.8% of all the species recorded (Tab. 3).

When the rank sequence of the families is compared to the ten most speciose families in the Cape Floristic Region as a whole (Goldblatt 1978, Tab. 3), some interesting differences emerge. Mesembryanthemaceae and Liliaceae are very under-represented in the Klein Swartberg high-altitude belt. Both these families are most diverse in the arid areas of the Cape, and so this is not surprising. Their places are taken by the Poaceae (from 14th to 4th position) and the Rosaceae (20th to 9th position). Within the ten most speciose families, the Asteraceae and Iridaceae have lost position relative to the Restionaceae and Proteaceae. The Asteraceae are possibly more diverse in the arid areas. The increased floristic importance of the Restionaceae and particularly the Poaceae is consistent with an increase in cover of Restionaceae and Poaceae with the Azonal Restioid Fynbos typical of the exposed summits of the mountains (Campbell 1985).

Distribution patterns of the flora

No distinct patterns could be detected, and distributions range from bipolar (*Deschampsia flexuosa*) to palaeotemperate (*Scabiosa columbaria*) to endemic to the Klein Swartberg. Genetic elements, as detected by Hedberg (1965) for the Afro-alpine flora, cannot be recognised so readily for this high-altitude flora. There appears to be no distinctive break in the distribution ranges: no two species have identical ranges, and there are no repetitive groups of distributions. Some species are endemic to the Klein Swartberg, others occur on nearby mountains (e.g. Great Swartberg), yet others are found on the Great Swartberg and the Kammanassie mountains, while others reach the Kouga mountains, etc. Nonetheless, to simplify the discussion we recognised the categories 'extra-Cape Floristic Region linking species', 'endemic species' and 'Cape Floristic Region species'. The latter category is the most common, and is discussed in the context of altitudinal zonation.

Extra-Cape Floristic Region linking species

There are only six species in this group, and several of them only reach to the Drakensberg. *Scabiosa columbaria* and *Deschampsia flexuosa* are peculiar for their vast distribution ranges. However, while *S. columbaria* is widespread within the Cape Floristic Region, and not restricted to the high-altitude regions, *D. flexuosa* is, in southern Africa, only found on the Klein Swartberg, and shows a remarkable disjunction between the East African volcanoes and the Klein Swartberg. Although Gibbs Russell et al. (1990) suggested that it may be introduced, this appears most unlikely, considering that in southern Africa it is only known from its very remote station on the summit ridge of the Klein Swartberg.

A number of species reach the Drakensberg, and associated high-lying land to the west of the Drakensberg. These would include *Senecio hastulatus*, *Homeria cookii*, *Restio sejunctus* and *Ischyrolepis schoenoides*. However, very few species are common to the mountains north of the Limpopo River. It is curious that there is not a greater floristic similarity to the Great Escarpment north of Graaff-Reinet, as these mountains exceed 2400 m. However, they are much drier, and seem to have more in common with the dry south-western margins of the Drakensberg than with the wetter quartzitic mountains of the Cape Fold ranges.

Tab. 4. Endemic and near endemic species on the Klein Swartberg (O. is an abbrevation for Oliver).

Species	KS	GS	Notes
Aspalathus patens	*	*	Kammanassie
Cliffortia crassinervis	*		
C. setifolia	*		
C. sp. nov. (O. 10019)	*		
Cromidon cf. *decumbens*	*		
Cyclopia aurescens	*		
Erica costatisepala	*	*	
E. gossypioides	*	*	
E. toringbergensis	*		
E. esteriana ssp. *swartbergensis*	*	*	
E. inamoena	*		
E. sp. nov. (O. 10000)	*		
Euryops glutinosa	*		
Holothrix pilosa aff.	*		
Heliophila rimicola	*		Rooiberg
Leucadendron dregei	*	*	
Pentameris glacialis	*		
P. swartbergensis	*	*	
Phylica costata	*	*	
P. stokoei	*		
Protea montana	*	*	Kammanassie
P. pruinosa	*	*	
Restio papyraceus	*		
Thamnochortus papyraceus	*	*	

Endemic species

Thirteen of the 123 species (10%) recorded from the Klein Swartberg above 1 800 m are endemic to the Klein Swartberg. The list of endemics would increase to 20% if species the from Great Swartberg and the Blesberg were to be included in the area (Tab. 4). However, other species reach the Rooiberg, or Touwsberg, or Laingsburg Witteberg, and it would make little sense enlarging the area used for determining endemism.

Of more interest is the distribution of endemics among the families. The frequency of endemics may be predicted to reflect the proportion of all the species found in each family (Tab. 5), and from this it is evident that some families have more than the expected number of endemics. These include the Ericaceae and the Rosaceae. The Rosaceae is expected to contribute three percent of all endemics, but actually contributes 27%! This is due to the three endemic species of *Cliffortia*. Fabaceae and Restionaceae contribute about as many endemics as would be expected, but the Asteraceae and Proteaceae contribute fewer. The Proteaceae present an interesting case, where three of the five species on the Klein Swartberg are restricted to the Klein Swartberg and the Great Swartberg, or some of the other surrounding mountains (Tab. 4). As the Proteaceae, with their large, spectacular inflorescences, are probably better collected than most other families, these figures may also be taken to suggest that the other families are under-collected on the surrounding mountains. The Asteraceae may similarly not be well-enough known on the Klein Swartberg. The most common species belong the difficult *Helichrysum* group, where new endemic species may well be filed under incertae in the herbaria, rather than be recognised as new species.

Altitudinal zonation

No detailed gradient studies have yet been published indicating the upper and lower limits of species on one mountain to test whether there are distinct breaks in the distribution ranges, similar to the study of Hamilton & Perrott (1981) for Mt Elgon. The apparently abrupt changes a mountaineer observes are clearly affected by local edaphic conditions, but from personal observation a change does occur at about 1800 m.

In this study, herbarium material for all Cape Floristic Region mountains was used. These collections rarely give precise altitudes, and never the lowest distributional limits. In addition, the 'high-altitude zone' would vary from mountain to mountain, and even on one mountain, due to variations in aspect and general climate. The observations suggest that each species has its own unique altitudinal range, and that these do not fall into discrete groups. Nonetheless, for the convenience of this discussion, the following three groups are used.

Ubiquitous Cape Floristic Region taxa

Included here would be the 17 species that range from sea level to the summit of the Klein Swartberg (e.g. *Elegia filacea, Pentaschistis eriostoma, P. malouinensis, Aspalathus rubens*). Several of these represent species complexes (e.g. *Elegia filacea, Erica hispidula* and *Pentaschistis eriostoma*), that may well, on critical examination, yield several ecologically more restricted species. These ecologically very broad species may not represent equivalent taxonomic units as the generally stenotypic species, and a detailed investigation of these species may be profitable. In some cases, such as *Gladiolus caryophyllaceus*, some differentiation has been observed, but is not adequate to justify formal taxonomic

Tab. 5. Distribution of endemic species among the ten most speciose families.

Family	Actual species	Proportion	Actual endemic	Proportion
Ericaceae	29	0.23	4	0.36
Restionaceae	16	0.13	2	0.18
Asteraceae	15	0.12	0	0.00
Poaceae	13	0.11	1	0.09
Fabaceae	7	0.06	1	0.09
Proteaceae	5	0.04	0	0.00
Iridaceae	4	0.03	0	0.00
Rutaceae	4	0.03	0	0.00
Rosaceae	4	0.03	3	0.27
Campanulaceae	3	0.02	0	0.00

Tab. 6. Correlation coefficients between the number of Klein Swartberg species found on each Cape Floristic Region area (Species), the distance between the area and the Klein Swartberg (Distance), the maximum altitude in each area (Altitude), its distance from the sea (Ocean). The significance levels are indicated in the row below the correlation coefficients.

	Species	Distance	Altitude	Ocean
Species	1.0000	-.6643	.8335	.6767
		.0036	.0000	.0029
Distance		1.0000	-.6131	-.5314
			.0089	.0282
Altitude			1.0000	.7366
				.0007

recognition (Goldblatt & Vlok 1989). This can be contrasted with *Holothrix pilosa*, where the differentiation is probably adequate to recognise formal subspecies, or *Romulea atrandra*, where the montane form is recognised at varietal level (De Vos 1972). The degree of differentiation may be more important than the formal taxonomic rank accorded for understanding the patterns of variation in these widespread species.

Taxa widespread in the mountains of the Cape Floristic Region

The majority of the 123 species recorded from the Klein Swartberg could be described as being montane. These species reach lower altitudinal limits of less than 1000 m, often to about 300 m, but they are restricted to the quartzitic soils associated with the mountains. Some of these species are found only at the lower margins of the study area on the Klein Swartberg, and do not appear to occur above 1900 m (e.g. *Hypodiscus synchroolepis*), while others appear to recognise no altitudinal boundaries (e.g. *Erica curviflora*).

Widespread high-altitude species

Included here are the species regarded as indicators for a high-altitude system. Generally these species are found above 1500 m, although the lower altitudinal limit of a species may to some extent be determined by the exposure of its habitat.

In addition to the endemic taxa, which obviously all belong to this category, we have included 21 species, although it is often difficult to decide where a species belongs, without having studied it over its whole distribution area. In some cases taxonomic monographs provide useful clues. For instance, Rourke (1969) notes that *Spatalla confusa* is a typical high-altitude species, with a prostrate growth-form, and a distribution restricted to the summits of mountains at altitudes of 1200 to 2100 m. Similarly, Williams (1982) notes that *Acmadenia teretifolia* is found 'only at very high altitudes' from the Cedarberg to the Great Swartberg. The Restionaceae, often being dominant in the high-altitude vegetation, provide good indicators: *Cannomois nitida, Ischyrolepis schoenoides, I. laniger, I. distracta, Rhodocoma alpina* and *Willdenowia stokoei* being typical of this vegetation, and absent from the more mesic mid-altitude types of vegetation. These species do not descend below 1500 m.

It would be highly desirable to construct a list of the taxa characteristic of these high-altitude systems. However, such a list would be dependent on the detailed study of several of these areas, rather than on the basis of the analysis of a single area together with information obtained from herbarium material. However, inferences only as to which species would most likely be characteristic of the high-altitudes can be made.

Statistical analysis of similarity patterns

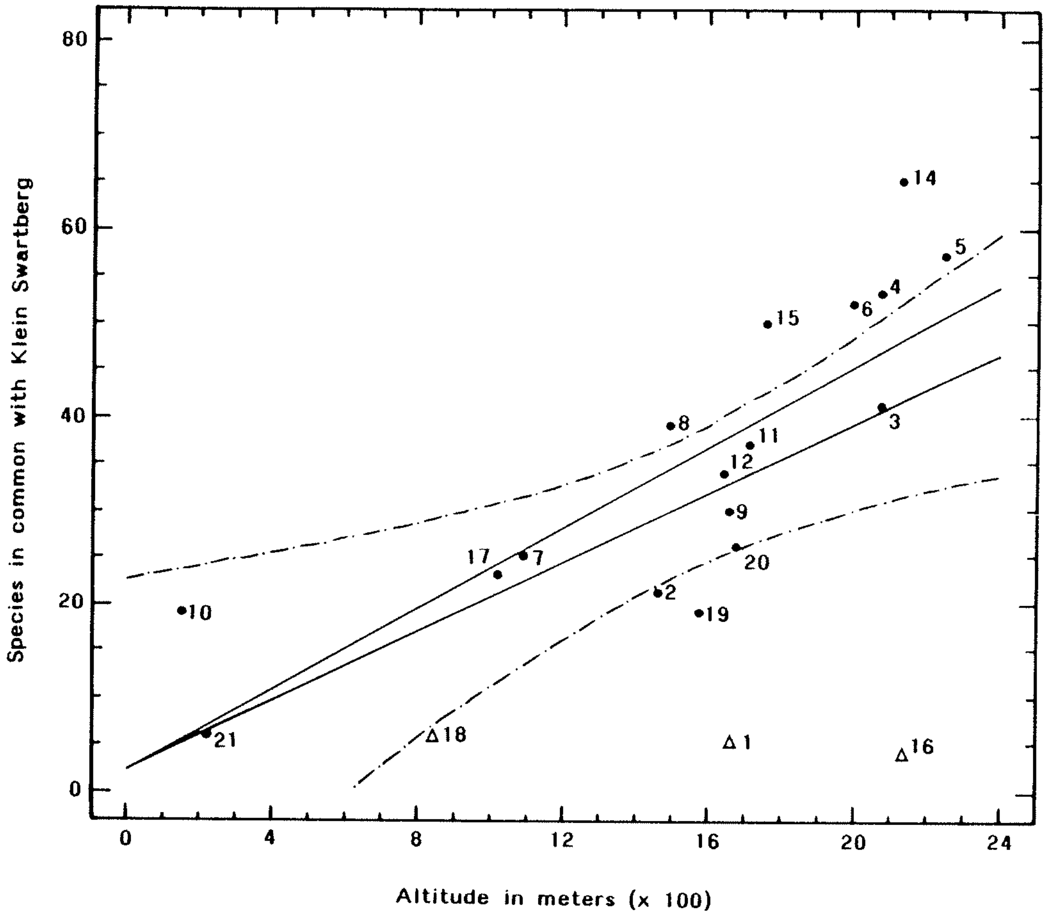
In order to test predictors of the distribution of the high-altitude species of the Klein Swartberg statistically, the Cape Floristic Region was divided into physiographical areas (Fig. 1), and the number of Klein Swartberg species found in each of these was determined from their distribution maps. For each of these areas the distance from the Klein Swartberg, the maximum altitude and the distance from the sea was determined. The relationship between these variables was determined by a product-moment correlation, the result of which is given in Tab. 6. There are some strong correlations among the 'environmental' variables. Distance to the ocean is strongly positively correlated to the maximum altitude in each area. This is consistent with the statement that the inland mountains are higher than the coastal mountains. There is a weaker negative correlation between the distance from the Klein Swartberg and the maximum altitude of the areas, which would be obvious as the Klein Swartberg is the highest mountain range in the Cape Floristic Region. While this is biologically trivial, it may cause some distortions in the correlations between the number of shared species and the environmental variables, as it will not be obvious which environmental variable is driving the correlation.

Geographical distance

The large role of gamma diversity, that is, replacement of species from one region to the other, has been well demonstrated for the Cape Floristic Region (Linder 1985; Kruger & Taylor 1979; Cowling et al. 1992). This would suggest that areas further from the Klein Swartberg should have less species in common with it, and this is supported by the significant correlation between the distance from the Klein Swartberg and the number of species held in common (Tab. 6).

It is obvious that using the complete list of species does lead to some obscuring effect from taxonomically poorly defined, eutopic species, and the proper test for this effect

Fig. 5. Regression of the number of species in common with the Klein Swartberg against the maximum altitude of each area, with the outliers (Hogsback, Roggeveld and Grahamstown) removed. The areas are numbered according to Fig. 1. The lower regression line is with the outliers included, the upper with them excluded. The broken lines indicate the 95% confidence limits for the regression with the outliers included.



would be the comparison with floras occupying similar areas (i.e. high altitude areas, above 1800 m). At least some common high-altitude species have vicariants – the best known being *Protea pruinosa* (Fig. 3E) from the Swartberg and *P. cryophila* from the Cedarberg (Rourke 1980). There may also be replacement by unrelated species: in the Cedarberg the most important high-altitude tussock restioid is *Ischyrolepis nana*, while from the Hex River mountains and Great Winterhoek mountains eastwards it is *Ischyrolepis laniger* and *I. distracta*. The relative contribution of sister-species replacement and replacement by unrelated species cannot as yet be quantified, but would be important in understanding the history of this high-altitude flora.

Distance from the ocean

Distance from the ocean is correlated both with altitude and with climate, with inland mountains being higher than the coastal mountains, and with a much larger climatic variation than the coastal mountains. The distance from the ocean is also significantly correlated with the number of species held in common with the Klein Swartberg, with a higher correlation coefficient than the distance from the Klein Swartberg (Tab. 6), suggesting that climate may be an important predictor of species distributions.

An inspection of Fig. 5 shows that areas which are under-represented in number of species are mountain ranges and areas close to the sea, while over-represented areas are more distant from the sea, indicating that distance from the sea complements altitude as predictor of species distributions.

Altitude as predictor

A simple test of the degree of altitudinal zonation in the montane flora is to calculate the correlation between the number of Klein Swartberg species found in each area, and the maximum altitude found of that area. If altitudinal zonation was well developed, then this correlation should be highly significant, as areas with progressively lower altitudes should only be able to support a progressively smaller number of high-altitude Klein Swartberg species. Altitude shows the best correlation with the patterns of species distribution, indicating that altitude is a much better predictor than distance or climate.

To test whether the high-altitude flora is derived from the Cape Flora or is a general African flora, the Roggeveld mountains, Amatole mountains and Grahamstown were left in the initial analysis, which gave a correlation coefficient of 0.59466 (Fig. 5). These three areas have only minute areas of fynbos, while the majority of the area has a tropical vegetation. With these areas removed, the correlation coefficient improves to 0.81054. The removed areas are indicated in Fig. 5. This corroborates the hypothesis that this high-altitude flora is essentially a part of the Cape Flora.

Conclusions

The high-altitude zone of the Cape mountains can be distinguished from the middle and lower slopes by a distinct vegetation structure, with a high dominance of Restionaceae and Poaceae. The dicotyledonous shrubs are mostly prostrate plants, except among rocks, where they may grow to a height of 1 m. Although similar vegetation may be found at lower altitudes in edaphically controlled sites, the floristic composition is quite different, and the prostrate dicotyledonous shrubs are absent.

This zone can also be distinguished floristically. There is no evidence for any abrupt boundaries, but several patterns emerge. The Poaceae and Restionaceae contribute relatively more species to the flora at these altitudes than at lower altitudes, and geophytic monocotyledons are generally rare. Proteaceae and Ericaceae are as common as at lower altitudes, but Asteraceae are less common. There appears to be a relatively distinct group of species that are restricted to the higher altitudes, and these can be used as indicators of this zone. The distribution patterns of this group are highly variable, with some species being endemic to the Klein Swartberg, whilst others are ubiquitous to the higher altitudes in the Cape Floristic Region.

There seems to be no abrupt interface between the flora and vegetation of the higher altitude areas and that of the middle slopes. This gradual replacement is expressed on many levels. At a structural level, the vegetation types grade from high-altitude into arid or water-logged types. Floristically it is likely that there will be a gradual change in the floristic composition along an altitudinal range. Phytogeographically the species do not appear to belong to discrete distribution patterns, but behave in an individualistic fashion. This gradualism hinders the understanding of the patterns in the rich Cape Floristic Region. However, this study suggests that there is a distinct high-altitude vegetation and flora, which may be regarded as a sub-alpine zone, but it would still require extensive study from other high peaks to establish a list of members of this flora.

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