VEGETATION GRADIENTS IN SOUTHERN CAPE MOUNTAINS

by

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CHAPTER 1

INTRODUCTION

The Southern Cape is best known for its extensive forest remnants. The fynbos which dominates in the mountain areas, however, is less well known and much less studied. It is a part of the famous "Capensis" flora of the winter rainfall region of the South Western Cape although rain falls in no distinct season in the region. The consequences of different rainfall seasonality for vegetation structure and diversity have yet to be studied.

Over the last decade interest in the Cape mountains and their flora has increased both scientifically, aesthetically and economically (Wicht 1971), and consequently land use practises and their environmental impact are being assessed more critically than in the past. The Directorate of Water Affairs, Forestry and Environmental Conservation (which includes the former Department of Forestry) is responsible for the Management of most Southern Cape mountain catchments and has initiated a programme of mountain catchment planning and research to ensure the conservation of water and biotic resources.

Southern Cape Mountain fynbos has been little studied in the past so that management and planners have had to draw heavily on Western Cape experience. This study arose from the need to define local vegetation patterns and their interdependence with animal life, climate and soil as a necessary prerequisite to vegetation mapping and interpretation of plant communities as animal and plant habitats and indicators of rainfall, soil and thus hydrology.

Fynbos is part of the diverse and complex Cape Floral Kingdom. Field taxonomy in fynbos is often problematic for trained botanists and is an overwhelming obstacle for mapping and monitoring of vegetation by untrained observers. Even the most unsophisticated observer, however, can recognize consistent variation in non-floristic characters such as vegetation height, density and the relative abundance of Proteaceae, small leaved shrubs and graminoid plants. A major aim of the study was thus to test the feasibility of deriving a non-floristic vegetation classification using easily learnt characters which had predictive value and was independent of the complication of high species turnover from one area to the next (Kruger & Taylor 1980). The derived classification could be tested in two ways 1) by comparing the communities extracted with floristically defined communities based on the same data set and 2) by assessing the consistency of location of communities and characters used to define them on environmental gradients.

Evergreen sclerophyllous shrublands of the world have long been recognized as characteristic of winter rainfall climates (Schimper 1903). Studies of ecological convergence in winter rainfall areas have proved a rich source of ideas and hypotheses both on the relationship of plant form and function, and the ways in which whole communities are structured (Specht 1969; Mooney and Dunn 1970; Parsons and Moldenke 1975; Naveh and Whittaker 1980; Cowling and Campbell

1980). The broader context of this study was thus to test (and develop) new hypotheses on the particular ways in which vegetation has adapted to impoverished soils in an effectively summer dry climate. Hypothesis testing, besides being of intrinsic interest in developing and stimulating ideas, may culminate in a scientifically based predictive framework for non-floristic phytosociological studies which would add greatly to their usefulness. Such a synthesis was a final, though optimistic, study objective.

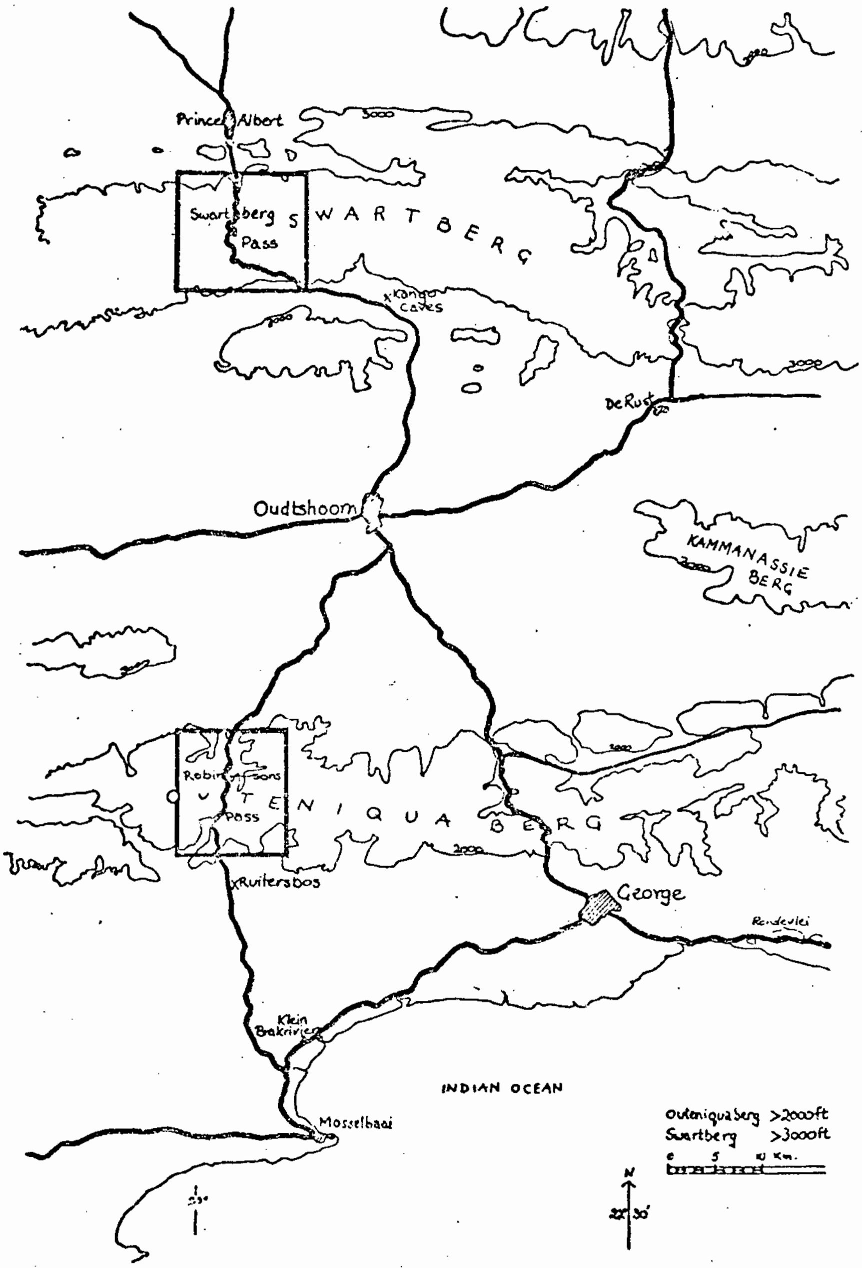


Fig. 1.1 Location of the Study areas.

1.1 LOCALITY

Two study areas were selected to allow comparisons between the coastal and inland mountains of the Southern Cape. An area in the Outeniqua mountains in the vicinity of Robinson's Pass, usually referred to as Ruitersbos after the forest station lying below Ruitersberg, was selected for the coastal study. The area was bounded by latitudes 33°56'S and 33°43'S and longitudes 21°56'E and 22°9'E.

The inland study area was in the vicinity of Swartberg Pass on the Groot Swartberg range bounded by lat. 33°23'S and 33°17'S and long. 22° to 22°6'E.

The study areas were selected (in approximate order of importance) for their ease of access, availability of mature veld relatively free of obvious human impact, and representativeness of the vegetation. Neither area was entirely satisfactory in all three respects but access limitations in the Swartberg and pest plant invasion and frequent fires in the Outeniquas strongly limited available choices.

The general location of the study areas is shown in Fig. 1.1.

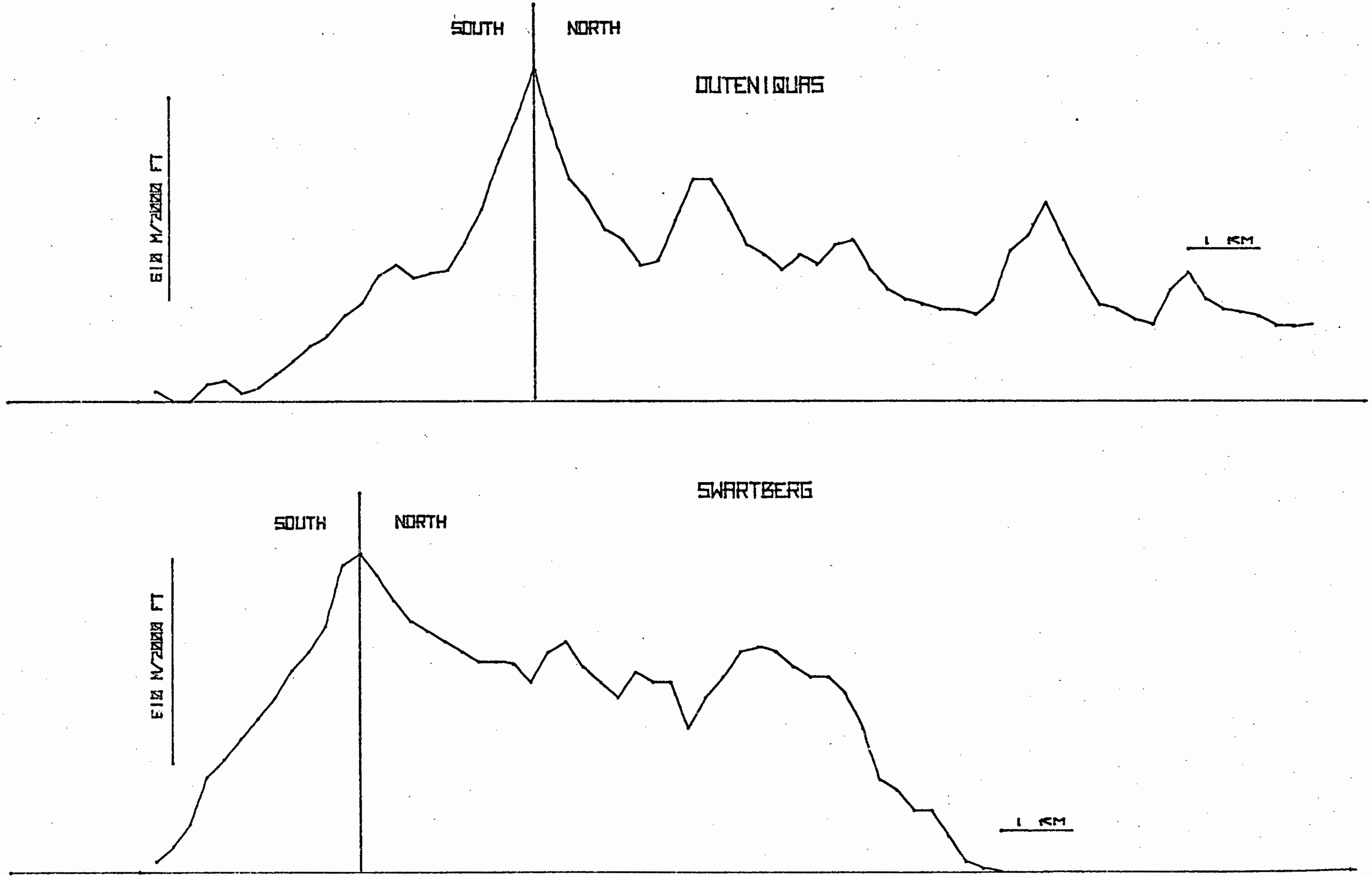


Fig. 1.2 Transects across the Swartberg (long. 22°02'25") and Outeniquas (long. 22°03'50") in the study areas. Vertical scale 5X horizontal. Areas left of the vertical line marking the watershed are generally referred to as "south slopes" in the text with "north slopes" to the right.

1.2 GEOLOGY AND GEOMORPHOLOGY

The Southern Cape landscape is dominated by two parallel ranges of Cape Fold Belt mountains striking in an east-west direction parallel to the coast line - the Swartberg (inland) and Outeniqua (coastal) ranges. Deeply incised remnants of a peneplain (or marine terrace) form the coastal forelands south of the Outeniquas. The broad, lower lying valley between the Swartberg and Outeniquas, the Little Karoo, is interrupted by island-like anticlinarial mountain ranges of which the Rooiberg and Kammanassie are prominent members.

The major geological formations are the Late Precambrian Nama System (Cango Formation), the Ordovician to Devonian Cape System, and Tertiary to Recent deposits. Enon conglomerates of the Cretaceous System form small but prominent areas of sculptured hills.

Cango Formation rocks outcrop at the Southern foot of the Swartberg Range and are composed of grey-wackes, shales, grits, siltstones, sandstones and limestone. Early Cambrian intrusions of granite occur south of the Outeniquas.

The Cape Supergroup follows unconformably on the Cango rocks and is made up of the Table Mountain Group, the Bokkeveld Series and the Witteberg Series. Table Mountain Group rocks are the main mountain builders and of greatest relevance to this study. Five formations have been identified in this group in the S. Cape mountains (Toerien 1976; Johnson 1976). The Peninsula Formation of Ordovician age is the lowest in the sequence and the thickest (±1 500 m thick) forming the high peaks and southern slopes of both the

Outeniqua and Swartberg Range. It is a white or pale grey quartzitic sandstone with relatively coarse false bedding. It is followed by the Cedarberg Formation (upper Ordovician age), a narrow siltstone and shaleband, highly carbonaceous in parts of the Swartberg, about 50 m thick. Shalebands are not as prominent a physiographic feature as in the Western Cape but can often be traced by their negative relief. The shaleband in the Robinson's Pass area is narrower than in the Swartberg and very inconspicuous. The Pakhuis formation of tillites found in the Western Cape is reduced to a thin zone of mudstone and sandstone with scattered weakly seriated pebbles, at the base of the shaleband (Rossouw et al. 1964) and is too narrow to be represented on a geological map at 1:50 000 scale. The Nardow Formation of the Western Cape (Rust 1967) is equivalent to three formations in the Southern Cape, the Tchando, Kouga and Baviaanskloof (Johnson 1976; Toerien 1976). The Tchando overlies the Cedarberg and consists of reddish brown or chocolate coloured (iron and manganese oxides) sandstones with thin, discontinuous, shale lenses to a depth of ±250 m. It is followed by the Kouga, formed of quartzitic sandstones distinguishable from the Peninsular by narrower cross bedding and a distinctive white colour, 300-400 metres thick. The Baviaanskloof is only 50-200 m thick and consists of two impure sandstone layer separated by a pale feldspathic layer. In the study areas it normally forms the lowest and most northerly strata of the Table Mountain Group (T.M.G.).

The Bokkeveld Group lies conformably over the T.M.G. and consists of alternating sandstones and shales. It is typically found in synclinal valleys between the mountains such as Gamkaskloof in the Swartberg and the Langkloof, north of the Outeniquas. Sandstones and shales of the Witteberg Group outcrop a few kilometres north of the Swartberg and outside the study area.

Tertiary formations are prominent as silcrete caps on peneplains north and south of Robinson's Pass on the Outeniquas.

Mountain areas of the Southern Cape are youthful landscapes formed by folding and faulting. Folding, initiated in the Middle Carboniferous, was renewed during the Permian and continued to the Upper Triassic. There is a regional trend of overfolding to the north. The southern slopes of the mountains are formed from overfolded anticlines. This is in contrast to W. Cape mountains such as Table Mountain which are preserved synclines. Faulting took place in the Middle Cretaceous with an estimated throw of about 3 000 m on the Cango Fault at the southern foothills of the Swartberg. A similar fault marks the southern foothills of the Outeniquas near Robinson's Pass. Younger rocks have been stripped exposing the Peninsula formation from southern slope foothills to mountain crests. The absence of extensive faulting on the northern margins, however, has lead to the preservation of the younger formations such as the Chando, Kouga and Baviaanskloof.

Erosional features are represented by remnants of a surface cut when the Enon was deposited at about 1 280 m in the vicinity of Swartberg Pass (Rossouw et al. 1964), and of an erosion level at 1 000 m, along the southern slopes of the Swartberg dated as Miocene-Pliocene and contemporaneous ? with surfaces cut both north and south of the Outeniquas in the Robinson's Pass areas.

The S. Cape Mountains form long east-west tending chains broken by narrow river valleys such as the Gouritz, Seweweeks, Meiringspoort etc. but, otherwise, with few apparent phytogeographic barriers in the form of marked terrain discontinuities. Elevation increases form the coastal mountains inland with maximum elevations of 1 362 m (Ruitersberg) and 1 521 m (Engelseberg) in the Robinson's Pass study area to 1 950 m (Waboomsberg) and1856 m (Oliewenberg) in the Swartberg Pass study area. The Western (Klein) Swartberg includes some of the highest peaks in the fynbos biome region. Whilst absolute elevation is not very high, relief is considerable and the south slopes, in particular, rise sharply from the lowlands; 1 040 m over 5 kms south of Ruitersberg and 1 160 m over 3,3 kms on the south slopes of the Swartberg (Fig. 1.2).

Swartberg, in the vicinity of Swartberg Pass, has steep slopes south of the watershed broken by gentler slopes of a peneplain relict at about 1 000 m. Bare rock and sloping cliffs form the higher reaches with a zone of large talus boulders below. Steep vertical cliffs are typical of the upper north slopes grading abrubptly to undulating terrain between 1 460 and 1 280 m which is deeply incised by juvenile drainage systems cutting deep, narrow kloofs. This plateau is bounded to the north by a very steep scarp dropping 500 m to the Karoo (Fig. 1.2).

Scree slopes and blocked stream beds attributed to periglacial action (de Goede, pers. comm. 1978) occur above 1 500 m on the highest peaks especially on the south slopes whilst talus slopes with a steeper angle of repose are common below cliffs on the drier northern slopes.

The Robinson's Pass area has steep southern slopes, relatively free of cliffs and boulders south of the watershed with precipitous cliffs and boulder-strewn slopes below, north of the watershed. The study area consists of a succession of anticlines and synclines forming hills and valleys of decreasing elevation extending into the Little Karoo (Fig. 1.2).

Peneplain remnants are conspicuous north of the watershed in the Klein Moeras River and Sebrafontein Valleys and below the southern foothills forming a coastal plateau extending nearly to the sea.

1.3 CLIMATE

There are very few weather stations in the Southern Cape mountains so that this account is biased towards lowland stations adjacent to the study area. The Outeniquas fall under Schulze's (1965) region A and the Swartberg under region K. The following account draws heavily on Schulze's summary of the climate for these regions.

Both areas receive rainfall throughout the year but amounts vary considerably in relation to topography. In the Outeniquas rainfall may exceed 1 100 mm on the high peaks dropping to 400 mm on north-slope foothills. In the Swartberg rainfall exceeds 750 mm at high elevation and drops sharply to below 200 mm on the northern foothills. The rain is mostly cyclonic and orographic with occasional thunderstorms. The latter are more frequent in the Swartberg. Snow occurs annually on the high peaks of the Outeniquas, but is more common (five or six falls per annum) and lies longer in the Swartberg.

The role of mist in augmenting precipitation is probably underestimated (Schulze and McGee 1978). No records on cloud cover are available in the study area but, following observations in the Western Cape (Marloth 1904; Nagel 1962; Kruger 1974) appreciable moisture is probably precipitated as mist, especially in the summer dry periods.

Annual sunshine duration is about 50% of the possible in region A and 70% of the possible in Region K (Schulze 1965). Orographic cloud is mostly restricted to south aspects and is more frequent, and lies at lower elevations, in the Outeniquas than in the Swartberg (personal observations).

Frost is practically unknown in the Outeniquas but can occur in the Swartberg, particularly in areas susceptible to cold air drainage, between June and August (Schulze 1965). The Outeniquas experience a mild temperate climate showing a clear maritime influence. Maximum temperatures range between 24,5°C in January and 19,4°C in June. Minimum temperatures range from 14,7°C in January and 8,2°C in June, for the coastal plateau. The thermal régime in the Swartberg is more continental with marked diurnal and annual temperature extremes. The Cango Caves, near the southern foot of the Swartberg Pass, have mean maxima of 31,2°C in January and 18,0°C in June and mean minima of 13,9°C in January and 3,4°C in June.

Hot dry bergwinds can result in warm temperatures in winter months, occasionally rising above 38°C.

Winds are mostly south to south-easterly in the summer and north-westerly in the winter.

1.3.1 Solar Radiation

Schulze and McGee (1978) have emphasised the significance of solar radiation in ecological and biogeographic studies, and have summarised seasonal and latitudinal trends for Southern Africa. The nearest stations measuring solar radiation are Cape Town and Port Elizabeth (Schulze 1965). Mean annual radiation is 475 and 431 cal cm^{-2} day^{-1} respectively. These compare with Mediterranean climate areas in S. Australia (440), California (420) and France (360) quoted by Specht (1969). Kruger (1974) estimated 318 cal cm^{-2} day^{-1} for a horizontal surface in the Zachariahshoek catchment in mountainous terrain in the Western Cape and mean radiation for the whole catchment as only 213 cal cm^{-2} day^{-1}. Potential solar radiation for both Cape Town and Port Elizabeth is 724 cal cm^{-2} day^{-1}.

In mountainous terrain slope and aspect have a marked effect on sunshine duration and potential radiation and thus plant life. Frank & Lee (1966), Schulze (1975), Swift (1976), and Holland et al. (1977) have published methods for estimating potential radiation on different slopes and aspects. Swift's (1976) algorithm was programmed on a Hewlett Packard 9820 calculator using a solar constant of 1,95 cal cm^{-2} min^{-1}. Potential radiation for a range of slopes and aspects for a latitude of $33^{0}30'$ south were calculated. The effects of slopes on potential solar radiation are shown in Fig. 1.3 and of aspect in Fig. 1.4.

There are striking differences between aspects and between different slopes. Potential radiation on all slopes and aspects is relatively similar in summer. In winter, however, radiation is strongly controlled by the low azimuth of the sun with steep north slopes receiving the highest, and steep south slopes the lowest, radiation.

Elevational effects on potential solar radiation are minimal for the latitudes under consideration (Lee 1963). Low net radiation figures recorded in mountainous terrain by Kruger (1974) are, therefore, largely due to attenuation by the atmosphere and particularly by higher cloud cover.

Sunshine duration has been measured near George, Oudtshoorn and at the Langkloof experimental farm near Joubertinia (Agricultural

TABLE 1,1. The Ratio of Actual to Potential Sunshine for Outeniqua, Langkloof and Oudtshoorn Experimental Farms. Potential Sunshine was calculated for a latitude of $33^{\circ}30'$ using Swifts (1975) algorithm.

	J	F	M	A	M	J	J	A	S	O	N	D	Year	Period yr.
Outeniqua (near George)	,49	,45	,48	,51	,56	,58	,62	,58	,48	,47	,47	,50	0,52	11
Langkloof (near Joubertina)	,66	,58	,60	,60	,59	,63	,67	,63	,57	,59	,58	,65	0,61	12
Oudtshoorn	,78	,70	,70	,76	,68	,71	,71	,71	,64	,66	,68	,74	0,71	8

TABLE 2,5. Mean Windspeed m_S^{-1} (ex Weather Bureau and Agricultural Technical Services, unpublished).

	Period (yrs)	J	F	M	A	M	J	J	A	S	O	N	D	Year
George	11	2,7	2,3	2,1	2,1	2,2	2,6	2,6	2,9	2,6	2,7	2,7	2,7	2,5
Langkloof	12	2,8	2,6	2,5	2,3	2,2	2,4	2,5	2,6	2,5	2,7	2,7	2,8	2,5
Oudtshoorn	8	1,5	1,5	1,4	0,9	0,7	0,8	0,8	1,0	1,0	1,3	1,6	1,6	1,2

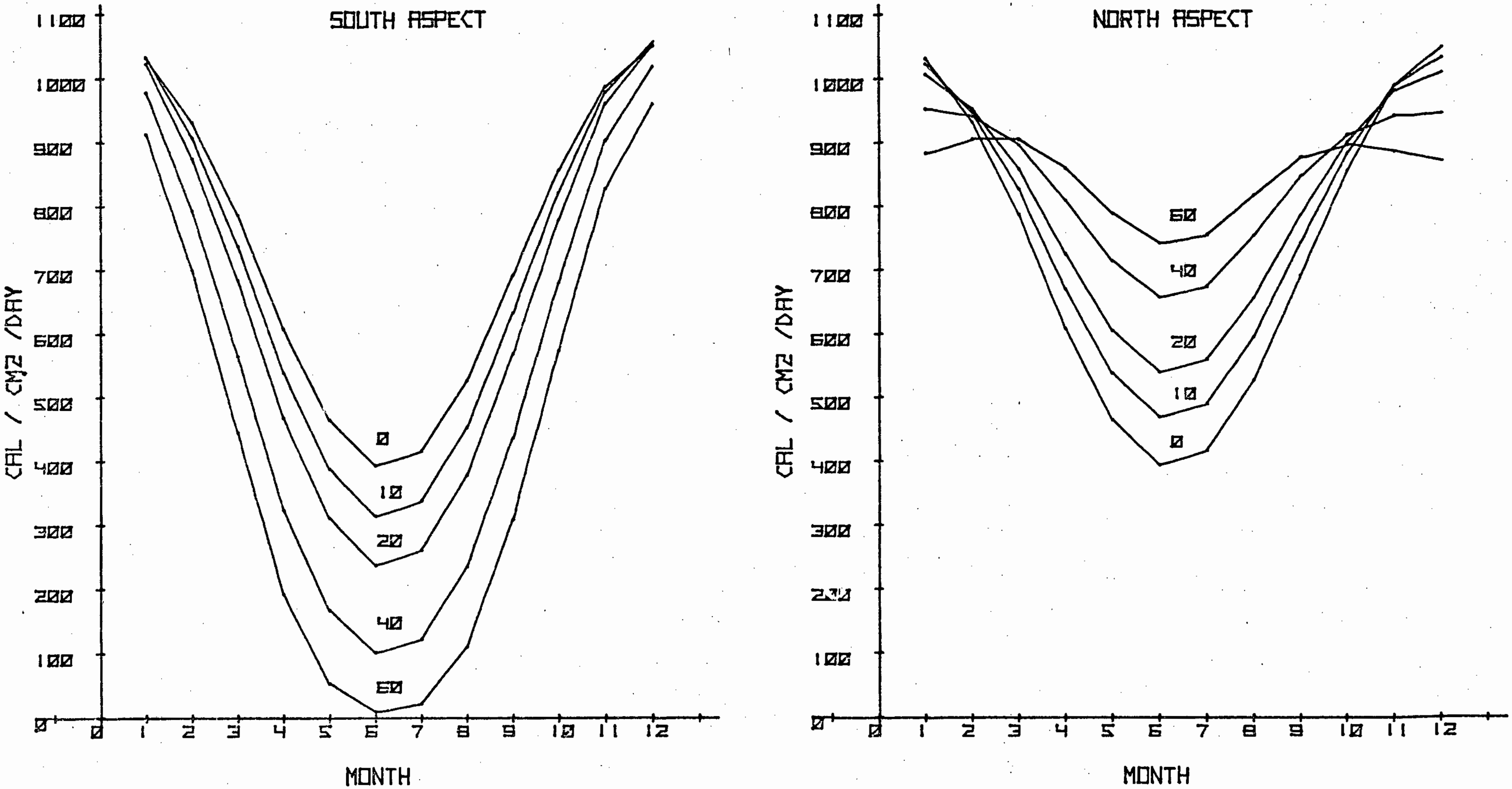


Fig. 1.3 The effects of slope on potential radiation (calories cm^{-2} day^{-1}) for a latitude of $33^{o}30'$ south. Calculated from Swift's (1976) algorithm. Percent slope is indicated on each curve.

Technical Services, unpublished). The ratio of actual to potential sunshine increases from the relatively cloudy coastal plateau to the northern foothills of the Outeniquas, and is greatest in the sub-arid Little Karoo (Table 1.1).

Orographic cloud occurs mostly on mid- and upper-south slope elevations, and only rarely on high northern aspects. Thus sunshine duration is probably least on higher south slopes of the Outeniquas, greater on the north and on both aspects of the Swartberg (although a high cloud cover is often present above about 1 600 m on the south slopes of the latter range).

1.3.2 Precipitation

The Southern Cape has rainfall distributed throughout the year. There are marked precipitation gradients in the region, mostly controlled by elevation, whilst the Little Karoo suffers from the rain shadow of the Outeniquas.

The Outeniquas and Coastal Forelands

Virtually no rain gauges are located in the mountains. Rainfall is said to be higher in the Outeniquas than in the Swartberg, rising from about 600 mm on S slope foothills to more than 1 100 mm on the peaks (Schulze 1965). Mean annual rainfall for seven stations ranging in elevation from 59 m (Mossel Bay) to 457 m (Jonkersberg) in the vicinity of the study area

TABLE 1,2. Mean rainfall (mm), Outeniquas (ex Weather Bureau, 1955, 1965 and unpublished).

Station	Altitude	Period (y)		J	F	M	A	M	J	J	A	S	O	N	D	Year
South																
Ruitersbos	229 m	20	mm	80,4	60,1	92,1	63,2	59,2	38,2	46,7	54,8	76,0	82,1	75,6	52,0	780,4
			d	7	7	9	7	6	5	6	6	8	9	7	6	83
Jonkersberg	457 m	41		101,3	98,6	127,4	76,9	68,5	46,9	62,7	79,9	99,9	99,3	114,6	99,4	1075,4
				9	9	10	8	8	6	7	8	10	10	10	9	104
North																
Wagenboomskraal	579 m	26		55	62,5	70,2	50,5	70,1	42,8	62,1	70,3	80,8	83,7	98,3	77,4	823,7
				5	4	5	5	5	4	6	5	7	7	6	5	64
Groot Doornrivier	533 m	35		15,8	14,0	18,7	20,8	27,7	15,5	26,5	22,5	20,4	20,5	25,1	11,4	238,9
				1	2	2	3	3	3	3	3	3	3	3	1	30

TABLE 2,3. Mean rainfall (mm), Swartberg. Sources as for Table 2,2.

Station	Altitude	Period (y)	J	F	M	A	M	J	J	A	S	O	N	D	Year
South															
Kangogrotte	640 m	21	29,3	28,1	43,9	39,5	30,0	29,6	23,1	32,9	22,7	31,7	29,9	22,4	363,1
Albertberg	1067 m	10	58,6	75,7	82,6	51,6	73,8	48	56,6	66,2	49,4	66,2	48,9	50,3	727,9
North															
Swartberg-Bos	1600 m	12	33,1	38,0	49,9	34,5	56,4	36,9	51,8	50,4	41,5	51,6	57,9	34,1	536,1
Kliphuisvlei	1370 m	10	28,9	36,4	38,1	29,9	50,3	41,3	45,9	46,1	42,5	40,4	24,3	27,2	451,3
Prince Albert	686 m	83	11,5	18,7	26,6	19,2	21,2	13,4	9,6	10,2	12,5	13,3	14,0	11,7	181,9

showed a linear increase of rainfall with elevation (mean rainfall p.a. = 255,8 + 1,769 altitude, r^2 = ,84, $P < ,01$). Rainshadow effects north of the Outeniqua watershed are apparent with a very rapid decline in mean annual rainfall from high north slopes, best described by a quadratic regression relationship.

Rainfall is mostly of low intensity and is cyclonic or orographic in origin. Mist precipitation is probably an important additional moisture input, especially in the summer months (Marloth 1904, 1907; Nagel 1962). Snow occurs two or three times a year, usually only on the highest peaks.

Thunderstorms are rare with between 5 and 10 days with thunder per annum (Schulze 1965).

Rainfall variability is low, with George showing the least variation of all stations (14% mean annual relative variability) in a table from Schulze (1965) with a range of data from South Africa. Tyson (1978) has detected cycles of drought with a periodicity of about 10 years for the Southern Cape, possibly related to cycles of sunspot activity with similar frequencies.

Table 1.2 gives rainfall statistics for selected stations in or near the study area.

Swartberg

A number of raingauges have been established over Swartberg Pass providing an unusual degree of coverage for montane areas. Unfortunately the location of some of these gauges is given incorrectly in

Weather Bureau publications and the precise location of the station Swartberg Pass 48/81 is in doubt.

The mountains are drier than the Outeniquas but topographic patterns appear to be similar. Mean annual rainfall for nine stations on the foothills of Swartberg ranging from 305 m (Besemkop) to 1 067 m (Albertberg) also show a linear increase of rainfall with elevation (mean annual rainfall = 129,98 + ,878 Altitude, $r^2 = 0,95$; $p < ,01$). The rate of increase with altitude was, however, substantially lower. Once again rain shadow effects on north slopes are apparent although few stations from mid-elevations are available. Rainfall declined rapidly from 725 mm p.a. at 1 600 m (cf. 775 mm at 1 067 m on south aspects) to 210 mm p.a. at 884 m on the northern foothills, but then only slightly to 182 mm p.a. at 686 m at Prince Albert on the edge of the Karoo.

Rainfall intensity is probably higher in the Swartberg than in the Outeniquas because of the greater frequency of convectional storms. Mist precipitation is probably significant only at high elevations (±1 500 m). Snow occurs five or six times per annum and may fall at elevations below 1 100 m, and is more persistent in the Swartberg than in the Outeniquas, sometimes lying for more than two weeks (personal observation).

Thunderstorms appear to be more frequent in the Swartberg than in the Outeniquas, with between 10 and 20 days with thunder per annum (Schulze 1965) and tend to be associated with high intensity rainfall.

Rainfall variability for Ladismith, on the Swartberg foothills, is appreciably higher than George at 21% relative variability per annum, but

<u>TABLE 1.4</u>. Mean monthly maximum and minimum temperatures (^{o}C) for selected stations in the study area. (Weather Bureau 1954; Weather Bureau unpublished; Agricultural Technical Services unpublished; Dept. of Forestry unpublished).

Station	Kangogrotte		Swartberg* Pass		Oudtshoorn		Langkloof		Ruitersbos		George	
Period	21		1		25		12		1		75	
Ht (m)	640		1600		335		671		518		221	
Month	MAX	MIN	MAX	MIN	MAX	MIN	MAX	MIN	MAX	MIN	MAX	MIN
J	31,2	13,9	20,2	8,5	32,2	15,3	25,5	13,7	20,8	13,1	24,5	14,7
F	30,9	13,9	19,7	9,7	32,3	15,4	25,2	14,0	23,3	14,7	24,4	15,2
M	28,2	12,8	19,1	10,9	30,0	14,0	24,3	13,3	22,1	14,1	24,0	14,4
A	24,9	9,5	18,7	10,9	26,7	10,7	21,4	11,1	21,2	14,1	22,4	12,0
M	21,4	6,4	13,5	6,9	22,5	6,7	18,4	8,5	19,1	11,9	21,1	10,3
J	18,0	3,4	10,8	4,7	19,9	3,3	16,7	7,1	17,5	10,8	19,4	8,2
J	17,5	3,0	12,4	5,8	18,9	3,4	16,1	6,0	14,8	9,5	18,6	7,4
A	19,3	4,4	10,6	5,4	21,3	4,8	16,3	6,0	16,3	9,4	19,2	8,1
S	21,6	6,1	11,3	3,7	23,2	7,3	18,2	7,2	17,7	9,9	19,1	8,9
O	24,1	8,0	13,5	3,5	25,9	9,9	20,5	9,0	19,1	10,0	20,0	10,5
N	26,9	10,4	17,2	6,3	28,2	12,4	21,8	10,5	22,4	12,6	21,7	12,1
D	29,0	12,1	19,6	9,8	30,4	13,6	24,2	12,2	23,7	14,6	23,0	13,3
Year	24,4	8,7	15,6	7,2	26,0	9,7	20,7	9,9	19,8	12,1	21,5	11,3
$Yr\frac{MAX+MIN}{2}$	16,6		11,4		17,9		15,3		16,0		16,4	

*Incomplete records.

this is not high by sub-continental standards (Schulze 1965). Table 1.3 gives rainfall statistics for selected stations in or near the study area.

1.3.3 Temperature

Kruger (1979) reports mean annual screen temperatures of 15° to 18°C for fynbos, with high montane sites falling below and arid fynbos above this range. Strong maritime influences result in cooler temperatures along the coast (15° to 16°C), becoming considerably warmer inland (17° to 18°C). Coastal areas also have a lower annual range (±4,5°C) than those inland (±11°C).

Mean temperatures of the warmest month (usually February) fall between about 20,5° to 24°C whilst the coolest months are largely enclosed by the 10° and 12,4°C July isotherms. Absolute maxima are relatively low in the coastal forelands, but frequently exceed 40°C inland. Frost is virtually unknown on the Outeniquas and coastal forelands, but occurs in the interior mountains.

Outeniquas and Coastal Forelands

No long term temperature records are available from the mountains. George, on the coastal plateau, has an annual mean temperature of 16,4°C reaching a maximum mean of 19,8°C in February and a coolest monthly mean of 13,0°C in August. An absolute maximum of 41,3°C has been recorded (in January) and absolute minimum of 1,3°C (in August).

Assuming regional lapse rates of ,005°C m^{-1} (e.g. Fuggle and Ashton 1978; Smith and Geller 1978) temperatures on high mountain peaks will be about 7^{0}C cooler than at George, i.e. with annual means of 9,4^{0}C. There is, however, very little information available to confirm these rates. Stations on the coastal forelands and the coast itself suggest rates of only 0,0027^{0}C m^{-1}. No quantitative information on temperature variation with altitude in mountainous areas is available.

Temperature statistics for selected stations are shown in Table 1.4.

Swartberg

Even less information is available on temperature régimes in the Swartberg. Cango Caves, in the Swartberg foothills, has a mean annual temperature of 16,5^{0}C. January is the warmest month at 22,6^{0}C mean and July the coolest at 10,3^{0}C mean. The annual range in temperature is thus appreciably greater than George (12,3^{0}C compared with 6,8^{0}C). Limited data is available from a weather station established near the top of Swartberg Pass (1 600 m) on a north aspect. Calculations, for one year's data only, give a lapse rate of about 0,0054^{0}C m^{-1}, reasonably close to that of Smith and Geller (1978). Mean annual temperature for the high montane station was 11,4^{0}C with a mean maximum of 15,6^{0}C and a mean minimum of 7,2^{0}C. March was the warmest month with a mean monthly temperature of 15^{0}C and September the coolest with a mean of 7,5^{0}C.

Temperature data are shown in Table 1.4.

Frost has been recorded for an average of 6,7 days p.a. at Oudtshoorn in the Little Karoo. Whilst frost has been seen in the hollows and valleys, particularly of the north slopes of the Swartberg, no records of frost frequency are available.

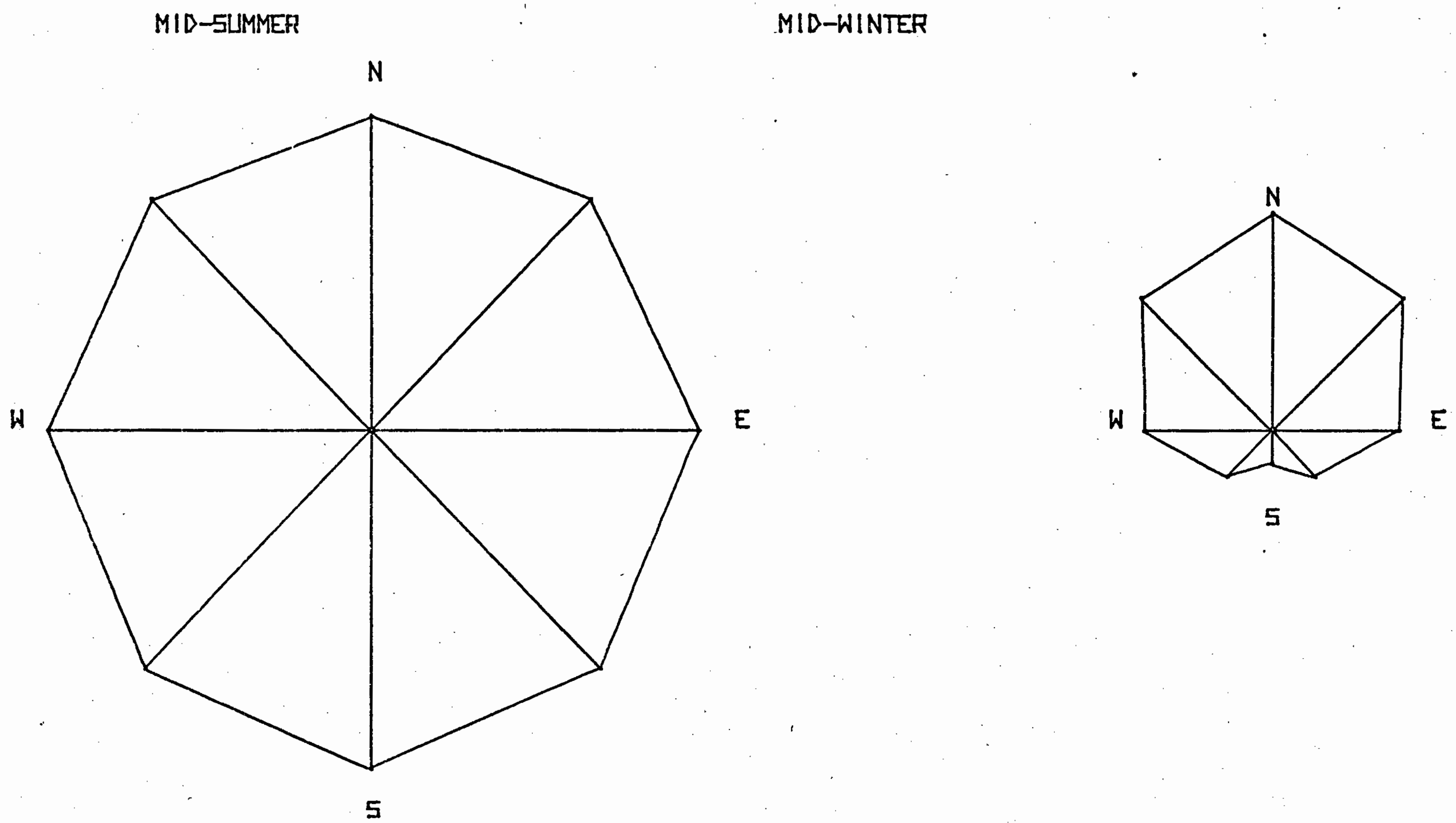


Fig. 1.4 The effects of aspect on potential radiation in mid-summer and mid-winter for a 40% slope calculated for Lat. $33^{0}30'$ south from Swift's (1976) algorithm. The length of each line from the centre to the circumference of the polygon is proportional to radiation.

1.3.4 Wind

The winds and weather of both study areas are controlled by the general circulation of South Africa. Jackson and Tyson (1971) describe the local conditions as follows:

"The winter circulation of the South Western Cape is associated with disturbances in the Circumpolar westerly winds, taking the form of a succession of eastward moving cyclones (depressions) and anticyclones. Originating in areas of cyclogenesis far to the south and west of Southern Africa, these disturbances first bring rain to the south-western and later to the south and south-eastern coasts and may even extend far inland. Fronts are associated with the depressions: warm fronts are diffuse, difficult to recognise and almost impossible to follow: cold fronts are more usual, sharper and more easily recognised. Following the passage of a cold front, winds back from north-west to west and south-west, pressure starts rising, temperatures fall and instability showers and storms may occur". This seems to be the pattern in the Southern Cape where rain is usually associated with westerlies and southwesterlies although in the S.W. Cape rain is usually associated with northwesterly pre-frontal winds.

The föhn-like bergwinds have been described by Tyson (1964) and Phillips (1931). They often precede winter anti-cyclones and are caused by dry subsiding air moving off the interior plateau in response to strong coastward pressure gradients. These hot, dry winds are important ecologically often resulting in abnormal fire hazard conditions. The great fire of 1869 which burnt large areas of indigenous forest followed a long period of bergwinds (Phillips 1931).

Summer weather arises from slight southward displacement of the subtropical high pressure belt over the oceans. On the surface this belt appears as a dynamic system of anticyclones which travel eastward toward and along the coast, blocking westerly cyclones" Kruger (1979). This is the cause of the strong south easterlies and warm dry conditons. However, mid-latitude depressions periodically penetrate inland bringing rains to the south coastal region and eastern continental areas. The Southern Cape thus receives rain throughout the year whereas the S.W. Cape, which is mostly skirted by summer mid-latitude depressions, is a winter rainfall area.

Data from wind stations at George are shown in Fig. 1.5 and Table 1.5. George has an annual mean wind speed of only 2,5 m s^{-1} compared with Cape Town (D.F. Malan) 4,0 and Port Elizabeth 4,3 m s^{-1}. Across the Outeniquas, The Langkloof Experimental Farm has a mean annual windspeed of 2,5 m s^{-1} while the Oudtshoorn Experimental Station has a wind speed of only 1,16 m s^{-1} (Agricultural Technical Services, Unpublished records 1970-1977). Table 1.5 shows monthly mean wind speed for Oudtshoorn and George.

The windrose for George (Fig. 1.5) shows a strong south easterly tendency in summer and a northwesterly tendency in winter, with no major directional tendencies in autumn and spring.

Very little information is available on windtrends with altitude. Kruger (1974) reports higher wind speeds in the mountains of the Jakkalsriver catchment (3,68 m s^{-1}) than in nearby lowland areas (Worcester Veld Reserve 3,13 m s^{-1}). Personal observations suggest that wind is much stronger at high elevations and is an important ecological factor there.

1.3.5 Synthesis of Climate

Moisture availability is frequently the major limiting factor in plant growth (Schulze and McGee 1978; Walter 1979). Rainfall is a poor indicator of available moisture since evaporation demand varies from place to place.

Walter-Lieth (1967) climate diagrams in which rainfall is graphed against temperature are frequently used by biologists to express moisture regime at a site. The implicit assumption is that temperature is approximately equivalent to evaporative demand and, by empirical selection of appropriate precipitation/temperature scales, periods of moisture shortfall should coincide with the temperature chart rising above the rainfall chart.

Climate diagrams for George, Langkloof and Oudtshoorn are shown in Fig. 1.6.

Schulze and McGee (1978) point out that Walter-Lieth climate diagrams have been superseded by less empirical approaches to moisture balance. Effective rainfall (the moisture potentially available to plants) can be estimated more directly as the difference between precipitation and potential evapotranspiration (PE). Potential evapotranspiration is the quantity of water needed for evapotranspiration if vegetation covered soil is freely supplied with water throughout the year. A

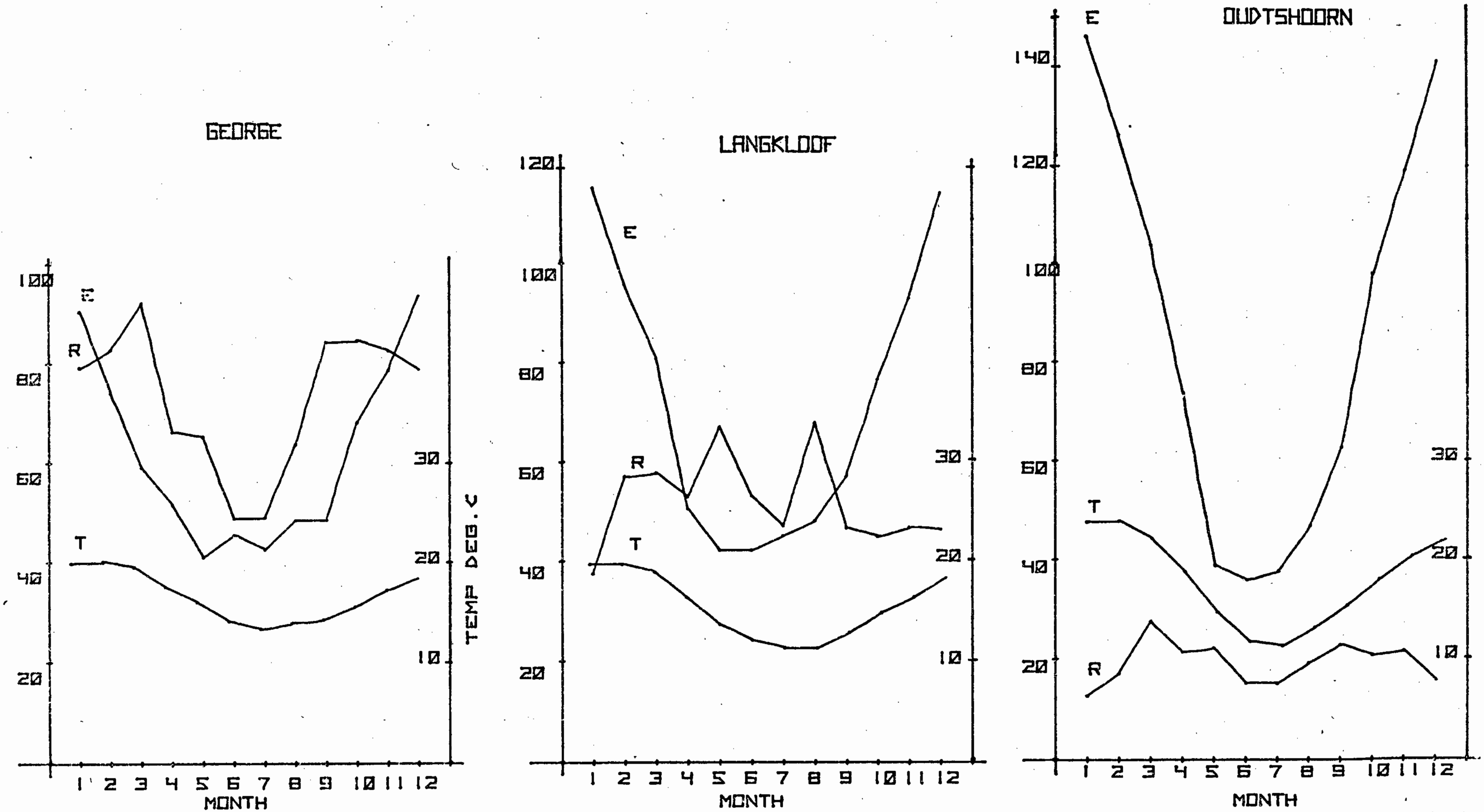


Fig. 1.6 Climate diagrams for George (G), Langkloof Experimental Farm (L), Oudtshoorn (O). T = temperature °C, R = rainfall (mm), E = Class A Pan evaporation ÷ 2 (mm). Duration of records in G - R83y, T75y, E6y; L - R12y, E12y; O - R81y, T25y, E8y. Rainfall and temperature data for G and O ex Weather Bureau (1960, 1965). Pan evaporation and Langkloof data ex Agricultural Experimental Farms (Outeniqua, Langkloof, Roodeheuwel, unpubl.).

number of methods have been devised for calculating PE from meteorological variables, usually as an aid to prediction of consumptive demand of crops in irrigation scheduling (Israelson and Hansen 1962).

Penman's (1948) equation and modifications of it (Montieth 1965) is the most soundly physically based method and has had the most successful application to biological and hydrological problems (Slatyer 1967). Penman's equation (ex Israelson and Hansen 1962) was programmed on a Hewlett Packard 9820 calculator. The equation requires relatively sophisticated meteorological input, including sunshine duration and daily wind run which were only available from Outeniqua, Oudtshoorn and Langkloof experimental farms.
Shortwave reflectivity (albedo) was assumed to be 0,2 throughout the year although Yates (1981) measured values ranging from 0,14 to 0,17 for Australian heathlands and quotes values of 0,14 and 0,10 for English heather.

Thornthwaite's (1948) method requires only temperature and latitude as data input and has therefore been widely adopted (Ward 1967; Kruger 1974; Schulze and McGee 1978). The method was developed under humid temperature conditions (New Jersey, U.S.A.) and underestimates by 40-50% of real values under arid conditions , Fig. 1.7. The exact magnitude of the underestimation depends on the extent of the aridity (Ward 1967; Hashemi and Habibean 1979). Nevertheless the Thornthwaite method is the most convenient and accurate for the limited data available and was consequently programmed on a Hewlett Packard 9820 calculator (algorithm ex Israelson and Hansen 1962, Table 2).

The difference between PE and rainfall provides a useful approximation of moisture balance and of the effective moisture régime. Figure 1.8 compares moisture balance for a number of stations in the study area with stations in the winter and summer rainfall area. The forest climate of Diepwalle, and more marginally of George, is strikingly represented by a moisture surplus for most of the year. The effective moisture régime of the renosterveld climate of Cango Caves and the fynbos climate of the Langkloof is unequivocally Mediterranean and typified by winter surpluses (Bond 1980).

Microclimatic variation in moisture régimes were investigated by modelling PE on different slopes and aspects (using Penman formula) with varying radiation input according to Smith's 1976 algorithm (see section on radiation). This procedure probably overestimates PE for south and underestimates for north aspects since temperature and humidity were held constant in the equation. The ratios of PE on different slopes and aspect to PE on a horizontal surface were calculated for Outeniqua Experimental Farm (E.F.), Langkloof E.F. and Oudtshoorn E.F. (Table 1.6). Ratios were nearly identical for Outeniqua and Langkloof station and the latter are not quoted. Oudtshoorn is significantly different showing a greater response of PE to slope and aspect in the winter months. Both the Outeniquas and the Swartberg have very similar trends in mean annual PE.

In the Outeniquas, potential evapotranspiration on a steep north slope is nearly twice as great as a steep south slope, but only 116% of a level slope. PE on a steep (60%) south slope is only 63% of PE on a level slope. There are marked seasonal variations in PE.

TABLE 1,6. The effects of slope on potential evapotranspiration (P.E.) on north and south aspects. The figures are ratio of P.E. on each slope to P.E. on a horizontal surface. P.E. was calculated from Penman's formula and the effects of slope and aspect were modelled by altering potential radiation values only, according to Swift's (1976) algorithm.

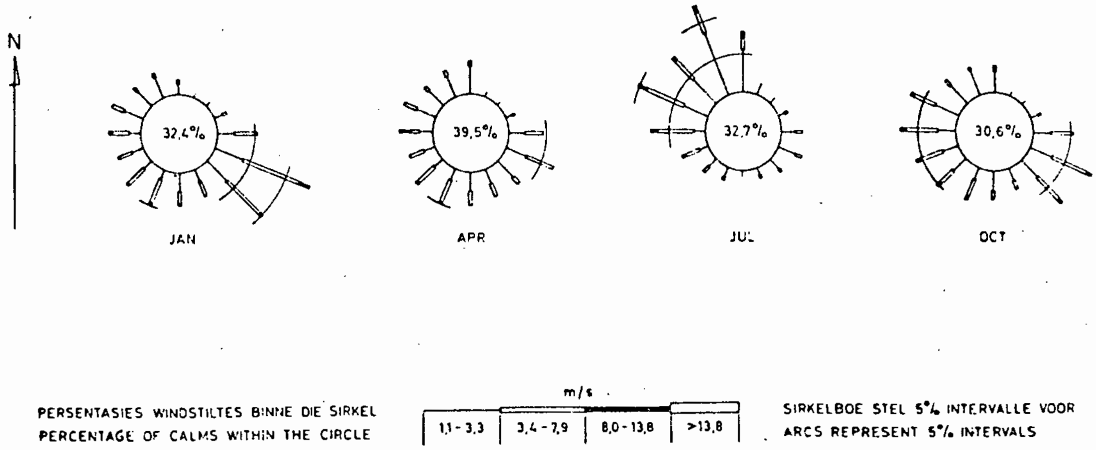
South	% Slope	J	F	M	A	M	J	J	A	S	O	N	D	$\bar{x}$ Annual
Outeniqua	30	,98	,93	,88	,65	,55	,53	,47	,61	,74	,86	,95	,98	,81
Oudtshoorn	30	,97	,90	,78	,52	,21	-	,09	,41	,68	,84	,92	,98	,79
Outeniqua	60	,90	,78	,63	,35	,20	,16	,11	,30	,52	,69	,86	,92	,63
Oudtshoorn	60	,88	,75	,53	,16	-	-	-	-	,36	,63	,81	,91	,61
North														
Outeniqua	30	,96	1,02	1,19	1,23	1,45	1,42	1,42	1,30	1,19	1,06	,98	,94	1,13
Oudtshoorn	30	,95	1,02	1,13	1,36	1,57	1,90	1,73	1,47	1,24	1,05	,94	,93	1,12
Outeniqua	60	,88	,98	1,22	1,38	1,70	1,74	1,74	1,48	1,26	1,03	,90	,83	1,16
Oudtshoorn	60	,85	,96	1,15	1,56	2,0	2,50	2,27	1,71	1,36	1,05	,88	,82	1,15

Most slopes and aspects have similar values for the summer months, but widely differing values for winter. Steep north slopes have a high evaporative demand throughout the year and show the least seasonal variation in PE. Steep south slopes vary from high PE in mid-summer to very low, or sometimes no PE in winter and show the greatest seasonal variation. These calculations thus provide some quantitative insight into the annual and seasonal effects of slope and aspect on moisture regimes.

The above discussion demonstrates the climatic context of the study as one of strong precipitation gradients related to altitude and major differences in microclimate and moisture regime controlled by topography. Dominant aspects on the east-west trending mountains are north and south, and the high relief results in steep slopes. Thus the consequences for plant growth are considerable.

Additional effects of elevation on climate have been poorly instrumented. Expected gradients are temperature, snow, cloud cover, mist precipitation and windrun. Any interpretation of vegetation gradients over mountains is complicated by the inter-dependence of these variables. I believe, however, that the emphasis placed on available moisture in this chapter reflects it's significance as a controlling factor in nature.

Fig. 1.5 Windrose for George (ex Weather Bureau, 1975 - Surface Winds. Climate of South Africa, Pt. 12).



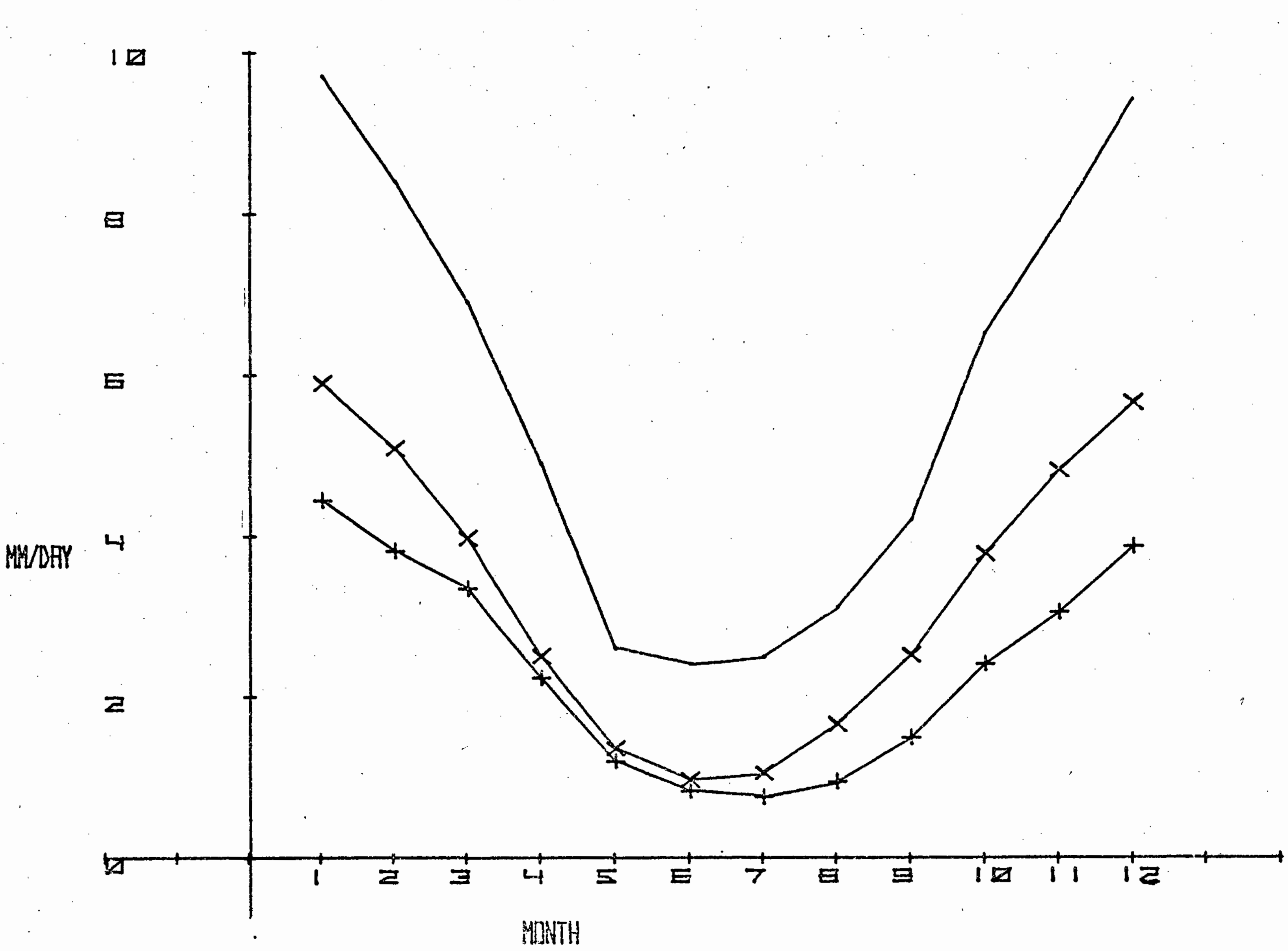


Fig. 1.7 Measured pan evaporation (———) and calculated evapotranspiration (PE) using Penman's equation (✕✕✕) and Thornthwaite's equation (+—+—+). An albedo of 0,2 was used for Penman's equation. Weather data from Oudtshoorn Experimental Farm (unpublished). Note that Thornthwaite's equation underestimate PE for arid areas.

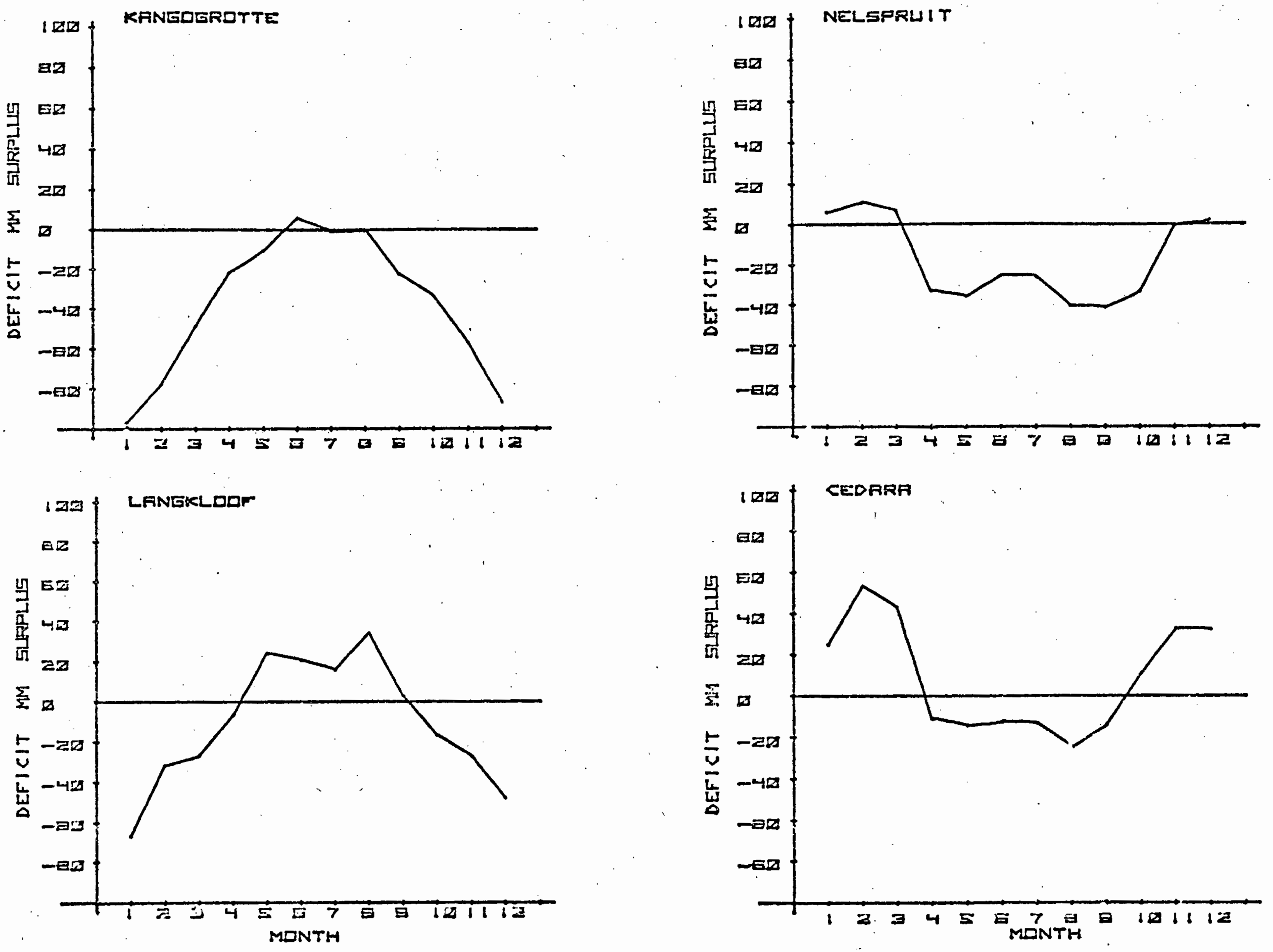

KANGOGROTTE
NELSPRUIT
LANGKLOOF
CEDARA
DEFICIT MM SURPLUS
100
80
60
40
20
0
-20
-40
-60
-80
1 2 3 4 5 6 7 8 9 10 11 12
MONTH

Fig. 1.8 (Cont.)

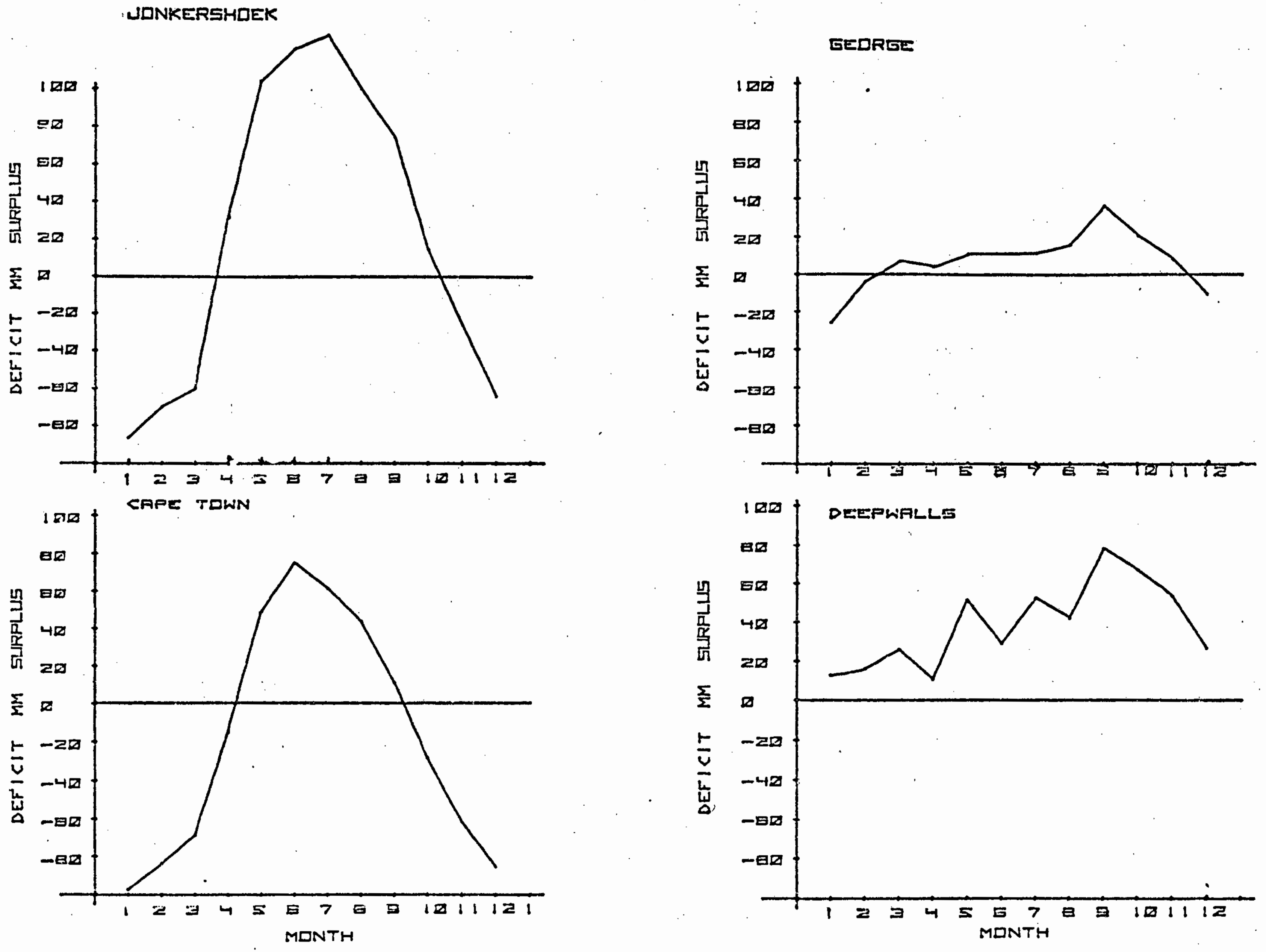


Fig. 1.8 Comparative water balance in winter rainfall (Jonkershoek, Cape Town), non-seasonal rainfall (George, Diepwalle, Kangogrotte, Langkloof) and summer rainfall areas (Nelspruit, Cedara). The y axis is monthly moisture deficit or surplus (R-PE) with PE calculated by Thornthwaite's equation. Data ex Weather Bureau (1960, 1965).

1.4 SOILS

Kruger (1979) described fynbos soils as structureless, acid to very acid, and with a very low base saturation. He stated that most are podsols or podsolized to some degree. There is textural variation according to parent material with sands and loamy sands predominating on the quartzites of the Table Mountain Group. He listed Mispah, Glenrosa and Cartref as the most common soil forms in mountain environments. Soils with yellow, reddish or brown horizons (Hutton, Clovelly, Glenrosa) are common in the warmer, interior mountains with lower effective precipitation. Podsolization, in contrast, is especially pronounced in the cooler, more humid, southern ecosystems. Boucher's (1978) description of Cape Hangklip soils and Lambrecht's (1979) review largely conforms with Kruger's generalizations.

Studies of fynbos soils in the Southern Cape mountains are very limited. Neethling (1970) briefly discussed mountain soils on the polar slopes of the Outeniquas. The Department of Agricultural Services has recently completed a land-type map of the 1:250 000 Oudtshoorn sheet, which covers both study areas and includes information on soils.

To supplement the scanty information on mountain soils, a number of observations were made on soil profiles in the two study areas. Profiles were studied by auger at each vegetation sample (Chapter 2.3), a poor technique in shallow, rocky soils, and by soil pits and exposures along roads. Soils were classified according to the South African binomial system (MacVicar et al. 1977). Laboratory analyses were undertaken by Saasveld, D.R. de Wet Forestry Research Station and the Citrus Exchange laboratories (see Appendix 1 for methods).

Mountain soils in the Southern Cape show complex distribution patterns with considerable variation in soil development and degree of weathering within small areas. Because of the steep topography, the processes of colluviation and deposition vary in intensity resulting in profiles of mixed origin and parent material. Butzer and Helgren (1972) recognized a series of palaeosols on the coastal forelands and deduced marked quatenary climatic change to account for their pedogenesis. Palaesols are probably poorly preserved on steep mountain slopes with their high erosion rates, but add additional complications to interpretation of an already complex soil pattern.

1.4.1 Swartberg

Swartberg soils are mostly apedal loamy sands and sandy loams, very stony on north and lower south slopes and with pH from 4-6. North slope soils show minimal B development and are typically Mispah and Glenrosa (SW6 and SW7 of Appendix 2). Red soils (Hutton and Oakleaf - Leeufontein series) occur locally on stable talus slopes and colluvial fans (SW5, SW8). Most north slope soils have developed in situ. A horizons are typically darker coloured at high elevations becoming dark brown at low elevations.

South slope soils have a more complex distribution and genesis. They are mostly moderately deep, dark coloured, acid (pH 3, 5 to 5,5) loamy sands and sandy loams with red, yellow or dark brown subsoils (Oakleaf - frequently Leeufontein, Hutton, Glenrosa and, more rarely, Clovelly form soils). The subsoils have mostly developed in situ, but A horizons are typically demarcated by a stone line indicating colluvial origin.

Deeper red and yellow soils occur on remnants of a Tertiary Surface at about 1 000 m (SW2). These soil patterns conform with Kruger's (1979) generalizations for soils of the drier, interior mountains.

1.4.2 Robinson's Pass

The most striking difference between the two study areas is the occurrence of eluviated (E) horizons and, rarely, podsols in the Outeniqua mountains. No E horizons were found in the Swartberg, probably because of insufficient water movement through the soil under the more arid climate. North slope soils on the Outeniquas are mostly moderately deep, very rocky or stony, loamy sands and sandy loams. E horizons occur in Cartref form soils on steep slopes at higher elevations (R5). Most of the mid- and lower-elevation slopes, however, have Mispah and Glenrosa Form soils (R8, R10). Moderately deep and deep red and dark brown soils (Hutton, Oakleaf Form) occur locally on talus slopes, pediments or remnants of Tertiary surfaces (e.g. R7, R9).

South slope soils, as in Swartberg, are more highly developed, more complex and more variable. There is no simple relationship with underlying geology or with elevation. The soils are mostly finer textured loams, fine sandy loams and sandy clay loams and very acid (pH 3,3 to 5,1). Deep and moderately deep red Hutton Form soils occur at lower elevations, apparently associated with relict erosion surfaces and frequently supporting <u>Protea aurea</u> communities. These soils sometimes overly yellow apedal subsoils (e.g. RX11) and are not included in the binomial classification system. Moderately deep Oakleaf and Glenrosa Form soils with dark brown subsoils occur at low- and mid-elevations, usually on steep or convex slopes (RX1, 3). They are sometimes associated with shallow and moderately deep, medium textured yellow soils (Clovelly Form) especially on clayey elements of the Cedarberg, Chando and Peninsula Formations. These soils usually have a stoneline separating the A and B horizons. Textural and consistence contrasts across the transition appear to restrict roots to the topsoil (RX12, RX6).

Cartref soils with eluviated, sandy, E horizons occur at higher elevations. Leucadendron uliginosum is frequently an indicator species, (e.g. RX4, RX5). The A horizons are mostly gravelly and detection of the E horizon by augering is difficult.

No true podsols were found in the study area (Cartref is formed by a process of eluviation, not podsolization and may be found, for example, in monsoonal climates in Mocambique!). A single profile (R2) and several augerings were located in soils with a horizon resembling the Bf (thin ironpan) horizon of podsolic soils defined by the soil survey of England and Wales (Avery, Claydon and Ragg 1977). These soils (sometimes termed placaquods - D. Grey pers. comm. 1980) had an A horizon rich in organic matter overlying a thin, but hard, iron duripan which strongly limited root penetration (RX2).

High altitude slopes below Ruitersberg supported deep peaty soils. No pits were dug in these soils and auger descriptions only were made. They consisted of a metre or more of highly organic material ($>$80%

weight loss by ignition) directly overlying rock. They occurred on very steep slopes (60%+) and appeared to be unstable. Crescent shaped depressions (up to 5 m in length and 3 m broad) occurred on them either devoid of vegetation or with a low graminoid/cryptogamous vegetative cover. These are presumably formed by soil slip.

The soils of the Robinson's Pass study area do not conform readily with Kruger's (1980) generalizations. Podsols, in particular, were not as common as anticipated. The distinction between Cartref form soils and podsols with remnant ferrihumic B horizons is not always easily made. A great deal more study will be needed to fully understand the complex patterns and the genesis of soils on the polar slopes of the Outeniquas.

1.4.3 Chemical Characteristics

Kruger (1979) has described mountain fynbos soils as "universally poor, with base saturation levels of around 20 to 40% (ratio of net exchangeable cations to cation exchange capacity), with negligible amounts of extractable phosphorus and low levels of total nitrogen (0,1 to 0,2%)".

Few soil analyses from mountain fynbos have appeared in the literature though some are available for the Southern Cape (Neethling 1970; van Daalen 1980). These mostly confirm the generalization (Cowling and Campbell 1980) that fynbos soils are poor in exchangeable bases with low levels of phosphorus and nitrogen. Van Daalen (1980) reported similarly low nutrient levels in the Knysna forests.

Soil samples from representative pits in the two Southern Cape study areas are shown in Appendix 1 and summary statistics in Table 1.7. The sample size is limited and the mean value can thus only provide a very general picture. The data is not adequate for defining plant nutrient régimes since bulk densities were not estimated (Mehlich 1980).

The data in Appendix 1 show a generally low level of exchangeable cations with dystrophic subsoils (MacVicar et al. 1977) under proteoid and/or ericaceous shrublands, mesotrophic in some xeric restioid or arid fynbos sites and eutrophic in Waboomveld, arid fynbos, and Karroid succulent shrublands. Subsoil base saturation appears to vary with moisture régime ranging from 10 to 25% on the more mesic southern slopes, 30 to 50% on upper north aspects, and 80-100% in relatively xeric restioid communities, waboomveld and arid fynbos. No generalizations can thus be made on the degree of leaching of fynbos soils (cf. Kruger 1979) though broad physiognomic/structural groups may correlate with particular leaching régimes.

An interesting feature of all but the driest sites, is the concentration of bases in the A horizon with Svalue and base saturation decreasing strongly in the B or E horizons. This strongly suggests nutrient concentration and retention by plants in a closed nutrient cycle similar to that of tropical rainforest (Walter 1979) with similar implications of ecosystem collapse if management practises break the cycle leading to permanent nutrient loss.

Australian workers have demonstrated the significance of phosphorus and nitrogen in structuring heathland vegetation analagous to fynbos (Beadle 1966; Loveless 1961, 1962; Specht 1975; Heddle and Specht

1975; Specht, Connor and Clifford 1977). Cowling and Campbell (1980) have suggested that low nutrient levels, especially phosphorus, are similarly important in fynbos. Soil analyses from the two study areas, whilst showing generally low phosphorus levels, differed significantly. Mean total phosphorus in the Swartberg was nearly six times higher (124 mg/kg) than Ruitersbos (23 mg/kg). R.L. Specht (pers. comm. 1979) has suggested that these differences may account for differences in grassiness between the two study areas (Chapter 4). R X 2, with total P of ,0007% is comparable with some of the lowest values reported by Groves (1980) whilst the Swartberg samples (e.g. SW 3, ,019%) exceeds Australian heathland values by several orders of magnitude.

Total soil nitrogen does not differ significantly between the two study areas with means of 965 (,097%) and 1238 (,124%) mg/kg in Swartberg and Ruitersbos respectively. These values fall within the general range of Australian heathland soils (Groves 1980).

The role of trace elements in fynbos nutrition is virtually unknown (Schutte 1960). The Ruitersbos forestry plantations are notorious for extremely poor pine growth due to manganese deficiency (Lange 1969). Manganese deficient areas are covered by a wide range of fynbos communities with no obvious signs of compositional changes or nutrient deficiencies in problem areas.

In summary, soils of the study areas are generally poor in bases, phosphorus and nitrogen, but with considerable local variation, especially in base status, according to the leaching régime. There are large differences between the coastal and inland ranges in total phosphorus and lesser differences in bases, especially calcium, with Swartberg having the richer soils.

TABLE 1.7. Summary Statistics for Selected Soil Analyses (See Appendix 2) from surface (A) and Subsoil (B) horizons. Svalue is the sum of exchangeable Na, K, Ca, Mg.

	n		$pH-CaCl_2$		S/100g clay		% Base Saturation		Total N ppm		Total P ppm		Bray 2 P ppm		%C
	A	B	A	B	A	B	A	B	A	B	A	B	A	B	
Swartberg															
South Aspects	4	4	4,24	4,47	12,1	2,6	36,3	80,8	1151	833	133	169	8,7	5,5	1,97
North Aspects	4	3	4,6	4,9	20,3	19,8	69,3	76,2	779	-	115	-	11	2	2,58
Total Mean	8	7	4,4	4,7	16,2	10,0	55,4	44,5	965	-	124	-	9,5	40	2,31
Ruitersbos															
South Aspects	4	3	3,94	4,17	21,0	14,2	38,3	40,2	1439	-	22	24	5	-	3,1
North Aspects	5	4	4,29	4,66	47,3	22,4	81,6	64,1	1078	-	24	-	4,8	-	2,72
Total Mean	9	7	4,13	4,45	35,6	18,9	62,4	53,9	1238	-	23	-	4,9	-	2,89

1.5 VEGETATION

Several recent reviews have appeared on the woody vegetation of the Southern and South-Western Cape Province (Taylor 1978; Goldblatt 1978; Kruger 1979; Boucher and Moll 1980). With the exception of the Knysna Forests, however, few detailed vegetation studies have been made in the Southern Cape.

Acocks (1953) recognized six veld types within the vicinity of the study areas (Table 1.8). The coastal ranges are more mesic than the Swartberg and evergreen, sclerophyllous Podocarpus, Ocotea, Cunonia forest occurs in moist, protected sites in the mountains. They exist in dynamic equilibrium (van Daalen 1980) with mesic ("hygrophilous", Taylor 1978) fynbos vegetation which occurs in similar habitats, but also over a wide rainfall gradient on nutrient poor soils. Coastal Rhenosterveld (Acocks veld type 46) occurs on Cretaceous and Recent sediments, with fynbos remnants on granite and silcrete plateaus between the Outeniqua mountains and the sea. A spinescent and succulent scrub (Acocks Gouritz River Scrub phase of Valley Bushveld, veld type 23) occurs on valley slopes within the area. Fynbos gives way to renosterbosveld and, in the little Karoo, to Succulent Mountain Scrub on base rich substrates north of the Outeniquas.

In the drier climate of the Swartberg, fynbos occurs widely on T.M.S. sandstone substrates. Very small forest remnants still occur in ravines with marked topographic shadeing e.g. at Waterval between Schoemanspoort and Rus en Vrede. Mountain rhenosterbosveld occurs extensively in the Cango Valley, on base rich soils on the southern Swartberg foothills. Acocks (1953) mapped no rhenosterveld on the northern foothills of the Swartberg and fynbos grades directly to Succulent Mountain Scrub on T.M.G. sandstones and Bokkeveld shales on dry, steep, north facing slopes.

The Outeniqua study area was entirely restricted to mountain fynbos whilst the Swartberg area included both fynbos and Succulent Mountain Scrub (Spekboomveld). Besides Muir's (1929) work in the Riversdale area and Phillip's (1931) Clementsian account of fynbos successional patterns in the Knysna Forests, no detailed published accounts of the vegetation of the Southern Cape coastal ranges could be traced. A vegetation map of the Moordkuil's catchment (immediately east of the Ruitersbos study area) using dominance type techniques (Whittaker 1978) has recently been completed as part of a catchment planning exercise (Seydack, Horne 1980, unpublished).

Vegetation studies in the inland mountains have been similarly neglected. Taylor (1979) has mapped the Rooiberg, an island like range in the Little Karoo, for catchment planning purposes. His units are largely physiognomic/physiographic but conform, in a general way, with vegetation patterns in the Swartberg and parts of the Kammanassie mountains.

Moffett and Deacon (1977) have studied the flora and vegetation in the vicinity of Boomplaas Cave, an archeological site, on the southern foothills of the Swartberg near the study area. They recognized seven vegetation types, one of which was Proteoid fynbos, two Elytropappus shrubland, one "Asteroid" Shrubland with Pteronia incana, Dodoneaea and Relhania, and three "bush" or woodland types. They discuss the evidence for a much more open, grassy vegetation in the late Upper Pleistocene before the Holocene warming over the last 10 000 years.

Recently, mountain fynbos of the eastern Swartberg (east of Meiringspoort) and western Swartberg (west of Gamkaspoort) has been mapped (by the author) at an extensive Scale of 1:100 000 for mountain catchment planning purposes (Seydack, Horne 1981). The units were defined by informal dominance mapping methods (Whittaker 1978) using mixed physiognomic/structural and floristic criteria. The units and their characteristics are listed in Table 1.9.

1.6 LAND USE

Both the coastal and inland study areas were confined to state forest land. Forestry objectives in mountain catchments include the protection of stream source areas and their management for maximum, sustained water yield, the conservation of mountain ecosystems and the provision of recreational facilities (Wicht 1970). Fire is the most widely used tool for water and conservation management and has the greatest land-use impact on ecosystem structure and dynamics. Variation in fire frequency (van Wilgen 1980; Bond 1980b), intensity (Rourke 1972) and season (Jordaan 1948, 1965; Bond 1980b) may radically alter the gross structure of the vegetation and also affect floristic composition (Kruger 1977; Campbell and van der Meulen 1980). The effects of fire season and frequency appear to be particularly pronounced in the drier inland ranges.

Fynbos in the Swartberg study area was relatively old over the sampling period (15-50 years since the last fire) probably as a consequence of fire suppression practises in the mid-decades of the century. Subsequent to field work most of the area has been burnt by fires ignited by lightning, arson, and prescribed burns. The absence of a proteoid layer in some areas was probably due to fire history.

Fynbos in the Ruitersbos area was between 12 and ±20 years old with (probably) older vegetation in the arid areas. No marked fire effects on the vegetation, such as eradication of the proteoid layer, were visible.

Other land-use impacts such as roadbuilding and grazing of livestock were negligible and appeared to have no significant effect on vegetation structure and floristic composition.

TABLE 1.8. Acock's Veld Types (1953) in the vicinity of the two study areas in relation to substrate and moisture régime. Veld type numbers in parentheses.

Moisture Regime	Base Rich	Base Poor
	Swartberg	
Mesic		False Macchia (70)
Intermediate	Mountain Rhenosterveld (43)	False Macchia (70)
Xeric	Succulent Mountain Scrub (25)	Succulent Mountain Scrub (25)
	Ruitersbos	
Mesic		False Macchia/Knysna Forest (4)
Intermediate	Coastal Rhenosterveld (46)	False Macchia (70)
Xeric	Valley Bushveld (23) Gouritz River Scrub	False Macchia

TABLE 1.9 Major Fynbos Vegetation units used in Catchment Planning in the Eastern and Klein Swartberg (Directorate of Forestry and Environmental Conservation 1980, 1981. Units were defined informally by mixed floristic/structural physiognomic criteria. The floristic composition, especially of non-Proteaceous shrubs, showed little resemblance between the two areas, but structure, habitat, and some Proteaceae and Restionaceae remained constant.

Symbol	Name	Habitat	Diagnostic Features
H_1	Communities of High Mountain Crests.	High mountains, especially south aspects. 1 800 m+.	Low Ericaceous and ericoid shrublands. Proteaceae occur only as low, spreading shrubs - no erect forms. "Unusually high" restioid cover in the west.
P_1S	Proteoid Shrublands of the Upper Southern Slopes.	Steep south aspects. ±1 400-1 800 m.	*Protea punctata* dominant where proteoids present. Ericaceae diverse and abundant. Grasses (*Pentameris* spp.) sedges and tufted, unbranched restios (*Hypodiscus alboaristatus*) relatively common. Tall restios absent.
P_2S	Proteoid Shrublands of the Lower Southern Slopes.	Steep to gently sloping S. aspects. ±950-1 400 m.	*Protea repens*, *P. lorifolia* typical. Ericaceae neither as common nor as diverse as P_1S. Less restios and more grasses and non-proteoid shrubs than the analagous P_2N. Tall restios present (*Cannamois dregei*, *Willdenowia teres*).
P_1N	Proteoid Shrublands of the Higher North Slopes.	Steep, rocky, N. aspects. ±1 750+.	Discontinuous Proteaceae patches dominated by *P. punctata*, *Leucadendron album*. Less shrub cover, fewer shrub species than S aspect analague (P_1S). Distinguished from P_2N by presence of *Hypodiscus synchroolepis*, *H. alboaristatus*, *Elegia parviflora*, and relatively high cover of grasses and/or tufted sedges. Tall restios present locally.
P_2N	Proteoid Shrublands of Mid- and upper North Slopes.	Steep, rocky, N. aspects. ±1 400-1 750 m.	Proteoids present but open or scattered, in a tall restio matrix. Non-proteoid shrubs poor in species with low cover but increasing in importance at higher elevations. Grasses are insignificant.
W_1	Waboomveld.	Lower S, E and W aspects.	Very variable. *Protea nitida* always present. "Subtropical" grasses, e.g. *Cymbopogon*, *Themeda*, *Heteropogon* characteristic. Compositate prominent Restios unimportant. *Cheilanthes eckloniana* usually present. Rich in deciduous geophytes.
A_1	Arid Fynbos.	Steep, rocky, mostly N. aspects. ±1 400 m.	Low, open or sparse shrublands dominated by shrubs. Total cover usually 50%. Tall restioids are sparse and restios seldom important. Grasses frequently visually prominent. Succulents (and sometimes bipinnate ferns) present.

CHAPTER 2

METHODS

2.1 SAMPLING STRATEGY

Primary sampling requirements are that samples should be representative of the vegetation studied and economically sited with respect to study objectives. Selection procedures in phytosociology remain controversial with essentially opposed viewpoints between the European schools of phytosociology and Anglo-American ecologists.

Mueller-Dombois and Ellenberg (1974) characterise the European approach as essentially subjective with or without preconceived bias and the Anglo-American as objective with sample location according to chance. Werger (1974) describes the Zurich-Montpellier Site selection method as "the most efficient way to find the units or associations, which are types abstracted from actually occurring stands or phytocoenoses, is to select for sampling those stands which may possibly be examples of such an association". Thus the observer must have a relatively detailed knowledge of the communities he wishes to study before he can select stands "typical" of preconceived associations. However, Werger recommends that prejudice about the expected results of a phytosociological study should be avoided in site selection! Ideal application of this sampling approach is dependent on the vegetation conforming with the "community unit hypothesis", i.e. that vegetation consists of natural entities in contact with each other along narrow boundaries (Werger 1974). If this hypothesis applies, selection of stands overlapping community boundaries will tend to be rare and associations defined analytically will be relatively distinct with few inter-grades.

The Zurich-Montpellier approach has been much criticised because of its subjectivity and apparent circularity of argument e.g. "associations are being studied in terms of samples taken in terms of associations" (Whittaker 1956). It would seem that subjective sampling procedures are prone to oversimplifying or even falsifying vegetation patterns because of a priori bias on what communities ought to be present and where (in terms of site) they should occur. An added disadvantage in many parts of Africa, and not least in the Southern Cape mountains, is that problems of access may bias results to easily reached vegetation with the justification, conscious or subconscious, that this is "typical". Thus, whilst subjective sampling location is perhaps the most economical strategy, it may be far from representative of the vegetation studied.

Objective techniques include random, stratified random and systematic sampling (Greig Smith 1964; Kershaw 1975; Shimwell 1970; Mueller-Dombois and Ellenberg 1974 etc.). The former are essential if probabilistic statistics are to be used for data analysis. Since this is not normally the case for most phytosociological techniques (Kruger 1974), these techniques, which are time consuming and therefore expensive, must be justified in other ways. Taylor (1969) and Kruger (1974) used systematic sampling in fynbos with poor results in terms of community abstraction. Many plots were placed on obvious community boundaries with markedly heterogeneous vegetation. Advantages in terms of representativeness of the real vegetation may thus be outweighed by analytical difficulties in abstracting vegetation types meaningful to the worker and by the added expense of field technique.

More recently, greater flexibility of sampling strategy seems to have been accepted. Werger 1974, for example, states that a Zurich-Montpellier analyses using stratified random, random or systematic sampling may also yield good results whilst Ivimey Cook and Proctor (1966) state that it is difficult to "collect any substantial body of phytosociological data to support a conclusion seriously at variance with the facts".

In this study samples were selected by random sampling (to avoid bias to easily accessible, and often unrepresentative vegetation) stratified by altitude (to allow equitable coverage of the main environmental gradient), but with subjective decisions on precise sample location.

Subjective decisions were reduced by defining criteria for rejecting plots. Reconnaisance surveys were used to identify suitable transects across the mountains from southern to northern foothills, with relatively easy access and with mature vegetation. Each transect was divided into six altitudinal belts each, north and south of the watershed. Four of these belts were located between the contour approximately enclosing the foothills and the contour halfway between the foothills and the mountain crest and two belts above the midway contour (Fig. 2.1).

No objective guides to sampling intensity are available. Sampling intensity used in this study was thought adequate to express vegetation and environmental gradients. Preliminary studies indicated relatively rapid vegetation change from mid-to low-elevations and these areas were, accordingly, sampled more intensively. Samples were located by random co-ordinates projected onto a 1:50 000 topographic map with a stratification of four samples to each altitudinal belt. In addition, up to four samples were located on the highest elevations in the study area. Fifty samples were eventually described on the Swartberg and sixty five in the Outeniquas, the high number in the latter reflecting the greater topographic variability.

Sample selection was subject to the following constraints:

1) the vegetation must be mature (i.e. eight years or more since the last fire)

2) the site must be free from marked topographic shading e.g. ravines were not sampled

3) the site must be free of disturbance e.g. by road building, heavy infestation of alien plants, excessive erosion

4) the sample must be approximately uniform within the plot in terms of surface type and relief

5) only north (337^{0} to $22^{0}50'$) and south ($157^{0}50'$ to $202^{0}50'$) aspects were studied.

The latter constraint was selected because these are the dominant aspects in the S. Cape mountains and the restriction should simplify environmental interpretation.

2.2 SAMPLE SIZE

Optimal sample size in phytosociological studies has received much study, but few firm guidelines have emerged (cf. summaries of research done in Greig Smith 1964; Shimwell 1970; Mueller-Dombois and Ellenberg 1974). Many studies bypass explicit consideration of sample size by using plot dimensions used by previous workers. Mueller-Dombois and Ellenberg for example suggest empirical values for temperate vegetation of 10-25 m^2 for dwarf-shrubheath, 50-200 m^2 for forest undergrowth and 200-500 m^2 for forests including canopy trees.

Sample size is a compromise between maximum information obtained and minimum effort expended. The problem has frequently been approached by the concept of minimal area - the "minimal size of area in which the community can be represented", Werger (1974). The most efficient sampling unit is then the size of, or slightly larger than the minimal area. The latter is usually assessed by examining graphs of species against area from successively larger plot sizes. Usually the slope of the curve decreases with increasing area and this is taken to be the minimal area. However, Werger (1972) has summarised the literature on minimal area, plot size and species area curves and concludes that an objective definition of minimal area seems impossible. He suggested a pragmatic approach using Gleason's (1925) expression for the species area curve

$$y = a + b \log e X$$

where a and b are constants calculated from a regression of species on area. Species number in 1 ha (calculated from the equation) are taken to have an information content of 100%. The investigator

TABLE 2.1. Estimates of mean plot size from species area curves for selected information levels (see Text).

Information Content(%)	40	50	60	70	80
Plot Size (m^2)	12,2	35,9	108,6	330,9	1021,9
Ratio of plot Size Increase for 10% Information increase	-	2,95	3,02	3,05	3,09

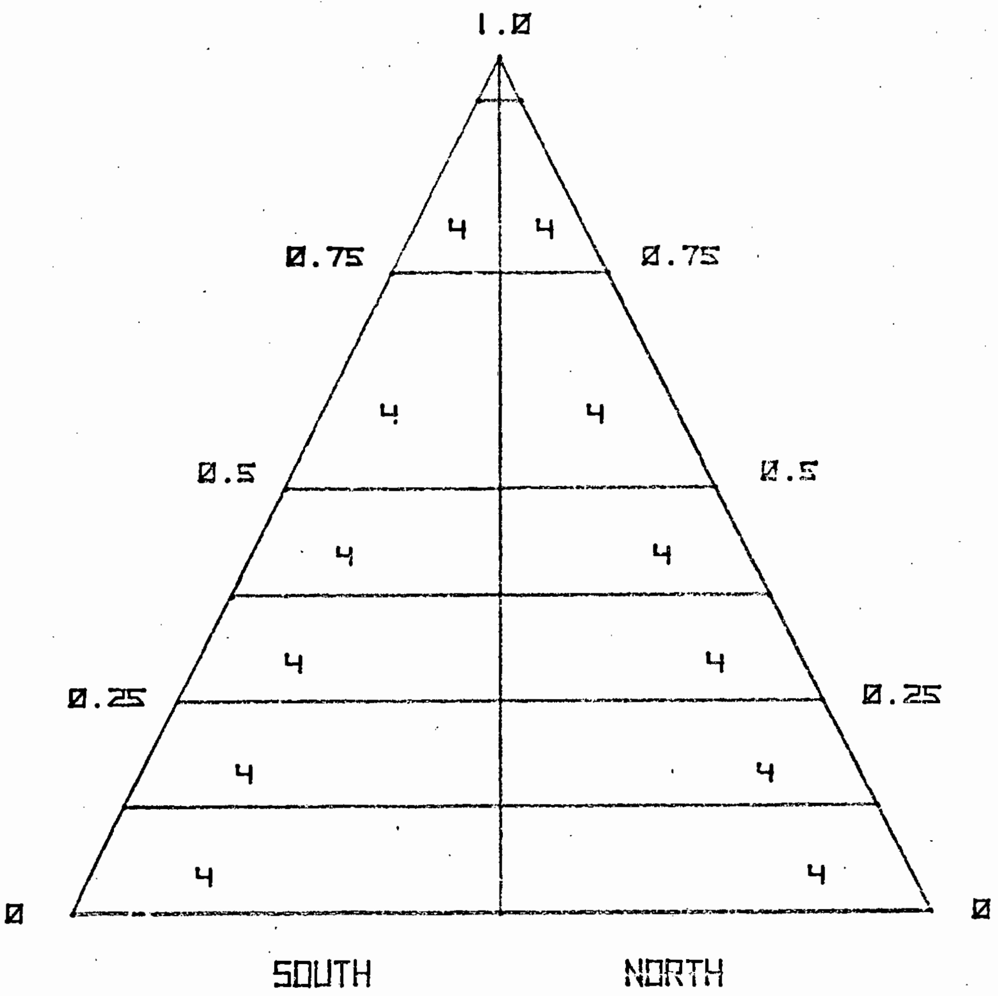


Fig. 2.1 Sampling Design. The triangle represents a mountain divided into north and south aspects. The contours altitudinal belts with four random samples/belts and four samples on the mountain crest (See taxt).

must make a subjective decision on the required resolution e.g. an information content of ±50% and calculates the expected area which is the desired plot size.

This approach was used in this study (Table 2.2). Nested plots containing plot sizes of 1, 5, 10, 50, 100, 500 and 1 000 m^2 were studied in the Swartberg (8 plots) and Ruitersbos (4 plots). For a 10% increase in information content (species number) a threefold increase in plot size is required. 50-60% information content yielded average plot sizes of 36 and 109 m^2 respectively.

These fall within the range used in several studies in fynbos e.g. Kruger 1974, 3 x 5 m; Werger, Kruger and Taylor 1972, 10 x 10 m; Taylor 1969, 5 x 10 m; McKenzie, Moll and Campbell 1977, 10 x 10 m. For a higher information content prohibitively large plot areas are required. A plot size of 5 x 10 m, with the long axis orientated perpendicular to the slope, was used in this study as a compromise between efficiency and optimal information content.

2.3 FIELD AND LABORATORY PROCEDURES

Vegetation

Percentage cover of species represented by above ground plant parts within the sample area was subjectively estimated. Rare species were given a cover value of 0,5%. Deciduous geophytes and annuals were recorded when seen, but not included in the analyses. Several species, especially forbs and some herbs, were excluded from the analysis because of identification difficulties. Additional species within a 2 m perimeter of the plot were recorded as present with a cover value of 0,1. Mean heights to the tallest vegetative portion of each species were estimated. In addition each species was classified according to a number of structural criteria (see below).

Total plant cover and total litter cover were estimated subjectively. Veld age was assessed by bud scale counts on Proteaceae or, in arid areas with no vegetation cues, arbitrarily assigned an age of 40 years.

Site

Site factors measured at each sample point are listed in Appendix 3 together with the codes used in analysis. The table is largely self-explanatory. Altitude was measured by a barometric-type altimeter calibrated against spot heights on a 1:50 000 topographical map. Slope was measured with an Abney Level. Aspect was measured with a prismatic compass and corrected for magnetic declination. Aspect was coded as two variables - a north - south component (cosine of true north) and an east-west component (sine of true north). The effects of slope and aspect on radiation were expressed as a radiation index (Frank and Lee 1966).

Soil augerings were made at each sample site and soil properties recorded. Augering is not a satisfactory sampling procedure in shallow, rocky soils. Excavation of soil pits is the only effective method in these conditions but is particularly time consuming in the inaccessable terrain. Estimates of effective depth were made, but these are of limited value without pits. Soil measurements were largely confined to the A horizon. Subsoil horizons were recorded but ignored in the analysis except in estimates of soil moisture regime. This pragmatic approach is the most convenient in the field but reduces the interpretive value of the data. *Protea nitida* veld, for example, appears to be confined to rather deep talus soils. These soils cannot be satisfactorily separated from shallow Mispahs overlying bedrock using soil augers thus obscuring soil-vegetation patterns.

Soils were described by standard techniques (Soil Survey Staff 1952). Permeability was measured by estimating the time interval at which water dropped onto a dry ped disappears. Categories were (i) very rapid - each drop disappears directly into the soil and no water film develops (ii) rapid - slight water film develops but disappear in less than one second (iii) moderate - water film disappears between 1 and 5 seconds (iv) slow - film disappears between 5 and 15 seconds and (v) very slow - greater than 15 seconds. Extremely slow permeability was found in some soils despite their coarse texture. Consequently water drop penetration time, a method for estimating water repellency, was recorded in the laboratory ([illegible] Richardson and Hole 1978). This variable was only recorded for the Ruitersbos study area.

pH was measured in a saturated water paste. Organic matter was measured by weight loss after heating at 475°C for 8 hours. Conductivity of a soil paste was measured for Ruitersbos only and corrected to a temperature of 15,8°C by the soils laboratory at Saasveld. Conductivity values had an unacceptably high measurement error as yet unresolved by this laboratory. The values are included in the analysis for Ruitersbos only since they provide the only direct approximation to cation status.

Geology was recorded from a 1:250 000 geology map but does not necessarily reflect soil parent material which may be an admixture of several sources of material. Rainfall was estimated from a 1:250 000 isohyet map. This is subject to several inaccuracies and isohyets are almost certainly too high for high elevations in the Swartberg and for upper and mid north elevations. An approximation to rainfall was also made by measuring the distance of a plot to a line drawn in an east west direction on the southern foothills. Surface Rock cover was estimated subjectively in four different size classes, whilst bare soil was separately estimated.

Some additional variables were recorded but were not used in the analysis. Landform position, for example, was difficult to express, particularly since top slopes and bottom slopes converge in steep, stepped terrain. Landform position is thus of doubtful value in mountainous terrain where moisture movement down slopes may be highly complex.

2.4 VEGETATION STRUCTURE

Floristic studies may be approached either at the level of species distribution in communities or continua, or at a phytogeographic level where patterns of speciation, migration and endemism are of interest. Studies of vegetation structure show a similar dichotomy with an interest either in physiognomy/structure as a tool for classifying and ordinating communities or as an expression of selective pressures operating over evolutionary time.

Early studies combined the two approaches especially for interpretation of world vegetation patterns in terms of climate (Schimper 1903; Raunkiaer 1934). Several physiognomic/structural classifications were subsequently developed with more purely phytosociological objectives (Fosberg 1967; Mueller-Dombois and Ellenberg 1974; Webb et al. 1970) whilst Walter's (1979) studies on the vegetation of the earth is an example of the purely ecophysiological perspective where no attempt is made at classification. Current interest in evolutionary ecology and the adaptive strategies of plants (Pianka 1978) has lead to a tentative synthesis, especially in studies testing structural convergence (Mooney and Dunn 1970; Parsons and Moldenke 1975; Parsons 1976; Cowling and Campbell 1980).

Physiognomic/structural characteristics for describing the appearance of plants and the communities in which they occur have suffered from a confusion of terminology (Shimwell 1971). Shimwell (1971) defined physiognomy as "the external appearance of the vegetation" and structure as "those characteristics related to the spatial distribution of the biomass", especially of whole plants rather than their component organs. Functional attributes are believed to differ by being of adaptive significance to the plant and include features such as periodicity, dispersal mechanisms and Raunkiaerian life form (Shimwell 1971). Curiously, Shimwell does not include leaf size as a "functional" attribute. Linder and Campbell (1979) have pointed out that "structure" may also be a "functional" characteristic in that it has adaptive significance. Given our lack of knowledge of the relationships between plant form and function, it seems that no a priori distinction can be made between functional, physiognomic and structural characteristics (cf. Webb et al. 1970). I shall thus refer to non-floristic characters as physiognomic/structural or structural (for brevity).

In the present study, I wished both to derive and test the effectiveness of a structural classification at a scale comparable to a floristic classification and to test and generate hypotheses on the functional significance of structural characteristics. The latter objective is discussed in Chapter 7.

The class of non-floristic vegetation attributes is enormous. Parsons and Moldenke (1975) selected only those known to have functional significance in their tests of convergence between Californian and Chilean vegetation. However, as Webb et al. (1970) have pointed out, adaptive features are difficult to distinguish from "indifferent" characters. I have followed their approach in selecting a range of attributes, some of apparent functional value, others frequently encountered in fynbos and related shrublands but of unknown significance.

Most structural classifications are based on synthetic growth forms combining several physiognomic/structural attributes, selected on an a priori (e.g. Mueller-Dombois and Ellenberg 1974) or a posteriori basis (Parsons 1976). The relative abundance of different growth forms is then used to derive a classification. An alternative approach, comparing stands on the basis of the relative importance of selected single characters, e.g. glaucous leaves, terete leaves etc. has seldom been used. In the present study I have used a combination of growth forms and single attributes, following Webb et al. 1970, but with the emphasis on the latter.

The floristic complexity and peculiar physiognomic/structural features of fynbos and other winter rainfall vegetation of the world, has lead to several attempts to explain, and classify vegetation structure (Marloth 1892; Schimper 1903; Bews 1925; Adamson 1931; Parsons 1976; Moll et al. 1976; Linder and Campbell 1978). Structural attributes were derived from these studies and from preliminary reconnaisance studies.

Characters noted in relèves and used in the analysis are listed in Table 2.2. Several categories (not listed) were absent in the study area. Others, such as canopy form, leaf aroma and leaf protection (e.g. waxes, resins) were too subjective for consistent field use. An attempt to measure Shrub leaf colour by Munsell charts was foiled by the species richness of the vegetation. Resprout or seed regenerative strategies could not always be recognized with confidence.

Leaf texture is a problematic character. It has the property, like many soil variables (consistence, structure, texture), of classes recognisable to most fieldworkers but difficult to objectively define. Laboratory analyses appear to show real differences in leaf specific weight (B. Campbell 1981 pers. comm.). The following guidelines are tentatively proposed (drawn from discussions with F. Kruger, B. Campbell, R. Cowling and A. Milewski):

Succulent - broken leaves express liquid when squeezed between thumb and forefinger

Semi-succulent ("fleshy") - No liquid expressed but leaves collapse with a rubbery or gelatinous texture when rolled between thumb and forefinger. Leaves relatively thick.

Sclerophyll - Leaves not as above. Breaking when folded. Leaves tend to maintain their shape on drying.

Orthophyll - Leaves thin, not as above, wilting on drying.

2.5 DATA ANALYSIS

There are two major opposing views on the fundamental characteristics of vegetation. The "community unit hypothesis", most explicitly stated by the Zurich-Montpellier School (Werger 1974) assumes that vegetation is discontinously distributed, as discrete units, and exists as natural types.

Early in the century, Gleason (1926) challenged this view and proposed that the distribution of a species is based on its individualistic response to the sum factors impinging on its environment. He proposed that communities varied continuously with gradual changes in abundance along environmental gradients.

These two theoretical arguments have stimulated the development of two major classes of vegetation analysis - classification and gradient analysis (Whittaker 1967; Orloci 1975). For applied purposes, classification has continued to be the most important since vegetation maps can be produced of the units of classification. Gradient analysis has mostly been used by phytosociologists to improve understanding of the relationships of classified units although it has been productive in the development of theoretical ecology (Terborgh 1971; MacArthur 1972). Recently Kessel (1979) has combined gradient analysis with computer technology in a technique, gradient modelling, which holds much promise for natural resource management. He combined gradient models of vegetation into a predictive system so that, for example, vegetation structure, floristics, fire behaviour and successional sequence could be predicted at any locality by specifying co-ordinates for location of a stand on the gradients. The system appears to be more flexible than vegetation maps at presenting information and, since information extraction is more selective, requires less training for interpretation (Kessel 1979). In practice, however, the human need to label will probably never make classification redundant.

Orloci (1975) has clearly stated a number of difficulties in the testing of the continuum and community unit hypotheses. The practical and philosophical difficulties of testing the two hypotheses has lessened the acrimony of the earlier debates (e.g. McIntosh 1967; Cormack 1971) and many vegetation studies use both ordination and classification techniques since the two are frequently complementary (Greig Smith 1964; McIntosh 1967; Orloci 1975).

TABLE 2.2. List of structural-functional characters determined for each species. Only species recognizable throughout the year were included in the analyses.

1. Synusiae (Kruger 1979) following Raunkiaer (1934).

Woody Plants - Tall shrubs > 150 cm (No trees were recorded in the study area).

Phanerophytes (Mid-height shrubs, 100-150 cm
(Mid-height shrubs 50-100 cm

Chamaephytes (Low shrubs 25- 50 cm
(Dwarf shrubs < 25 cm

Hemicryptophytes
Graminoid (Poaceae
(Cyperaceae
(Restionaceae (including <u>Schizaea</u>)

Forbs
Bipinnate Ferns

Geophytes including only evergreen (e.g. <u>Aristea</u>, <u>Corymbium</u>) and semi-deciduous species (e.g. <u>Watsonia</u>)

Classes 2-10 recorded for shrubs and forbs only.

2. <u>Leaf Shape</u>:

Narrow (leaf length > 6X diam.) Divided into small (< 5 mm diam.) and large
Broad (leaf length < 6X diam.)
Aphyllous (leaf-like phyllodes were described as leaves e.g. in <u>Thesium</u>, <u>Asparagus</u>).

3. <u>Leaf Size</u>:

leptophyll	(< 25 mm^2)
nanophyll	(26- 225 mm^2)
microphyll	(226-1125 mm^2)
mesophyll	(2026-182 mm^2)
aphyllous	

4. <u>Leaf Pubescence</u>:

None, on top only, on lower side only, on both sides.

5. <u>Leaf Form</u>:

Isobilateral (most Proteaceae)
Terete (cylindrical, circular in cross section)
Linear (Leaf length > 6X diam.)
Rolled (Ericaceae)
Rolled (non-Ericaceous e.g. <u>Phylica</u>, <u>Passerina</u>, <u>Metalasia muricata</u>, <u>Disparago ericoides</u>)
Other.

Table 2.2 (cont.)

6. Leaf Arrangement:

Elytropappoid i.e. Leptophyllous, adpressed, scale like leaves e.g. *Elytropappus rhinocerotis*, *Helichrysum ericoides*, *Phymaspermum appressum*, *Stoebe capitata*

Decussate e.g. *Penaea cneorum*
Fascicled e.g. *Cliffortia tuberculata*, *Theilera guthriei*, *Aspalathus hystrix*
Whorled including all Ericaceae in the study area
Trifoliate
Lobed e.g. *Paranomus dregei*, *Ursinia anethoides*
Compound (excluding trifoliate)
Cupressoid e.g. *Widdringtonia nodiflora*, *Brunia nodiflora*, but excluding minute, scale-like elytropappoid leaves
Rosette e.g. *Mairea caffra*, *Alepidea capensis*
Undefined.

7. Leaf Texture (see Text):

Orthophyll, intermediate, sclerophyll, semi-succulent (e.g. *Clutia ericoides*, *Lobostemon paniculatum*, *Eriocephalus africanus*, *Zygophyllum fulvum*), Succulent-intermediate, very succulent.

8. Post-fire regeneration (Martin 1964; Kruger 1970):

Only the dominant regeneration strategy for shrubs was coded
Seeds stored in soil
Canopy stored seed (Serotiny)
Resprout from rootstocks
Resprout from undamaged above-ground stems (e.g. *Protea nitida*).

9. Deciduosity:

Evergreen, Winter deciduous, Summer deciduous, Unknown.

10. Spinescence:

Leaf spinescence (e.g. *Cliffortia ilicifolia*), Stem Spinescence.

11. Geophyte - Leaf Size:

Small (leaves < 10 cms long), Medium (11-50 cm), Large (> 50 cms).

GRAMINOID HEMICRYPTOPHYTES

12. Height:

0-25 cm, 26-50, 51-75, 76-100, 101-150, 151+.

Table 2.2 (cont.)

13. Tussock Size:

Tussock size was measured as the apparent mean diameter of a graminoid individual at ground level

Single stemmed, < 5 cm, 5-10 cm, 11-25 cm, > 25 cm.

14. Restionaceae - Growth Forms:

Plumose e.g. *Thamnochortus argenteus*, *Restio rhodocoma*, *R. giganteus*
Coarse, branched stems (coarse = stems > 2 mm diameter) e.g. *Willdenowia teres*
Fine, branched stems (fine = stems < 2 mm diam.) e.g. *Restio sejunctus*, *R. triticeus*
Coarse, unbranched stems e.g. *Cannamois dregei*
Fine, unbranched stems e.g. *Hypodiscus synchroolepis*.

15. Cyperaceae - Growth Forms:

Broad, leafy sedges (i.e. grasslike) broad defined as 5 mm+ e.g. *Tetraria involucrata*
Narrow, Leafy sedges, narrow defined as <5 mm e.g. *Tetraria ustulata*, *T. fimbriolata*
Fine, Restioid - hard, erect, stem-like leaves, fine = < 1 mm e.g. *Ficinia nigrescens*
Coarse Restioid coarse = > 1 mm e.g. *Tetraria cuspidata*
Spreading, mat form e.g. *F. ramosissima*.

16. Poaceae - Growth Forms:

Restioid - nearly leafless, hard stemmed grasses e.g. *Ehrharta ramosa*
Sclerophyllous, coarse. Hard leaved grasses, usually with rolled leaves, coarse = leaf breadth 2 mm+ e.g. *Pentaschistis eriostoma*
Sclerophyllous, fine. Fine = leaf breadth < 2 mm e.g. *Merxmuellera stricta*
Orthophyllous. Soft leaved grasses, usually with relatively broad not inrolled leaves, e.g. *Themeda triandra*, *Erhrharta dura*, *Heteropogon contortus*, *Pentaschistis ampla*
Stoloniferous, e.g. *Brachiairia serrata*.

Classification

Classifications may be monothetic (divisions based on a single attribute) or polythetic (many attributes), agglomerative (group formed by fusion of samples) or divisive (groups formed by division of the set or subset) (Orloci 1975).

Divisive techniques are attractive since they resemble the familiar taxonomic keys, allow selection of a priori attributes and facilitate recognition of plots not included in the original "sampling universe" (Williams and Dale 1965). Association analysis and related methods (Williams and Lambert 1960; Lambert and Williams 1962) were widely used monothetic divisive techniques but class divisions on the chance occurrence of single species produced many misclassifications

(Taylor 1969; Kruger 1974). A polythetic divisive technique, indicator analysis, based on the division of ordinations, has been recently developed (Hill et al. 1975; Hill 1979). This offers the benefits of divisive methods without the limitations of monothetic class choices. Hill (1979) claims that the method is similar to the traditional tabulation methods ofthe Zurich Montpellier School particularly in its classification by both species and stands.

The method is further discussed in Chapter 4 and 5.

Agglomerative classificatory methods, particularly "cluster analysis", have become widely used in phytosociological studies. These generally work by the calculation of an index of similarity or resemblance between all pairs of individuals within a data set. The indices are thus used to group individuals within "clusters" by a variety of grouping procedures (Williams 1971; Orloci 1975; Mather 1976; Webster 1977). Results of the classification are highly dependent on the index of similarity and the grouping algorithm used (Webster 1977; Campbell 1978). In South Africa, cluster analysis has often been used as a rapid sorting procedure with final classification by Braun-Blanquet tabulation methods (Moll and Campbell 1975; Glyphis et al. 1978; Laidler et al. 1978).

The Braun-Blanquet technique, which involves subjective, iterative sorting of species and stands (Werger 1974) has been successfully used in fynbos studies (Taylor 1969; Werger et al. 1972; Boucher 1977, 1978). Despite early criticisms of its subjectivity the method works well to the extent of being used as a test of the effectiveness of numerical methods, especially with increasing recognition of the need for subjective decisions in using "objective", quantitative techniques (Campbell 1978; Walker 1974).

Gradient Analysis

Whittaker(1967) defined two types of gradient analysis. Direct gradient analysis is the ordering of species or stands along known environmental gradients. Ordination, synonymous with indirect gradient analysis (Whittaker 1967; Shimwell 1971) is the ordering of samples by their own characteristics along one or more axes of variation.

Gradient analysis is theoretically attractive because of the similarities between gradient models and Hutchinson's (1957) development of the hypervolume niche model and current interest in competition along resource gradients (Terborgh 1971; MacArthur 1972; Pianka 1978). This has stimulated the development of many numerical ordination techniques.

Austin 1980, has emphasised the dependence of ordination techniques on underlying assumptions of species distribution on gradients and has pointed out that no general theoretical framework yet exists. The consequences are significant and several authors have shown the distortion of axes caused by linear or Gaussian assumptions of species distribution (Swan 1970; Noy Meir and Austin 1970; Gauch, Whittaker and Wentworth 1977).

Gauch et al. (1977) compared several ordination techniques and found that the simple Bray Curtis (1957) technique was most satisfactory followed by reciprocal averaging (Hill 1973). Reciprocal averaging has become a widely used ordination technique despite its characteristic "arch" or "horseshoe" distortion of the first and second axis (Gauch et al. 1977).

Recently the method has been refined to remove the arch and correct scale distortions at the ends of the axes (Hill and Gauch 1980). The new method, termed "Detrended correspondence analysis" is available as a Cornell Ecology Program - DECORANA and was used in this study.

CHAPTER 3

SITE ANALYSIS - ENVIRONMENTAL GRADIENTS

3.1 INTRODUCTION

Gradient analysis of vegetation is linked with Hutchinson's (1957) model of the hypervolume niche (Whittaker 1967). When the fitness of an organism is plotted along a resource gradient, a bell shaped curve usually results. For two resource gradients, fitness can be plotted simultaneously on two axes, for three gradients three axes and continuing for n gradients on n axes to obtain an n-dimensional hypervolume enclosing the complete range of conditions under which an organism can exist and produce offspring.

The hypervolume model, whilst productive of theory, is difficult to apply in the field since the number of resources defining the niche is potentially infinite. A necessary preliminary is the selection of those resource gradients on which competition is effectively reduced, i.e. on which most species can be placed with minimal niche overlap (Pianka 1978). Gradient analysis has proved to be an effective tool for this purpose (Whittaker 1967; Kessel 1979).

Indirect gradient analysis (Whittaker 1967; Shimwell 1970) ordinates vegetation stands relative to each other and the main axes of variation may thus be compared <u>post hoc</u> with possible resource gradients. In an alternative approach, direct gradient analysis, the ecologist uses his intuition to select gradients representing the major resources to which plant species are responding. Stands are then ordinated along these gradients to observe how (if at all) the vegetation does, in fact, respond.

Direct gradient analysis is the more powerful approach since it involves (at least) implicit hypothesis testing - if there is no perceivable response to a gradient then it is probably of minor importance in structuring vegetation. Indirect gradient analysis suffers from weak, ad hoc explanations for vegetation patterns.

I have assumed that the major gradients on which plant species are sorted are those representing the physical features of the site. I have used principal components analysis (PCA) to generate those (orthogonal) axes which maximise the variance in a set of environmental variates.

PCA is a powerful, robust technique for summarising the major trends of variation in a set of variables. Altitude, for example, is a gradient to which vegetation appears to respond strongly though altitude per se has no direct bearing on plant growth. PCA provides a concise summary of variables responding in a similar way to altitude permitting a better understanding of the "complex altitudinal gradient", the variables associated with it and the direction of variation.

Easily measured variables, which are strongly correlated (heavily loaded) with the principal components, may then be selected as axes for direct gradient analysis. I have avoided using the position of the stands themselves on the principal components because the axes are not easily generalized to new study areas.

The aims of the PCA study were thus 1) to define the major environmental gradients independently from vegetation and to explore relationships between site variables and 2) to use the principal components to generate axes for direct gradient analysis and to test whether vegetation structure is, indeed, related to these gradients.

3.2 Methods

PCA (or the related technique of factor analysis) has been widely used in vegetation studies (Goodall 1955; Boaler 1966; Gittins 1969; Ross, Morris 1971; Orloci 1975; Isebrands, Crow 1975 to list but a few). Several authors have shown that the method is inappropriate where non-linear relationships between variables are common. Species distributions are characteristically non-linear and the resultant distortions have lead to decline in the use of PCA in vegetation studies in recent years (Swan 1970; Noy-Meir and Austin 1970; Gauch, Whittaker & Wentworth 1977).

The assumption of linearity is probably less problematic in analyses of environmental factors. Mather (1976) discussed examples in physical geography and Webster (1977) and Jeffers (1979) provide examples of applications in soil and site research. PCA has been used in South African environmental studies by Dyer (1979) for rainfall anomalies, Bosch (1977) for distinguishing soil features and van Daalen (1980) for characterising fynbos and forest sites.

Theory

Numerous descriptions of the analysis have been published. The following brief outline is drawn mostly from Isebrands & Crow 1975; Orloci 1975; Webster 1976; Mather 1976 and Dyer 1979.

PCA is a technique that provides a mathematical transformation of the data and, in this sense, is not a statistical model. One set of variables is transformed into another component set with the following properties:

1) the first component accounts for the largest possible proportion of the variance, the next component for the largest proportion of the remaining variance and continuing until all variance is accounted for
2) the new component set is a linear function of the original set
3) the components are orthogonal, i.e. independent of each other
4) the total variance in the original data set is preserved in the component set.

The principal components model can be simply expressed as follows

$$Z_j = a_{j1} PC_1 + a_{j2} PC_2 + .. + a_{jn} PC_n$$

where Z_j is variable j and each variable is expressed as a linear combination of n (total number of variables) new uncorrelated components PC_1, PC_2 ..... PC_n.

Each component is itself defined as a linear combination of the n original variables.

$$PC_i = a_i 1 x_1 + a_i 2\ X_2 + \ldots\ldots\ a_{in}\ X_n$$

where PC_i is component i, X_1 is variable 1 and a_i 1 is the "loading" or principal component coefficient of variable 1 on component i.

Computational methods, which involve matrix manipulations and solving for eigen roots and vectors, are not discussed here (see Mather 1976).

Frequently the results of PCA are ambiguous with, for example, a number of variables loaded significantly on more than one component. To facilitate interpretation the axes may be "rotated". Axis rotation involves the manipulation of axes about the origin until some alternative position is reached. This position generally approaches, as far as possible, a set of criteria known as Thurstone's Simple Structure (Child 1970), the most important of which is that each original variable should contribute strongly to one of the components (factors) and little to the others.

Two broad classes of rotation exist- orthogonal rotation where axes are maintained at 90° and oblique rotation where this constraint is lifted. In oblique rotation the assumption of indepence of componenents (factors), i.e. that they lack any significant correlation between them, is lifted. Oblique rotations have been criticized, especially in the behavioural sciences, for their susceptibility to subjective manipulation by the experimenter (Child 1970; Webster 1977). For this reason orthogonal rotations have often been preferred. Analytical solutions are now available for the oblique case and their greater flexibility for non-orthogonal components may lead to their wider use (e.g. Carleton 1980 for vegetation applications).

Analysis

The results of PCA are dependent on the variables selected for analysis and should, as far as possible, cover the "domain of interest" (Mather 1976). I used the variables listed in Appendix 3 These were selected to represent a category of independent variables such as rainfall, altitude and geology, dependent variables such as pH, organic matter, soil colour etc. and a small number of vegetation variables to identify the possible significance of components to plant growth (see e.g. Boaler 1966).

The most important omissions were variables expressing nutrient régime and effective soil depth. pH and conductivity (Ruitersbos only) are correlated with base status and provide some indication of nutrient status. Augering was used for soil depth determination, but accurate measurements of effective depth and the frequency of crevices in parent material for deep root penetration, can only be obtained from soil pits. Unfortunately both sets of data are expensive to collect.

No data transformations were used except for water drop penetration time which was approximately normalised by a logarithmic transformation.

The data was analysed on the SPSS factor analysis program using a principal components option with communalities set at one (i.e. no estimate of error variance was made). The scale of variable measurements differed widely and data was consequently standardised by using a correlation matrix as data input.

The extracted components were subjected to a Varimax (orthogonal) rotation (see Webster 1977).

3.3 Results

Results are shown in Tables 3.1, 3.2, 3.3 & 3.4.The two study areas are discussed separately.

(a) Swartberg

The first component accounted for 33,8% of the variance and the first three components for over half the total variance (Table 3.1). The first component reflects a radiation/aspect gradient dividing north and south aspects. North aspects are more rocky with stonier soils than south aspects. Vegetative cover and phytomass (Sum Cover) are higher on south than on north aspects, although veld age is greater in the latter (Horne (1980) has reported lower fire frequencies on north than on south aspects in the Central Swartberg over a period of 29 years (1950 to 1978)).

The second component, which is not independent of the first, is interpreted as an altitudinal/rainfall gradient. It is interesting that

TABLE 3.1 First four latent roots and vectors for PCA of site variables from Swartberg, North and South Aspects, after Varimax rotation.

	Roots			
	1	2	3	4
Root	11,14	3,77	2,38	1,95
% Variance	33,8	11,4	7,2	5,9
Cumulative %	33,8	45,2	52,4	58,3

Variates	Vectors			
	1	2	3	4
Altitude	-,106	-,692	-,118	,074
Slope	,196	,008	,783	-,273
Aspect EW	-,564	,204	,056	-,239
Aspect NS	,882	,077	-,049	,291
Radiation Index	,815	,142	-,205	,305
Effective Soil Depth	-,161	,334	,166	,614
Depth of A horizon	-,109	,119	-,079	,816
Hue of A	,133	-,002	-,211	-,028
Value of A	,138	,787	,044	,114
Chroma of A	,049	,711	,066	-,059
Texture of A	-,053	-,094	,142	,095
Consistence of A	,102	-,175	-,053	-,077
Stoniness of A	,772	,058	,180	,010
pH of A	,138	,399	,008	,112
Organic Matter of A	-,056	-,813	,121	-,188
Permeability of A	,405	-,158	-,166	,244
Geology	,544	,576	,149	,069
Isohyet	-,484	-,564	,085	,209
Foothill Dist.	,900	,200	,028	-,125
Total Rock Cover	,846	,145	,042	-,050
Stones 13 cm	,696	,169	-,192	-,029
Stones 25 cm	,254	,103	,113	-,162
Rock 100 cm	,031	-,110	,237	-,025
Rock 200 cm	,285	-,037	,085	,253
Bare Soil	,781	,356	,060	-,259
Litter Cover	-,577	-,389	,086	,421
Total Plant Cover (T)	-,760	-,411	,041	,150
Sum of Plant Cover (S)	-,894	-,086	-,083	,188
Ratio T/S	-,822	,115	-,139	,190
Exposure	-,018	,015	,817	,193
Moisture Index of Soil	-,673	-,187	,315	,030
Erosion	,420	,728	-,078	,096
Veld Age	,755	,131	,366	-,173

this component explains far less variance than the radiation component and that aspect appears to control most variation in the measured variates. Several soil variates are significantly loaded on the altitudinal component, including organic matter, soil colour value and chroma (soils are darker at higher elevations). Soil erosion increased at lower elevations.

Slope and exposure were strongly loaded on the third component and top and effective soil depth on the fourth component. The remaining components are loaded in single factors only and explain negligible proportions of the total variance.

Because of the marked dichotomy between north and south slopes, the data were analysed separately for the two aspects.

<u>South aspects</u>. The first component accounted for 23,3% of the total variance and the first four components for 57,6%. The first component represents a rainfall/altitude gradient on which soil organic matter increases and pH decreases with altitude. Consistance is finer and depth of the A horizon is shallower with increasing elevation. Soil erosion increases towards dry, low elevations.

The second component relates to rockiness with high loadings of total rock cover, stones of 25 cm diameter and degree of stoniness in the A horizon. Total vegetative cover decreases and Soil hue increases with greater rockiness. The third component defines a radiation gradient with which the subjectively derived soil moisture index and exposure index are correlated.

Vegetative cover and phytomass are not strongly loaded on altitudinal, radiation, or rockiness gradients but total cover is weakly loaded on the two former components. The influence of slope orientation on phytomass (the summed cover of all species) is apparently reflected on the fourth component, which overlaps with third component.

North aspects. The first component explain 34,5% of the total variance and the first four components 63,5%. The first component again represents an altitude/rainfall gradient, but the extremes of moisture gradient are greater than on the south aspects and this is clearly reflected in high loadings of "dependent" vegetation variates (Total Cover, Sum Cover, Litter and percentage Bare Soil). Lighter coloured soils, with less organic matter, are found at lower elevations and rockiness (especially small rock sizes) increases. Veld age is related to altitude with old veld at low elevations.

The weak loading of soil pH on this component is significant. Unusually low pH was found in some mid-elevation sites and (if not a laboratory error) may represent relict pre-weathered material which has been preserved on the gentler plateau slopes.

The second component is broadly equivalent to the third component of the south slope analysis and reflects relief and, consequently, radiation. Soil texture has a high loading on this component which is not easily interpreted.

Both the third and fourth components describe rockiness (rocks of ±100 cm diameter) which is negatively correlated with soil depth, stoniness in the A horizon and soil consistence.

TABLE 3.2 PCA of Site Variables, Swartberg. Component loadings above 0,3 are indicated for the first four components of a Varimax rotated matrix for south and north slopes respectively.

Roots	1		2		3		4	
	S	N	S	N	S	N	S	N
Roots	7,70	11,38	4,79	3,69	3,4	3,25	3,12	2,64
% Variance	23,3	34,5	14,5	11,2	10,3	9,9	9,5	8,0
Cumulative %	23,3	34,5	37,9	45,6	48,2	55,5	57,6	63,5

Variates	Components 1		2		3		4	
Altitude	,942	0,935						
Slope		,429		,687	,835			
Aspect EW	,301						,436	
Aspect NS					,470		,709	
Radiation Index		,326		,721	-,803			
Total Depth						,834		
Depth A	-,457					,782		
Hue			,702					
Value	-,382	,472						
Chroma		,579						
Texture				,798				
Consistence	,563							,737
Stoniness of A			,650		,369		-,365	,909
pH of A	-,846		-,301					
Organic matter	,784	-,541		,389		-,324		
Permeability								
Geology	-,349	,874						
Isohyets	,939	-,933						
Foothill Dist.	,948	,944						
Rock Cover		,821	,814					
Stones 13 cm		,425					-,401	
Stones 25 cm		,325	,808					
Rock 100 cm						-,453		-,572
Rock 201 cm								
Bare Soil		,920						
Litter		-,87						
Total Cover	,404	-,902	-,430					
Sum Cover		-,686					,891	
Ratio		-,4					,887	
Exposure				,313	,491			
Moisture Index	,318	-,493			,487			
Erosion	-,792	,79					,360	
Age		,70			,556		-,614	

(b) Ruitersbos

Ruitersbos data were analysed as above by first examining the complete matrix and then separately analysing north and south slopes.

Complete Data Set

The first component accounts for 38,6% of the variance and the first three components for 57,4% (Table 3.3). The first component, as in Swartberg, represents a radiation/aspect gradient. North aspects are rockier than south aspects, soils are less leached with a droughty soil moisture index and higher pH and textures of the A horizon are sandier and more friable. Water repellency is more strongly developed on north than on south aspects and soils are paler.

The second component (10% of the total variance) is interpreted as a moisture gradient, but is not orthogonal to component one or three (elevation) with high loadings shared by several variables. Vegetation cover and phytomass (Sum Cover) are strongly loaded suggesting a greater dependence on moisture than aspect or elevation per se. Soils are stonier in dry areas with coarser textures and paler colours in the A horizon. Apparent soil erosion increases with decreasing rainfall and decreasing vegetative cover.

The third component (8,8% of the variance) is an altitudinal gradient but shares high variable loadings with both radiation and moisture components. Slopes are steeper at high elevations, rainfall increases, pH decreases, and organic matter and water repellency increase with increasing altitude.

TABLE 3.3 First four latent roots and vectors for PCA of site variables from Ruitersbos, North and South aspects, after Varimax rotation.

	Roots			
	1	2	3	4
Root	13,52	3,49	3,08	2,06
% Variance	38,6	10,00	8,8	5,9
Cumulative %	38,6	48,6	57,4	63,3

Variates	Vectors			
	1	2	3	4
Altitude	-,006	-,061	,914	,059
Slope	-,002	-,114	,815	,064
Aspect EW	-,052	-,009	-,141	,108
Aspect NS	,824	,371	,013	-,096
Radiation Index	,839	,226	-,160	-,142
Effective Soil Depth	-,119	-,171	-,197	,824
Depth of A horizon	-,368	-,161	,392	,739
Hue of A	-,123	-,309	,344	-,021
Value of A	,447	,508	-,339	-,113
Chroma of A	,297	,382	-,389	,001
Texture of A	-,682	-,501	,085	,108
Consistence of A	-,763	-,215	,332	,231
Stoniness of A	,572	,519	-,066	-,246
pH of A	,509	,276	-,670	-,024
Organic matter of A	-,379	-,107	,492	,669
Permeability of A	,075	,147	,158	,257
Geology	,043	,622	-,125	-,295
Isohyet	-,243	-,589	,567	-,105
Foothill Dist.	,254	,853	-,037	-,169
Total Rock Cover	,695	,619	-,051	-,050
Stones 13 cm	,183	,749	-,293	-,009
Stones 25 cm	,512	,410	-,021	-,002
Rock 100 cm	,710	-,164	,286	-,132
Rock 200 cm	,184	,071	,129	,022
Bare Soil	,091	,666	,003	-,261
Litter Cover	-,110	-,883	,039	,101
Total Plant Cover (T)	-,194	-,889	,175	,057
Sum of Plant Cover (S)	-,355	-,746	,131	,057
Ratio T/S	-,331	-,606	,141	,034
Exposure	,177	-,149	-,193	-,125
Moisture Index of Soil	-,633	-,451	,198	,416
Erosion	,242	,665	-,176	-,115
Veld Age	,077	,560	-,532	-,051
Conductivity	-,009	,200	,108	-,082
Log WDPT	,480	-,200	,503	,294

The fourth component expresses soil depth, which is related to organic matter content (peaty soils are deep).

South Aspects. The first component accounts for 26,6% of the total variance and the first three components for 53,8%. Examination of ordinations of plot scores on the first two components indicates that these are not strictly orthogonal, but appear to follow a quadratic relationship along a single trend of variation. The first two components together account for 45% of the variance and can be interpreted as a complex altitude/moisture gradient. The "independent" variates altitude, slope, radiation index, rainfall, distance from foothills, and geology are strongly loaded on the first and weakly or moderately loaded on the second component.

The soil variates, organic matter, log WDPT, conductivity, permeability, consistence, total depth and depth of A horizon were all significantly loaded on either the first or second component, increasing with increasing elevation, higher rainfall or lower insolation.
Soil pH and chroma, however, decreased with increasing elevation.
Veld age was the only vegetation variable significantly loaded on the first two components.

The third component, accounting for 8,7% of the variance, describes rockiness with the variates total rock cover and stones 25 cm diameter both significantly loaded. The exposure index was also moderately loaded on this component. Soil colour value was weakly loaded with increasing rockiness. The vegetation variable sumcover and ratio of total to sum cover are both strongly loaded on the rockiness component and, surprisingly, increase with increasing rockiness.

The fourth component also describes a rockiness/vegetative cover gradient, but with rocks of 100 cm, bare soil and total cover, having the most significant loadings.

North aspect. The first component accounts for 35,6% of the total variance and the first three components for 52,5%. As for the south aspect analysis, the first two components are related to each other, both defining an altitudinal/moisture gradient, the first loaded more heavily on rainfall (and distance from foothills) and the second more on altitude. The two components together account for 44,6% of the variance. Vegetative cover and phytomass (Sum Cover) increases with increasing rainfall whilst veld age decreases. Water repellency increases with increasing rainfall.

Soil pH decreases, organic matter increases and soil consistence is firmer with increasing altitude, but altitude is a poor predictor of vegetative cover (and available rainfall) in the complex topography of the north slope study area.

The third component accounts for 7,9% of the variance and reflects stoniness (total rock cover, stoniness of the A horizon and stones <13 cm) and soil depth. Soil texture is also strongly loaded on this component becoming coarser with higher rock cover or shallow soil depth.

TABLE 3.4 PCA of site variables, Ruitersbos. Component loadings above 0,3 are indicated for the first four components of a Varimax rotated matrix.

	Roots							
	1		2		3		4	
	S	N	S	N	S	N	S	N
Roots	9,05	12,46	6,27	3,16	2,98	2,76	2,17	2,44
% Variance	26,6	35,6	18,5	9,0	8,7	7,9	6,4	5,6
Cumulative %	26,6	35,6	45,1	44,6	53,8	52,5	60,2	59,5

Variates	Components							
	1		2		3		4	
Altitude	,776	,318	,461	,632				
Slope	,783	,345	,35	,476				
Aspect EW							-,475	,826
Aspect NS	-,353							,870
Radiation Index	-,83	,442	-,307	,411				
Total Depth	-,309		,644			,646	-,349	
Depth A			,924	,330		,480		
Hue								
Value	-,337	-,364			,474			
Chroma	-,628	-,309						
Texture						,797		
Consistence			,674	,873	-,304		,300	
Stoniness of A		-,359				-,555		-,328
pH of A	-,818			-,821				
Organic Matter		,324	,852	,642				
Permeability			,773					
Geology	,664	-,43	-,415	-,525		-,309		
Isohyets	,769	,646		,458		,350		
Foothill Dist.	,886	-,726		-,484				
Rock Cover		-,330			,698	-,515	,319	
Stones 13 cm		-,598				-,406		
Stones 25 cm					,713			
Rock 100 cm		,487			,376		,549	,336
Rock 201 cm								
Bare soil		-,508					,833	
Litter	-,369	,773						
Total Cover		,748					-,834	
Sum Cover		,932			,911			
Ratio		,909			,913			
Exposure		,437		-,363	,510			
Moisture Index			,711	,326	-,473	,624		
Erosion		-,372						
Age	-,51	-,773	-,355				-,335	
Conductivity	,590						,338	
Log WDPT	,372	,659	,517				,304	

3.4 DISCUSSION

PCA was an effective technique for summarising relationships between the environmental variables in this study. Patterns of variation are similar on the two ranges suggesting a fair measure of generality.

The interrelationship between mountain structure (especially their east-west trend) and the radiation budget imposes the major pattern on environmental variation. In Chapter 2, I showed that potential evapotranspiration is nearly twice as great on steep north than on steep south slopes. Moisture availability is a key factor controlling vegetation establishment and rates of chemical weathering. Garland (1979), has suggested that aspect differences and their effects on vegetation establishment, weathering and sheet erosion account for the asymmetry of Drakensberg valleys. He reports contrasts of skeletal soils, poor in organic matter and clays and lacking true profile development on north slopes with deeper, organic rich profiles on south slopes. Sheet erosion processes are active on north whereas soil creep processes predominate on south slopes (Garland 1979).

The same pattern is found in the two study areas. On north aspects relatively more water is evaporated and less moisture is available in the soil solution than on south aspects. Greater rockiness of north slopes could be attributed to slower chemical weathering rates and more rapid stripping of soil material by sheet erosion. Less intense weathering may also account for coarser soil textures (and therefore more friable consistence) on north aspects. Whilst soil depth, measured by auger, showed no significant loading on radiation components, soil pits confirmed the expected pattern of predominantly shallow soils on north and deep soils on southern aspects. Pedogenesis is more advanced on south slopes with the development of mature soils such as Hutton and Clovelly Forms, whereas skeletal Mispah or Glenrosa lithosols are typical of north slopes. It is not clear, however, whether the south slope soils are a product of more intense weathering or slower rates of erosion with consequent preservation of palaeosols.

The second major control on site variables is the altitude/moisture gradient or, more particularly, precipitation and temperature. These two climatic factors vary together and it is difficult to unravel their relative effects. However, rainfall and altitude are not closely related on the north slopes of the Outeniquas because high sub-ranges north of the main watershed fall in a rainshadow. Thus a component describing "moisture" as distinct from altitude could be described for Ruitersbos although few variates were loaded exclusively on one or the other component.

Soil organic matter and pH of the A horizon are strongly correlated with altitude (the north slopes of Swartberg are an exception for reasons stated earlier). Meentemeyer (1978) has recently developed a model for predicting organic matter decomposition rates from actual evapotranspiration (AE). Using data from many biomes of the earth, he showed that (leaf) litter decay rates are strongly correlated with AE and, especially at higher AE, lignin content of the litter. His model would satisfactorily explain organic matter accumulation at higher elevations as a function of reduced evapotranspiration. It is interesting to note that organic matter is not significantly loaded on the "moisture" component of the Ruitersbos plots but is correlated with altitude suggesting that temperature controls on litter decay are the more significant. Water repellency is strongly correlated with organic matter and hence with altitude. The decrease of pH with increasing altitude may be a function either of increased leaching or associated with organic matter and the release of organic acids (Hanawalt, Whittaker 1977).

Vegetative cover is largely controlled by the altitude/moisture gradient. Cover increases with increasing moisture availability but apparently reaches an asymptote level (using subjective estimates) at relatively low levels of moisture availability since there were no significant loadings of cover variables on either of the south slope analyses (cf. Specht 1981). It is significant that cover is correlated with the moisture component in the Ruitersbos analysis, but not with the altitude component.

The inverse relationship of veld age and altitude and the greater age of veld on north aspects may not be entirely trivial. Horne (1980) plotted the distribution of fires in the Swartberg and showed highest incidence of lightning fires near the mountain peaks and on southern aspects so there is a higher probability of finding old stands on north aspects and low elevations.

3.5 CONCLUSIONS

Three major axes of variation of site variables can be identified. The most important of these is the radiation gradient which, since radiation drives the hydrological cycle, I shall interpret as primarily an available moisture gradient. The complex altitudinal gradient accounts for the greatest proportion of the remaining variance. It is not, however, independent of the moisture gradient. Thirdly a gradient defining rockiness accounted for significant variance in both study areas.

The PCA confirmed and expanded intuitive understanding and, to that extent at least, was successful. In retrospect, an oblique rotation would have been preferred to an orthogonal rotation to distinguish more clearly the relative response of variates to the aspect and moisture gradients.

CHAPTER 4

CLASSIFICATION OF PLANT COMMUNITIES

4.1 INTRODUCTION

Floristic classifications were derived from the relevés using subjective absolute cover estimates as importance values. Floristic classifications are of rather limited practical value in fynbos management. High species turnover along geographic gradients (Kruger and Taylor 1980) places high demands on the ecologist's ability in field taxonomy for limited returns in increased ecological understanding. Species assemblages, with similar ecological tolerences, may show little taxonomic resemblance because of this delta diversity. This reduces the generality and usefulness of a formal phytosociological approach to parochial studies in small areas (e.g. Taylor 1969; Kruger 1974; Moll and Campbell 1976; McKenzie et al. 1977; Boucher 1978). High delta diversity results in a real problem in extrapolation and interpretation of ecological studies since comparable communities elsewhere may not be recognizable on floristic criteria and existing structural classifications are too coarse. The problem could be resolved by selecting indicator species of wide geographic distribution, but narrow ecological tolerance (if they exist!), by identifying structural categories bound to particular site constraints but less area dependent than floristics for successful classification or, perhaps, by attempting classifications at the generic or familial level (assuming that higher taxa remain restricted to a particular site)(Del Moral & Denton 1977).

I attempted a structural approach here. Since structure is likely to be less sensitive than species to environmental variation, i.e.

trends of variation will tend to be more quantitative than qualitative, a floristic classification may be used as a standard for comparison of the success of a structural classification (Webb <u>et al</u>. 1970; Knight and Loucks 1969; Walker 1975).

4.2 METHODS

The range of classification methods available has been discussed in Chapter 2. I used two-way indicator species analysis (TWINSPAN, Hill 1979) which is an improved version of indicator species analysis (Hill, Bunce & Show 1975). TWINSPAN is a divisive polythetic technique which constructs a classification of samples and then uses this to obtain a classification of the species. The two classifications are then combined to obtain an ordered two-way table, resembling a Braun-Blanquet table. Details of the method are described in the TWINSPAN manual for program CEP-41 in the Cornell Ecology Program series and are only described briefly here.

The first step is to create a dichotomy by ordinating the samples (using Reciprocal Averaging - RA, Hill 1973) and dividing the ordination at its middle. Differential species (i.e. species with clear ecological tolerances) occurring mostly on one or other side of the dichotomy are identified next. An improved ordination is constructed using the differential species to weight each sample for a new sample score and this "refined" ordination is then divided to derive the desired dichotomy. The final stage in the process parallels RA by repeating the division of ordinations, but by ordinating the most highly preferential species rather than samples. This, the "indicator" ordination, is not essential to the method, but provides simple criteria for re-identification of the groups and allows summarization of the classification in a table similar to that used in the Braun-Blanquet method.

TWINSPAN works on presence/absence of species. Quantitative data are accomodated by creating "pseudospecies" at pre-selected thresholds. Thus, e.g. Cannamois dregei might have cover values of 3%, 20% and 45% in three separate samples. Pre-selected cut-off (threshold) levels may be: 0 5 15 25. Thus the three samples would contain the following pseudospecies:

Sample 1	- 3%	Cannamois dregei 1
Sample 2	- 20%	Cannamois dregei 1, 2, 3
Sample 3	- 45%	Cannamois dregei 1, 2, 3, 4

It is then possible to have Cannamois dregei as an indicator at level 1 (present) or, for example, at level 3 (exceeding 15% cover). Pseudospecies are particularly useful for continuously varying data such as structural attributes, or stem diameters in successional forest series.

Several options are available for the user. The default option, using pseudospecies cut off levels of 0, 2, 5, 10 and 20% proved as/or more effective than alternatives attempted, and was used in all floristic analyses. The user may also weight different levels of pseudospecies e.g. the higher cover values may be accorded greater significance as indicators and be weighted accordingly. No weighting was used in the floristic analyses.

The size of the final groups is controlled by specifying a minimum group size for subdivision (a group of 5 sample plots was used) and a maximum level of divisions. Six levels were used in all analyses. Species occurring in only one stand were ignored in the analyses.

4.3 RESULTS

Ruitersbos

Twenty groups were defined by the successive dichotomies of which 12 can be readily identified ecologically. The division hierarchy is shown in Fig.4.1together with the most effective indicator species. Species of doubtful taxonomic identification (usually Cyperaceae) have been omitted as indicators. Species composition of the groups is summarised in Table4.1, which resembles a Braun-Blanquet Table. The sequence of species in the TWINSPAN results was altered using Braun-Blanquet techniques to give the results in the table. Numbers refer to pseudospecies levels i.e. 1 = 0-2; 2 = 2,1-5; 3 = 5,1-10; 4 = 10,1-20; 5 = 20+.

The vegetation groups

Four major groups can be recognized. Group A is arid fynbos, Group B is more mesic fynbos including grassy Waboomveld with renosterveld affinities, and relatively xeric restioid veld with seed regenerating

FIGURE The dendrogram produced by two-way indicator species analysis for Ruitersbos showing indicator species at each dichotomy, group name and number of stands in each group (in parentheses).

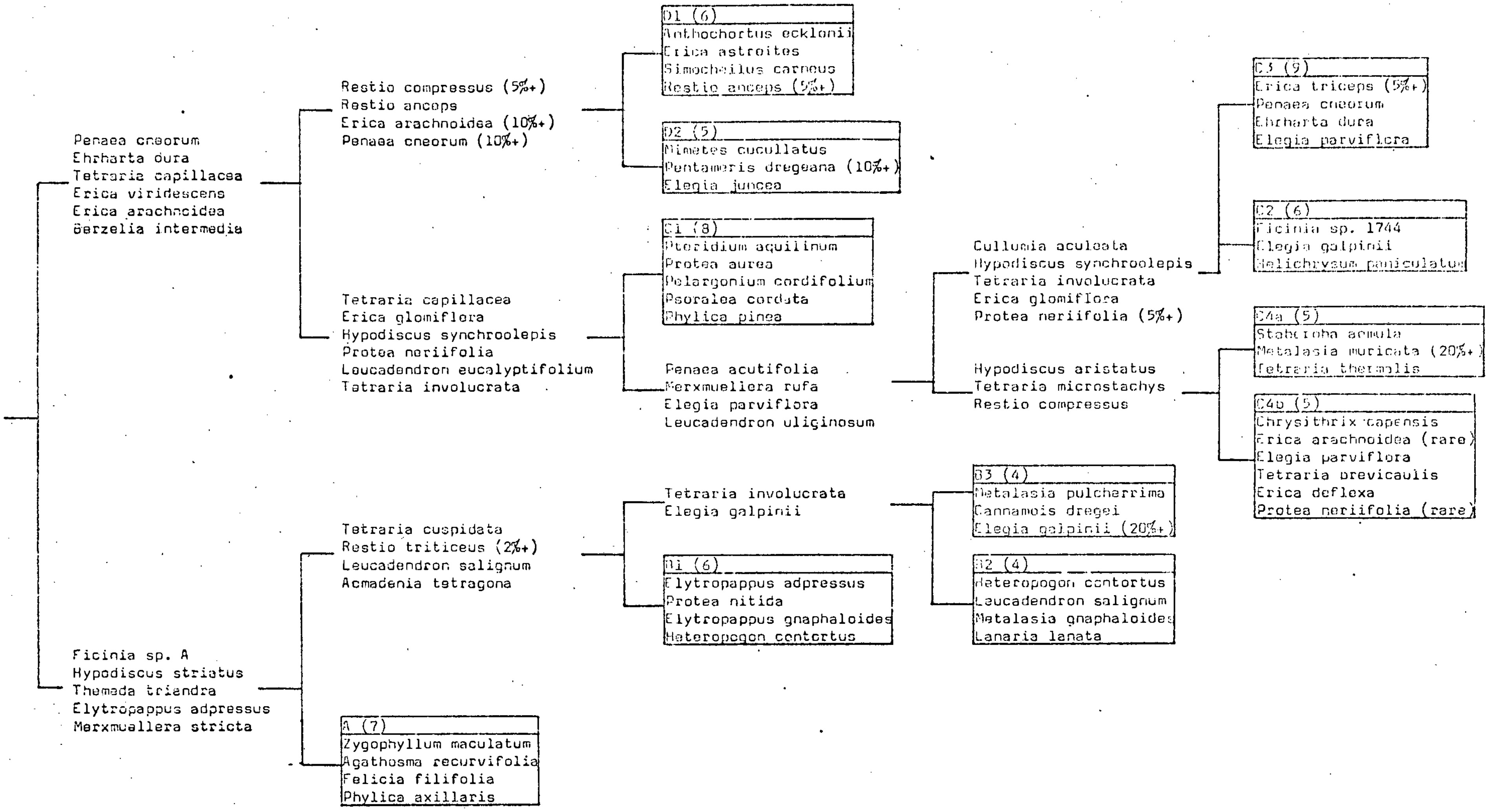
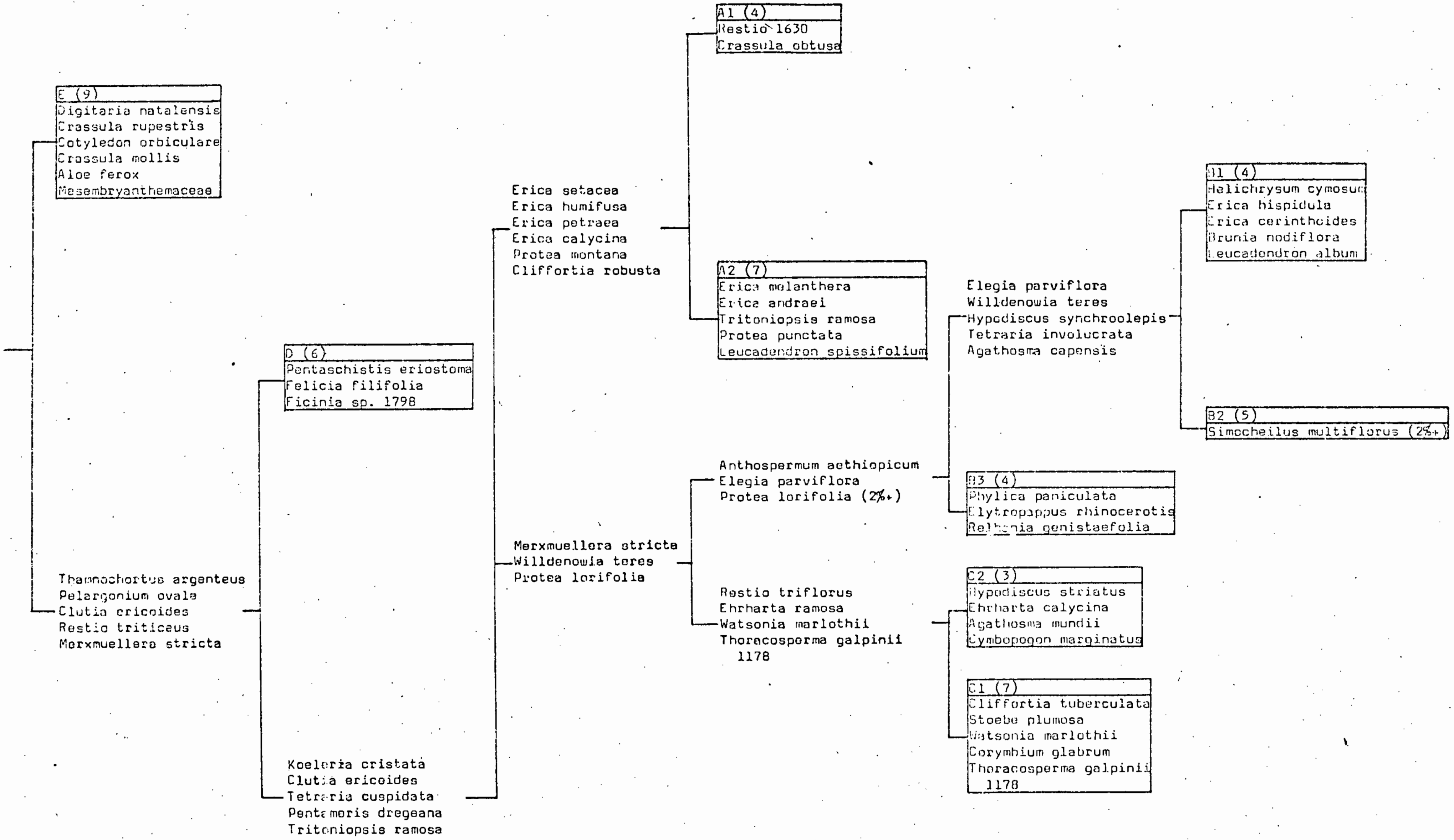


FIGURE The dendrogram produced by two-way indicator species analysis for Swartberg showing indicator species at each dichotomy, group name and group size.



Proteaceae. Group C is a large group including most stands with a visually prominent canopy layer of Proteaceae. Group D includes the short, closed, ericoid heathlands of high elevations and peaty soils where Proteaceae are sparse or absent.

The composition of the groups is discussed in detail in Chapter 5 .

Swartberg

Eighteen groups were defined of which 9 have been described since they are readily recognisable. Indicator species, and the divisive hierarchy, are shown in Fig. 4.3. Species whose field identification is difficult have been omitted as indicators. The groups are less discrete than those of Ruitersbos (Table 4.2)confirming intuitive feelings that, in the latter area, communities are associated with particular habitats whereas Swartberg vegetation shows no sharp discontinuities. The group of Karroid plots at low elevations on north aspects is, however, sharply discontinuous with the adjacent fynbos. Sampling has been somewhat uneven and a higher sampling intensity would have allowed more subtle differentiation, e.g. in B3 vegetation of the southern foothills.

The vegetation groups

Five larger groups have been defined (up to the fourth level of division). Group A includes short, closed, ericoid heathlands with no distinct proteoid layer at high elevations on south slopes. In habitat and structure, but not in species composition, it resembles

Ruitersbos Group D. Group B includes all the remaining stands of the south aspects and one north aspect stand, usually with a visually prominent upper stratum of Proteaceae and a mixed graminoid, restioid, ericoid understorey.

Group C is similar to Group B, but includes only north aspect plots. These are distinguished by floristic differences and the generally greater, prominence of restios and relative scarcity of shrubs. Groups B & C are comparable to the large Group C of Ruitersbos.

Group D is an arid fynbos unit with no or rare Proteaceae, and is often characterised by the grass Pentaschistis eriostoma. It is comparable to group A of Ruitersbos.

Group E is confined to the Swartberg and is a form of succulent Karoo which, under particularly arid conditions, may be found growing on sandstone substrates.

DISCUSSION

Indicator species analysis has not, to my knowledge, been previously used in South Africa. Hill et al. (1975) report on its application in Scottish pinewoods and it has also been used in studies of British mires (Daniels 1978) and French pastures (Basset 1978).

The method performed well and the units extracted were readily identifiable. In a previous mapping exercise in the Moordkuil's catchment adjacent to the Ruitersbos study area, substantially the same groups were extracted as significant for mapping purposes using in formal dominance mapping techniques (Whittaker 1978). A similar, more extensive, approach in the eastern Swartberg also identified substantially the same major groupings as those in the TWINSPAN analysis (Table 1.9). However, whilst the subjectively selected units were difficult to describe accurately (being based largely on intuition), TWINSPAN provides a succinct summary of floristic composition of the final table together with indicator species for easy recognition.

Traditional phytosociological techniques (Werger 1974) have been successfully used in fynbos classification, but are slow and difficult to use with large numbers of species (Werger et al. 1972; Boucher 1978). The problem has been partially resolved by the computer aids for preliminary sorting (Boucher 1977; McKenzie et al. 1977). Kruger 1974 and Taylor 1969 used the monothetic divisive "association analysis" with only limited success, partly because of the limitations of a rigid sampling strategy. Campbell and Moll (1975) and Linder and Campbell (1979) have used polythetic agglomerative techniques (group-average sorting with the Canberra or relativized Czekanowski measure, Campbell 1978) with fair success, but indicators defining group are difficult to extract.

Two way indicator species analysis appears to have advantages over all these techniques. The method is close to the tabulation method in concept (Hill 1979) and produces a reasonable final table. It is, however, very much faster, and easily copes with large numbers of species, typical of fynbos. The method is computationally more efficient than cluster analysis (which is faster than association analysis), requiring less storage space (Hill 1979) and has the distinct advantage of listing indicator species so that final groups are readily identified.

One problem with cluster techniques is the formation of closed hierarchies in which it is difficult to fit new data without complete re-analysis. If the indicator analysis has been based on representative samples, allocation of new individuals to the classification does not require re-analysis, as misclassifications are less common. For example, a separate classification of 28 South aspect plots from Ruitersbos, although altering final plot order, extracted exactly the same groups as the analysis for the whole data set (65 plots). Allocation of new plots is much simplified by the use of indicator species. The possibility of misclassification is reduced, relative to association analysis (Williams & Lambert 1959), by polythetic rather than monothetic choices at dichotomies.

Perhaps the main difficulty with TWINSPAN is that the program is long and complicated, and some sections lack "elegance" (Hill 1979). This may reduce comprehension by the user. Another problem, which appears in the Ruitersbos data, is the ordering of dichotomies. If two, small, outlier groups are successively split from a larger, more homogeneous group, and the larger group is then itself divided, then the latter subgroups will be ordered by their relationships to the two outlier groups and not to the general trend of the table (Hill 1979). The species analysis, which orders species in the final table, is not satisfactory. For both floristic and structural analyses (Chapter 5) manual sorting of species using Braun-Blanquet tabulation methods was necessary. In general, though, the method appears to offer a robust, practically useful classification technique of wide generality which may be used in unaltered form or as a basis for final manipulation by Braun-Blanquet techniques.

Group

Table 4.1 RUITERSBOS FLORISTIC TABLE

Group	A1				A2							B1					
Relevé No.	1	2	3	4	7	8	9	10	11	5	6	12	13	14	16	15	17
Differential Species of high montane heaths (A1)																	
Euryops bolusii		1	1														
Ficinia nigrescens 1175	1	1	1														
Restio sp. 1630	1	2	3	1													
Crassula obtusa	1	3		1													
Cliffortia robusta	2	2	1			1			2								
Erica petraea	3	3	1	1	3	3											
Erica(?) hispidula 1162	1		1	1													
Erica nervata	1	1	1		1	1											
Species common to high montane and Protea punctata heath (A1, A2)																	
Cliffortia integerrima		1		3	2	1	1										
Protea montana	1	1		1			1	1	1	1							
Elegia? vaginulata	1	1	1	1		1	1		1	1							
Erica setacea			1	1	1	1	1	1	1	1	1	1					
Erica calycina	1	1			1	1	1	1	1	1							
Differential species of Protea punctata heath (A2)																	
Erica transparens					1	1				1	1						
Erica humifusa					1	1	1		1								
Ficinia cf filiformis?					1	1	1		1		1	1	1				

Table 4.2 SWARTBERG FLORISTIC TABLE

CHAPTER 5

COMMUNITY DESCRIPTIONS

5.1

The communities defined by floristic analyses, their site characteristics, vegetation layering and species diversity are discussed in the following section.

Plant species were determined by Stellenbosch herbarium, Compton Herbarium and Bolus herbarium and nomenclature in this chapter and Tables 5.2 and 5.3 follows their usage. Duplicate specimens are housed in the herbarium at Saasveld Forestry Research Station. Cyperaceae and Ericaceae (especially minor genera) were diffidult to identify and specimen numbers are quoted where determinations are doubtful or have yet to be made.

Relevés have been grouped into layering categories according to a classification described in 5.2. Sub-formation categories follow Campbell et al. (1981) ex Specht (1979). Categories relevant to the study areas are listed in Table 5.1 below.

TABLE 5.1. Nomenclature used for sub-formation description of shrublands from Campbell et. al. (1981).

Height of dominant stratum		Projective canopy cover of dominant stratum %	
Tall	2 m+	Closed	75-100
Mid-high	1 -2 m	Mid-dense	50- 75
Low	0,25-1,0	Open	25- 50
Dwarf	0,25	Sparse	5- 25

5.2 VEGETATION LAYERING

Layers, or vegetation strata, may be readily identified in fynbos. For example, Proteoid shrublands typically have an upper canopy layer of Proteaceae with a more or less distinct understorey (Taylor 1978; Kruger 1979). Vegetation stratification is an important community attribute and an attempt was made to define objective stratification categories.

Methods

Each species in each relevé was assigned a cover value and a mean height. Structural categories were defined by calculating relativized Czekanowski coefficients (Campbell 1978) between plots using cover values for all species in each of eight height classes, viz. 0-25, 26-50, 51-75, 76-100, 101-150, 151-200, 201-250 and 250+ cms.

The plots were subsequently classified by a group averages Cluster analysis (Webster 1977; Campbell 1978) to give stratification categories.

Results

Swartberg and Ruitersbos data were analysed separately. In both areas three broad categories could be identifed from the cluster groups 1) a unimodal layering with maximum cover in one or two adjacent layers (symbol U) 2) a bimodal layering with maximum cover concentrated at two separate levels (symbol B) and 3) a trimodal layering with three distinct, non-adjacent layers or with no distinct stratification, but with cover evenly spread over 1 m 50+ (symbol T). (Fig. 5.1).

These three main categories were subdivided according to the height of the dominant layers (Tables 5.2, 5.3). Histograms of the proportion of cover in each height class are presented in Figure 5.1.

Discussion

The results confirm subjective impressions of layering in fynbos communities and provide a useful classification of this community charactristic. Unimodal types occur primarily at high elevations (low closed heathland) or in arid fynbos (low open shrubland). In situations where the proteoid layer is poorly developed at mid elevations (usually a result of fire history) a unimodal layering may occur, but the dominant layer is higher (75-100 cms) than arid fynbos or high montane heath.

Bimodal layering is typical of proteoid shrublands with a heath understorey, or where restioids predominate in relatively xeric situations.

Trimodal layering is most common in mesic fynbos where, however, the layers are not distinct. A proteoid canopy is usually present with shrubs and graminoid life forms occurring from ground level to the canopy. Trimodal layering is also found in the more mesic variants of Waboomveld with a sparse canopy of <u>Protea nitida</u>, sometimes mixed with a layer of somewhat shorter broad sclerophylls, a mid stratum of leptophyllous and nanophyllous shrubs and a lower stratum of grasses, restios, sedges, subshrubs and forbs.

It is interesting that the results derived from the cluster analyses on a relatively large data set of height classes largely conforms with results from a similar, but subjective study in a structural workshop held by the fynbos biome project (Milton and Odendaal, unpublished manuscript, 1977) with data collected in the Western Cape.

The stratification classes listed in Tables 5.2 & .3 have been used in the community descriptions that follow.

<u>TABLE 5.2</u>. Vegetation Layering Classes, Swartberg.

The classes were obtained by group averages cluster analysis on a matrix of relativized Czekanowski Coefficients. Cover values in eight height classes (see text) were used as importance values.

Class	Sub-class	Symbol
Unimodal	1) Modal layer below 0-25 cms. 80% of the total cover below 50 cms. Maximum Height 100 cms.	U1
	2) Modal layer 26-50 cms with 80%+ of the total cover below 50 cms. Maximum Height 100 cms.	U2
	3) Modal layers 26-75 cms. 90% of the total cover below 75 cms. Maximum height 150 cms.	U3
	4) Modal layers 51-100 cms. Maximum height 200 cms.	U4

Table 5.2 (Cont.)

Class	Sub-class	Symbol
Bimodal	1) Two distinct layers with peak cover at 26-75 cms and 101-150 cms. Max. height 200 cms.	B1
	2) Much the same as 1 but with less than 20% of total cover in the upper layer.	B2
	3) Two layer at 26-50 cms and 76-100 cms respectively.	B3
Trimodal	1) Three layers with peak cover at 26-50 cms, 75-100 cms and 150-200 (rarely 250) cms. Maximum height 250 cms.	T1
	2) No distinct layering with relatively even cover distribution across height classes. Maximum height 200 cms.	T2

TABLE 5.3. Vegetation Layering Classes, Ruitersbos. See Table for legend.

Class	Sub-class	Symbol
Unimodal	1) Modal layer 26-50 cms. Maximum Height 150 cms.	U1
	2) Modal layers 26-75 cms. Maximum Height 150 cms.	U2
Bimodal	1) Peak cover at 101-150 cms and 201-300 cms.	B1
	2) Peak cover at 26-75 cms and 101-150 cms. Maximum Height 200 cms.	B2
Trimodal	1) No distinct layering. Cover fairly evenly distributed to maximum height of 300 cms+.	T1
	2) Modal layer 101-150 cms with relatively even cover distribution below. Maximum Height 150 cms.	T2

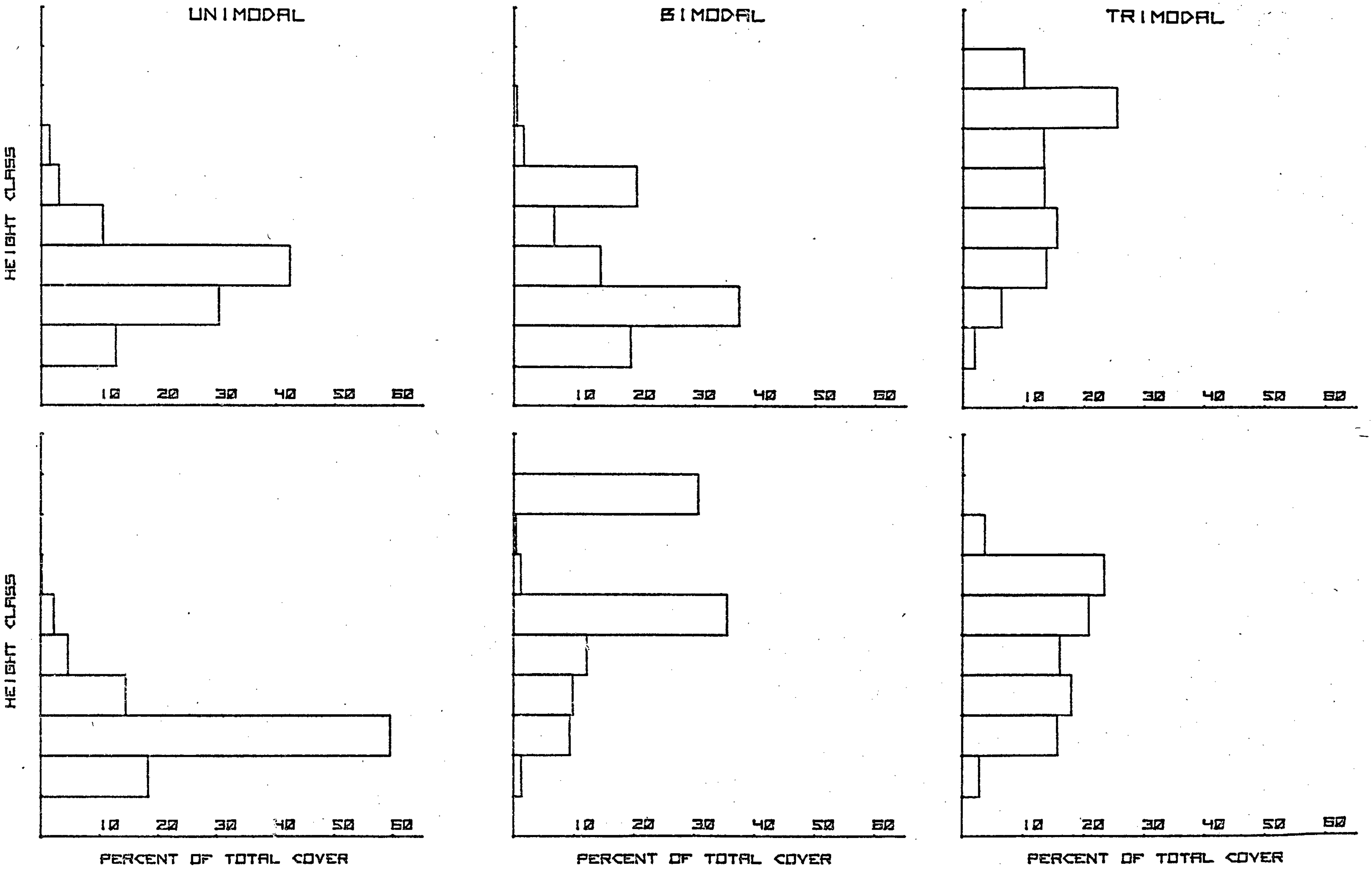


Fig. 5.1 Vegetation Layering showing unimodal, bimodal and tri (or a-) modal examples. Height classes, starting from the lowest histogrambar, are 0-25 cm, 26-50, 51-75, 76-100, 101-150, 151-200, 201-250 and 251-300 cm respectively.

COMMUNITY DESCRIPTIONS

Ruitersbos

D Ericaceous heathlands of the upper south aspects. These communities are exposed to south-east clouds bringing mist precipitation in summer. They are dominated by ericaceous shrubs with Peneaceae, and Bruniaceae. Restios are important in D1 which unit appears to be unique to the coastal ranges. Hard inrolled grasses are frequent, together with sedges, in D2 which is analagous to A1 of the Swartberg.

D1 Simocheilus carneus - Restio anceps community

Sub-Formation: Low closed Shrubland. (Low narrow-sclerophyllous heathland, Kruger 1979).

Stratification: U1, U2 (see 5.2).

Habitat: The community occurs on very steep (33^0-65^0) southern aspects at mid to high elevations (700-1 350 m). These slopes are directly exposed to rainbearing south-west winds and receive appreciable mist precipitation in summer.

Soils: Soils are shallow or moderately deep, acid (pH 3,3-3,6) and peaty (Organic Matter 30-80%, rarely 10-15% at low elevations). A horizon directly overly hard rock or gley or, at lower elevations, thin (20 mm) indurated ironpan. These soils are not adequately defined in the binomial system. Although the soils are wet, rapid moisture movement on the very steep slopes probably prevents stagnation and development of anaerobic conditions.

Vegetation: The community occurs on steep, south aspects at cool, wet, higher elevations of the Outeniquas, exposed to south-east cloud bringing additional mist precipitation. Indicator species are Anthochortus ecklonii, Erica astroites, Simocheilus carneus and Restio anceps. Ericoid shrubs particularly E. arachnoidea and Simocheilus carneus predominate in the dense canopy at 50-100 cms intermingled with dense mats of Restionaceae (R. anceps, R. compressus) or Cyperaceae. A low, indistinct ground layer of rosette forbs, evergreen geophytes, Drosera and bryophytes occurs at 0-10 cm.

Soil slumps are common on the steeper slopes and Pentaschistis steudelii is a common pioneer on the freshly exposed bare peat.

Diversity: The unit is mostly rather poor in species. Near the highest mountain crests, however, relevé diversity is high with a number of unusual high montane endemics. S* 25-40 ($\bar{x}$ 34,3); H' 3,27-4,05 ($\bar{x}$ 3,68); S.I. ,84-,9 ($\bar{x}$,87).

D2 Erica arachnoidea - Pentameris dregeana community

Sub-Formation: Low open (mid-dense) shrubland. (Low, narrow-sclerophyllous heathland, Kruger 1979).

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* Species Diversity parameters are S = Number of species in 5x10 m relevé, H' is the Shannon Wiener Index $-\sum pi \log_2 pi$ and S.I. is Simpson's Index $\sum pi^2$ where pi is the proportional contribution to total cover by each species.

Stratification: U1.

Relevés: 57, 58, 59, 60, 61.

Habitat: The community occurs on steep (43-66^{o}) Southern aspects at high elevations (900-1 300 m), usually further inland than D1 and less exposed to rain or mist precipitation. Surface stones or rocks are present and A horizons have rare to frequent stones. The soils are typically Cartref or humic Mispah Form, and, although moist, are not wet as in D1. Soils are rich in organic matter, but not peaty (O.M. 12,4-19%), pH 3,5-4,0.

Vegetation: The community is essentially single layered and dominated by mid-dense cover of ericoid and penaeoid shrubs (Erica arachnoidea and Penaea cneorum) common in the canopy at 50-80 cms. Mimetes cucullatus and Protea cynaroides occur as occassional proteoid emergents. The herbaceous element is intermingled with the shrubs. Pentameris dregeana, a hard leaved grass, is common together with Cyperaceae and restios. A poorly defined ground layer of rosette plants and geophytes occurs.

The only character species of the community is Pentameris dregeana. Whilst D2 shares many species with D1, Restio anceps is rare or absent whereas Mimetes cucullatus and Elegia juncea, both indicators of more xeric conditions, are typical of the drier D2.

Diversity: The relevés were slightly richer in species than the wet heaths of D1. S 29-46 ($\bar{x}$ 38,2); H' 3,37-4,1 ($\bar{x}$ 3,69); S.I. ,82-,91 ($\bar{x}$,86).

C Mesic Proteoid shrublands. These occur on both north and south aspects over a wide range of elevation. The proteoid layer varies from scattered emergents (C4) to a closed canopy (C1). Typical Proteaceae are P. neriifolia, P. aurea and Leucadendron eucalyptifolium.

C4 Erica viridescens - Hypodiscus aristatus community

Sub-Formation: Tall open (mid-dense) shrubland, rarely tall open Proteoid Shrubland with tall mid-dense heath understorey.

Stratification: Variable. U2, B1, B2.

Relevés: C4a:46, 1, 2, 3, 4 C4b:5, 6, 7, 9, 10.

Habitat: The community occurs on steep (23^o to 46^o) north aspects at higher elevations (850-1 300 m). Surface rock cover varies from about 10 to 65% averaging about 40% mostly of larger rock sizes. Two variants are recognized (see below), with the Tetraria thermalis variant occurring on soils with frequent stones in the A horizon and the Chrysithrix capensis variant on soils with only rare stones. The soils are Cartref or, rarely, humic Mispahs (Chrysithrix variant), fairly rich in organic matter (7,6-11,8%, $\bar{x}$ 10,3) and acid (pH 3,8-4,6, $\bar{x}$ 3,96).

Vegetation: The community is two layered with an open canopy of the tall (1,5 m+), green-flowered Erica viridescens and a denser understorey (,5-1 m) of ericoid shrubs, Cyperaceae and Restionaceae.

Leucadendron uliginosum is occasionally common in the canopy with scattered Leucadendron eucalyptifolium. Protea neriifolia occurs sporadically in the moister phases (C4b).

There are no exclusive character species. Indicator species include Restio compressus, Tetraria microstachys (both also in D1 and D2 of the south slopes), Hypodiscus aristatus, Erica densifolia and Centella sp. Two sub-communities can be recognized:

C4a Erica viridescens - Staberoha aemula - Tetraria thermalis sub-community

This occurs on shallower, stonier and drier sites than C4b and has several species in common with C3.

Indicator species are Staberoha aemula (also present in C2 and C3), Tetraria thermalis, T. fimbriolata, Penaea acutifolia (both also in C2 and C3).

C4b Erica viridescens - Protea neriifolia - Erica deflexa sub-community

The sub-community occurs on moist sites with few stones and a deeper A horizon.

Indicator species include Chrysithrix capensis, Erica arachnoidea, E. deflexa, Tetraria brevicaulis, Restio strictus and Elegia parviflora. Several of these are found only in D1 and D2 on south aspects indicating that this is the most mesic north slope community.

Diversity: C4 is relatively poor in species. S 21-37 ($\bar{x}$ 30,2); H' 3,11-4,32 ($\bar{x}$ 3,61); S.I. ,81-,93 ($\bar{x}$,86).

C3 Protea neriifolia - Leucadendron eucalyptifolium - Erica triceps community

Sub-Formation: Medium (1,5-2,5 m) mid-dense proteoid shrubland with mid-dense heath understorey.

Relevés: 43, 44, 45, 47, 49, 51, 52, 13, 42.

Stratification: Mostly T1, sometimes U1 or U2.

Habitat: The community occurs at mid-elevations (700-850 m), mostly on steep (24°-47°) south aspects, rarely on north aspects (Relevé 13) in sheltered situations.

Surface rocks and stones are generally rare (0 to 70%, $\bar{x}$ 14% cover). A horizons were relatively stone free in the relevés sampled. The soils are mostly moderately deep, acid (pH 4,0-5,2, $\bar{x}$ 4,4) loams and sandy loams with dark brown or dark yellowish brown B_{21} horizons (Glenrosa, Clovelly). These soils are typical of Peninsular and Chando formations on south aspects where clay lenses occur in the sandstone. Organic matter in the A horizon ranges from 4,9-14,1% ($\bar{x}$ 8,6%).

Vegetation: The community is two to three layered with a mid-dense canopy of Leucadendron eucalyptifolium and/or Protea neriifolia. Erica viridescens frequently occurs in the overstorey with the proteoid elements. A mid-dense understorey from ,8-1,2 m is dominated by ericaceous shrubs (E. triceps, E. glomiflora) intermingled with restioids and Cyperaceae (Tetraria capillacea, T. involucrata). A diffuse stratum from 5-35 cms is present consisting mainly of grasses (Ehrharta dura, Merxmuellera rufa) and sedges.

The proteoid layer changes fairly abruptly to Leucadendron uliginosum, probably associated with a change to stonier, Cartref soils. The L. uliginosum community is poorly represented on south aspects in the Robinson's Pass area and consequently undersampled and the relevés of this visually distinct community were thus classified with C3.

There are no exclusive character species. Erica triceps was generally abundant and an indicator species (occurring also in D2). Other character species are Hypodiscus alboaristatus and Cliffortia stricta. Protea cynaroides and Mimetes cucullatus are frequently present.

Diversity: The community is rich in species (35-48, $\bar{x}$ 41,8); H' 3,13-4,63, $\bar{x}$ 3,9; S.I. ,81-,94, $\bar{x}$,88.

C2 Protea neriifolia - Erica viridescens - Hypodiscus synchroolepis community

Sub-Formation: Medium open proteoid shrubland with mid-dense restioid heath understorey.

Relevés: 8, 11, 12, 14, 18, 20.

Stratification: T1, T2.

Habitat: C2 occurs at mid-elevations (750 to 1 000 m) on sloping to steeply sloping (11°-68°) north aspects, generally on rocky sites (rock cover 60-80%). Soils were stony, shallow, moderately acid (pH 4,4-5,4, $\bar{x}$ 4,9) Glenrosa. Organic matter in the A horizon is moderate (5,4-12,8, $\bar{x}$ 8,13).

Vegetation: This community occurs below C4 and is a xeric north slope equivalent of C3. Plots 18 and 20 are transitional to, and more mesic than B3. *Erica viridescens* is common in the 1,5-2,0 m overstorey with *Protea neriifolia*. *Penaea acutifolia* is a characteristic narrow-leaved shrub in the understorey, but shrubs are otherwise inconspicuous in this layer. Herbaceous plants dominate in the understorey, particularly *Hypodiscus synchroolepis*, *Tetraria involucrata*, *T. cuspidata*, *H. striatus* and, in four of the six relevés, the tall (1 m+) *Elegia galpinii*.

There are no exclusive character species. *Ficinia* sp. (1744), *Helichrysum paniculatum* and *Elegia galpinii* are indicator species.

Diversity: The community is relatively poor in species (S = 29-39, $\bar{x}$ 33,2); H' 3,37-3,99, $\bar{x}$ 3,7; S.I. ,85-,89, $\bar{x}$,87.

C1 Protea aurea - Pteridium aquilinum community

Sub-Formation: Tall (2,5-4,0 m) mid-dense proteoid shrubland with tall mid-dense shrub understorey.

Relevés: 38, 39, 40, 41, 48, 50, 55, 56.

Stratification: T1 and B1.

Habitat: The community occurs on lower (400-750 m) south slope foothills on gently sloping to sloping (10^0-36^0) southern aspects. It is largely confined to moderate deep and deep, red and yellow sandy loam and sandy clay loam soils (Hutton, Clovelly) on Tertiary peneplains or their scarps. Surface rocks are rare or absent and A horizons are generally free of stones. A horizons are moderately acid (pH 4,5-5,5, $\bar{x}$ 4,9) and fairly rich in organic matter (6,5-15,5, $\bar{x}$ 11,0). Pinus radiata grown on similar soils in the vicinity sometimes suffers from Manganese deficiencies (Lange 1968).

Vegetation: The community has a tall, dense, proteoid canopy dominated by Protea aurea frequently associated with Leucadendron eucalyptifolium. P. coronata occurs locally on more shallow, rocky soils. The rare Leucospermum formosum is restricted to this community.

The understorey is generally tall (1-2,0 m+) and dense except in old stands where it is suppressed by the proteoid canopy. Leptophyllous shrubs are common and diverse overlying a lower herbaceous layer where sedges dominate. Restioids are rare. Ferns and forbs (e.g. Psoralea cordata) are frequent.

The community has several exclusive character species and, like the D communities, is distinctive apparently because of sharp soil discontinuities.

Character species include Protea aurea, Pteridium aquilinum, Psoralea cordata, Pelargonium cordifolium and Phylica pinea.

Diversity: The community is moderately rich in species (S 25-49, $\bar{x}$ 38,8); H' 3,13-4,09, $\bar{x}$ 3,68; S.I. ,8-,9, $\bar{x}$,86.

B Xeric Proteoid Shrublands. These communities are confined to mid and lower elevations north of the watershed on the Outeniquas. Indicator species in the proteoid layer include P. lorifolia, P. repens, P. nitida and Leucadendron salignum. Restionaceae dominate the understorey except in Waboomveld where C4 type grass taxa are important.

B3 Elegia galpinii - Metalasia pulcherrima community

Sub-Formation: Tall (1-2,0 m), open restioid heath with scattered Proteaceae.

Stratification: B2.

Relevés: 15, 19, 21, 22 see also 18, 20.

Habitat: B3 occurs at mid-elevations (800-1 000 m) on relatively xeric, steep (30-45^{o}) north aspects. There are generally abundant, large surface rocks and boulders (50-90% rock cover) and soils are shallow, stony loamy sands (Mispah), with a pH of 5,3-5,6 and low organic matter content ($\bar{x}$ 4,6%).

Vegetation: This distinctive community is characterised by the tall, unbranched restioid Elegia galpinii in the overstorey associated with rare to frequent Protea repens and/or P. lorifolia, and Metalasia pulcherrima.

Shrubs are poorly represented in terms of cover and number of species and some (e.g. Cliffortia pulchella) show a tendency to stunting in this community. Restioids predominate with E. galpinii, Hypodiscus aristatus, Cannamois dregei, Hypolaena purpurea and Hypodiscus striatus. Characteristic species include Metalasia pulcherrima, E. galpinii (also in C2), and Gnidia sp.

Diversity: The community has moderate species diversity (S 25-38, $\bar{x}$ 32,5; H' 3,07-3,85, $\bar{x}$ 3,53; S.I. ,76-,88, $\bar{x}$,83.

B3 is a distinctive community restricted to the western Outeniquas between Outeniqua and Robinson's Pass. Although generally poor in shrub species, several rare Proteaceae occur in this unit including Leucadendron ericifolium (once thought to be extinct), L. olens and Leucospermum secundifolium.

B2 Leucadendron salignum - Erica brachycentra community

Sub-Formation: Variable.

Stratification: B2, T1.

Relevés: 16, 17, 25, 30.

Habitat: The unit occurs on relatively xeric North aspects at mid-elevations (680-950 m) on steep slopes (30^0-48^0). The community is heterogeneous, perhaps due to undersampling and shows strong affinities with B3 and less so with B1. Surface rocks are smaller, with less cover than B1 (15-30%), whilst pH ($\bar{x}$ 5,45) and organic matter ($\bar{x}$ 4,55%) are comparable. Soils are mostly stony loamy sands (but deeper than B1) (Glenrosa).

Vegetation: The unit is poorly defined by character species, but *L. salignum*, *E. brachycentra* and *Metalasia gnaphaloides* are centred in this community. *Heteropogon? contortus*, a subtropical (C4?) grass species, is the first representative of this group to appear on the xeric end of the moisture gradient.

Diversity: The community is moderately rich in species, S = 35-38, $\bar{x}$ 36,5; H' 3,64-4,24, $\bar{x}$ 3,95; S.I. ,84-,92, $\bar{x}$,89.

B1 *Protea nitida* community (Waboomveld)

Sub-Formation: Mostly low open woodland or tall open shrubland with a graminoid-shrub understorey.

Relevés: 23, 24, 26, 27, 28, 32.

Stratification: B2, U2.

Habitat: Waboomveld occurred at mid to lower elevations (900-600 m), mostly north of the watershed, on relatively steep slopes (16-61°). It occurs on all aspects but, due to the sampling strategy, was recorded only from north, north-east and north-west facing slope. Surface rocks are common (55-85% cover), but mostly of smaller size classes (12,5-50 cm diameter). Waboomveld commonly occurs on loose rock or stabilised talus slopes (Kruger 1979), especially on east- and west aspects on north-south valleys incising the mountains. The soils are generally very stony loamy sands or sandy loams, moderately acid (4,3-5,7, $\bar{x}$ 5,3) with low organic matter contents in the A horizon (1,7-4,1, $\bar{x}$ 3,2%) and are moderately deep or deep, with dark brown or dark reddish brown subsoils (Oakleaf).

Vegetation: Waboomveld is a three layered community, with a sparse proteoid canopy, a tall shrub layer (75 cm - 1 m 50) and a low shrub/forb/herbaceous layer (5 cm - 50 cms). Grasses are particularly conspicuous in this lower layer and include species typical of grassland or savannah areas of the sub-tropics (Heteropogon contortus, Brachiairia serrata, Aristida diffusa, Themeda triandra). Geophytes, especially deciduous geophytes, are common and diverse, but were not included in the analysis because of their ephemeral character.

The shrub component varies from essentially fynbos elements to renosterveld elements with Compositae (Elytropappus gnaphaloides, E. adpressus, Stoebe capitata) becoming prominent.

Waboomveld is discussed by Taylor (1978) and Kruger (1979), both of whom consider it as a major sub-category of mountain fynbos.

Diversity: Waboomveld is typically rich in species, perhaps because it lies on the ecotone between fynbos and renosterveld. Relève 52 was unusually species poor and, in several respects, is closer to community A (arid fynbos). For this reason it is ignored in the following statistics: S 40-49, $\bar{x}$ 44,8; H' 4,05-4,99, $\bar{x}$ 4,54; S.I. ,86-,96, $\bar{x}$,92.

A Phylica axillaris - Felicia filifolia community - Arid fynbos

Sub-Formation: Low open or sparse shrubland.

Stratification: Mostly U1, U2.

Relevés: 29, 31, 33, 34, 35, 36, 37 (32 has affinities).

Habitat: Arid fynbos occurs at low elevations (750-600 m) on the northern foothills of the Outeniquas on steep to gently sloping northern aspects. Unlike waboomveld, this community occurs on shallow soils over hard rock (Mispah) or with thin dark brown subsoils (Glenrosa). A horizons are acid to neutral (pH 5,2-5,6, $\bar{x}$ 5,4) with a low organic matter content (2,2-4,9, $\bar{x}$ 3,4%).

Vegetation: Arid fynbos is a single layered community though a very poorly defined, seasonal understorey of annuals or deciduous geophytes sometimes forms a second layer. Ericoid shrubs, mostly low (1,0 m) dominate the community. Grasses, sedges and restios generally have low cover. Small succulent Crassulaceae occur in the ground layer.

Character species include *Zygophyllum maculatum*, *Felicia filifolia*, *Phylica axillaris* and *Agathosma recurvifolia*.

Two sub-communities could be distinguished - the one more closely allied to B1 (Waboomveld) (relevés 29, 31, 33) indicated by *Eroeda* sp., *Elytropappus adpressus*, *E. gnaphaloides*, and the other a more arid community (relevés 34, 35, 36, 37) indicated by *Passerina obtusaefolia*, *Agathosma recurvifolia*, *Diosma apetala* and *Chrysanthemoides monilifera*.

Arid fynbos is discussed by Taylor (1979) and Kruger (1979).

Diversity: Diversity is variable with both rich and poor sites. S 17-35, $\bar{x}$ 27,9; H' 3,21-4,39, $\bar{x}$ 3,76; S.I. ,84-,93, $\bar{x}$,87.

SWARTBERG

A Ericaceous Heathlands of the upper South slopes.

Protea punctata and Leucadendron album are characteristic proteoids, but erect Proteaceae are replaced by low procumbent species at higher elevations. Ericaceae and ericoid leaved Rosaceae dominate the heathland. Grasses with hard, inrolled leaves are common in the herbaceous layer associated with restios and sedges. Rosette forbs with broadleaves appressed to the ground occur in the ground layer.

A1 Erica petraea - E. nervata community

Sub-Formation: Low closed or mid-dense heathland.

Stratification: U1, U2, U3.

Relevés: 1, 2, 3, 4.

Habitat: The community occurs at high elevations (1 400-1 900 m) on peaks, ridges and amongst cliffs on south aspects. Slopes vary from very steep to gentle (on mountain tops). Surface rocks are generally abundant and soils are shallow, stony Mispahs or, rarely, Clovelly forms. They are acid (pH 4,1-4,6) and relatively high in organic matter (5,0-9,0%).

Vegetation: The community is single layered and dominated by ericaceous shrubs with up to 14 species counted in a relevé. High altitude endemic Proteaceae (e.g. P. montana, P. venusta, Leucadendron *dregei*) occur as low shrubs often forming procumbent mats. The herbaceous element is intermingled with the shrubs and consists of Poaceae, Restionaceae and Cyperaceae in approximate order of importance. A poorly defined layer of low rosette forbs and geophytes occurs as a ground layer. The community is structurally and ecologically similar to D2 on the Outeniquas.

Character species are not clearly defined due to the limited sample number. *Restio* sp. (1630), *Crassula obtusa*, *Cliffortia robusta*, *Erica petraea* and *E. nervata* were, however, typical of the community.

Diversity: The community has moderate species richness. S 32-43, $\bar{x}$ 35,8; H' 3,61-3,96, $\bar{x}$ 3,84; S.I. ,87-,9, $\bar{x}$,88.

A2 *Protea punctata - Erica melanthera, E. andraei community*

Sub-Formation: Low mid-dense shrubland with scattered emergent proteoid shrubs.

Stratification: U1, U2, U 3.

Relevés: 7, 8, 9, 10, 11, 5, 6.

Habitat: A2 occurs at mid to high elevation (1 300-1 600 m), on steep (35-65°) South aspects, lower, or less mesic than A1. Surface stones, mostly of diameter 25-50 cms, are frequent covering 15-50%. Soils are moderately deep, but stony, loamy sands or sandy loams with reddish brown or yellowish brown subsoils (Hutton, Clovelly, Oakleaf).

They are acid (pH 4,3-5,2, $\bar{x}$ 4,8) and relatively rich in organic matter (4%-11%, $\bar{x}$ 6,3%).

Vegetation: The community is essentially single layered and dominated by ericoid and ericaceous shrubs. Proteaceae, especially P. punctata, Leucadendron spissifolium and L. album are typical emergent shrubs, the former to ±150 cms, but with sparse cover. Similar vegetation elsewhere in the Swartberg suggest that low Proteoid cover in this community is probably due more to past fire history than environmental controls. The herbaceous element is dominated by grasses (Pentameris spp., Pentaschistis sp.) and tufted, mostly unbranched restioids (Hypodiscus alboaristatus, H. synchroolepis, Elegia spp.) with Cyperaceae subordinate.

Low forbs, geophytes and ferns occur as a sparse ground layer. The community (or related communities) is widespread at upper mesic elevations in the Swartberg, Kammanassie and Rooiberg ranges and is distinguished by the presence of Protea punctata and the dominance of Ericaceae in the shrub layer.

Characteristic species include Erica setacea, E. calycina, E. melanthera (also B1), Leucadendron spissifolium and Hypodiscus alboaristatus.

Diversity: The community is relatively species rich, S 40-49, $\bar{x}$ 44,6; H' 3,78-4,6, $\bar{x}$ 4,23; S.I. ,87-,94, $\bar{x}$,91. The community is particularly rich in Ericaceae with more than ten species being recorded in some 5 x 10 m relevés.

B Proteoid Shrublands of Mid and Lower South Slopes. These shrublands are dominated by Protea repens, P. lorifolia and P. eximia. Ericaceae seldom have significant cover in the small leaved shrub layers. Restios and sedges dominate the herbaceous layer with subtropical grasses increasingly important at lower elevations.

B1 Transitional Protea punctata, Brunia nodiflora community

Sub-Formation: Medium, open proteoid shrubland with mid-dense understorey.

Stratification: T1, T2, B1.

Relevés: 12, 13, 14, 16.

Habitat: This transitional "community" occurs at mid-elevation between ±1 100-1 200 m on relatively gentle (13-27°) slopes on south aspects. Surface stones are generally rare, but boulders (100-200 cm diameter) occur locally. Soils are mostly moderately deep loamy sands or sandy loams with dark reddish brown or very dark brown B horizons (Oakleaf, Hutton), usually stony in the A horizon. pH lies between 4,8 and 5,5 and organic matter between 3,9 and 6,2%.

Vegetation: This "community" is transitional between the Protea punctata, Erica heaths of mesic upper elevations and the mixed proteoid shrublands of mid and lower elevations on south aspects. The proteoid layer is generally well developed with P. punctata, Leucadendron album and more xeric species such as *P. eximia* and *P. lorifolia*. The understorey is generally not distinctly layered. *Brunia nodiflora* is a characteristic shrub together with *Erica hispidula*, *Stoebe cinerea*, *Cliffortia tuberculata* and *Anthospermum aethiopicum*. The transition from low altitude *Leucadendron salignum* to high altitude *L. spissifolium* occurs in this zone. Grasses (*Cymbopogon plurinodis*, *Merxmuellera stricta*) dominate the graminoid synusia with restioids of subordinate importance. Rosette forbs are rare or absent in the groud layer.

The community often extends as tongues into B2, especially on deeper soils and/or near drainage lines.

Character species are poorly defined and the community is recognised more by the presence or absence of species characteristic of A2 or B2 than by its own unique species compliment.

Diversity: The community is moderately rich in species, S 39-49, $\bar{x}$ 42,8; H' 3,31-4,12, $\bar{x}$ 3,81; S.I. ,82-,92, $\bar{x}$,87.

B2 *Protea lorifolia - Simocheilus multiflorus* community*

Stratification: T1, B2.

Relevés: 15, 17, 18, 19, 35.

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* Doubtful determination. (Bond 956). This and other minor genera of Ericaceae sent to Mr. E. Olivier, National Herbarium, Pretoria, for checking.

Habitat: This community is typical of lower mid-elevations (1 000-1 200 m) on relatively gentle slopes (9-21%) on south aspects. It also occurs in limited areas at higher elevations (±1 400 m) on steep north aspects. Where slopes are steeper on south aspects the community is usually replaced by Waboomveld (B3 in part). Soils are mostly shallow or moderately deep loamy sands with very dark brown or dark reddish brown subsoils (Glenrosa, Hutton, rarely Oakleaf). They are acid (pH 4,8-5,2 with pH 4,0 in the north slope relevé) with relatively low organic matter content (3,3-6,4%). Surface rocks are not conspicuous on south slopes (10-30%) and are mostly small (50 cm diameter). North slope phases are very much more rocky and soils are shallow Mispah or Glenrosa.

Vegetation: The community is widespread at lower mid-elevations in the Swartberg and other Little Karoo ranges. A proteoid layer between 1,5 and 2,0 m is usually present with *Protea repens*, *P. eximia* and *Leucadendron rubrum*. *P. lorifolia* frequently forms a distinct understorey at ±1 m associated with more widely scattered *L. salignum* and local populations of *L. barkerae* and/or *Leucospermum cuneiforme*.

The community is easily distinguished from A2 by the low diversity of ericaceous shrubs though *Simocheilus multiflorus* may contribute significant cover. Other shrubs include *Agathosma* spp., *Passerina obtusaefolia*, *Cliffortia tuberculata*, *Disparago ericoides*, *Metalasia muricata*, *Anthospermum aethiopicum* and many more. Restionaceae (*Willdenowia teres*, *Restio triticeus*, *Cannamois dregei*, *Hypodiscus striatus*) and Cyperaceae (*Tetraria ustulata*, *T. cuspidata*) dominate the herbaceous layer with grasses (Merxmuellera stricta) subordinate. Pelargonium ovale is one of the few common forbs. Character species include Agathosma mundii, Tetraria cuspidata and Helichrysum paniculatum.

Diversity: The community is moderately rich in species, S 40-45, $\bar{x}$ 42,8; H' 3,23-3,76, $\bar{x}$ 3,48; S.I. ,79-,87, $\bar{x}$,83.

B3 Protea nitida - P. repens, Phylica paniculata communities

Sub-Formation: Medium, mid-dense proteoid shrublands with heath understorey and medium heathlands with proteoid emergents.

Stratification: B1.

Relevés: 20, 21, 22, 23.

Habitat: B3 consists of two communities, floristically similar, but, because of the sampling procedure, undersampled for phytosociological community characterisation. They occur on low elevations (900-1 000 m) on southern foothills of the Swartberg. Waboomveld (Protea nitida) occurs on steep (50-70°) scarp slopes above the Cango fault, on rocky terrain or on talus slopes. Soils are moderately deep or shallow Glenrosa and Oakleaf Forms with a pH of 5,1-5,2 and 2,7-3,2% organic matter. On the pediment below the scarp Protea repens, P. lorifolia shrublands occur on gentler slopes ($\pm 30^{\circ}$) in soils derived from sandstone colluvium overlying shale at depth, and providing a relatively mesic soil moisture regime. Surface stones (25-50 cms diameter) vary from rare to common near the T.M.S. scarp. The soils have a pH of 5,1-5,2 and are low in organic matter (1,1-1,6%).

Vegetation: The communities are ecotonal between heathlands and shrublands of shale derived soils. Protea nitida, Leucadendron rubrum and L. salignum occur on steeper rocky site as emergents whilst P. repens with occasional P. eximia forms a distinct canopy at 1,5 m with a second layer at 1 m of P. lorifolia and L. salignum on foothill pediments. Phylica paniculata, a tall ericoid shrub, is prominent in the understorey with Stoebe spp., Erica spp., Agathosma mundii, A. capensis and Anthospermum aethiopicum. Renosterveld shrubs including Elytropappus rhinocerotis, Relhania squarrosa, R. genistaefolia and Rhus lucida occur sporadically.

Tall coarse restioids (Willdenowia teres, Cannamois dregei, Hypodiscus striatus, Restio fruticosus) dominate the herbaceous layer with frequent grasses, mostly of subtropical affinities (Cymbopogon plurinodis, Brachiairia serrata, Themeda triandra) and rare sedges. The fern, Cheilanthes ecklоniana, is a character species of the ground layer and rare succulents occur.

Phylica paniculata, Elytropappus rhinocerotis and Relhania genistaefolia are character species.

Diversity: The unit is rich in species. S 42-56, $\bar{x}$ 47,8; H' 3,59-4,47, $\bar{x}$ 3,9; S.I. ,84-,91, $\bar{x}$,87.

C Proteoid Shrublands of the Mid and Upper North Slopes. The communities of this group are not well defined since they form a continuum of gradually changing floristic composition. The proteoid layer is particularly susceptible to fire history and its potential presence can often only be inferred from scattered emergents or local dense stands.

C1 Cliffortia tuberculata - Thoracosperma galpinii (1178) community

Sub-Formation: Low and Medium mid-dense shrublands with proteoid emergents and medium open proteoid shrublands.

Stratification: U3, U1, U4/T1, U4, U1, T2.

Relevés: 28, 29, 30 - 25, 26, 27, 34.

Habitat: C1 occurs on gentle to steep (16-50°) North aspects at upper mid and upper elevations (1450-1650+ m). Surface stones and rocks are frequent to (mostly) common (25-65% cover). Soils are shallow or moderately deep and stony loamy sands or sandy loams and sandy clay loams on/or near shale bands (Glenrosa, Mispah, rarely Hutton, Clovelly). pH ranges from 4,4-5,0, $\bar{x}$ 4,8 and organic matter from 3,8-8,4%, $\bar{x}$ 5,6%, staining the A horizon a very dark grayishbrown to black.

Vegetation: The unit is not a distinct community, but a continuum of closely related high elevation communities. A low ericaceous heathland with grasses (Pentameris spp.) prominent and Hypodiscus alboaristatus the dominant restio occurs at the highest elevations with scattered Protea punctata, Leucadendron album or L. spissifolium. This is analagous to A2 of the south aspects, but is very much poorer in ericaceous species (1-2 compared with 5-10+). At lower elevations, on more droughty soils or on xeric aspects, this community is gradually replaced by a heathland with Ericaceae subordinate to other shrubs (e.g. Cliffortia tuberculata, Anthospermum ciliare, Metalasia pallida etc.) and with Restionaceae (Hypodiscus synchroolepis, Willdenowia teres) and Cyperaceae e.g. Tetraria ustulata dominating the herbaceous layer instead of grasses. Protea repens and P. lorifolia replace P. punctata in this zone. The sub-community is approximately equivalent to B1 and the more mesic phases of B2 of the south aspects, but approximately 250 m higher at its lowest limit.

Character species for C1 include Cliffortia tuberculata, Stoebe plumosa, Watsonia marlothii and Corymbium glabrum most of which occur in A2 or B1, but which are restricted to C1 north of the watershed.

Diversity: Species richness varies from low to relatively high. S 30-49, $\bar{x}$ 39,3; H' 3,17-4,25, $\bar{x}$ 3,84; S.I. ,79-,92, $\bar{x}$,87.

C2 Protea repens - P. lorifolia - Hypodiscus striatus community

Sub-Formation: Medium open proteoid shrubland with mid-dense restioid-shrub understorey.

Stratification: B3, U3, U4.

Relevés: 24, 31, 32, 36 (33).

Habitat: The community occurs on steep to sloping (18-40°) north aspects at mid-elevations (±1 300-1 400 m). Surface stones and rocks are abundant (55-85%) with both large boulders (100 cm - 200 cm+) and small stones (13 cm diameter). Soils are shallow, rocky, loamy sands with no or minimal B development (Mispah, Glenrosa). pH is between 5,0 and 5,7 ($\bar{x}$ 5,3) and organic matter is relatively low (2,7-6,6%, $\bar{x}$ 4,4).

Vegetation: The community is typically two layered with a proteoid canopy overlying an understorey dominated by restioids with shrubs subordinate. *Protea repens* and *P. lorifolia* are typical canopy dominants sometimes associated with *Leucadendron rubrum* and the shorter *Paranomus dregei*, *Protea harmeri* and *Leucospermum wittebergense*. Medium (50-75 cms) and tall (75-120 cms), coarse restios predominate in the understorey, especially *Cannamois dregei*, *Restio fruticosus*, *R. hystrix*, *Hypodiscus striatus* and *Willdenowia teres*. *Themeda triandra* and *Cymbopogon marginatus* are rare C4 type grasses associated with *Ehrharta calycina*. *Tetraria ustulata* is locally common towards the transition to C1. Shrub species (which are subordinate to graminoids) include *Agathosma mundii*, *Acmadenia sheilae*, *Agathosma capensis* and *Anthospermum ciliare*. Renosterveld genera such as *Elytropappus adpressus* and *Relhania* spp. are rare, but present.

The community has affinities with the *Protea repens* - *P. lorifolia* phase of B3 on the southern foothills (but displaced 200-300 m higher in elevation). Character species include *Agathosma mundii* and *A. capensis* both of which are not, however, restricted to the unit.

Diversity: The community is moderately low in species richness. S 24-37, $\bar{x}$ 32; H' 3,52-4,05, $\bar{x}$ 3,82; S.I. ,87-,89, $\bar{x}$,88.

C Arid Fynbos. This group includes arid fynbos, the most xeric communities on the Swartberg gradient. Proteaceae are rare or absent, total cover is low (usually 30% Foliage Projective Cover) and, unlike C2, Restionaceae become subordinate to shrubs towards the drier end of the gradient. Succulent plants and malacophylls are frequent, but seldom have high cover value. The community is equivalent to (but drier than) A of Ruitersbos.

D1 *Passerina obtusaefolia - Felicia filifolia - Pentaschistis eriostoma* community

Sub-Formation: Low and medium open heathland.

Stratification: B1, B2, U3, U4.

Relevés: (36, 33), 38, 37, 39, 40, 44 (43).

Habitat: Steep to gently sloping (12-40°) north aspects between ±1 200 and 1 350 m. The sites are typically very rocky (70-85%) with very shallow sandy and loamy sand soils (Mispah, Glenrosa). The soils are more acid than expected (see discussion in Chapter 1) with a pH range of 4,6-5,1, $\bar{x}$ 4,9 and with organic matter also relatively high (3,1-5,3%, $\bar{x}$ 4,6). There is wide variation in these values which may reflect laboratory error rather than ecological reality!

Vegetation: The unit is not homogeneous and shows a cline from relevés closely related to C2 with rare Proteaceae and Restionaceae (36 and 33) common to ones where Restionaceae form an insignificant component. The structure is simple with only one distinct layer in which shrubs predominate. Shrubs include *Passerina obtusaefolia*, *Metalasia pallida*, *Felicia filifolia* (characteristic species), *Aspalathus hystrix*, *Phylica floccosa* and *Anthospermum tricostatum*. The tufted grass, *Pentaschistis eriostoma* is characteristic of the unit and is locally common. Restionaceae include *Restio fruticosus* and *Hypodiscus striatus* and sedges the characteristic dwarf, fine leaved *Ficinia* sp. (1798).

Diversity: Arid fynbos is poor in species (annuals and deciduous geophytes not included). S 15-24, $\bar{x}$ 21,3; H' 3,08-3,52, $\bar{x}$ 3,31; S.I. ,77-,87, $\bar{x}$,84.

E Succulent Karroid Shrublands. Succulent Karroid shrublands replace fynbos on steep North aspects below the 300-350 mm rainfall isohyet. They are easily distinguished from fynbos by the absence of Restionaceae, but other graminoid and shrub genera are less exclusive. Karroid shrublands occur on Table Mountain Sandstones and Bokkeveld shales with relevés on the former substrate showing a stronger floristic relationship to arid fynbos.

E1 Crassula rupestris - Digitaria natalensis community

Sub-Formation: Medium Open Succulent Shrublands.

Stratification: B3, B2, U3.

Relevés: (43), 41, 42, 48, 49, 50, 45, 47, 46.

Habitat: Karroid Shrublands occur on the steep scarp marking the northern limits of the Swartberg. The community replaces arid fynbos on steep (30-70°) north aspects below about 1 100 m. The sites are very rocky (75-90% rock cover) with small, medium and large rocks represented. The rocks are either Table Mountain Group sandstones in situ or T.M.G. talus overlying shales at varying depths. Soils are very stony. Mispah, Glenrosa or Hutton Form with pH varying from 4,3-6,9, $\bar{x}$ 5,33 and low organic matter (2,4-6,6%, $\bar{x}$ 4,06). Some of the lower pH values and higher organic matter values are probably due to laboratory error. pH values averaging ±5,5 and organic matter of ±2,5% are probably more typical.

Vegetation: The vegetation is generally a mosaic of small leaved or succulent shrubs with local clumps of Portulacaria afra or broad-leaved, non-succulent shrubs such as Rhus glauca and Euclea undulata. Crassula rupestris is a conspicuous succulent shrub with Crassulaceae and Mesembryanthemaceae in general well represented. Asteraceous shrubs are common, particularly Eriocephalus africanus and Pteronia incana.

Grasses are the most important herbaceous element and predominantly subtropical taxa such as *Digitaria natalensis*, *Themeda triandra* and *Aristida diffusa*. Geophytes, nearly all deciduous, are diverse in species, but were excluded from the relevé analysis.

Character species include *Digitaria natalensis*, *Crassula rupestris*, *Colyledon orbiculata*, *Aristida diffusa* and *Aloe ferox*.

Diversity: The unit is relatively poor in species (excluding annuals and deciduous geophytes). S 18-29, $\bar{x}$ 22,9; H' 3,21-4,09, $\bar{x}$ 3,51; S.I. ,78-,92, $\bar{x}$,86.

CHAPTER 6

STRUCTURAL CLASSIFICATION

6.1 INTRODUCTION

In chapter four, I discussed the benefits of structural classifications at a scale where floristic variation is due to phytogeographic patterns as well as site variation. In this chapter, I discuss an attempt to construct a physiognomic/structural classification for the study area.

Physiognomic/structural classifications (referred to hereafter as structural for brevity) have been widely used on a world or continental scale (Warming 1909; Fosberg 1967; Mueller-Dombois and Ellenberg 1974). Their use at a smaller, local scale has been greatest in the rich and poorly known tropical floras (Beard 1955, 1978; Webb et al. 1970). The generality of the physiognomic approach rests on the (convergence) assumption that "physiognomy expresses biotope conditions and that similar biotopes in different parts of the world will exhibit, and can be recognized by, vegetation of similar physiognomy" Beard (1978). A major weakness of the assumption is that "local influences are sometimes pronounced because different growth forms are available in different geographic areas" (Beard 1978).

The idea of similar lifeforms in similar biotopes has been explicitly tested in the winter rainfall climates of California and Chile whose floras are unrelated (Parsons and Moldenke 1975; Parsons 1976). They provided support for the hypothesis that vegetation growing in similar sites in the two areas should show greater resemblance than vegetation in different environments in the same study areas. Convergence is never exact, however, and the question remains "how similar must structure be before one can assume identical biotopes".

An interesting example of the problem is the theory that evergreen sclerophyll shrublands in the winter rainfall regions of the world show structural convergence as an adaptation to the peculiar climatic features (Schimper 1903; Cody & Mooney 1978). An opposing hypothesis, however, proposes that sclerophyll and other "convergent" features of fynbos are an adaptation to substrate and independent of rainfall seasonality (Johnson and Briggs 1975; Cowling and Campbell 1980).

The use of structural criteria to define biotopes is thus constrained by 1) the complexity of selective pressures operating in the evolution of plants (e.g. co-evolution between plants and available seed vectors, Milewski 1980) 2) historical factors of disturbance (e.g. Jaksić and Fuentes 1980 on the effects of herbivores in Chile, Feely 1980 on the role of man in structuring Southern African savannah woodlands) and 3) problems of phylogeny e.g. the absence of Eucalyptus in South Africa (See also Chapter 7).

Structural Classification in Fynbos

Despite its floristic diversity, the Cape fynbos shows a remarkable convergence of growth forms including reduction in leaf size, sclerophyll evergreen leaves, the prominence of ericoid forms in unrelated families, small size, woody character and large root systems of shrubs and rarity of succulence and thorniness (Bews 1925).

Adamson (1931) suggested that fynbos structure and succession was best understood in terms of growth forms. The species composition of any growth forms appeared, to him, to vary in a largely random way so that growth form composition was the more stable feature. These observations on the convergent nature of fynbos and the constancy of structural relative to floristic composition provided an early stimulus to physiognomic classification of fynbos (Adamson 1938).

Adamson's early work has been followed by Taylor's (1978) and Kruger's (1979) descriptions of the fynbos biome which are essentially physiognomic rather than floristic. Moll <u>et al</u>. (1976) developed a system for habitat classification using quantitative structural criteria on the premise that these are easier to collect than species based classifications. Bond <u>et al</u>. (1980) sought correlations between fynbos structural variables and rodent populations and showed that these were more significant than floristic criteria in defining rodent habitats. Linder and Campbell (1978), presented a quantitative attempt at structural classification of fynbos. They used polythetic, agglomerative cluster techniques and found that results were dependent on selection of suitable similarity coefficients but that successful classification was feasible.

The present study arose from the need to plan and manage mountain catchment areas in the Southern Cape by staff with limited botanical knowledge. Physiognomic classifications have been widely used in similar circumstances, especially in the tropics, with apparent success (Beard 1955, 1978; Webb et al. 1970). The requirements of an effective physiognomic system are a) the classes should have predictive value i.e. each class should occur within a limited range of climatic, edaphic, hydrological conditions b) structural groups should correspond with floristic groups within any one area (c) a single class should respond in similar ways to perturbations such as fire and grazing d) structural classes should have relevance to faunal assemblages where possible (e.g. Moll et al. 1976; Bond et al. 1980) and e) recognition of classes should be objective and simpler to apply than floristic classifications. In addition, the study should allow the testing (and generation) of hypotheses relating growth form distribution to resource gradients.

6.2 METHODS

Growth forms and structural features of the vegetation used in the analyses are discussed in Chapter 2. Each shrub or forb listed in a relevé was allocated a nine digit code with the value of each digit representing a single category within a class of structural attributes. The main classes were 1) Raunkiaerian life form 2) leaf shape (broad, narrow or aphyllous) 3) Raunkiaerian leaf size 4) the presence and location of pubescence (upper, lower or both leaf surfaces) 5) leaf type e.g. isobilateral, linear, terete etc. 6) leaf arrangement e.g. decussate, whorled, fascicled, rosette form 7) leaf texture e.g. sclerophyll, orthophyll, semi-succulent, succulent 8) deciduosity and 9) dominant fire regeneration type e.g.

serotinous*, resprouting from rootstock etc. Graminoid life forms were allocated a four digit code referring to a) type i.e. grass, restio or sedge b) height c) tussock diameter and d) growth form category, e.g. unbranched restio, grassy sedge, hard-leaved grass etc. Geophytes were allocated a two digit code; the first representing their geophyte growth form and the second leaf length. Finally, bipinnate ferns were allocated a single digit, representing this specific growth form (see Table 2.2 for a list of growth forms).

Schizaea pectinata, a restioid-like fern, was allocated a graminoid code. Bobartia spp., restio-like geophytes were listed as geophytes and Lanaria spp., sedge-like geophytes, were referred to geophytes and not to sedges. Deciduous geophytes and annuals were not included in the analysis because sampling was spread over several seasons.

The importance of each structural category in a relevé was assessed by summing the total cover of the relevant category for all species in the relevé using a program developed on a Hewlett Packard 9820 calculator. The categories were then used as attributes (a total of 115) with cover as importance value in a TWINSPAN analysis (Hill 1979). TWINSPAN, a divisive polythetic classification, has been discussed in Chapter 4. Several different pseudospecies levels were used in separate analyses and, in one analysis, species with

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* Serotinous has been used throughout the text for Proteaceae which retain seed in cones or capitula for more than one year. The term is never used in the alternative context of late flowering. Bradyspory (brady-Gr. bradys, slow) appears to be a more precise synonym (Kruger pers. comm. 1980) but could not be found in available botanical glossaries.

high cover were heavily weighted. Despite Linder and Campbell's (1978) success with relativized data, no analyses were made with transformed or relativized data since direct cover values appeared to be more useful for eventual field use of the classification (but see Discussion and Chapter 7).

6.3 RESULTS

TWINSPAN proved relatively effective using cover categories of 0, 5, 10, 25 and 50 percent. Relevé groups conformed, to a greater or lesser extent, with groups defined by the floristic TWINSPAN (Table 6.1). Differentiation of arid groups, however, was less successful with poor discrimination between arid fynbos and Waboomveld in the Ruitersbos data set.

Although indicator species (i.e. structural attributes) were very useful in defining the relevé groups, structural variables were poorly sorted in the final table. Tabulation methods were thus used to sort variables into a more satisfactory groupings and several additional variables which had not been included in the initial analysis because of data sorting procedures were added. These were: stem spinescence, leaf spinescence, the ratio of non-proteoid shrub/ graminoid cover, and the proportion of non-proteoid shrubs with ericaceous, non-ericaceous inrolled, and semi-succulent leaves respectively (Tables 6.2, 6.3).

Tabulation procedures resulted in a more effective classification of arid fynbos and Waboomveld relevés in the Ruitersbos data set and

TABLE 6.1 Group Similarities between Floristic and Structural Classification. Similarities were calculated by Sorensen's Coefficient (Shimwell 1970), S.I., where S.I. = 2c/a+b.100 and c is the number of relevés common to a pair of floristic and structural groups and a and b are the number of relevés in each group. The coefficient ranges from no similarity 0, to identical 100.

Ruitersbos			Swartberg		
Group Symbol		S.I.	Group Symbol		S.I.
Floristic	Structural		Floristic	Structural	
Heathlands					
D1	H1	91	A1	H1S	75
D2	H2	91	A2	H2S	86
C4	H3	86			
Mean		89,3			80,5
Proteoid Shrublands					
C3	P1	82	B2	P1Sa	80
			B1	P1Sb	100
C1	P2	94	B3	P2S	100
C2	P3	60			
Mean		79			93,3
Restiolands					
B3+B2	R1	67	C1	R1a, R1b	80
			C2		89
Mean		67			84,5
Dry Shrublands					
B1	W1	92	D1	A1S	100
A	A1	92			
Mean		92			100
Karroid Shrublands					
			E1	K1	100
Mean for Study Area		83,9			90,0

of two restioid and one heathland relevé in the Swartberg data set. In general, however, TWINSPAN produced a readily interpretable grouping of relevés for the cover categories selected.

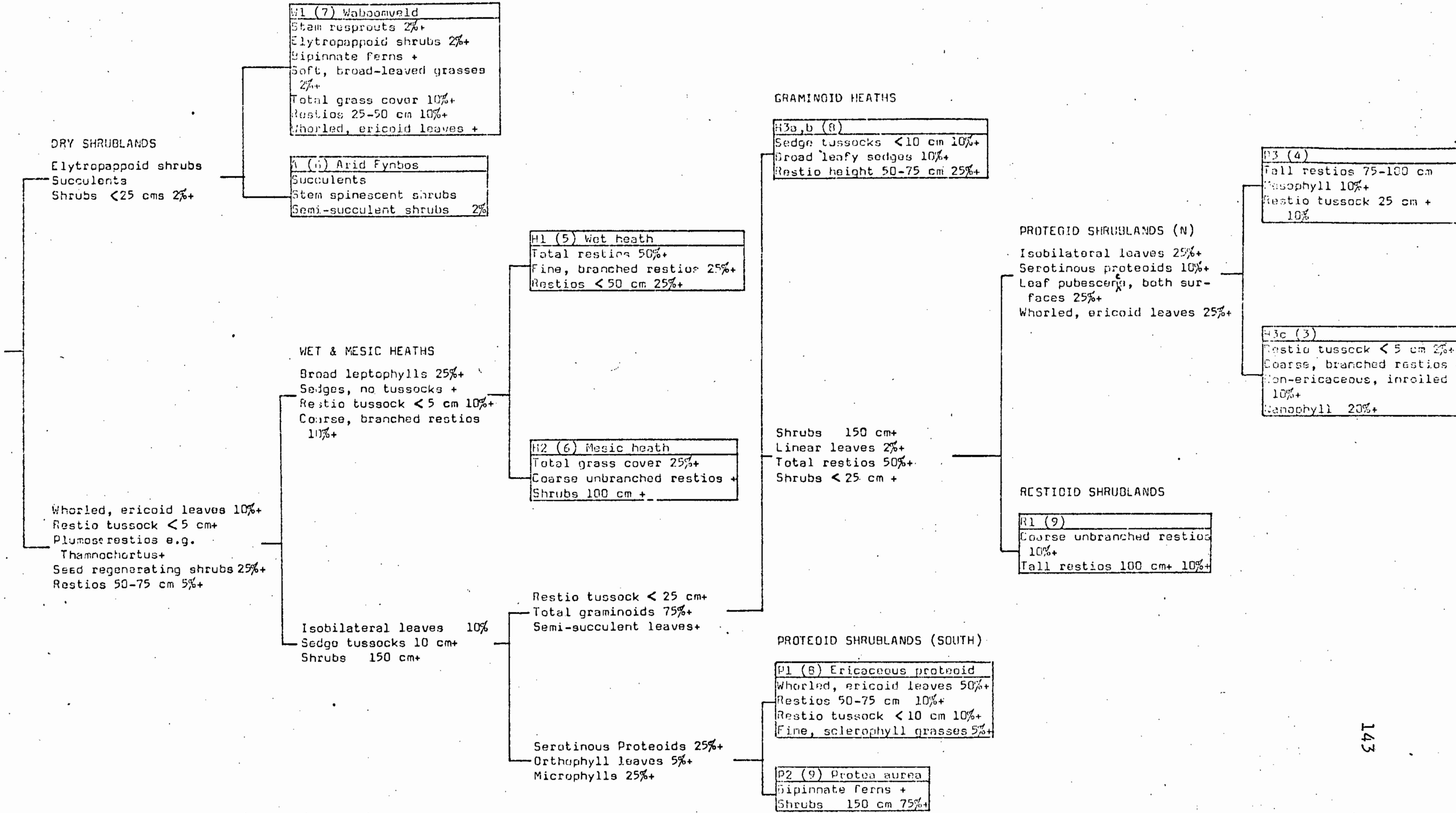
6.4 STRUCTURAL TYPIFICATION

Five major structural groups could be identified (Tables 6.2, 6.3). These were ericaceous communities lacking tall broad-leaved shrubs, proteoid shrublands with a mixed understorey of shrubs and graminoids, restioid communities with or without a proteoid layer and with small leaved shrubs subordinate, and xeric, non-ericaceous shrublands with low proteoid cover. The latter group includes waboomveld and arid fynbos (Taylor 1978). Non-fynbos shrublands included only Karroid succulent shrublands on the northern foothills of the Swartberg.

The structural and ecological characteristics of the main groups are described below followed by a structural typification of vegetation on the Outeniqua and Swartberg gradients (Sect. 6.6, 6.7). The division hierarchy and indicator attributes are shown in Figs. 6.1, 6.2.

In the descriptions I have used the concept of taxocenes (Peet 1978). A taxocene is a group of taxonomically related organism utilising similar resources. Competition or selection to avoid competition is greatest between members of the same taxocene. Important taxocenes for the structural typification of fynbos are proteoids (most Proteaceae and possibly other taxa such as Laurophyllus capensis), Ericaceae, Restionaceae, Cyperaceae and Poaceae.

FIGURE 6.1 Modified TWINSPAN dichotomies for structural classification, showing indicator characters at each division, RUITERSBOS. Community symbols as in Section 6.7, 6.8. Number of relevés in parentheses.



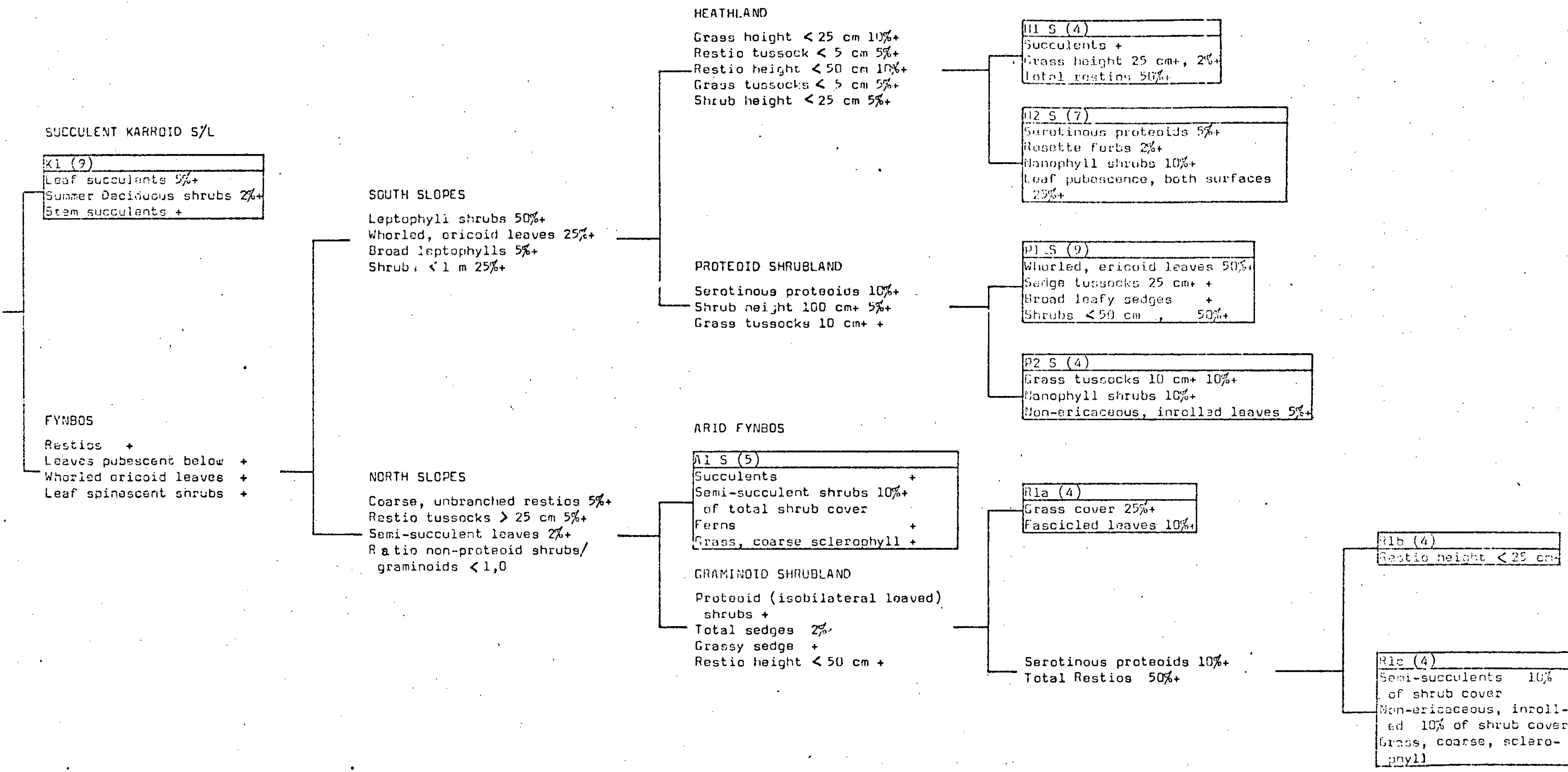
Grubbiaceae, Peneaceae and Bruniaceae resemble Ericaceae in their habitat requirements in the Southern Cape. However, these and other small leaved shrub families have been grouped into a broad category of non-ericaceous shrubs.

6.4.1 Heathlands - On Terminology

Specht (1979) has recently introduced a definition of heathland which differs from common usage. In Britain and Europe heathlands are shrublands dominated by Ericaceae, particularly Calluna (e.g. Gimingham 1972). Schimper (1903) referred to the similarity between heath and "the poorest sclerophyllous formations of the warmer districts with moist winters". He considered the resemblance superficial since heathlands are confined to poor, often peaty soils whereas evergreen sclerophyll shrublands are climatically limited and cover a range of soil types. More specifically, the characteristic features of heathland are a consequence of the dominance of Ericaceae, i.e. a taxonomic rather than adaptive legacy.

Specht (1979) has recognized that the shrubland formations occurring on poor soils in the winter rainfall areas of Australia and the Cape differ in a number of features from shrublands on base-rich soils in the same climate. He uses the term heathland for shrublands on poor soils redefining the term to include 1) vegetation of an evergreen sclerophyll nature 2) the presence, but not necessarily dominance, of the heath families Ericaceae and Grubbiaceae (in South Africa) and 3) distribution limited to nutrient-poor soils (Specht 1979).

FIGURE 6.2 Modified TWINSPAN dichotomies for structural classification showing indicator characters at each division, SWARTBERG. Community symbols as in Sections 6.7, 6.8. Number of relevés in parentheses.



I have retained the common usage of the term heathlands as (usually) low evergreen shrublands with a relatively high total cover dominated by Ericaceae. This is more or less equivalent to Taylor's (1978) ericoid-restioid zone. Pinus, Betula or Eucalyptus tree overstoreys over Ericaceous communities are best referred to as woodlands with heath understoreys. By analogy, proteoid communities in fynbos with their distinctive, broad-sclerophyll, isobilateral leaves are proteoid shrublands with, in mesic sites, heath understoreys.

Specht's (1979) dichotomy of shrubland types can be accomodated by referring to fynbos (nutrient poor) and non-fynbos (e.g. renosterveld, Karroid) shrublands. I thus follow Taylor (1978) in using the indigenous term fynbos rather than "older ambiguous terms such as Sclerophyllous Bush, Sclerophyllous Scrub, Maquis, Macchia and Heath".

Major Structural Groups in the Study Areas

6.4.2 Heathlands (Symbol H)

Heathlands are low (,5-1,5 m) shrublands with a high vegetative cover dominated by Ericaceae. Ericaceae form not less than 50% of non-proteoid shrub cover. Peneaceae, Grubbiaceae and Bruniaceae are typical heath associates on the coastal ranges, but usually absent in the inland mountains. Heathlands are typical of high elevations (1 000 m+) but may extend to lower elevations especially on soils with seasonally or perennially high water tables.

Proteoid shrubs are poor in species and do not exceed 10% cover. Prostrate, spreading species are characteristic of high elevations in the inland mountains (Protea montana, P. venusta, Leucadendron dregei). Graminoids are important components and usually exceed, or equal, total small-leaved shrub cover. The relative cover of grasses, restios and sedges is of diagnostic significance in distinguishing heathland types. Rosette or prostrate soft-leaved forbs and evergreen geophytes are characteristic of the ground layer.

Heathlands have been discussed by Taylor (1978) under his "ericoid-restioid" zone and by Kruger (1979) as "narrow sclerophyllous heathland and graminoid heathland".

6.4.3 Proteoid Shrublands (Proteaveld) (Symbol P)

Proteoid shrublands are medium (1-2 m) or tall (2 m+) communities with an overstorey of isobilateral, broad-leaved proteoid shrubs. Serotinous Proteaceae (seed stored in the canopy) dominate in the overstorey.

Proteoid shrublands occur over a wide range of elevations (450-1 000 m) in areas with a rainfall of 600-1 000 mm+.

Proteoid shrublands are layered communities with two or three layers including the proteoid canopy and one or two understorey layers dominated by shrubs and graminoids. Three major understorey types were identified. The most mesic is a heathland understorey dominated by Ericaceae (50%+ of all non-proteaceous shrubs). In drier areas non-ericaceous shrubs predominate as a second major category. Especially on north aspects, graminoids, particularly restios, dominate the understorey over a wide altitudinal range. This latter group is described below under restioveld. Proteaceae are visually prominent members of the community. Unfortunately their diagnostic value is limited by major fluctuations in plant density in response to fire history. Fire season and weather conditions within the first two years after fire may cause tenfold or more variations in proteoid density - especially in the inland mountain ranges (pers. obs.). In mapping exercises it is important to recognize communities with the potential to develop a proteoid canopy since management prescriptions may alter. I have attempted to recognize "potentially" proteoid shrublands, even when a proteoid canopy is lacking, by considering understorey characteristics but the problem is by no means resolved.

Structural features of Proteoid shrublands are discussed by Taylor 1978 ("proteoid zone") and Kruger 1979 (broad-sclerophyllous scrub or open scrub).

6.4.4 Restioid Shrublands (Restioveld) (Symbol R)

Restioid shrublands are low to mid-height graminoid shrublands dominated by Restionaceae. They are characteristic of north aspects on both coastal and inland ranges of the Southern Cape, on shallow, rocky soils (Mispah, Glenrosa) over a wide altitudinal range.

Tall (1 m+) coarse-stemmed restios with broad tussocks (e.g. Cannamois dregei, Willdenowia teres) are characteristic growth forms. Fine leafy sedges (e.g. Tetraria ustulata) and restioid sedges (e.g. T. cuspidata) are usually present but subordinate to the restioid element.

Proteaceae are generally present and may be visually dominant, but proteoid density in successive generations may fluctuate widely in this veld type. Small-leaved shrubs typically have a lower total cover than graminoids. Low shrubs ($<$ 50 cms) are common but visually subordinate to restios.

At their mesic extreme, restioid shrublands are characterised by a high cover of fine leaved grassy sedges, fine stemmed restios less than 75 cms tall and a higher proportion of ericaceous shrubs in the non-proteoid shrublayer. At the xeric extreme, Rutaceae with aromatic leaves are often common together with inrolled non-ericaceous and/or semi-succulent leaved shrubs. Tall (1 m+) coarse, unbranched restios are characteristic.

Taylor (1978) apparently groups restioid shrublands with the "ericoid-restioid" zone - "open restioid communities of drier inland ranges containing a mixture of coarse, rigid, tufted species of _Cannamois_, _Hypodiscus_ and many other species separated by bare soil". Kruger (1979) does not explicitly recognise the type which he appears to include, in part, in arid fynbos and "herbland" of mountain crests.

Laidler _et al_. (1978) describe a restioid shrubland from Table Mountain which seems to conform with Southern Cape restioveld characteristics. I will argue (Chapter 7) below that the prominence of restios is related to a set of edaphic conditions and not to an elevational gradient.

6.4.5 Dry Shrublands (Symbol W - Waboomveld, A - Arid Fynbos)

Dry shrublands include Waboomveld and Arid Fynbos (Taylor 1978). They occur at mid- and low-elevations with a mean annual rainfall of 250 to 750 mm. Dry shrublands intergrade with proteoid veld with a non-ericaceous understorey or restioveld. They are distinguished from these types by a number of characteristics. Tall serotinous Proteaceae are usually absent but are replaced by an open or sparse cover of species surviving fire by root sprouts, epicormic shoots, or soil stored seed.

Non-ericaceous shrubs dominate the small-leaved shrub strata. In-rolled, non-ericaceous leaves, and elytropappoid or semi-succulent ("fleshy") growth forms are well represented. Stem spinescence and stem and leaf succulence characterise the more xeric phases.

The graminoid layer is usually low with soft, broad-leaved C4 type grasses present (especially Themeda triandra). Restios are always present, but the cover is typically low and distribution is patchy with discrete tussocks separated by several metres.

Total cover is typically less than proteoid shrublands with non-ericaceous understoreys, ranging from 50-80%. Annuals and deciduous geophytes are common in the openings and relatively diverse but were not included in the analyses.

Kruger (1979) characterised Waboomveld, which often correspondse with the more mesic of the dry shrubland types, by the presence of 1) Protea nitida as the only prominent tall shrub 2) low, multi-stemmed (= fire resprouting) broad sclerophyllous shrubs 3) cupressoid (including elytropappoid) low shrubs and 4) the presence of Poaceae, especially broad, soft leaved types. Additional features in the two study areas are 1) the prominence of non-ericaceous shrubs and 2) the presence of bipinnate ferns.

Taylor (1978) defined arid fynbos, the most xeric of the dry fynbos shrublands, by 1) low total crown cover (50%) 2) simple structure without distinct layering 3) preponderance of ericoid shrubs with few Proteaceae and 4) restioids mostly rare and only locally conspicuous. Kruger (1979) applied a less restrictive definition where the dominance of proteoids, graminoids or shrubs may vary widely, but cover remains low and site conditions subarid to arid.

In addition to features listed by Taylor (1978), arid fynbos in Southern Cape mountains is characterised by the dominance of the shrub growth form, low cover of graminoids, and a high proportional cover of grasses to restios Kruger (1979) includes some restioveld in arid fynbos although acknowledging the wide altitudinal range of the common restio species. Because there is a distinct structural change from arid fynbos to restioveld, I prefer, however, to exclude the latter from the concept of arid fynbos.

6.4.5 Succulent Karroid Shrublands

On the northern foothills of the Swartberg, fynbos vegetation gives way to succulent Karroid Shrublands on steep, north-facing slopes below ±1 100 m. The underlying geology varies from quartzitic Kouga sandstone to a mixed talus of sandstone boulders and shale. There are no raingauges in the immediate vicinity, but the isohyet map gives the annual precipitation as 300-350 mm.

Karroid shrublands intergrade with arid fynbos and share several taxa, especially on the sandstone substrates. However, they were well defined as a structural group by the TWINSPAN analysis with the absence of restios being the most consistent indicator. A single relevé, with less than 5% restio cover, was included in the Karroid group.

Proteoids are entirely absent and microphyll and larger leaf sizes, where present, are invariably succulent (*Aloe*, *Cotyledon*).

Ericaceous shrubs are absent, but non-ericaceous shrubs with inrolled leaves (*Phylica*, *Passerina*, *Polygala*) occur and may be common on sandstone substrates. Spinescent leaved shrubs, characteristic of fynbos, do not occur in Karroid shrublands (with the notable exception of *Aloe*) but stem spinescence is characteristic occurring in a wider range of taxa than in fynbos. Summer- deciduous shrubs were entirely restricted to Karroid shrublands and did not occur in either the Swartberg or Outeniqua arid fynbos. Shrub leaf texture in these species is orthophyllous. Semi-succulent shrubs occur (e.g. *Eriocephalus*) but their proportional cover is less than arid fynbos. Karroid succulent shrublands are distinguished from fynbos by a succulent cover of 5%+. The proportional contribution of sclerophyllous shrubs is thus lower than any fynbos communities.

The graminoid layer is dominated by tussocks of strongly deciduous perennial, soft-leaved grasses (*Digitaria*, *Themeda*, *Aristida*). Semi-evergreen hard-leaved grasses (e.g. *Pentaschistis eriostoma*) are absent. Karroid shrublands differ strikingly from all but arid fynbos in their low sedge cover (0-2%).

Annual grasses, forbs and deciduous geophytes are relatively common but were not included in the structural analysis.

Total vegetative cover is similar to the range for arid fynbos, but a distinctive feature is the patchiness of the cover. Small trees or tall shrubs, mostly with berry-like fruits form small clumps in a manner quite different from the apparent random spacing of Proteaceae in fynbos.

Taylor (1972, 1978) has attempted to define fynbos floristically by "the lack of single species dominance and/or the conspicuous presence of members of the family Restionaceae". Physiognomically he defines fynbos by the presence of a restioid element "tufted plants with near-leafless tubular or wiry non-woody stems", an ericoid element of shrubs with "small, narrow often rolled leaves" and the general, but not obligatory, presence of Proteaceae.

Kruger (1979) has suggested that Restionaceae are the only constant and differential floristic element.

This study tests only one interface with non-fynbos shrublands and cannot therefore contribute a more refined physiognomic/structural definition of fynbos. Leaf spinescent sclerophyll shrubs appear, however, to be exclusive to fynbos shrublands on nutrient poor soils.

6.5 DISCUSSION

6.5.1 On the use of TWINSPAN

Campbell (1978) has discussed a number of problems associated with the use of similarity coefficients for classification of quantitative data. TWINSPAN is not free of these implicit data standardisation problems. The use of different pseudospecies cut-off levels produces different classifications and, in the absence of a priori criteria for setting these levels, the "success" of a classification must be judged subjectively. The problem is most acute for quantitative data where attributes are represented in most relevés and group discrimination is based entirely on quantitative cover differences.

In practice, selection of intuitively reasonable cut-off levels gave acceptable results, but the inherent subjectivity in the method limits its value as a test of the hypothesis that floristic classifications in any area can also be defined by structural criteria.

6.5.2 On the value of structural classifications

Three criteria seem important in assessing the value of a classification 1) is recognition of classes simple and independent of subjective bias 2) do the units have any meaning in the real world i.e. do they correspond, in this case, to environmental and/or floristically defined classes 3) how generally applicable is the classification?

(a) Recognition of Structural Types

To facilitate type recognition, structural characters should be recognizable in the field, free of observer bias, and easier to learn than species of an area. Plant height, tussock diameter, Raunkiaerian leaf size class, and leaf shape (broad-narrow) mostly fit these criteria. Most of the remaining characters are more susceptible to observer bias. Leaf texture (sclerophyll, semi-succulent etc.), for example, may be interpreted differently by different observers. Laboratory analyses of leaf specific weight may be used in this case, but the field applicability of the classification is thereby reduced. Recognition of grasses, sedges and geophytes is often complicated by growth form convergence, especially to a restioid type e.g. Bobartia, Ficinia, Ehrharta ramosa. Grasses sometimes mimic evergreen geophytes, e.g. Ehrharta dura, and geophytes "grassy" sedges, e.g. Lanaria lanata. Structural classification is thus not a panacea for avoiding taxonomic problems in fynbos.

Several characters require a knowledge of temporal variation e.g. deciduosity and fire regeneration strategies although the latter may often be recognized by characteristics such as multi-stemmed shoots at ground level in resprouting shrubs (Martin 1966).

Leaf type and leaf arrangement (e.g. ericoid, linear, terete, isobilateral, whorled, decussate, fascicled) are relatively free of subjective error and mostly easily recognizable.

Graminoid growth forms, e.g. coarse, unbranched restios, grassy sedges, fine, wiry grasses may have rather subjective class limits but reference to common representative species is a helpful aid.

Structural classification, unlike their floristic counterpart, depend more on quantitative rather than qualitative variation in vegetation attributes (compare Tables 4.1, 4.2 and 6.2, 6.3). Subjective cover estimates are notoriously subject to observer bias (Greig Smith 1964) however, and misclassifications will be more frequent. Structural classifications are invariably polythetic and therefore less easy to use than floristic classifications where monothetic, or nearly monothetic, choices may often be adequate.

Finally, the sum cover of structural attributes is more difficult for field use than total cover estimates since it involves an assessment of the degree of layering in a stand of vegetation.

Despite these limitations, the potential advantage of structural classifications remain the ease and rapidity with which structural attributes can be collected, by relatively inexperienced observers, in a rich, complex and poorly known flora (Webb _et al_. 1970).

(b) Structural Classifications and their interpretation

Webb _et al_. 1970, attempted the first rigorous test of the relative success of structural and floristic classification at a local level in a study of Australian rainforests. They measured success by the degree to which floristic and structural data recovered environmental information and concluded that both systems were effective "to a reasonable and comparable extent".

The degree to which structural and floristic classifications correspond with altitudinal and moisture gradients is discussed in Chapter 7. Both systems appear to be equally effective predictors of general environmental conditions. The correspondence of structural and floristic groups is shown in Table 6.1. Since both classifications involved some manipulation by tabulation methods, the similarity is greater than that produced by TWINSPAN alone. Nevertheless it is clear that there is little information loss in using structural methods to define vegetation types. These results confirm Webb et al.'s (1970) conclusions that structural classifications can be effective at the local level.

(e) On generality

The wider applicability of studies based on intensive sampling within a much larger sampling universe is always open to doubt. The most important limitation of this study is its restriction to mature fynbos. The relative cover of life forms in fynbos changes with time after fire (Adamson 1931; Kruger 1977). Outside the mature stage of fynbos succession (±10-40 years after fire) the classification is useless. Floristic classifications, based on presence-absence criteria, are less sensitive to community age.

Past fire history is a second major limitation. Proteaceae are particularly sensitive to fire régime and differences in fire season may produce twenty fold differences in the ratio of seedlings to adults (Bond 1980). In the Swartberg Pass area two heathland types were defined (Fig. 6.2) but there is good evidence from elsewhere in the Swartberg that the lower heathland usually has a canopy of Protea punctata and/or Leucadendron album, remnants of which can still be seen in the study area. Failure to recognize the "proteoid potential" of this unit would lead to serious errors in, for example, climate prediction from vegetation.

No experimental work has been done on the effects of Proteaceae removal on understorey components which may or may not respond. Thus use of understorey criteria rather than the proteoid nature of the canopy to define proteoid shrublands is not necessarily a solution. The problem was stated by Hills (1960 quoted in Webb et al. 1970) as "the significance of variation in any one feature is dependent upon the total effect of all the features in the complex".

The wider applicability of the classification in the coastal and inland mountains remains to be tested. Recent surveys at a reconnaisance scale (1:100 000) of the Swartberg, however, indicate a general correspondence of the major structural units (Table 1.9).

6.6 CONCLUSIONS

The study has demonstrated that structural classifications may be successfully used at the local level in fynbos. Structural types resemble floristically defined communities and are as useful as predictors of "site potential". B. Campbell is currently developing a structural classification for mountain fynbos and associated shrublands within the Capensis region (Linder and Campbell 1978). Judging by results in this study, his classification may be expected to contribute to an understanding of ecological relationships, have practical applications in fynbos management, and be easier to use than a floristic system.

Limitations of structural methods should, however, be noted to avoid their uncritical use. The dependence of structural methods on fire history (including veld age) is the most problematic. Attributes open to subjective interpretation, e.g. leaf texture, should be avoided as monothetic class indicators since inexperienced users will make mistakes and experienced users may tend to vary their choice of attribute according to the results they wish to obtain (see e.g. Stock 1976 on the South African Soil Classification).

Table 6.3 SWARTBERG STRUCTURAL TABLE

Group	H1					H2						H3a				H3b				H3c			P1								P2									P3				R1									W1							A1					
Relevé No.	84	85	53	62	63	54	57	58	83	59	81	2	3	5	4	8	7	8	47	1	9	10	42	43	44	45	48	49	51	52	25	38	39	40	48	50	55	41	56	11	12	14	13	15	18	23	22	19	21	16	17	30	24	27	23	33	32	26	20	31	34	36	37	33	35
Altitude (m)	1190	1350	855	1170	1310	720	1000	1105	1090	1260	965	965	870	1195	1050	1300	1215	935	730	1055	1060	1140	845	710	800	860	920	850	800	810	890	430	460	800	890	725	475	705	800	850	780	785	820	985	990	815	855	850	965	930	795	820	685	655	697	700	660	842	690	620	590	760	700	600	680
Drought Index X100	20	38	55	20	43	69	69	56	56	28	56	153	181	83	83	28	28	167	97	153	167	83	97	83	83	69	69	69	69	69	236	238	238	230	139	97	181	181	181	139	167	153	181	339	83	167	167	167	167	83	167	167	250	431	542	383	390	250	264	250	653	611	625	380	611
Aspect	S	S	S	S	S	S	S	S	S	S	S	N	N	N	N	N	N	N	S	N	N	N	S	S	S	S	S	S	S	S	N	S	S	S	S	S	S	S	S	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N
Stoniness of A.	1	1	1	1	1	1	3	2	1	1	3	3	3	2	3	2	2	3	3	3	2	2	1	1	1	2	1	1	3	3	2	2	1	1	1	1	1	1	1	3	2	3	2	3	4	3	4	3	3	3	3	3	4	3	3	3	3	3	3	3	4	4	4	3	3
Restio tussock 5-10 cm	3	4	3	4	3	1	1	+	+	1	1	1	+	1	+	1	2	1	1	+	2	3			1	1	1	1	1	2	1				3	1		+	1		1	1	+	1	+	1	1		1	+	1	1	1	1	1	1	1	3	1	+				+	
Restios, fine branched	6	4	3	4	3	1		1		+	+	1	+	1	1	1	+	1	1	1	1	+	+	+	1	1	+	2	1	1	1	+	1		1	1	1	3	1	2	1	1	1	1	1	1	+	1		+	1	1	4	1	1		1	+	1	+				+	
Restio height 25-50 cm	6	4	3	4	3	1		1		+	+	1		1		1	1	1		1	1		+					1	+		2	+	1		1		1	3	1	1	2	1	+	1	+	2	1	1	1	1	1		2	2	2	1	2	3	2	1	+			1	
Restios, no tussock	4	2	1	1	+	+						+	+	+	1	1	1		+	1		+	+					1	+	1			+			1	2	+	2	+			1					1					2			+			+						
Sedges, mat-forming	+	+			+																																1																												
Grass tussocks 5-10 cm	2	2	2	1	1	+	3	4	3	3	1	1	1	1	2		1	1		+	1	1	2						+		+	+	+	1			1			+	+	1	+		+	+		+	+	1	1	1	+	1	1	1	1	1	2	1	+			+	1
Grass height < 25 cm	2	2	2	1	1	1	1	4	3	3	2	1	1	+		2	1	1	2	1	1	1	+	1	1	1	2	1	1	3	2	+		+		+		+		+		1	+	+	+	+		+		2	2	1	1	1	2	1	2	2	3	+	+	+	+	+	1
Grasses, fine sclerophyllous	2	2	2	1	1	1	4	4	3	3	2	1	1	1	1	1	1	2	2	1	1	1	2	1	1	1	2	1	1	2	+		+	+		+		+		+	+	1	+	1	1	+	+	+	+	1	1	1	1	+	1	+	1	1	2	+	+	+	+	+	1
Total grass	2	2	2	1	3	1	4	4	3	3	3	1	1	2	2	2	1	2	2	1	1	3	2	1	2	2	2	1	1	3	3	1	1	1	+	+	1	2	2	+	+	1	1	1	1	+	+	+	+	2	2	2	2	2	3	1	3	2	3	1	1	1	1	1	1
Broad leptophylls	4	2	4	4	4	3	5	4	3	5	5		+	1	+		+	+	1		2	2	1	+	+	1	1	1	1	+	3	1	1		1	1	1	1	2	+	1	1	1	+	2	1	1	1	1	1	3	1	+	1	1	1	1	2	1	2	1	1	1	3	+
Restios, coarse branched	1	2	3	3	2	3	1	2	2	3	3		+		2		1	3		+	2	+					+	+					+				2		1	+				+		1	+	+	+				1	+		+									
Restio height 75-100 cm	1	2	3	3	2	3	1	2	2	3	3				2					1	3	1			+		+	+	+	1	+		+			1	2		1	3	3	4	1		1	1	+	4	1	2		4	1			+			+			2			
Restio tussock < 5cm	1	2	3	3	2	3	1	3	2	3	3		+	2	+	1	1	1	1	1	1	2	+	+	1	1	1	2	1	1	+	+	1		1	+	1	3	1	+	+	1		+			+	+	+				3	+											
Sedges coarse restioid	+	+	2	+	1	1	+	1	2	1	2	1	+							+									1	+																																			
Sedge height < 25 cm	+	1	+		2	1	1	2	1	1	+	1		1	+	+	+	+	+					1	1		1			1	1	+	+			+	+							+	+	+	+	+	+	+	1	+	1		+	+	+	+				+	+		
Sedges fine restioid		1	+		1	1		1	+	+	1						+						1	1			1	1	+		+	1	1	1		+	+	+				1	2	+		+	+	+	+	+	+	+	1	+	+		+	+				+	+		
Berzelioid shrubs	3	+	1	3	2	1	1	+	2	+	+		+		+	+	+		1				+	1	1		1		+	1				1	2	+	+	+				+	1	+						+	1	2								1		+	+	+	
Rosette forbs	+	+	+	+	+	+	1	+	+	+	+					+											+	+	+	+	+			+		+		+						+			+		+		+	+	+	+	+		+	+	+	+	+			+	
Geophytes, leaves < 10 cm	+	+	+	+	+	+	+	+	+	+	+								+				+	1	+	+	+		+	+		+															+					+	+	+					+	+					
Sedges, no tussock	+	+	+		1	+	+	+	+																																																								
Lobed leaves	+		+		+							+	+		1		1	+			1	1		+		+			+	+			1		+		3	+		+		+			+	+				+		+							+		+				
Sedges broad-leafy			+		+			+	+	+		3	3	4	2	4	2	+		1		+	+	1	+	+		+	1	1				+		1		+	+	+	1	1	2	+	1	1	+	+	1	1	+	1	1	1	1		1	1							
Sedge tussocks 10-25 cm						2	1		+			1	3	4	2	4	2	2	2	1		+	+	3	2	3	+		2	1			1	1		1	2	1	1	1		2	3	2	1	1	1	+	1	3	+		1	2	1		1	1	+						
Total sedges	+	1	2	+	2	3	1	2	2	2	3	4	3	4	2	4	2	2	2	2	1	1	2	4	3	3	2	1	3	2	1	1	1	1	1	2	3	1	1	2	1	2	3	2	2	2	2	2	1	3	2	1	2	3	1	1	1	2	+	1		+	+	+	
Restio tussock 10-25 cm		+	+		+		2	2	2	+	+	3	3	2	2	1	4	3	3	1	2	+	4	4	2	3	2	2	2	1			+	+			1	1	+	2	2	1	2	+	1	4	4	4	2	1	1	1	1	2	1		1		1	1	+	2	2	1	
Grasses, broad orthophyllous	+	+			2		+		+		2	1	1	1	1	1	+	1	+	+	1	2	+	1	1	1	1	+	+	1	3	1		1			1	1	2	+			+	+	+					2	2	1	2	1	1	1	1	2	1	+	+		+		
Grass tussock < 5 cm	+	+	1		2	+	1		1		3	1	1	+	+	2	+	1	2	1	1		+	1	2	2	2	1	1	3		+		1		+		2	2	+			+	1	+		+			+	2		+		+		+			1	+	+	+		+
Narrow leafy sedge			+		1	2	1	+	1							1	1	2	2		1	1	+	3	3	3	1		2	2				1			2	+	1	2	+													1	1		1			+			+	+	
Compound leaves							+												+				+			+		+	+	1		+			+				+																										2
Ferns			1								+																					1	+	+	2	3	1	+	1														+	+	+	+	+	+	+						
Undefined shrub leaf arrangement	1	1	1	1	1	1	2	1	1	2	1	+	2	+	+	1	1	2	2	4	5	4	4	4	4	4	5	6	6	5	4	5	6	5	6	6	6	6	6	4	3	3	3	2	3	5	3	4	3	2	6	5	3	3	3	4	3	3	3	4	2	1	2	2	2
Isobilateral	+	1	1	1	1	1	1	1	1	1	1	+	2	+	+	1	1	2	2	3	4	3	4	4	3	4	5	6	5	5	3	4	4	5	5	5	5	6	5	4	3	3	3	1	2	2	1	+	2	+	5	4	2		2	2	2	1	1	2					
Microphylls	+	1	+	+	1	+	1	+	+	1	+	+	2	+	+	1	+	2	1		+	2	4	4	2	+	+	5	5	5	2	4	5	5	5	6	5	2	5	+	1	+	2	+	+	1		1	+	1	4	4	2	1	2	+	2	1	+	2	1		+		+
Serotinous						+				+	+	+	1	+	+		+	+	1	4	4	2	4	4	3	4	4	6	5	5	1	4	4	4	5	5	4	5	5	4	3	2	2	1	1	1			1	+	4	4								2					
Shrubs, large, narrow leaves			+	+	+	+				+	+	+	2	+	+	+	1		1	3	4	2	4	4	2	4	5	5	5	5	3	1	4	1	5	3	1	4	+	1	2	3	3	1					+	+	5	4	1	+	1	1	1	+	1	2	+	+	+	+	1
rubs 150 cm+						+			+	+	+	+	2					+	1	4	4	2	4	4	3	4	4	6	5	5	3	5	6	5	5	6	5	6	5	4	3		4	+	+	3		3		1	4	4	2	+	1	1			1						
on-ericaceous, rolled leaves	+	2			+		1	+	+	2		2	2					+	1	3	1	2	1	1	3	1		3	2	1	+	2	1	+	+	4	2	1	2	1	1	+	1	1	1				1	2	1	1	1		2	3	3	+	1	3	1	1	1	1	2
thophyll leaves	1	+	+	+	+	+	1	+	1	1	1		+	+	+	+			1	+	1	+	1	1	+	1	+	1	2	1	1	2	2	1	1	1	2	2	2	+	+	+	+	+	+	+	1	+	+	+	+	+	+	+	+	+	+	1		+	+	+	+	+	+
esophylls	+	+	1	1	+	1	1	+	1	+	+				+				1			+		1	+	+	+	2		+	1		1	+	1		+		1	4	3	2	2	1	2	1			1			+	2		1	1		1	1						
estio height 100-150 cm			+										+					2															+							2	1	1		3	4	2	4	2	3					2				1			1		+		2
estios coarse, unbranched							2	1	1	1	1	1	1	1	2	2	4	2	+	1	1				1	1	2	1	1	2	+				3	1		+	+	2	1	1	1	3	4	2	4	3	3	2	1	4	1	2	+	1	1	2	1	+	1		+	+	2
estio tussock 25 cm+			+												1	1	+	2		1	2	1									1		+							4	3	4	2	3	4	2		2	3	2		4		2		1		1			1	1			2
hrubs < 25 cm					+											+		+		+				+				+		+	+	+	+	+	+		+	+	+	+		2	+	4	+	+	1	+	1	1	1	1	+	1	1	1	1	+	1	1	1	1	1	1	1
tem resprouts																															1																			+		+	2	+	1	2		1	1		+				
lytropappoid shrubs																																																					1	+	2	1	1	+	3	1	+	+	+	2	
rasses, stoloniferous																																																							1			+	+						
hrubs, semi-succulent leaves		+	+	+	+		+	+	+	+				+	+	+	+	+	+	+	+	+	+									+	+							+	+	1	+	+	1	1	1	+	+	1	+	+	+	1	+	+	+	+	1	1	2	1	2	1	2
ucculent shrubs																																																							+		+		+	+	1	+	+	1	1
tem-spinescent shrubs																																+	+																										+	+	1	+	+	+	+
rasses coarse sclerophyllous																				+																																	+	1	2	+	1	1	1	1	+	1	1	1	1
hrubs, aphyllous																																																									+					+	+		
erete	3	+	1	3	2	1	1	+	2	+	+	+	+		1	+	2	+	2	+	+	1	+	+	+	1	1	+	+	2	+	+	+	3	2		+	+	2	+	+	1	1	1	+	3	+	3	+	+	1	2	+	2	+	+	+	+	1	2	2	2	2	1	
ecussate shrubs	+	2	2	2	1	4	1	2	3	2	2		1	+	1	1	1	2	1	1	1	1	2	2		1	1	1	1	2	1	4		1	1	+	1	2	+	1	2	1	1	1	3	1	+	+	1	+	2	1	+	1	2	+	1	1	1	1	2	+	1	+	2
estios fine unbranched	1	2	1	2	2	+	+	1	1	+	1	3	3	2	1	1	1	1	3	1	3	4	4	4	2	3	1	2	2	1	1			+				1	1	3	3	4	2	1	1	3	1	4	1	1	+	1	1	1	1	1	2	2	1	1	+	1	1	1	+
eaves pubescent, lower surface	1	1	4	1	1	1	5	4	3	4	5	2	2	1		+	+	1	1	3	2	2	2	1	3	1	1	3	2	1	1	2	2	+	+	5	2	1	2	1	2	1	2	1	2	2	1	2	2	2	1	2	2	1	3	3	4	2	4	4	2	1	2	1	1
hrubs, large, broad leaves	1	2	2	3	2	4	2	2	3	3	2		+	+	1	2	1	3	1	1	1	1	2	2	2	1	1	3	1	2	2	6	3	5	2	6	5	4	5	4	3	1	2	1	2	2	1	1	3	2	2	2	3	2	2	2	1	2	2	2	1	+	1	1	2
ndefined shrub leaf form	1	2	2	2	2	4	2	2	3	2	2		1	1	1	1	1	2	1	1	1	1	2	2	1	1	1	2	2	2	2	4	2	1	2	3	2	2	2	1	1	1	2	1	1	1	1	1	2	2	2	2	2	2	2	2	1	2	4	2	2	1	2	3	+
anophylls	3	3	3	3	2	4	1	2	3	2	4	+	1	+	2	1	2	2	3	4	5	3	3	2	2	4	5	2	2	2	3	4	1	2	3	3	2	2	1	2	3	2	2	2	3	1	2	1	2	2	3	2	1	3	2	1	1	2	2	2	1	1	1	1	1
eophytes, evergreen	1	1	1	1	+	+	2	+	1	1	1	1	+	1	+	1	1	+	1	+	+	1	+	1	+	+	+	+	1	+	2	1	+	1	+		+	+	1	1	+	1	1	+	+	+	+		+	1	1	1	1	+	+	1		+	+	+					
orbs	+	+	+	+	+	+	+	+	+	+	+			+	+	+	+		+		+	+	+	+	+	+	+	+	+	+	+	+	+	+	2		+	2	2				+	+	+	+	+	+	2		+	+	+	+	+		+	1		+				1	
hrubs 50 - 100cm	6	4	6	6	5	6	6	5	6	5	6	+	2	4	3	2	2	1	6	1	2	5	3	4	6	5	6	5	5	5	3	3	2	6	4	3	6	3	5	2	2	3	3	2	4	1	2	3	3	2	3	3	3	3	4	1	3	2	4	1	2	3	3	1	
eptophylls	6	3	5	6	5	4	5	4	5	5	5	4	5	4	3	3	3	4	3	5	3	5	5	5	6	5	6	5	5	4	5	4	4	6	3	5	5	4	6	3	4	3	5	4	4	5	3	4	4	2	5	3	3	3	3	4	5	3	3	4	3	3	3	3	3
estio height 50 - 75 cm	1	2	2	2	2	1	3	2	2	1	1	3	3	3	2	2	4	3	3	1	2	4	4	4	2	3	2	2	2	2			+	+	3	1	+	1	2	2	2	1	2	1	1	3	1	1	+	+	1	1	4	1		1		1	1			1	2		+
edge height 50-75 cm	+	+			+			+	+	+	2	3	3		+	3	1		+	1		1	+	1	+	+	+	+	+	1				+		1		+	1	2		1	1	1	+			+	+			+			+			2							
eaves pubescent, both surfaces	4	2	2	4	4	3	1	+	1	1	1	4	3	3	2	2	2	4	1	6	5	4	4	3	2	4	5	1	1	1	2	4	1	3	3	3	2	1	1	3	3	3	3	1	3	1	2	1	2	1	1	1	+	1	1	+	+	+	1	1	+	+	1	1	1
rass height 25-50 cm	+	+			2		4		+		2		1	2	2	2	+	2	+	+	1	2	2	+	+	1	+	+	+	+	2	+	+	1	+		1	2	2	+	+		+	+	+		+			1	2	1	1	1	2	+	+	3	2	1	+	3	1	+	+
horled leaves	5	3	4	5	4	3	5	4	4	4	5	4	3	4	2	2	2	3	5	4	2	3	5	5	5	5	5	4	5	3	3	2	1	4	2	2	3	3	4	3	3	3	3	+	3	1	2	1	3	1	3	1			2		1	+	+	+					
ricaceous inrolled leaves	5	3	5	5	4	3	5	4	5	4	5	4	4	4	3	3	3	3	5	4	3	4	5	5	5	5	5	4	5	3	4	2	+	4	2	2	3	3	4	3	3	3	4	4	3	3	2	3	4	1	3	1	1	2	2		1	2	+	+					+
arrow leptophylls	4	3	2	3	2	2	2	1	4	1	4	4	5	4	3	3	3	4	6	5	3	5	5	6	6	5	5	6	6	5	3	4	4	6	4	5	5	4	5	3	3	3	5	4	5	5	3	4	4	2	3	3	3	3	4	3	4	3	4	4	3	3	3	2	3
edges 25-50 cm	+	+	+	+	1	3	1	1	2	1	2	+	2	4	2	2	2	2	2	1	+		2	3	3	3	+	1	3	1	1	+	+	1			2	+	+	+	1	2	3	2	1	2	2	2	+	3	1	1	1		+	+	2	2	+	1			+	2	
hrubs 100-150 cm		1	+		1	+	+	+	+	1	+	4	4		2	+	3	4	+	4	2	3	4	3	2	+		2	2	1	3	2	2	+	2	4	2	3	1	3	3	3	2	1	3	3	+		1	1	+	1	1		1	+	+		+	2	1			+	2
ascicled leaves		1	1		1		+	+	+	+		2	2	2	2	2	2	+	+	3	2	2	2	1	2	1	2	2	2	2	3	3	3	1	+	4	2	+	2	+	+	2	2	4	1	1	1	+		2	1	2	1	2	1	1	3	2	1	1	1	2	2	1	+
inear leaves	+	1	1	+			+		+	+		+	1	+	1	+	+	+	+	1	1	1	+	1		+	2	1	1	2	2	3	3	1	+	+	3	1	2	1	2	1	2	1	3	1	1	1	1	+	2	2	1	2	2	1	3	2	1	2	1	1	+	1	1
hrubs 25-50 cm	1	2	+	1	1	1	+	+	2	2	+		1	1	1	2	2	1	2	+	2	1	2	1	2	1	1	+	1	+	4	4		+	+	1	1	+	2	1	1	1	1	2	+	1	2	2	4	1	4	2	1	2	2	3	3	2	2	4	2	1	1	3	2
non-ericaceous, inrolled	+	2			+		1			2		2	2					1	+	3	1	2	1	1	3	1		3	2	1	+	2	2	+	1	3	2	1	1	1	1		1	1	4				1	2	1	2	2		2	4	3	1	1	3	2	3	3	2	3
estios, plumose e.g. Thamnochortus argenteus		+	+		+		1	1	1	+	+	+	+	+	+	+	+	+	1	+	+	+	+	+		+	+	+	+	1				+			+		+		+	1	+			+							1	+					+			2	1		
edge tussocks 5-10 cm		+	+		+		+	+	+	+	1		+	+	+	+	1	2			1		+	2	2	+	+	1	1	1	1	+	+	1	1	1		+	1	1	+	+	1	+	1	2	1				1	+		1	+		+	1	+	+			+	2	
edges, medium restioid	+	+			+	+	+	+	1	1	2	+		+	+	+	+	1	+	1	+	+		+	1	+	+	+	+	+	1		1		1	1	+	+	1	+	+	1	2	1	1	2	1	2		3	1	+	1	+			2	1	+	1					
rasses, no tussock										+							+	+		+	+		+	+						+	+		+	+															+				+		1		+	+						+	
edge tussocks 25 cm+												3								+											+													1	+					1		+					+								
otal Restios	6	5	5	6	4	3	3	3	3	4	3	3	3	3	3	3	4	4	3	2	4	4	4	4	2	3	3	3	2	3	2	+	1	+	3	2	2	4	3	4	4	5	3	4	4	4	5	5	4	3	2	5	5	3	2	2	2	3	2	1	1	2	2	1	2
otal graminoids	6	6	6	6	6	5	5	6	5	6	6	6	6	6	4	5	6	6	4	3	5	5	5	6	4	5	4	3	4	4	4	1	2	2	4	2	4	4	4	5	4	6	5	5	5	5	5	6	4	5	3	6	6	5	4	2	3	4	4	2	1	3	2	2	7
otal non-proteoid (NP) shrubs	6	5	6	6	5	6	6	6	6	6	6	4	5	4	4	3	4	5	6	5	4	5	6	6	6	6	6	6	6	5	5	6	5	6	4	6	6	4	6	4	5	4	5	5	5	5	3	5	5	3	5	4	3	4	5	4	5	4	5	5	3	3	3	3	3
atio NP shrubs/total graminoids	5	4	5	6	5	6	6	4	6	5	5	4	5	4	5	3	4	4	6	7	4	5	6	5	7	6	7	7	7	6	7	7	7	7	6	7	7	6	7	4	6	3	6	5	6	5	3	4	6	3	7	4	3	5	6	7	7	4	7	7	7	6	7	7	7

Table 6.2 RUITERSBOS STRUCTURAL TABLE

Group	M1				M2							P1a					P1b				P2				R1a				R1b				R1c				A1					K1								
Relevé No	1	2	3	8	4	5	6	7	11	10	9	34	17	18	19	15	16	13	14	12	22	23	20	21	29	30	28	31	35	26	25	27	24	32	36	33	39	40	44	37	38	43	41	42	48	49	50	45	47	46
Altitude	1705	1870	1865	1585	1445	1415	1325	1480	1470	1295	1805	1550	1100	1065	1080	1190	1180	1185	1100	1145	945	945	958	952	1610	1805	1485	1310	1460	1465	1805	1415	1358	1328	1288	1372	1204	1255	1335	1234	1325	1220	1900	1105	945	1095	1095	1095	945	905
Drought index X 100	110	250	210	187	170	240	161	194	208	232	139	378	333	347	403	282	236	264	333	333	347	347	333	238	282	282	292	361	264	361	282	361	431	375	488	583	881	583	881	853	853	847	847	792	784	819	750	819	792	750
Aspect	S	S	S	S	S	S	S	S	S	S	S	N	S	S	S	S	S	S	S	S	S	S	S	S	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N
Stoniness of A	2	3	3	2	2	2	2	3	2	2	2	3	2	2	2	2	2	2	2	2	2	2	2	2	4	4	4	4	2	4	4	3	3	4	4	3	4	4	3	3	3	4	3	4	4	4	4	3	4	4
Succulent, intermediate	+	1	+	+	1																+		+			+						+			1		+	+		+	+	1	2	1	1	1	1	1	1	2
Forbs	+	+	+	+	+	1	1	1	1	1	+	1	+	+	+	+	+	+	+	+	+	+	+	1	1	1	+			1	+	+	+	+				+												
Rosette	+	+	+	+	1	1	1	1	1	+	+	+	+	+	+	+	+	+	+	+	+	+	+	1		+									1	+				+	+									
Restios, fine branched	1	+		2	+	1	3	4	3	1	1	2	1	1	+	1	1	+	1	+	1	+	1	1	1	1	1	1	1	1	1	+	6	1		2	+													
Leaves pubescent both surfaces	3	1	2	2	4	3	2	3	4	2	4	4	+	1	1	1	2	6	2	6	3	1	1	1	1	1	1	1		1	1	+	+	+	2	+	+	+	+	+	+	1	1	2	2	5	2	1	1	+
Broad leptophylls	5	2	3	4	4	2	4	3	1	2	4	+	+	1	1	1	2	2	2	3	2	2	2	1	1	1	+			+	+	+		1	2				+	+	+		+	+	+	1	+		1	2
Grass height < 25 cm	2	1	2	3	2	3	3	2	2	3	3	1	1	+	1	1	1	1	+	1	1	1	1	+	3	3	+	+		2	1	1	+	1	+	+						+	+	1		1		1		+
Grass tussock < 5 cm	2	1	2	3	2	3	2	1	2	3	3	1	1	+	+	1	1	+	+	+		+	1		1	1	+	+		+	1	+	+	+	+	+				+	+	+	+	+	1	1	1	+	+	+
Sedge tussock 10 - 25 cm			+	1				+	+	+	+																																							
Shrubs < 25 cm	1	4	3	1	1	1	1	1	2	1	3	1	+	+	1	+	1	+	2	1	+	+	+	+	1	1	+	+	2	+	+	1	+	1	2	+	+	+		1	1	+	+	+	+	+	+	+	+	
Restio height 25-50 cm	2	4	2	3	2	2	3	5	2	2	3	3	2	1	1	+		1	1	1	1	1	1		3	3	2	2	1	2	4	1	6		2	3	+			1	1									
Restio tussock < 5 cm	1	3	4	1	2		2	4	2		2		1	1	+	1	1	+	1		1	+	1	1	1	3	1	1		1	1			1		2	+													
Restio tussock 5-10 cm	1	3	4	1	2				2		2	2													1	1	1	1	1	1	1	1	6	1	1	2	+													
Restio height < 25 cm			4	1	+	+	+		3	+		2					+	+				+			1	3	+	+	+	1	+	+																		
Grasses aphyllous		1	+	+		+	+					+												1	+	+	+	+	+	+	+	+	+	+	1															
Ericaceous, rolled	7	4	4	6	5	3	5	6	4	3	4	4	4	4	4	5	4	2	3	2	+	+	1	+	+	+	1	2		+	4	1		+	2	+														
Whorled leaves	6	5	3	6	5	3	5	6	4	3	4	4	4	4	4	3	4	2	3	2	+	+	1	+	+	+	1	+			4	1		+	2	+														
Shrubs 25-50 cm	6	2	3	6	4	3	5	4	5	3	5	5	5	5	5	5	4	2	1	1	1	1	2	1	2	3	2	1	2	1	4	2	1	2	3	1	1	1	2	1	1	2	1	1	2	2	2	2	2	+
Grass tussock 5-10 cm		+	1	+			+	+	+		+	1		+		+			+	1	1	+		+																		+	1					+	1	+
Sedge height 50-75 cm	+						1		1	1					2	1	1	+										1		+				4		+														
Leaves pubescent, lower surface												1	2	1	1		+			1	2	1	+	1							+																			
Berzelioid shrubs						+		+	+	2					1	+	+	+	+	+	1	+	1					+				+								+	+				+		+		+	+
Narrow leptophylls	5	4	3	6	4	3	3	5	6	4	4	6	6	5	5	6	5	5	3	5	3	4	5	5	4	3	3	2	1	1	5	2	2	2	4	1	3	3	3	2	2	3	1	3	3	5	3	2	2	+
Shrubs 50-100 cm	3	+	1	3	2	3	3	4	3	3	3	1	4	4	4	5	6	3	4	6	5	5	3	2	1	1	1	1	1	+	1	1	2	1	1	1	2	3	1	2	2	1	1	3	3	5	3	2	2	2
Terete leaves		3	2	+	+	1	1	+	+	2	2	2	2	1	3	1	2	4	1	1	3	+	2	+	2	1	1	+		1	2	1	+	1	3	1	1	2	2	1	1	2	+	2	2	5	3	+	1	
Mesophylls		2				1	1	+	1	+	+	1	4	6	6	3	4	2	3	3	4	3	1	1				+	3	4	+	1	2	2	3	2								+	+	+	+	+	+	+
Sedge height 25-50 cm	+			2		1	1	+	1	1	2	1	2	2	1	1		+	+	+	+	1	+	+	1	1	2	+	1	1	+	3	3	+	2									1	+		+	+	+	
Sedge tussocks 25 cm+	+			+		1	1		2	1	1	+	1	2	2	2	1	+							1	1	1	1	1	1		3	3	4	1															
Sedges broad-leafy	+		+	1		1	1	+	2	1	1	+	1	2	2	2	1	+							1	1	1	1	1	1		3	3	4	1															
Restio tussocks 25 cm+				+				+		+		3	+	1	+	+	+		+	2		+					1	1	5	2	3	3	1	2	3	3				1	1									
Restios, coarse branched		1								+		3	+	1	+	+	+		+	+							1	+	3	1	3	+	+	+	3	1	+			+	+									
Shrubs 150 cm+		+				+	+	+		+	3	3	1	4	4	1	1	5	3	3	4	4	1	3			1	3		4																+				
Microphyll		+	+	+	1	1	+	1	+	1	4	3	+	1	1	1	2	5	1	2	4	4	2	2		+	1	+	+			2	2	2	1	+	+	+	+	+	+	+	+	1	+	1	1	1	+	1
Grasses, broad orthophyllous	+	1	2	1	1	1	+	+	+	+	+	1		+	+	+	+	+	2	1	1	+	1	+	+	+		1	+	+		+	1	1		+						2	2	2	1	+	2	2	3	3
Non-ericaceous, rolled	+		+	+		1	1		3	1		1	1	1	1	1	1	+	1	1	1	3	4	5	2	+	+	1	1	+	1	1	1	1	1	1	2	3	2	+	+	2	+	2	1	1	1	1	1	
Grass tussocks 10-25 cm									+	2		+	+	1	+	+	+	2	4	2	2	2	3	3		+	3	3	1	2	1	1	2	2	2	3	2	2	2	2	2	3	2	2	1	+	2	2	3	3
Stem resprout shrubs																						+	1	2				+															2	+	+	1	1	1	+	2
Ferns																					+		1	+															+	+	+	+	+	+	+	+	+	+	+	+
Grass height 50-75 cm														+					3		2	+	2	2					2	+			+	+			2	1									1			
Grasses, stoloniferous													+		+						+	+	+																							1	+	1		+
Shrubs, leaf arrangement undefined	1	1	2	1	4	2	2	2	1	2	5	5	4	6	6	4	6	7	6	6	7	6	5	6	4	2	2	2	4	4	2	3	3	3	5	2	+	3	3	2	2	+	1	1	2	2	1	3	1	1
Isobilateral	1	+		+	1	1	1	+	1	1	4	4	4	6	6	4	5	5	5	4	6	6	2	3	+		1	1	3	4	+	2	3	3	3	2														
Serotinous	1	+		+	1	1	1	+	1	1	4	4	4	6	6	4	5	5	5	4	6	6	1	3	+		1	2	3	4	1	2	3	3	3	2														
Large, broad-leaved shrubs	+	2	+	1	3	2	2	3	2	1	4	4	4	6	6	4	5	5	5	3	4	4	3	4	1	1	1	1	3	4	1	1	2	2	3	2	+	+		+	+	+	2	2	1	2	1	2	1	2
Restios, coarse branched			4	1	+	+	+		3	+		2					+	+				+			1	3	+	+	+	1	+	+																		
Restio height 75-100 cm										+		3	1	2	1	+	1		3		+							+		3		3	3	2	3	2	1	2												
Restio height 100 cm+														1							1	+						1	4	+			1		+	3				1	1									
Restios, coarse, unbranched				+				+				1		1					3		+	1			+		+	1	3	2	+	3	1	2	1	3	1	2		1	1	1								
Sedge tussocks 5-10 cm	1					+	+					1	1				+	+		+	+	+			1	+	+	+	+	1	+	+	+	+	2									1	+		+	+	+	
Sedges, narrow leafy												+															+			+	+		+	+	+	+														
Shrubs, aphyllous																									+	+		2			+	+						+							+	1	+	+	+	
Shrubs, elytropappoid																					1	+	1			+					+	+	+		1		1													
Grasses, coarse sclerophyllous	3		1	1	+		1	+			+			+	+	+	1	+	3			+	2	1											1	2	2	1		1	1	1								
P semi-succulent, non-proteoid	+		+	+		+	+		+	+	+	+	+	+	+	+	+	+	1	2	+	+	+	+	1	+					+		+	1	2	1	1	2	2	1	1	2	+	+	1	1	1	1	+	
Succulence (very)								+							+									+		+						+				+	+	+		+	+	1	+	+	2	1	1	1	1	+
Shrubs, deciduous																					+		+	+											1							+	1	+	+	1	1	2	1	2
Succulence (intermediate)	+	1	+	+	1																+		+			+						+					+	+		+	+	1	2	1	1	1	1	1	1	2
Grasses, fine sclerophyllous	2	+	1	3	2	3	2	1	2	4	3	2	1	1	+	1	1	2	+	2	1	2	3	3	3	3	3	3	2	2	1	1	2	2	1	1	+	1	2	+	+	1	1	1	2	1	1	+	1	1
Fascided leaves	4	1	2	2	2	1	2	2	4	1	3	2	1	1	+	2	2	1	1	3	1	2	1	1	2	2	2	2	1	1	1	1	1	1	1	+	1	1	1	1	1	2	+	2	2	5	3	1	1	2
Linear leaves	2	1	1	1	3	1	2	2	2	2	3	2	1	1	1	2	2	2	2	4	2	2	1	2	2	2	2	+	1	1	1	1	1	1	1	+	2	1	1	1	1	+	1	1	2	1	1	1	1	+
Undefined shrub leaf form	+	1	1	1	4	2	2	3	1	1	3	2	1	+	1	1	2	2	1	3	2	2	3	3	1	2	+	3	2	1	1	1	1	1	1	1	+	1	1	1	1	1	2	2	1	3	2	3	2	3
Nanophylls	1	1	1	1	4	2	2	3	1	1	3	2	1	1	1	1	1	1	3	4	2	2	2	3	2	2	1	2		1	1	1	1	1	3	+	1	2	2	1	1	1	2	2	2	2	2	2	2	3
Grass height 25-50 cm	3	1	1	1	1	+	+		+	2		2	1	1	+	1	1	2	2	2	1	2	3	2	+	+	3	3	1		2	1	2	2	2	3	+	1	2	2	2	3	3	2	2	1	2	2	3	3
Restios, fine unbranched	2	3	4	2	3	1	2	+	2	3	2	2	2	2	2	1	1	1	2	+	+	+	1		2	3	2	2	+	3	1	1	2	2	2	1	1	1	1	3	3									
Restio tussocks 10-25 cm	+	2	2	3	+	2	2	1	2	2	1	3	2	2	2	1	1	1	4	1	1	1	1		2	2	2	2	+	3	1	1	2	2	2	2	2	3	2	3	3	1								
Total Restios	3	4	5	4	3	2	3	5	3	2	3	5	2	3	2	1	2	1	4	2	1	1	2	1	3	4	3	3	5	4	4	4	7	3	4	4	2	3	2	4	4	1								
Restios, plumose (eg. Thamnochortus)	+	2	2	2	+	1	1	+	1	1	1	2	1	1	1	+	1	+	1	1	1	+			1	2	1	1	+	1	1	1	1	+	+	2	+	1	1	1	1									
Sedges, fine restioid	1	+	1	1			+	+	1		1			+			+	+		+		1	+	+	+	+		+		+		+	+	+		+	+	1	+	+	+									
Sedge height < 25 cm	1	+	1	1		1	+	+	3	+	1	+		+		+	1	+		+	+	1	+	+	1	+	+	+	+	1	+	+	+	+		+	+	1	+	+	+									
Grasses, no tussock	3	1	2	1	+	+	1	+			+	2	+	+	1	+	1	+	+	+	+	1	2	2	3	3	+	1	2	1	1	1	+	+												1	+	1		+
Sedges, medium restioid	1	+	+	1		1	1	+	2	1	1	1	1	1		+	1	+	+	+	+	1	1	+	+	+	+	+	+	1	+	+		+	1									1	+		+	+	+	
Geophytes, evergreen	+	+	+	+	+	+	+	+	+	+	+	1	+	+	+	+	+	+	+	+	2	1	1	+	1	1	+	+	+	+	+	1		+	+										+	+	+			
Lobed leaves						+	+	+	+	+		+	+			1	1			+			+	+	+	1		1				+	+			1						+		+						
Shrubs, resprout	1	1	1	2	2	2	2	3	3	4	2	3	2	1	3	2	3	4	3	2	3	2	2	1	2	2	2	1	2	1	2	2	1	1	3	1	2	3	1	2	2	3	+	3	2	2	2	1	1	+
Total grass cover	4	1	3	3	2	3	3	2	2	4	3	3	1	1	1	1	2	2	4	2	2	2	4	3	3	3	3	3	2	3	2	1	2	2	2	3	2	2	2	2	2	3	3	2	2	2	2	2	3	3
Large, narrow-leaved shrubs	1	+	+	+	2	1	+	1	+	1	1	2	+	1	1	+	2	+	1	3	4	4		1	1	1	1	1	2	+	+	2	2	2	1	1	+	1	1	1	1	+	+	1	2	1	2	1	1	
Leptophylls	7	4	4	7	6	4	6	2	6	4	6	6	6	5	6	6	5	5	4	6	4	4	5	5	4	3	3	1	3	1	5	2	2	2	4	2	3	3	2	2	2	3	+	3	3	5	3	2	2	+
Total graminoids	5	4	6	6	3	4	4	5	5	5	5	6	3	4	3	3	3	3	6	3	3	3	4	3	4	6	5	5	6	6	4	6	7	6	6	6	2	3	3	4	4	3	3	2	2	2	2	2	3	3
Total shrubs	7	5	5	7	7	4	6	6	6	5	7	7	7	7	7	7	7	7	6	7	7	7	6	7	4	3	3	4	5	5	5	3	3	4	6	3	3	3	3	2	2	3	3	3	4	6	4	3	3	3
Total non-proteoid (NP) shrubs	7	5	5	7	7	4	6	6	6	5	6	6	6	5	6	6	6	6	4	6	4	4	6	6	4	3	3	3	3	1	5	3	2	2	5	2	3	3	3	2	2	3	3	3	4	6	4	3	3	3
Ratio NP shrubs/total graminoids	+	+	+	+	1	+	+	+	+	+	+	+	1	+	1	1	1	1	+	1	1	1	+	1	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	1	1	1	1	+	+
Total Sedges	+	1	1	1	4	2	2	3	1	1	3	2	1	+	1	1	2	2	1	3	2	2	3	3	1	2	+	3	2	1	1	1	1	1	1	1	+	1	1	1	1	1	2	2	1	3	2	3	2	3

6.7 STRUCTURAL TYPIFICATION - RUITERSBOS

The two study areas are discussed separately. Convergent and divergent structural features are compared in Chapter 7.

H HEATHLANDS

H1 Wet Heathlands (= Wet Heaths)

Sub-Formation. Low closed ericaceous shrubland.

Relevés. 53, 62, 63, 64, 65, 65 (53, 54, 62, 63, 64, 65)*

Floristic Equivalent. D1 *Simocheilus carneus* - *Restio anceps* community.

Description. The wet heaths occur on southern slopes directly exposed to rain bearing winds and south-easter, mist bearing clouds. They are confined to peaty soils with a high water table for most of the year, at elevations from 700 m to mountain crests. In all situations examined, wet heaths at their lowest altitudinal limits were confined to "hard pan" podsols (placaquods) - soils with an organic rich A horizon overlying a thin, brittle ironpan which impedes root and moisture penetration.

Wet heaths are characterised by 25%+ cover of fine, branched restios less than 50 cm tall and a total restioid cover greater than 50%. Low mat forming sedges are entirely restricted to wet heaths and have

* Relevés of the floristic equivalent of the structural type are listed in parentheses.

a structure strongly convergent to the dominant restios (R. anceps, Anthochortos ecklonii). The unit lacks coarse, unbranched restios typical of drier heaths.

H2 Mesic Heathlands

Sub-Formation. Low, mid-dense ericaceous shrubland.

Relevés. 54, 57, 58, 59, 60, 61 (57, 58, 59, 60, 61).

Floristic Equivalent. D2 Erica arachnoidea - Pentameris dregeana community.

Description. Mesic heathlands typically occur on better drained soils than wet heaths. In the Robinson's Pass area they occur on the high mountains (900 m+) usually inland of the first range and thus in a slight rainshadow. The soils are typically stony, moderately deep, Cartref or Mispah with relatively high organic matter, but no peaty accumulations.

Mesic heaths are distinguished from wet heaths by 25% or more total grass cover mostly of fine, hard-leaved grasses without distinct tussocks. Coarse unbranched restios are usually present, frequently with a low cover (< 5%), but absent in wet heaths. Total restio cover is less than 50% whereas wet heaths have a cover of 70-100%. The restioid proportion of graminoids is less than 50% whereas in wet heaths it is generally 75%+.

H3 Graminoid Heathlands

Sub-Formation. Low and medium, mid-dense, graminoid ericaceous shrublands.

Relevés. 1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 47 (1, 2, 3, 4, 5, 6, 7, 9, 10, 46).

Floristic Equivalent. C4 *Erica viridescens* - *Hypodiscus aristatus* community.

Description. Graminoid heathlands are mostly confined to the highest elevations on north aspects. They form a continuum from relatively wet heaths to *Leucadendron uliginosum* shrublands (with a proteoid cover exceeding 15%) and a heath understorey (relevés 1, 9 and 10). Soils are typically shallow, humic Mispahs onto bedrock or thin ironpans overlying bedrock and fluctuate from seasonally waterlogged to droughty. The proteoid phase occurs on deeper Cartref soils which, whilst better drained, are also subject to seasonal extremes of soil moisture.

Graminoid heaths are distinguished from mesic and wet heaths by the visual prominence of graminoid growth forms. These communities frequently have a tall open canopy of *Erica viridescens*. Non-proteoid shrubs have a total cover of 30 to ±75% in contrast to 100%+ in other heathlands. Three subtypes have been distinguished. The transitional proteoid type (H3a) (relevés 1, 9 and 10) is clearly differentiated from the remaining types by > 15% cover of tall (150 cm+) serotinous, proteoids, and low sedge cover (< 20%). Shrubs with non-ericaceous inrolled leaves have a cover of 10%+. The remaining two subtypes are distinguished on the basis of their sedge cover. H3 a approximates loosely to Tetraria thermalis communities. It is characterised by a high cover (50%+) of broad leafy sedges with broad tussock diameters (10-25 cms). Broad leafy sedges are replaced by narrow leafy sedges as the characteristic growth forms in H3b. Coarse unbranched restios are characteristic of H3b, fine unbranched restios of H3a.

Restios in all H3 communities are typically of medium (50-100 cm) height, unbranched and with relatively broad tussock diameter (e.g. Hypodiscus aristatus, Elegia parviflora, E. juncea).

P PROTEOID SHRUBLANDS

The two shrub dominated understoreys typically have from 2-20% soft leaved (malacophyllous) cover, a characteristic they share with mesic and wet heaths.

P1 Proteoid Shrublands with a Heath land (Heathy) Understorey Sub-Formation.

Medium and tall mid-dense or dense proteoid shrublands with an ericaceous understorey.

Relevés. 42, 43, 44, 45, 46, 49, 51, 52 (13, 42, 43, 44, 45, 47, 49, 51, 52).

Floristic Equivalent. C3 Protea neriifolia, Leucadendron eucalyptifolium, Erica triceps community.

Description. Proteoid shrublands with an ericaceous understorey occur primarily on steep south aspects at mid-elevations (700-850 m). They occur on relatively well drained moderately-deep loamy soils (Glenrosa, Clovelly) without signs of seasonal waterlogging and with a relatively high moisture-holding capacity.

Proteoid shrublands with heath understoreys are characterised by 50% or more of the non-proteoid shrubs bearing ericaceous leaves. They are distinguished from *Protea aurea* communities (usually with a predominantly non-ericaceous understorey) by the presence of the broad, soft leaved grass *Ehrharta dura*, greater than 20% cover of mid-height unbranched restios (50-75 cms) and the frequent presence of 10% or more narrow, leafy sedges.

P2 Dense Proteoid Shrublands with a non-ericaceous shrubby understorey

Sub-Formation

Relevés. 25, 38, 39, 40, 41, 48, 50, 55, 56 (38, 39, 40, 41, 48, 50, 55, 56).

Floristic Equivalent. C1 *Protea aurea* - *Pteridium aquilinum* community.

Description. *Protea aurea* shrublands are mostly restricted to lower elevations (400-750 m) on south aspects. Soils are generally deep reddish-brown loams and sandy loams or very dark-brown moderately deep loams. The soils are well drained and have a high moisture holding capacity.

Protea aurea may form woodlands with a dense canopy and a sparse cyperoid understorey. In the areas sampled, however, the understorey is tall, of high cover, and with no distinct layering. The understorey is predominantly of non-ericaceous shrubs (less than $\frac{1}{3}$ of non-proteoid shrubs are ericaceous) but heathy understoreys do occur at mesic extremes, where layering usually becomes more distinct.

Protea aurea shrublands are easily distinguished from other mesic proteoid shrublands by the presence of bipinnate ferns (Pteridium aquilinum). Total graminoid cover is lower than P1 ($<$ 10%) but increases in the more ericaceous types to 50%+. Other characteristics, defined by absence rather than presence, are discussed under C3 above.

P3 North-aspect Proteoid Shrublands with a mixed ericaceous/graminoid understorey

Sub-Formation. Medium open Proteoid Shrublands with mid-dense graminoid heath understorey.

Relevés. 11, 12, 13, 14 (8, 11, 12, 14, 18, 20).

Floristic Equivalent. C2 Protea neriifolia, Erica viridescens, Hypodiscus synchroolepis community.

Description. The community is the north aspect equivalent of P1, occurring on moderately deep sandy-loam soils.

North aspect Proteoid shrublands have a proteoid layer at 1,5-2,0 m with which the tall Ericaceous shrub E. viridescens, is associated as in most mesic north-aspect communities. The proteoid layer is never as dense as on the south aspects (30-60% cover). Shrubs in the understorey are relatively sparse and restios and sedges predominate (total graminoid cover 75%+).

P3a is the most mesic of the proteoid/graminoid shrublands of the north aspects. Unbranched, fine, broad-tussock restios of 75-100 cms (Hypodiscus synchroolepis) are characteristic of this type ((20)-40%+). Shrub species with pubescence on both upper and lower leaf surfaces are characteristic (30%+). The tall, coarse, unbranched restios typical of more xeric sites on shallow sandy soils occur but generally with less than 10% cover.

RESTIOID SHRUBLANDS (Restioveld)

R1 Proteoid-Restioid Shrublands

Sub-Formation. Medium mid-dense restioid shrublands with emergent proteoids.

Relevés. 15, 16, 18, 19, 20, 21, 22 (15, 19, 21, 22, 16, 17, 25, 30 - see also 18, 20).

Floristic Equivalent. B3, B2 Elegia galpinii, Metalasia pulcherrima community, Leucadendron salignum, Erica brachycentra community.

Description. The community is confined to mid-elevations (700-1 000 m) on steep north aspects characterised by shallow, sandy, stony soils. Most of these soils were strongly hydrophobic and thus the soil climate is probably very droughty. Plots 17 and 30 were anomalous in being relatively heterogeneous with Plot 17 in particular having deeper, sandy loam soils.

R1 is readily distinguished from the more mesic P3, which is usually on deeper, more loamy soils, by the taller restio layer characterised by prominent, tall (1 m+), coarse, unbranched, broad-tussocked restios (20%+). The proteoid layer is sparse (< 30%) except for the anomalous plots 17 and 30. The cover of serotinous (canopy stored seed) species is significantly lower than P3 (R1 0-10%; P3 18-55% - plots 17 and 30 are again anomalous) and resprouting proteoids become relatively more important. Ericaceous shrubs have mostly < 30% cover whereas P3 has mostly 30%+.

W1 Dry Shrublands with Scattered Proteoid Emergents (Waboomveld)

Sub-Formation. Low to medium mid-dense to open shrublands.

Relevés. 23, 24, 26, 27, 28, 29, 32 (23, 24, 26, 27, 28, 32).

Floristic Equivalent. B1 *Protea nitida* community.

Description. Waboomveld occurs at mid- and lower-elevations (600-900 m) on north aspects (and, outside the study area, south of the Outeniquas). It thus occupies a broadly similar altitudinal range to restioid shrublands but extends to lower, drier elevations. However, waboomveld is confined to talus slopes or other sites of colluviation with moderately deep or deep, stony, loamy sand or sandy loam soils (Hutton, Oakleaf). These soils are well drained and have a higher moisture storage capacity over the whole profile than typical restioveld soils.

Waboomveld in the Southern Cape is structurally diverse with a highly variable understorey usually dominated by non-Ericaceous shrubs, sometimes with ericoid leaves, sometimes with elytropappoid leaves. Soft-leaved C4 type grasses are characteristically present, sometimes in a proteoid savannah-like formation of nearly pure grassland. Restios are always present though usually sparse.

Characteristic features of Outeniqua Waboomveld are the presence of tall shrubs or small trees surviving fire by epicormic sprouting (Protea nitida, Maytenus oleoides). Serotinous proteoids are absent but resprouting or soil-stored seed types occur. Bipinnate ferns are restricted to this type (and to the tall dense Protea aurea shrublands, also with a non-ericaceous understorey). Grass cover is relatively high (10%+ total cover), mostly of soft-leaved, C4 type taxa (Themeda triandra, Heteropogon contortus, Brachiaria serrata, etc.). Elytropappoid shrubs are always present, usually with a cover of 5-15% and rarely up to 50% (Elytropappus adpressus, E. rhinocerotis, Stoebe capitata). Semi-succulent leaved shrubs are present but seldom form more than 10% of the total non-protecid shrubcover. Inrolled, non-ericaceous leaved shrubs are often common occurring as 10% or more of the non-proteoid shrubs in 5 out of 8 relevés.

Restioids are present, but total cover seldom exceeds 25% except in types transitional to restioveld. Low restios (< 50 cms) characteristically form a large proportion of total restio cover.

A1 Arid Fynbos

Sub-Formation. Low open Shrublands.

Relevés. 31, 33, 34, 35, 36, 37 (Relevé 31 was an anomalous, arid, *Protea repens* community with Waboomveld affinities). (29, 31, 33, 34, 35, 36, 37).

Floristic Equivalent. A. *Phylica axillaris* - *Felicia filifolia* community.

Description. Arid fynbos occurs on the lower northern foothills of the Outeniquas at elevations of 600-750 m. Mean annual rainfall is between 350 mm and 550? mm according to regional isohyet maps. Soils are shallow stony Mispahs or Glenrosas. Arid fynbos is always confined to TMG sandstones and quartzites and is the most xeric undisturbed community found on this substrate in the Outeniquas. On shales or deep, colluvial sandy loam soils, there is a sharp transition to renosterveld with mesembs common. On heavily grazed farming land renosterveld replaces arid fynbos but fynbos elements such as Restionaceae and Rutaceae persist.

Outeniqua arid fynbos is characterised by its low total cover (±60%), the presence (but low cover < 5%) of succulent plants and stem spinescence. Semi-succulent shrubs reach their highest proportional cover in this community (±10-40% of all shrubs). The proteoid layer was absent in relevés sampled but local populations of the rare *Leucospermum pluridens* and *Paranomus dregei* extend into arid fynbos in the area.

Non-ericaceous shrubs dominate the community withgraminoids generally insignificant (ratio of shrubs to graminoids 1,3-5,7:1) in contrast to waboomveld where graminoids remain important. Non-ericaceous inrolled leaved shrubs (Phylica, Passerina) are common forming 14-45% of all shrub cover. Low shrubs (< 25 cms) are characteristic of both arid fynbos and waboomveld. Ericaceae were absent in all the relevés sampled but do occur sporadically in arid fynbos.

The grass component is characterised by broad, soft-leaved, C4 type grasses and hard-leaved, coarse grasses (Pentaschistis eriostoma) but with total cover never exceeding 10%. Sedges are very rare or absent. Total Restio cover never exceeded 25% cover but restios were always present. The tall, coarse, tussock restio, Restio fruticosus - arid phase, occurs near the transition to renosterveld. Despite its visual prominence, the discrete tussocks of this species, usually separated by several metres in undisturbed veld, cannot be mistaken from the relatively continuous restio layer in restioveld.

6.8 STRUCTURAL TYPIFICATION - SWARTBERG

Vegetation structure in Swartberg is broadly similar to Ruitersbos. Non-ericaceous Proteoid Shrublands on lower south slopes grade to proteoid shrublands with ericaceous understorey and to heathlands at high elevations. On north aspects small areas of graminoid heathland occur at high elevations grading rapidly to restioid shrublands with a proteoid overstorey. Proteoid cover declines with increasing aridity and, in arid fynbos, restioid cover also declines and shrub cover increases. Unlike Ruitersbos, however, arid fynbos is replaced by Karroid succulent shrublands on sandstones or sandstone talus over shales on the northern foothills of the Swartberg.

The most striking difference between the two gradients is the relative abundance of grasses and scarcity of sedges in Swartberg relative to Ruitersbos.

HEATHLANDS

Swartberg heathlands mostly occur on southern aspects from 1 300 m to mountain crests at 1 800 m+. As in the Outeniquas, heathlands are characterised by <10% proteoid cover, and a high proportion (50%+) of low ericaceous shrubs. Leptophyllous broad-leaved shrubs are common as in H1 and H2 of the Outeniquas. Restios with narrow tussocks (<10 cms) are common, usually with a cover of 10%+.

H1S - High montane heathland

Sub-Formation: Low, closed to mid-dense, ericaceous shrubland.

Relevés: 1, 2, 3, 8 (1, 2, 3, 4).

Floristic Equivalent: A1 *Erica petraea* - *E. nervata* community.

Description: High montane heathland occurs from ±1 600 m to mountain crests at 1 870 m, and was only sampled on steep, south aspects. Cliffs and bedrock outcrops are extensive and the community is consequently fragmented and patchy. The vegetation is subject to high winds, cold temperatures, persistent snow and orographic summer cloud. Soils are mostly shallow, rocky Mispah and Glenrosa, relatively rich in organic matter, but not as rich as comparable communities on the coastal ranges.

H1 is a low, dense, single layered community distinguished from H2 by the absence of shrubs taller than 150 cm, the presence of succulents (Crassula obtusa and/or Mesembs) and the greater prominence of restios (±50%+). The unit was undersampled, but the increasing cover of restios at high elevations has been seen elsewhere in the Swartberg range.

H2 S - Mesic Heathlands with Protea punctata

Sub-Formation: Low, mid-dense, ericaceous shrubland.

Relevés: 4, 5, 6, 7, 9, 10, 11 (5, 6, 7, 8, 9, 10, 11).

Floristic Equivalent: A2 Protea punctata - Erica melanthera - E. andraei community.

Description: Mesic heathlands occur from ±1 300 to 1 600 m, on steep south aspects. The climate is less extreme than H1 but short duration snowfalls may be expected at least once yearly. Soils are generally deeper than H1 and are mostly moderately deep Oakleaf, Hutton, Clovelly and more rarely Glenrosa form.

Mesic heathlands resemble H2 on the Ruitersbos transect but are probably derived from proteoid shrublands. Scattered proteoids occur but never exceed 10% cover. The unit is distinguised from H1 by a lower restio cover (< 50%), 2%+ of forb cover, especially rosette forbs, and a frequently higher cover of nanophylls (10%+ in 5 out of 7 relevés). Shrubs with linear leaves mostly exceed 10% cover, here, but have lower cover in H1 S.

There is some evidence from elsewhere in the Swartberg that proteoids, especially Protea punctata and Leucadendron album, can form a mid-dense overstorey in this unit, dependent on fire history and elevation.

PROTEOID SHRUBLANDS

Only those proteoid shrublands with a proteoid canopy and a shrub dominated understorey are discussed here. These are widespread from 900 m - 1 300 m on the south slopes of the Swartberg and occur on coarse textured, moderately deep Hutton and Oakleaf soils.

Proteoid Shrublands are distinguished by 50%+ proteoids especially serotinous types regenerating from canopy stored seed. Understorey characteristics are the prominence (50%+) of mid-height shrubs (50-100 cms) and a relatively low total graminoid cover ($<$50%). Shrubs are generally more prominent than graminoids with a ratio exceeding 1,5:1 in 11 out of 13 relevés.

Proteoid shrublands showed continuous structural variation in the Swartberg and units are thus ill-defined.

Pl S - Proteoid shrublands with a heathy understorey

Sub-Formation. Medium, rarely tall, open to mid-dense proteoid shrublands with a dense (ericaceous) shrubland understorey.

Relevés. 12, 13, 14, 15, 16, 17, 18, 19, 34, (12, 13, 14, 15, 16, 18, 19, 35).

Floristic Equivalent. B1 Transitional Protea punctata, Brunia nodiflora community, and (B2) Protea lorifolia - Simocheilus multiflorus community.

Description. P1 occurs at mid-elevations from 1 000-1 200 m on south-facing slopes with a similar structural type displaced ±400 m higher at 1 400 m-1 600 m on high north-facing slopes.

The soils are mostly moderately deep, coarse-textured Hutton, Oakleaf and Glenrosa form.

P1 is a layered proteoid community with a canopy of serotinous Proteaceae always exceeding 50% cover. Additional features separating the understorey from heathland types are the relatively low total graminoid cover (mostly < 50% cover), less than 10% cover of short (< 25 cm), non-tussocked (diameter < 5 cm) grasses, and rare restios with broad tussocks and coarse, branched stems.

The unit is distinguished from drier proteoid shrublands by the presence of broad-tussocked, leafy sedges (e.g. Tetraria involucrata) a total cover of 75%+ ericaceous shrubs, (P2 mostly < 25%) and total cover of 50%+ low shrubs (< 50 cms) (P2 mostly ≤ 25%).

The set of relevés is not homogeneous and may be rather arbitrarily divided into two subsets P1a and P1b the former approximating the floristic B2 with Protea lorifolia prominent and the latter with the more mesic P. punctata present. P1b is distinguished structurally by fewer low shrubs (< 75% < 50 cms), a decrease in ericaceous cover (mostly < 50%), an increase in broad-leptophyll cover (10%+) especially of non-ericaceous inrolled leaves, a lower cover of fine, unbranched large tussock restios (mostly $<$ 10%), and 10% or more cover of shrubs with leaves pubescent on both surfaces.

P2 S - Dry Proteoid Shrublands

Sub-Formation. Variable. Tall or medium open to mid-dense proteoid shrublands.

Relevés. 20, 21, 22, 23 (20, 21, 22, 23).

Floristic Equivalent. B3 *Protea nitida* - *P. repens*, *Phylica paniculata* communities.

Description. These are the most xeric of the south facing fynbos communities occurring from 900- 1000 m. Soils are moderately deep or shallow Glenrosa and Oakleaf form.

This is not a homogeneous type and includes a relatively mesic Waboomveld (20, 21) and a serotinous proteoid community dominated by *Protea repens* (22, 23). The Waboomveld occurs on steep, rocky sites, the *P. repens* community on gentle pediment slopes. P2 is characterised by the presence of stoloniferous grasses (*Brachiairia serrata*), elytropappoid shrubs, ferns, and the presence of species surviving fire by epicormic sprouting. Ericaceous shrubs are rare ($<$10% cover) whilst shrubs with non-ericaceous inrolled leaves are common (mostly 25%+). Nanophyllous shrubs increase in cover in dry proteoid types (10%+) (50 cm+). Tall, broad tussock grasses are common graminoids (10%+).

Shrubs visually dominate graminoids (ratio of non-proteoid shrubs to graminoids > 1,5:1).

NORTH ASPECTS

As in the Ruitersbos study area, graminoids are conspicuous on north facing slopes and relative (non-proteoid) shrub cover declines. Restioveld occurs over extensive areas from ±1 300 m-1 600 m+, mostly with an open or sparse proteoid element. The structural analysis failed to distinguish distinct communities, as did the floristic analysis, and physiognomic/structural attributes varied continuously over the altitudinal gradient.

R1 S - Restioveld

Sub-Formation. Variable. Low and medium, mid-dense or open restioid shrublands sometimes with an open or mid-dense proteoid overstorey.

Relevés. R1a 28, 29, 30, 31 R1b 25, 26, 27, 35 R1c 24, 32, 33, 36.

Floristic Equivalent. C1 Cliffortia tuberculata - Thoracosperma galpinii (1178) community. (28, 29, 30 - 25, 26, 27, 34). C2. Protea repens, P. lorifolia, Hypodiscus striatus community (24, 31, 32, 33, 36).

Description. The unit occurs from ±1 300 m-1 650 m+ on steep to gently sloping, rocky north aspects. Soils are mostly shallow, rarely moderately deep at higher elevations, and stony (mostly Mispah and Glenrosa form).

The unit differs from south slope communities by the low cover (< 10%+) of 50-100 cm tall shrubs, low ericaceous cover (< 10%) in most instances, and total graminoid cover exceeding total non-proteoid shrub cover.

A cline from mesic to xeric types can be recognized. R1a is the most mesic group occurring at high elevations on deeper soils. It is characterised by a relatively high grass cover, exceeding 25%, low proteoid cover (< 10% - a fire artefact?), relatively low restio cover (mostly < 50%), and 10%+ fascicled leaves.

At lower elevations (R1b), grasses decline in importance and total restio cover increases to 50%+.

Towards the xeric extreme and intergrading with arid fynbos (R1c), semi-succulent leaves increase in importance, coarse, hard, wiry grasses appear and non-ericaceous, inrolled leaves occur on a higher proportion of shrubs.

A1 S - Arid Fynbos

Sub-Formation. Low and medium open shrubland.

Relevés. 37, 38, 39, 40, 44 (37, 38, 39, 40, 44).

Floristic Equivalent. D1 Passerina obtusaefolia - Felicia filifolia - Pentaschistis eriostoma community.

Description. Arid fynbos is the most xeric fynbos community occurring north of the watershed at ±1 200-1 350 m. Soils are shallow, rocky, sandy Mispahs. The transition from predominantly restioid veld to a shrub-dominated vegetation occurs in this unit, but is less clear cut than the Outeniquas. Swartberg arid fynbos also differs from the Outeniquas type by the increased importance of relatively tall shrubs (> 10%) which help to distinguish it from restioveld (< 10%).

Characteristic features distinguishing A1 from restioveld are the absence of broad-leaved proteoids, the absence of leafy sedges (e.g. *Tetraria ustulata*) and narrow tussock diameter (< 5 cms) of other sparse sedges present and the absence of Ericaceae. Non-ericaceous inrolled leaves are common. Semi-succulent leaves are prominent in shrub species (> 10% of all shrub cover is semi-succulent)and succulents are present, but with low cover (< 5%).

Coarse, hard-leaved grasses (*Pentaschistis eriostoma*) are indicators but with low cover (< 10%). Total restio cover is usually > 25% increasing rather gradually towards Restioveld at higher rainfalls and/ or elevation.

K1 - Succulent Karroid Shrubland

Succulent Karroid Shrublands replace fynbos on sandstone substrates below the 300-350 m isohyet on steep north aspects.

Sub-Formation. Medium Open Succulent Shrublands.

Relevés. 43, 41, 42, 45, 46, 47, 48, 49, 50 ((43), 41, 42, 45, 46, 47, 48, 49, 50).

Floristic Equivalent. E1 Crassula rupestris - Digitaria natalensis community.

Description. Succulent Karroid Shrublands occur on steep north facing slopes on the northern foothills of the Swartberg. They replace arid fynbos on T.M.G. sandstone below ±1 100 m under rainfall of 300-350 mm and extend onto mixed sandstone/shale substrates to ±950 m. Soils are mostly very rocky, Mispah, Glenrosa or Hutton Form with very shallow to moderate (±100 cms) depth.

The characteristics of the type have been discussed earlier in Section 6.4.5. There is considerable variability within the unit dependent on elevation and substrate. Low shrubs with ericoid, semi-succulent and succulent leaves predominate on pure sandstone soils and rare restios may still be present. At lower elevations clumps of tall shrubs occur in a matrix of succulent, semi-succulent, or deciduous low shrubs. Nanophylls are common.

CHAPTER 7

GRADIENT ANALYSIS

"To the popular mind, a botanist is still a man who carries a big tin on his back, collects all kinds of little weeds and calls them by long names. But such work is only the preparation for the real study. It is very interesting and also very useful to science, but, if the collector stops short there, he is a botanist only to the same extent as the sportsman who shoots birds and stuffs their skins is a zoologist" Marloth (1892).

7.1 INTRODUCTION

In this chapter I shall attempt to interpret physiognomic/structural features of the vegetation in terms of their function. A plant must be fitted to its environment or die. Sessile organisms, for the duration of their lifespan, must weather drought, flood, predators and competition from their neighbours, with no possibility of flight. We should be able to perceive those stresses most significant to the life of a plant by an understanding of the functional significance of its physiology and morphology. The measure of its success is the Darwinian criterion of the number of offspring produced which survive to reproductive maturity (Pianka 1978).

The extent to which plants can exploit opportunities available to them is limited by genetic constraints on phenotypic plasticity. Taxa with limited plasticity are conservative in habitat selection whereas plastic species may adapt to enter new environments. In comparing different vegetation of the world there is an unresolved difficulty in deciding which features are due to phylogenetic constraints on phenotypic plasticity and which are adaptive. Schimper (1903) for example argued that the absence of annuals in the Cape fynbos was "unimportant" in comparison to the many convergent features with Mediterranean sclerophyll shrublands. Recent authors (Goldblatt 1978; Cowling and Campbell 1980), however, use the absence of annuals as important evidence for nutritional control of sclerophylly in fynbos.

Moll et al. (1980) have argued that the scarcity of trees in fynbos in comparison with similar shrublands in Australia is due to fire history. Eucalyptus, however, is one of the few tree genera with ectotrophic mycorrhiza in the world (Pinus, which occurs in European heathlands, is another) (Lamont 1981). The South African tree flora appears to have no ectotrophic mycorrhiza (Laughton 1964) so that a phylogenetic argument is equally plausible. In the discussions that follow, I have assumed that most features are adaptive though I remain aware of the philosophical problems.

Both floristic and structural data were analysed by direct and indirect gradient analysis (Whittaker 1967). For brevity, results of the latter will not be discussed here since the conclusions are similar to those developed from direct gradient analysis. The section ends with an interpretation of the structural classification and its predictive uses.

7.2 METHODS - Selection of Gradients

Main trends of vegetation change could be related to elevation and aspect (Chapter 4,5,6). Successional variations in community structure were insignificant since only mature vegetation was sampled.

Altitudinal and "topographic moisture" gradients have been widely used in direct gradient analysis (Whittaker 1975; Whittaker and Niering 1975; Kessel 1979). Altitude is related to a complex of factors such as temperature, rainfall, snow, wind etc., some of which have been identified in this study by PCA (see Chapter 1.3 and 3). "Topographic moisture" as used by Whittaker (1975) and his students is a subjective measure of local moisture régime as affected by topographic shading and radiation differences associated especially with aspect but also with slope. Topographic moisture is synonymous with slope/aspect and therefore radiation gradients in this study since ravines and similarly shaded areas were not sampled. Environmental factors covarying with slope/aspect and hence moisture gradients in the study areas are discussed in Chapter 3 and 1.3.

In Chapter 1.3 I calculated the effects of slope and aspect on evapotranspiration in the Outeniquas and Swartberg. Extension of the approach allows for a quantitative expression of local moisture régime using a moisture index based on water balance considerations. Specht (1972, 1981) has developed a moisture index calculated as:

$$Ea/Eo = K\ (P-R+S)$$

where Ea = actual evapotranspiration, Eo = pan evaporation, P = precipitation, R = runoff, S = extractable soil water and k is an

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$$Ea/Eo = K\ (P-R+S)$$

where Ea = actual evapotranspiration, Eo = pan evaporation, P = precipitation, R = runoff, S = extractable soil water and k is an "evaporative coefficient" for the relevant plant community. The index has been successfully used to express climatic factors significant to vegetation in Australia and New Guinea and has recently been applied in South Africa (Specht 1972; Specht and Moll 1981). Unfortunately insufficient data was available for calculation of the index at each stand. A crude estimate was made by calculating the ratio of R-PE to PE (Table 7.1).

Thornthwaite (1948) developed a moisture index from his PE formula which has been widely used in relating vegetation to climate on a regional scale (Schulze and McGee 1978). The index is calculated as 100 (S/PE)-100(D/PE) where S is moisture surplus, D is moisture deficit and PE is potential evapotranspiration.

Specht's index is a measure of the relative intensity of drought, whilst Thornthwaite's combines both deficit and surplus. Neither estimates the duration of the dry season. It seems reasonable to assume that plants will suffer more from an extended period of deficit than a brief period even if the total deficit is identical. I have thus combined both the duration and intensity of drought into a "drought index" (Table 7.2) calculated by the number of months in which moisture deficits exceeded subjectively defined limits. The relationship between the drought index (D.I.) and rainfall for level areas is shown in Table 6.3.

The three indices were compared by assessing their ranking of permanent study sites on the Outeniquas and Swartberg relative to a ranking based on "ecological intuition" (cf. Linder and Campbell 1978). Both

TABLE 7.1. Procedure for calculating moisture surplus and deficit for different slopes and aspects. All the calculations were programmed on a Hewlett Packard 9820 calculator.

1. Using latitude (to the nearest half degree) and average monthly mean temperatures from the nearest station (Kangogrotte - Swartberg, George - Outeniquas, Weather Bureau 1965) calculate Thornthwaite's PE. Temperatures may be corrected for regional lapse rates where information is available (±0,5°C/100 m, Fuggle and Ashton 1979, see also Smith and Geller 1979). No correction was made in this study since altitude was used as a second axis.

2. Multiply monthly PE by the ratio: PE corrected for slope and aspect/PE on a horizontal surface. The ratio was calculated for N and S slope only by altering the radiation input in Penman's equation using Swift's (1976) algorithm (Chapter 1.3). Data from Oudtshoorn Experimental Farm were used for Swartberg and Outeniqua Experimental Farm for the Outeniquas (Agricultural Technical Services, unpubl.).

3. Calculate monthly rainfall from annual rainfall (from 1:250 000 isohyet maps) adjusted according to monthly distributions in nearby rainfall stations. In this study annual rainfall/12, i.e. even seasonal distribution, was assumed.

4. Subtract monthly PE estimates from rainfall to obtain surplus/deficit.

5. Calculate Moisture or Drought Indices.

TABLE 7.2. Procedure for calculating Drought Index. Calculations were programmed on a Hewlett Packard 9820 Calculator.

1. Obtain monthly PE and rainfall (R) data using slope, aspect and altitude adjustments if required.

2. Calculate monthly surplus/deficit.

3. Sum the number of months with deficits falling into five classes with 20 mm increments and divide by the potential number of months with a deficit (i.e. No. of classes x 12). The index ranges from 0 - no deficit, to 1 - severe and prolonged deficit (> 80 mm throughout the year).

Example:

	J	F	M	A	M	J	J	A	S	O	N	D
R	60	60	60	60	60	60	60	60	60	60	60	60
PE	100	110	90	70	60	50	50	60	70	80	90	100
Deficit (R-PE)	-40	-50	-30	-10	0	0	0	0	-10	-20	-30	-40

No. of months with deficit exceeding			Potential number of months
1.	0 mm	8	12
2.	20 mm	5	12
3.	40 mm	1	12
4.	60 mm		12
5.	80 mm		12
	TOTAL	14	60

Drought Index = $^{14}/60$ = ,23

TABLE 6.3. Rainfall Equivalents of Drought Index on Level terrain.

Outeniquas	Annual rainfall (mm)		300	400	500	600	700	800	900	1000	1100	
	Drought Index		,68	,58	,46	,38	,26	,18	,11	,07	,01	
Swartberg	Annual rainfall (mm)	200	300	400	500	600	700	800	900	1000	1100	1200
	Drought Index	,69	,60	,56	,49	,43	,35	,28	,25	,18	,13	,07

Thornthwaite's index and the modified Ea/Eo overestimated the droughtiness of north facing aspects. The drought index conformed closely to subjective rankings of the sites on a moisture gradient. G. Breytenbach (pers. comm. 1981) has found that the drought index is a good predictor of rodent zoo-mass and species diversity whereas neither of the moisture indices were significantly correlated. The index is being tested as a predictor of litter production and site quality in pine plantations and may prove to have wider usefulness in the Southern Cape.

The moisture and drought indices are independent of soil properties allowing separate interpretation of soil-plant interactions. Soil depth, which effects both the nutrient pool and soil moisture régime, appeared to be a significant additional source of variation. Rockiness, especially of small rocks, and stoniness of the A horizon are correlated with soil depth (Chapter 3) and were used to define a soil depth/rockiness gradient.

Soil nutrients may be important in structuring plant communities (Specht 1979; Cowling and Campbell 1980). The study was, however, almost entirely restricted to base-poor T.M.G. Sandstone substrates and soil nutrients, especially cations, did not seem to vary independently from altitude or moisture gradients (Chapter 1.4). Thus plant variation was studied only in relation to complex altitude, moisture and rockiness gradients.

7.3 RESULTS AND DISCUSSION

The distribution of communities, taxocenes and physiognomic/structural features was plotted on two dimensions using altitude, drought index or rockiness as axes. Drought index and altitude satisfactorily ordinated plots. The two axes are not completely independent since rainfall is correlated with altitude and the moisture régime at a site varies with altitudinal differences in temperature. The dependence of the drought index on inaccurate isohyet data probably causes some data anomalies but, unfortunately, no better information is available.

In some cases hypotheses have been proposed elsewhere to explain structural patterns and the gradient distribution may be used as a test. In others, however, the distributions themselves are used to generate hypotheses.

7.3.1 Woody Plants - Taxocenes

In this section I discuss taxonomic groups, with particular emphasis on phytogeographic aspects.

(a) Proteaceae (Fig. 7.1). Proteaceae are also discussed under regeneration strategies below.

Proteaceae are most abundant at intermediate positions on the moisture and altitudinal gradients (Drought Index (D.I.) ,1-,4). They are absent in arid areas (D.I. > ,6). Under comparable moisture régimes (aerial climate) cover is lower on north than on south aspects. However, north slope soils are often shallower than south and high seedling mortality in the more droughty soils, seems a plausible explanation for lower densities.

No explanations have been offered for the decline in Proteaceae cover at high elevations, and/or wet peaty soils. Mean windspeed seems to increase with elevation (pers. obs., Grace 1977), but no measurements are available. Strong winds limit plant height by wind-clipping (Grace 1977 reviews wind effects on plants) so that Proteaceae gain no height advantage over their shrub and graminoid competitors. Strong winds may also limit seed-set of tall bird and insect-pollinated species by limiting their foraging time (most Proteas appear to be rodent pollinated at high elevations in the Swartberg, Wiens and Rourke 1977).

In moist, peaty soils of Ruitersbos, Proteaceae are rare even at low elevations (plot 16). Australian workers have conflicting views on the effects of waterlogging, but experimental evidence (Lamont 1976) suggests that some taxa, at least, are tolerant of waterlogging showing stimulated proteoid root production. Demographic problems such as high seedling mortality from fungal pathogens (associated with wet sites) have still to be investigated.

The upper limit of Proteaceae is probably not temperature limited. Assuming an average 5°C drop in temperature in the last glacial maximum (Deacon 1979) the upper limit of the "proteoid" zone would drop by 1 000 m if temperature was limiting, necessitating extensive invasion of adjacent shale soils.

Figure 7.1-7.7, 7.9-7.17, 7.19, 7.23, 7.24. Gradient diagrams.

The x axis is the Drought Index representing a moisture gradient from mesic (left) to xeric (right). Note that the scale changes on the Ruitersbos gradient above D.I. 0,3 to allow a greater spread of mesic points. The y axis is altitude (m).

Aline has been drawn through the scatter of points to separate relevés on north (right) and south (left) aspects.

Graph symbols are

•	absent
+	0-2%
1	2,1-10%
2	11-25%
3	26-50%
4	51-75%
5	76-100%
6	101-150%
7	151+%

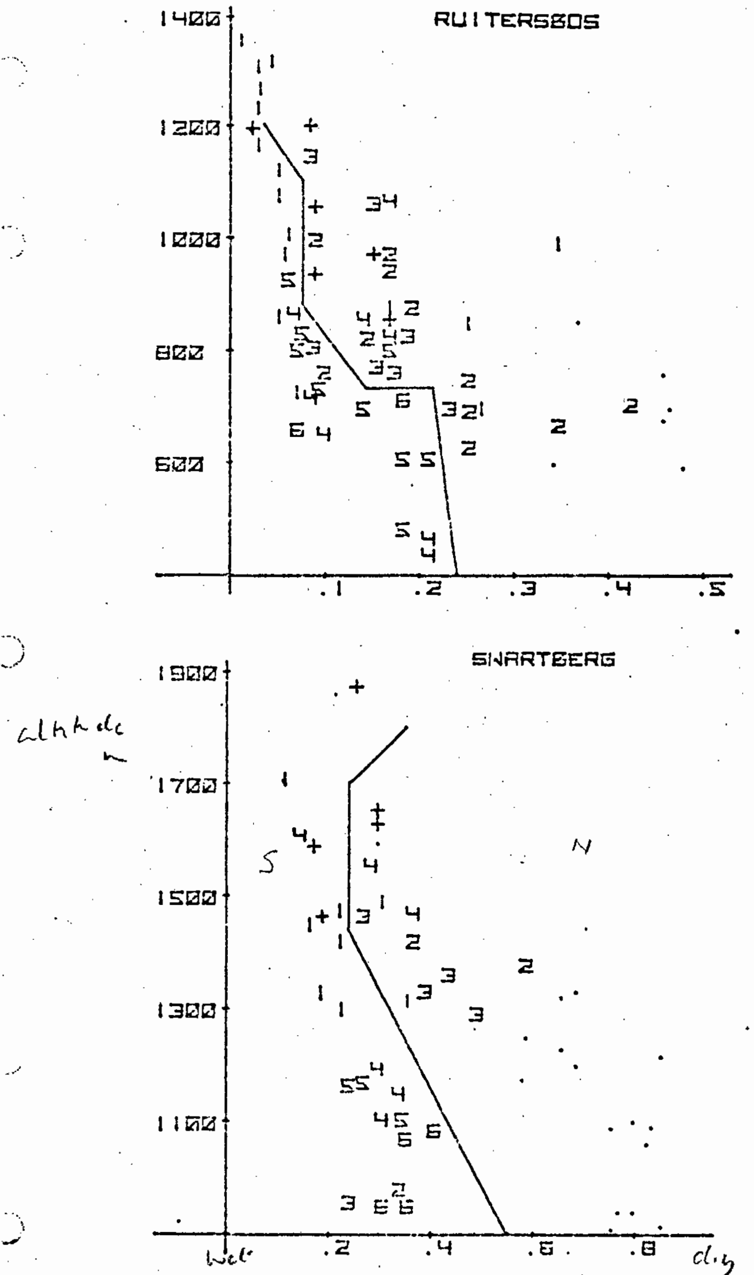

Fig. 7.1 Proteaceae - Isobilateral leaves.

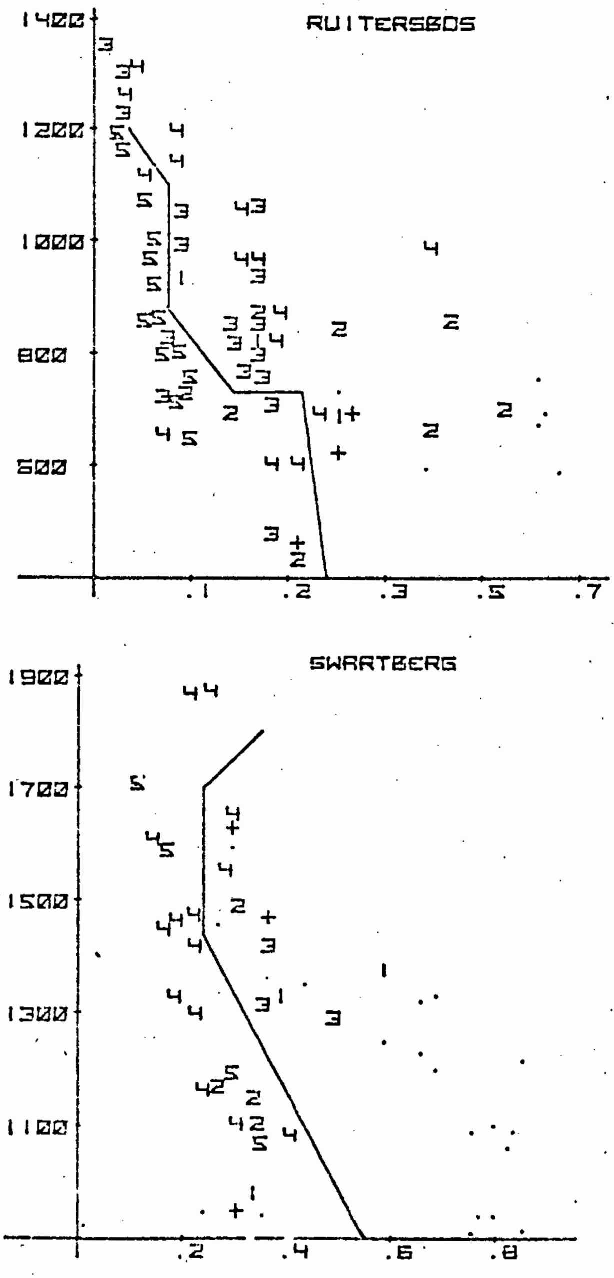

Fig. 7.2 Ericaceae.

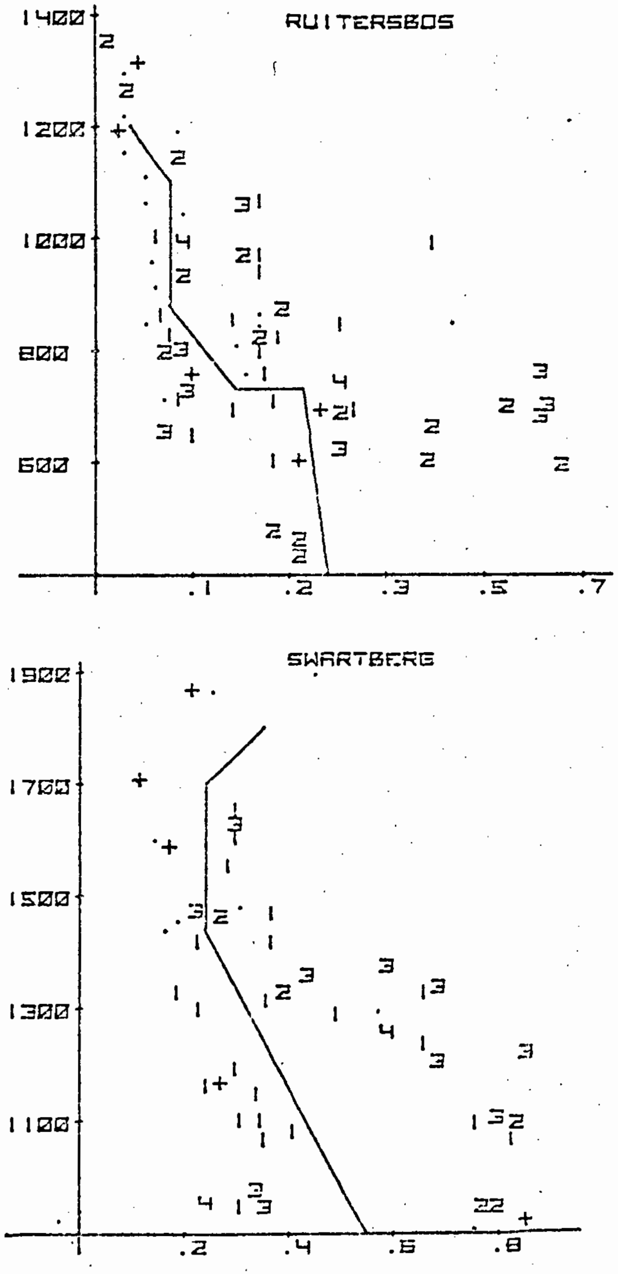

Fig. 7.3 Non-ericaceous shrubs with ericoid leaves.

(b) Ericaceae (Fig. 7.2).

The family, especially Erica, is mostly restricted to mesic sites (D.I. 0-,3). Ericas are thus far more widespread in the coastal than the inland ranges. Within the same range of moisture régime, ericaceous cover does not vary greatly from mid- to high elevations, though species numbers increase at upper elevations (Chapter 4).

Small (1973), noting the parallel development of xeromorphy in arid and nutrient deficient environments, suggested that species adapted to poor soils would be pre-adapted to arid areas and vice versa. Ericaceae are typically xeromorphic with sclerophyllous, evergreen, small inrolled leaves. Their centre of distribution on the gradients is moist, cool, nutrient-poor soils. Following Small (1973), I suggest that the family has radiated from such ancestral centres into arid areas by virtue of pre-adapted xeromorphy. Minor genera have penetrated most deeply into arid areas and are also the most recently evolved in the family (Oliver 1976).

(c) Non-Ericaceous Ericoid Shrubs (Fig. 7.3).

Non-ericaceous shrubs with inrolled leaves (e.g. some taxa of Phylica, Passerina, Cliffortia, Metalasia, Stoebe, Disparago, Polygala etc.) are common in relatively xeric areas (D.I. $>$,3), but also in moister areas where Ericaceae are rare. The two taxocenes appear to compete. Ericaceae cover is inversely proportional to other ericoid leaved taxa (r = ,65, n = ,40, p $<$,001 for Swartberg).

(d) Elytropappoid Shrubs (Fig. 7.4).

Several Asteraceous genera have independently evolved elytropappoid leaves (e.g. Elytropappus, Stoebe capitata, Helichrysum ericoides, Phymaspermum appressum). The small leaves, vertical leaf orientation, and reduction in transpirational area caused by the leaves being tightly adpressed to the stem, all reduce waterloss.

Elytropappoid shrubs are particularly common in dry Waboomveld shrublands (D.I. ,25-,5), on relatively deep fertile soils. They have a wider amplitude on north aspects of the Swartberg occurring from leached soils at high elevations to arid fynbos though usually on xeric microhabitats such as boulder crevices. The life form is replaced by densely pubescent, usually fascicled leaves in Succulent Karroid Shrubland.

7.3.2 Woody Plants - Physiognomic - Structural Features

(a) Deciduosity (Fig. 7.5).

Woody plants may evade drought by deciduosity or endure it as succulents or evergreens. Winter rainfall areas of the world have optimal growth seasons in autumn and spring - summer is too dry and in winter day-length is too short and temperatures too cool (Mooney et al. 1975). Schimper (1903) suggested that the dominance of evergreens in Mediterranean type climates was due to their capacity for opportunistic growth when conditions are favourable. His hypothesis has been supported by studies in Mediterannean California and Chile

(Mooney and Dunn 1970; Morrow and Mooney 1974; Mooney et al. 1975; Poole and Miller 1975; Miller and Poole 1979).

An alternative hypothesis, that the difficulty of acquiring nutrients in poor soils selects plants with longer lived leaves, has also been proposed (Monk 1966; Small 1972). Evergreen sclerophyllous plants are widely distributed on nutrient-deficient soils in Australia (Beadle 1962, 1966; Loveless 1961, 1962). The dominance of this life-form in Mediterranean climate areas of Australia has been attributed to nutrient deficiency rather than rainfall seasonality (Johnson and Briggs 1975; Specht 1979).

Virtually no deciduous shrubs were found at Ruitersbos. Deciduosity was relatively common in succulent Karroid shrublands in Swartberg (D.I. ,7+) on sandstone and sandstone/shale substrates. Rare deciduous shrubs also occur in Waboomveld on soils with a relatively high base status (Appendix 2). Unlike chaparral, however, fynbos shrubs are overwhelmingly evergreen (Cowling and Campbell 1980) supporting the nutrient hypothesis.

Miller (1981) has suggested that evergreen shrubs penetrate more deeply into arid areas in the Cape than in New World shrublands because of higher summer rain. His hypothesis would predict greater deciduous cover in the Western Cape than the Southern Cape under comparable rainfall conditions. According to Campbell (pers. comm. 1980) drought deciduosity is common in parts of the Cedarberg so that a comparison with Swartberg could provide a test.

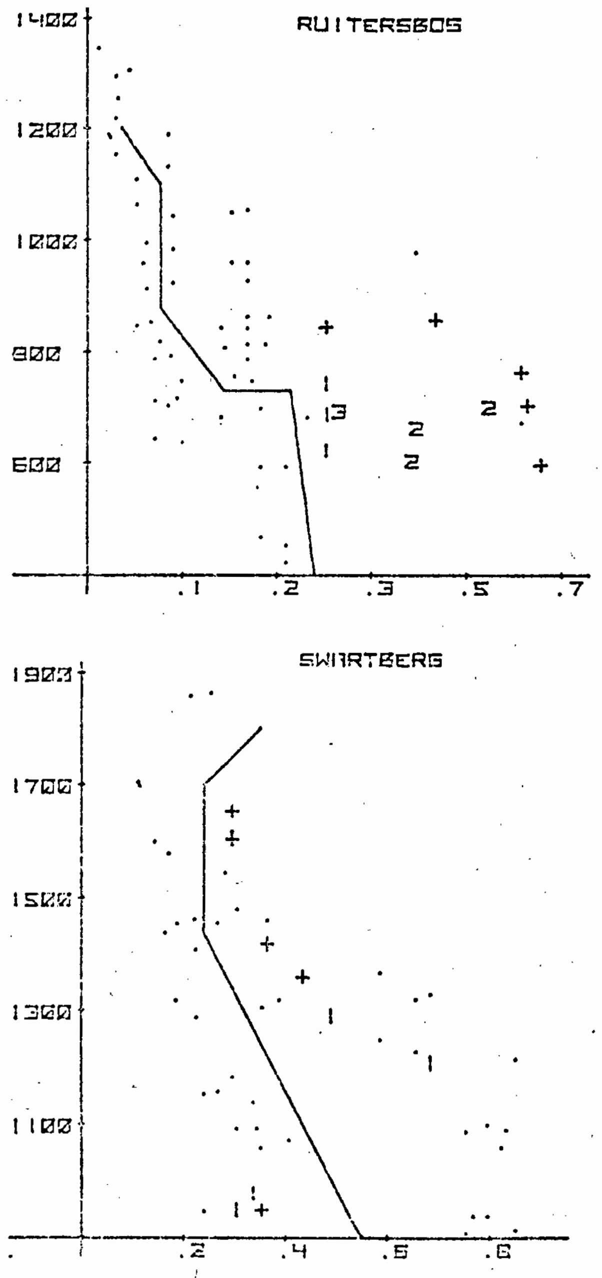

Fig. 7.4 Elytropappoid shrubs.

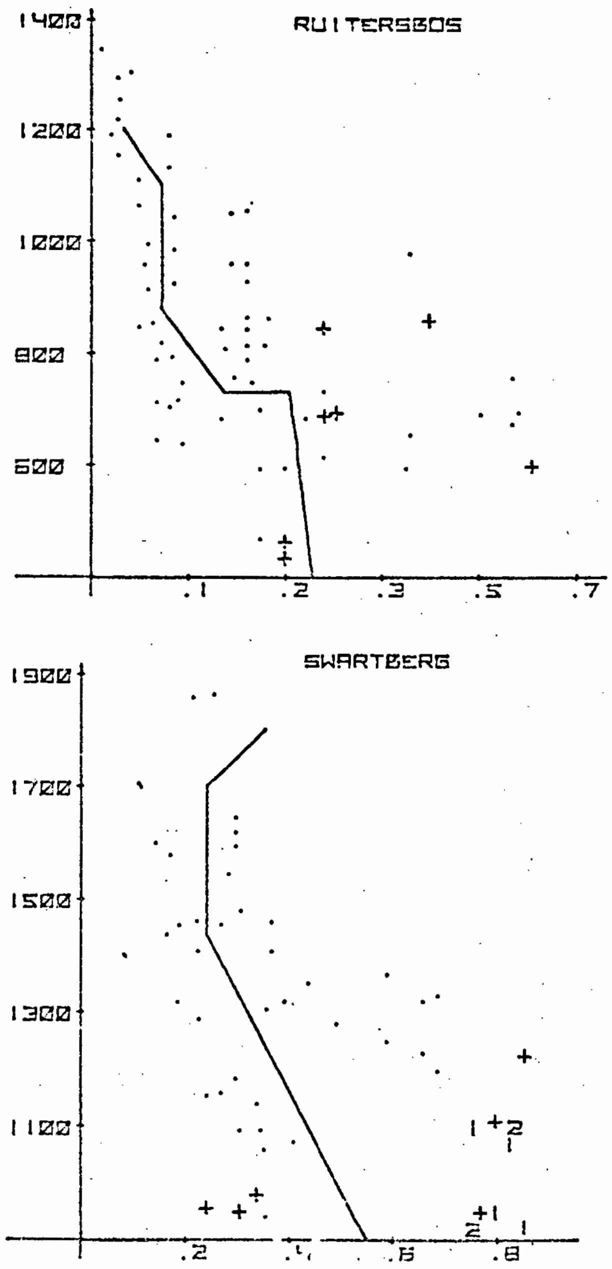

Fig. 7.5 Deciduous shrubs.

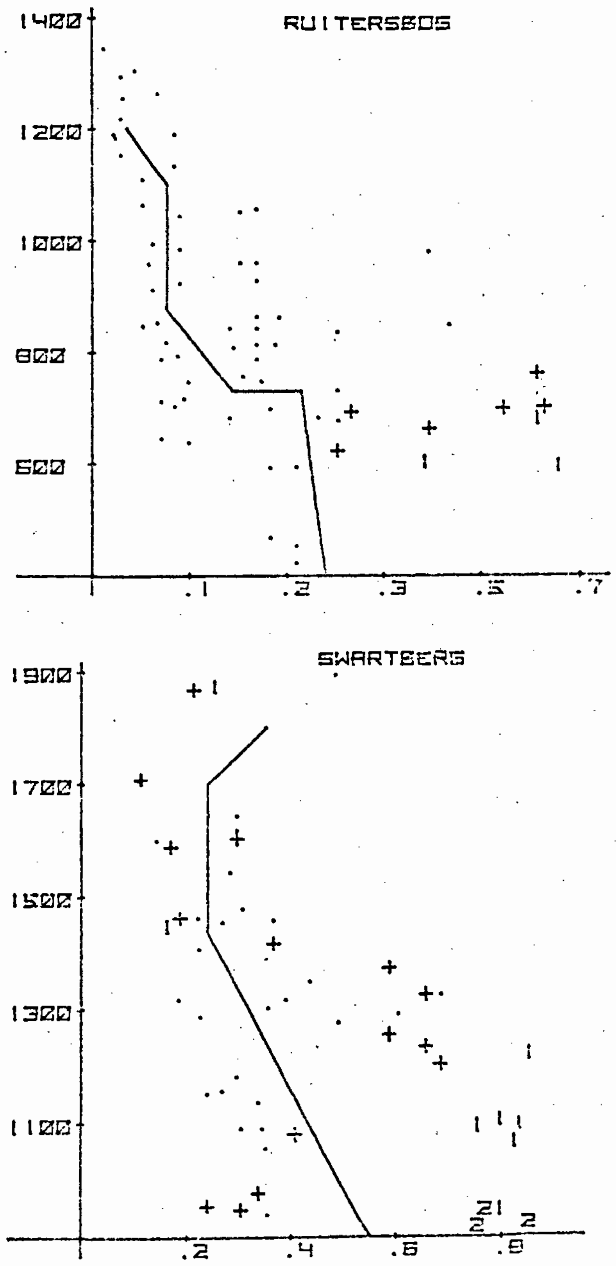

Fig. 7.6a Succulent shrubs.

(b) Succulence and Semi-Succulence (Fig. 7.6).

Succulents typically show high ratios of carbon gain to water loss, but low rates of carbon fixation so that they are at a competitive disadvantage where water is adequate for other plant strategies (Mooney 1970).

Succulents show the expected distribution with maximum cover in arid areas of low phytomass, especially arid fynbos and succulent Karroid veld. Succulents also occur at high elevations in the Swartberg, but are confined to xeric microhabitats on rocks and boulders with no vascular plant competition.

Semi-succulent (= "fleshy") shrubs are widely distributed on altitude and moisture gradients (Fig. 7.6), but their highest proportional cover is in arid fynbos. They are less common in arid areas with base-rich substrates.

The physiology of water loss and carbon gain of semi-succulent plants has yet to be investigated.

(c) Leaf Size

Absorbed solar radiation can raise leaf temperature well above air temperatures substantially increasing water loss. Small leaves maintain lower temperature under heat stress so that they should dominate in arid environments (Gates and Papian 1971; Parkhurst and Loucks 1972; Smith and Geller 1980). Californian and Chilean shrublands conform with heat budget predictions of leaf size (Parsons and Moldenke 1975).

Fig. 7.7 shows leaf size distribution in the Swartberg. Leptophylls are by far the dominant strategy in the two study areas. Mesophylls and microphylls are rare in arid areas (D.I. ,5+) conforming with moisture budget predictions, but are also rare at cool, moist, upper elevations. Nanophylls have a bimodal distribution being most common at low, xeric sites, but also occurring at mesic, high elevations.

Cowling and Campbell (1980) related the dominance of small leaves in fynbos to nutrient poor substrates following the Australian work of Loveless (1961, 1962) and Beadle (1962, 1966). Givnish and Vermeij (1976) developed an energy balance model in which both photosynthesis and transpiration are significant in determining leaf size. They suggested that plants can "afford" to transpire heavily only if potential photosynthetic rates are high. Nutrient limitations in poor soils limit photosynthetic rates, transpirational losses are thus relatively more "expensive" and small leaf size becomes the optimal strategy (Givnish and Vermeij 1976). Their model seems to fit understorey shrubs in the study area but Proteaceae remain an enigma.

Within the predominantly leptophyllous leaf class, heat budget considerations may influence leaf dimensions (Fig. 7.8a, b). Broad-leaved Ericaceae dominate in moist heaths with narrow-leaved species in arid areas, as predicted by these models. *Phylica* shows a parallel trend with broad-leaved species in the mesic range of the genus (*P. pinea*, *P. paniculata* in *Protea aurea* and *P. nitida* shrublands in the Swartberg respectively) and narrow-leaved species in arid fynbos (*P. floccosa*, *P. axillaris*).

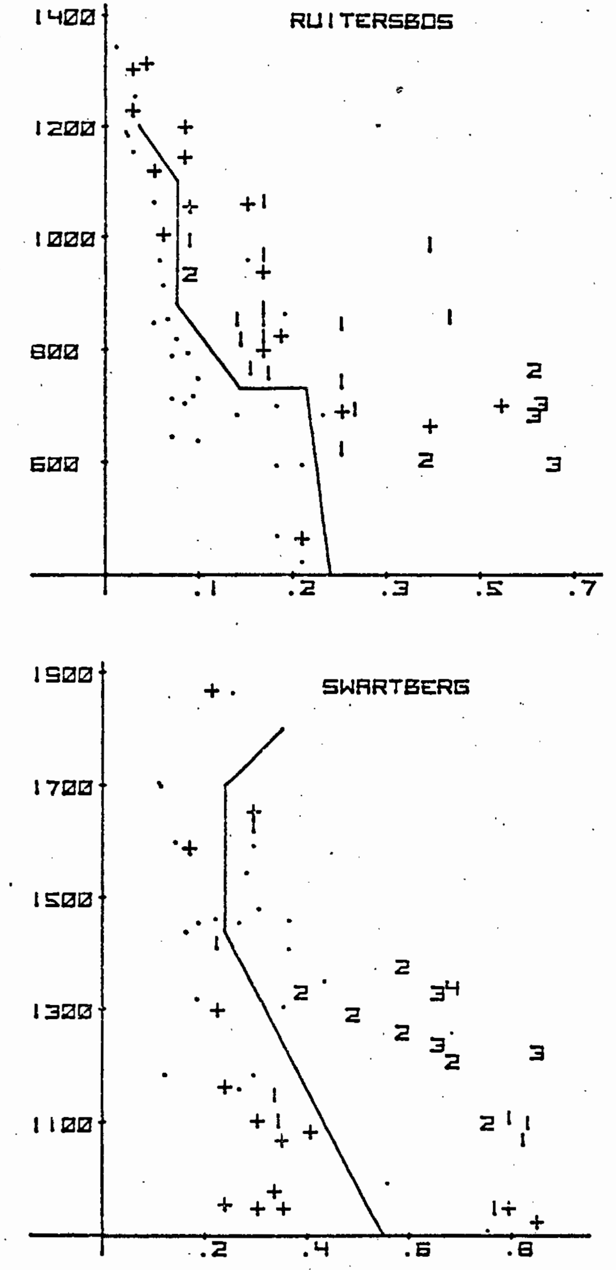

Fig. 7.6b Semi-succulence. Percentage of total shrub cover.

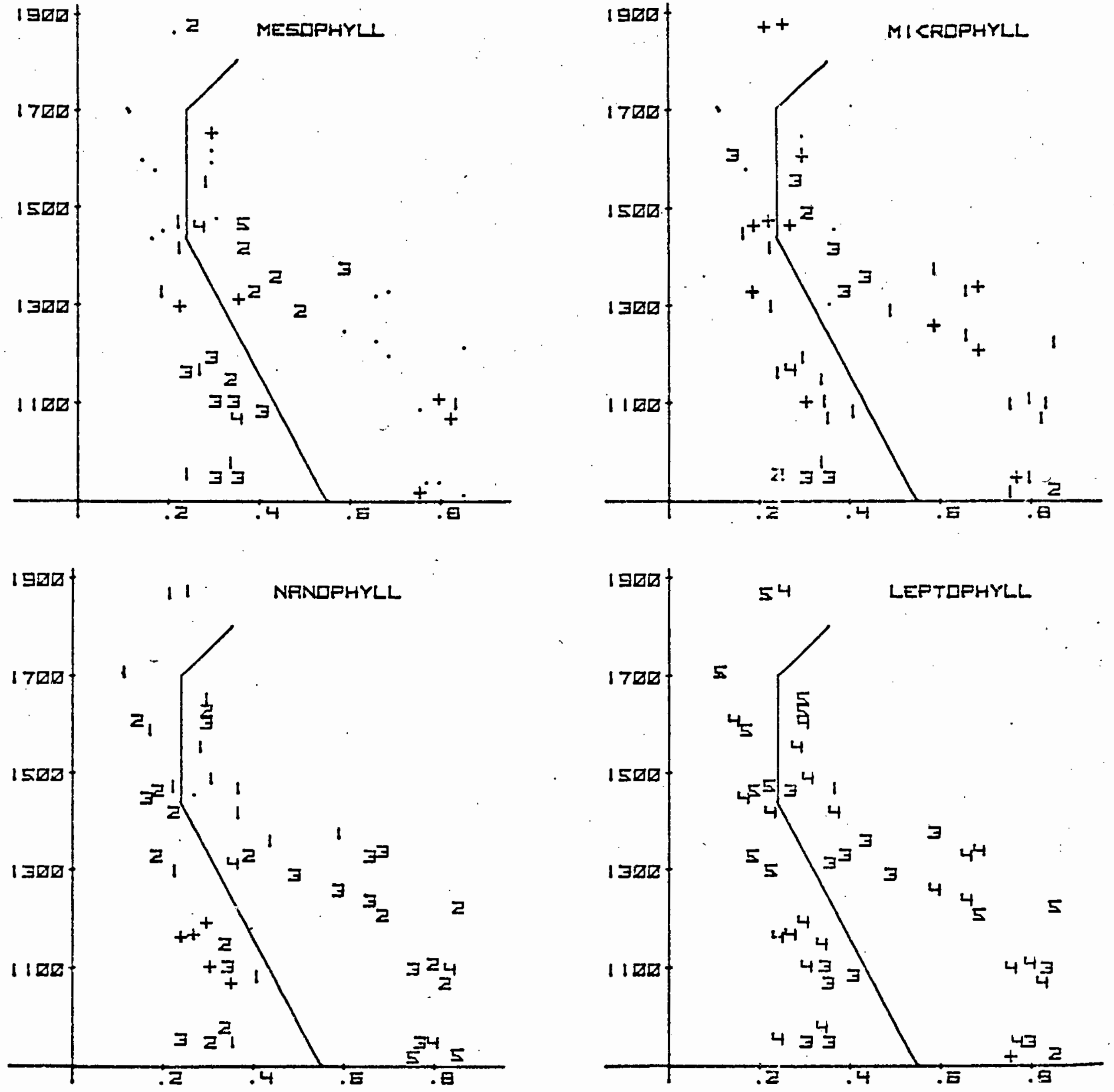

Fig. 7.7 Shrub leaf-size, Swartberg. Percentage of shrubs in each Raunkiaer leaf class.

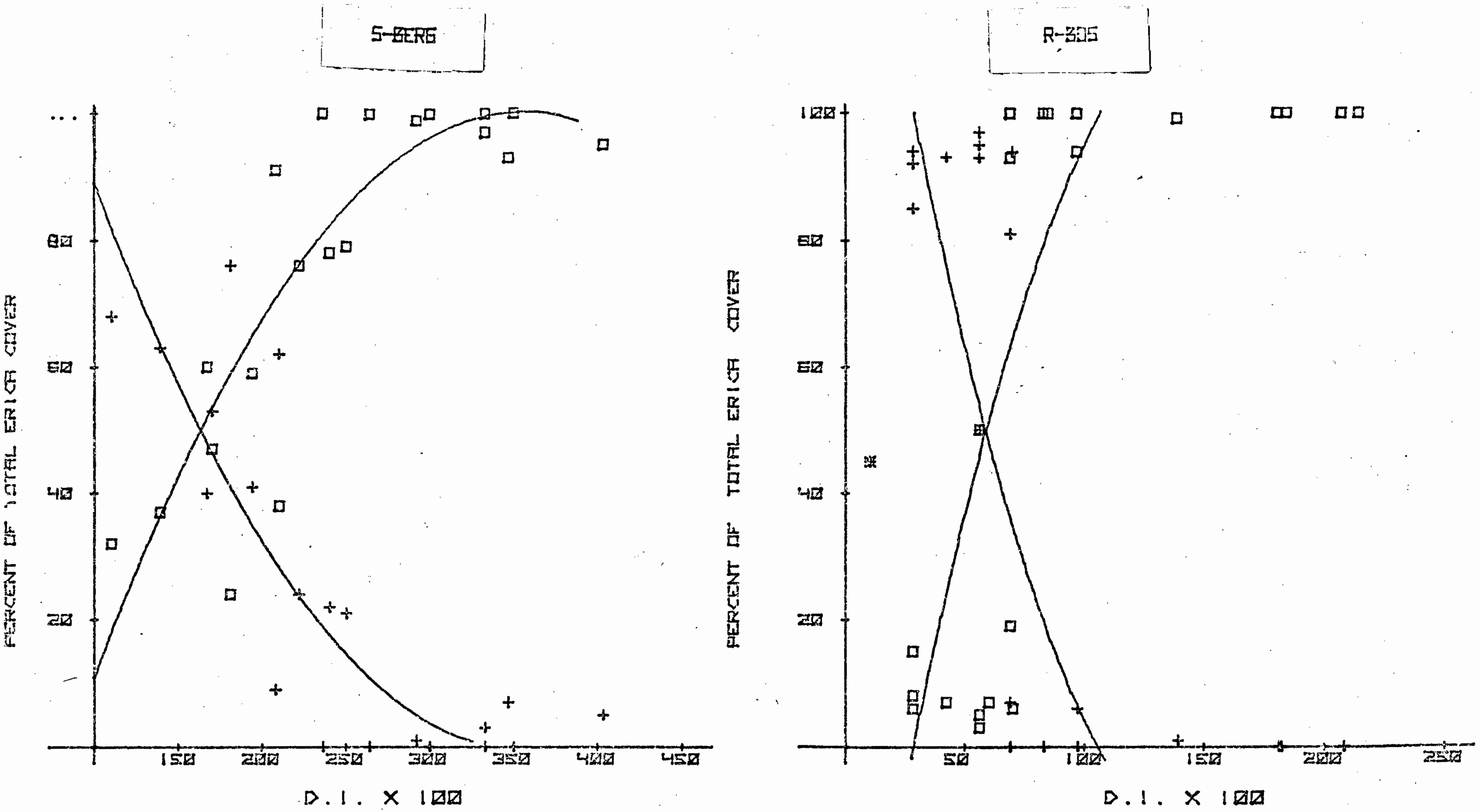

Fig. 7.8a Relative abundance of broad (+) and narrow-leaved (□) Ericaceae along a moisture gradient (mesic left, xeric right). D.I. = Drought Index.

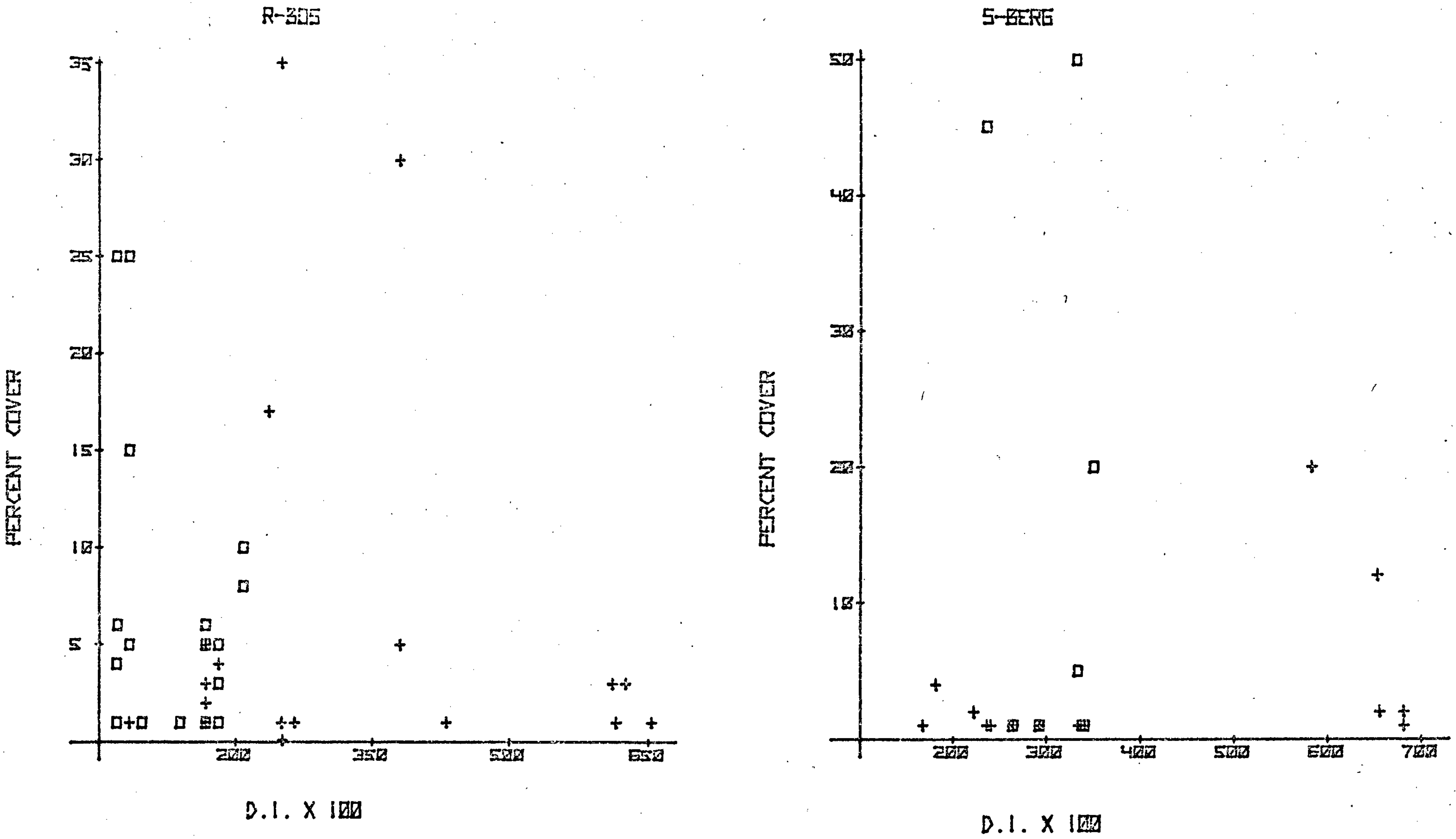

Fig. 7.8b Percentage cover of broad (☐) and narrow-leaved (+) Phylica spp. along a moisture gradient (mesic left, xeric right). D.I. = Drought index.

(d) Spinescence

Plant defences against herbivory are dependent on their total survival strategy - succulents, for example, cannot evade predators by dropping their leaves since production rates are too slow. Leaf spinescence should be rare in short-lived, orthophyll leaves since investments in mechanical tissue are expensive in relation to leaf duration. Evergreen, sclerophyll species have a hard, rigid structure so that leaf spinescence is a cheap defence.

Parsons and Moldenke's (1975) study seems to supports the prediction that leaf spinescence should be most common in evergreen sclerophyll shrubs though they found no trends and could suggest no functional significance for leaf spinescence. Leaf spinescence occurred in 22% of Californian and 17% of Chilean individuals at their foothill site (evergreen, sclerophyll), 1% in montane, 0% in maritimal and 13 and 3% respectively of desert sites (Parsons and Moldenke 1975).

Leaf spinescence is widespread in the two study areas (Fig. 7.9) but rare in Swartberg Karroid vegetation (succulent or deciduous) and Ruitersbos Heathlands and tall, closed protea shrublands (soft leaves). Patterns of leaf texture thus support the hypothesis.

Stem spinescence is very rare in fynbos (Fig. 7.9, and Bews 1925). Sclerophylly is associated with low leaf N, P, high fibre content, tannins and phenolics (Loveless 1961, 1962; Janzen 1974). In addition, food is presented in small bite-sizes reducing selectivity of intake. This battery of defences is more a consequence of selection to climatic and nutrient constraints but no less effective in deterring herbivores.

In arid areas, where evergreen sclerophyll strategies cannot be sustained, a new set of defences is encountered of which stem spinescence is one. The distribution of stem spinescence (Fig. 7.9) and its absence on any evergreen, sclerophyll shrub supports the above interpretation of the "sclerophyll syndrome".

7.3.3 Woody Plants - Regeneration Strategies

There is a general increase in seed-regenerating, woody species towards cool, moist, high elevations in the Swartberg whereas, in Ruitersbos, resprouting species are common in heaths on peaty soils (e.g. Penaea cneorum) (Table 5.2). Regeneration strategies were difficult to assign with certainty to many shrub species so I shall discuss the variable and well documented strategies of Proteaceae only (Williams 1972; Rourke 1972; Moll et al. 1981). Distribution of regeneration strategies along environmental gradients should provide insight into their adaptive significence (cf. Thompson 1978), but must be interpreted cautiously because of the dependence on past fire history.

The distribution of the four Proteaceae strategies, serotiny*, soil-stored seed, root resprouts and stem resprouts, is shown in Fig. 7.10. Serotinous species are absent at xeric sites but also at high elevations on peaty, waterlogged soils in the Outeniquas (H1, H2, H3). They dominate the vegetation in mesic sites (D.I. ,1-,3) at mid-elevations. Soil-stored seed species are never common, occurring

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* Serotiny is defined here as retention of the seed in cones or capitula for more than one year.

sporadically towards the drier end of the serotinous range (D.I. ,15-,2 in Ruitersbos) but also on wet peaty soils in the Outeniquas. Root resprouts are never common but have the widest distribution on both altitudinal and moisture gradients. Stem resprouts (*Protea nitida*) are confined to low, dry situations on deep, relatively fertile, talus soils.

Serotinous species are typically r selected (Stearns 1976; Pianka 1978) in their reproductive strategy producing relatively large quantities of seed adapted to long distance dispersal when openings are created. Their population size varies with fire régimes and seedling densities may change by several orders of magnitude as a result of fire season alone (Bond 1980). They are poorly buffered against unfavourable fires since seeds do not persist in the soil (pers. obs.) and the seed reservoir is thus dependent on reproductively mature adults. Cycles of local population extinction and recolonisation are typical, especially on drier, north aspects. Their failure to penetrate arid areas is probably due to their complete dependence on seedling survival in the critical period after fires where mortality from drought is high. Their absence in waterlogged or high altitude sites is probably also due to seedling failure from, for example, damping off, wind damage or short growing seasons.

Proteaceae with soil stored seed are relatively more k selected. Dispersal distance is probably short and the strategy is typical of highly site-specific taxa (e.g. *Mimetes*). Buried seed may remain viable for long periods (several fire cycles e.g. *Mimetes stokoei*, Rourke 1976) so that the strategy is relatively more buffered than seroting to unfavourable fires and should thus occur over a slightly wider range of conditions. Generally, however, the two strategies

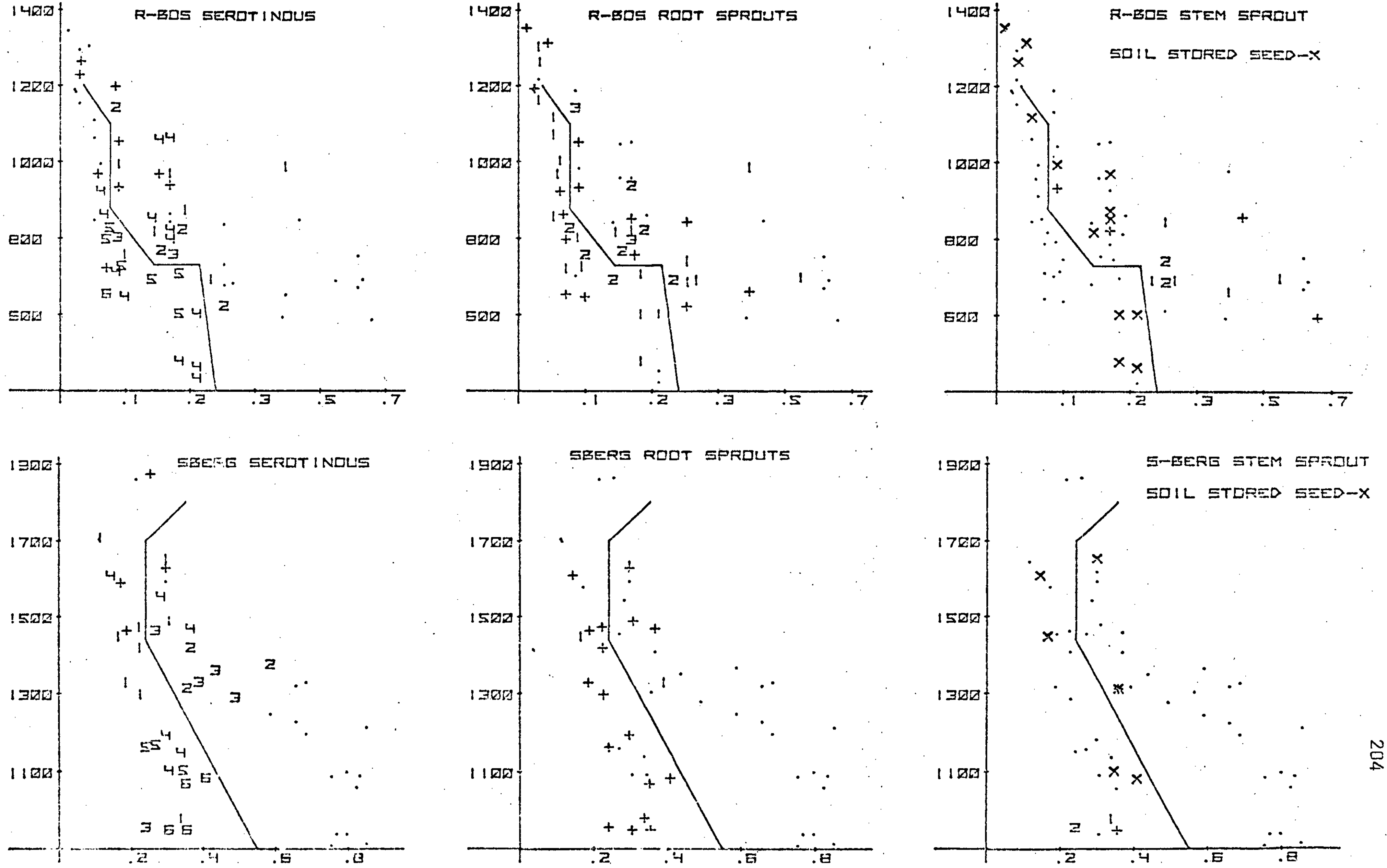


Fig. 7.10 Proteaceae Regeneration Strategies. S-Berg = Swartberg, R-Bos = Ruitersbos. Soil stored seed (X).

are competitive and serotiny will be the more successful.

Root resprouts are highly buffered against adverse fires having the capacity to persist with minimal mortality. Their failure to dominate the vegetation remains an unsolved mystery (cf. Keeley 1977; Carpenter and Reicher 1979; Moll et al. 1981).

7.3.4 Graminoid Growth Forms - Taxocenes

Restio, grass and sedge distribution along environmental gradients is discussed below, with the main emphasis on distribution of the taxonomic groups rather than particular physiognomic/structural features. A general discussion of the role of graminoid life forms in structuring fynbos follows in the next section.

Restios (Fig. 7.11). Total restioid cover varies in a relatively complex way with altitude and moisture gradient. On south aspects, there is a decline in cover from high, moist elevations to low, xeric elevations on both study areas. Under comparable moisture régimes, restio cover is higher on north than on south aspects. Both study areas show declining restio cover at low and/or xeric elevations on north aspects. Restio are absent in arid areas of the Swartberg (D.I. > ,7, which, however, coincides with a change in geological substrate).

In Chapter 6, I showed that several structural feature of restios are sufficiently site-specific to be of diagnostic value (Table 6.2, 6.3). Apparent tussock size is a useful character and the distribution of large tussocked (diam. > 25 cms) and small tussocked (dia-

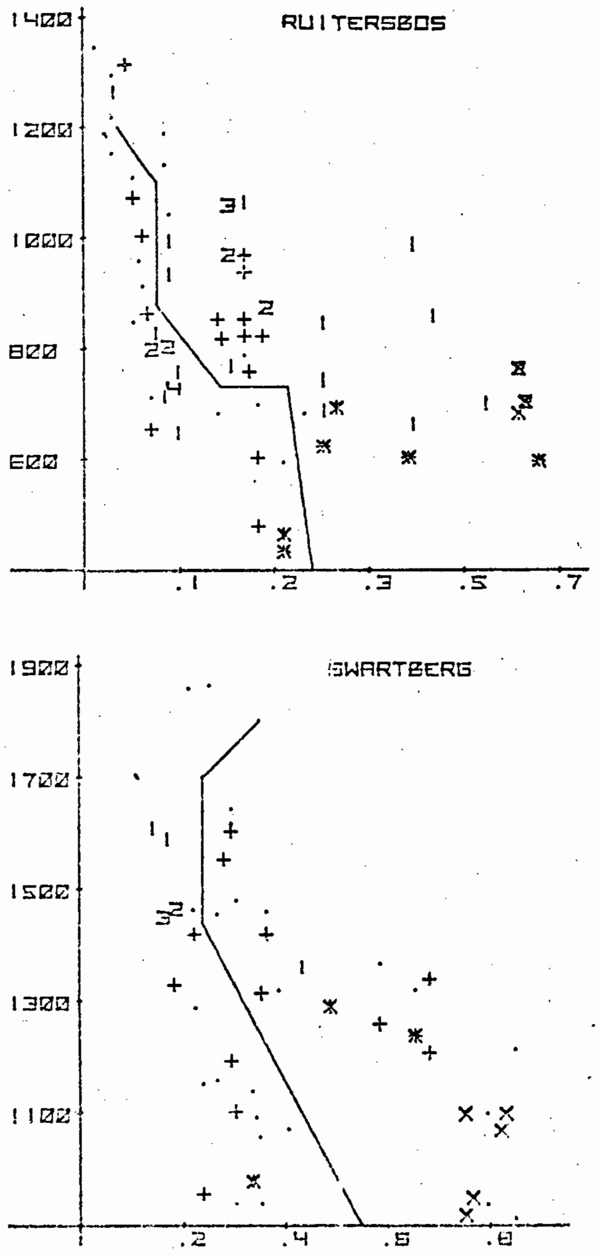


Fig. 7.9 Leaf Spinescence and Stem Spinescence (X).

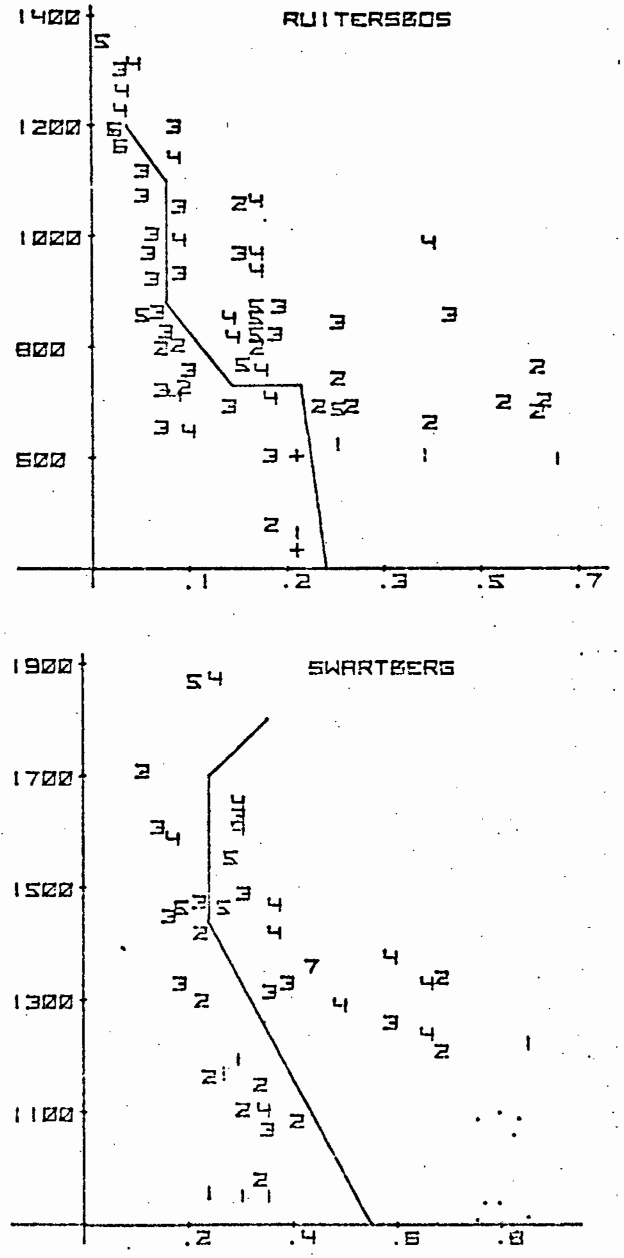


Fig. 7.11 Total Restios.

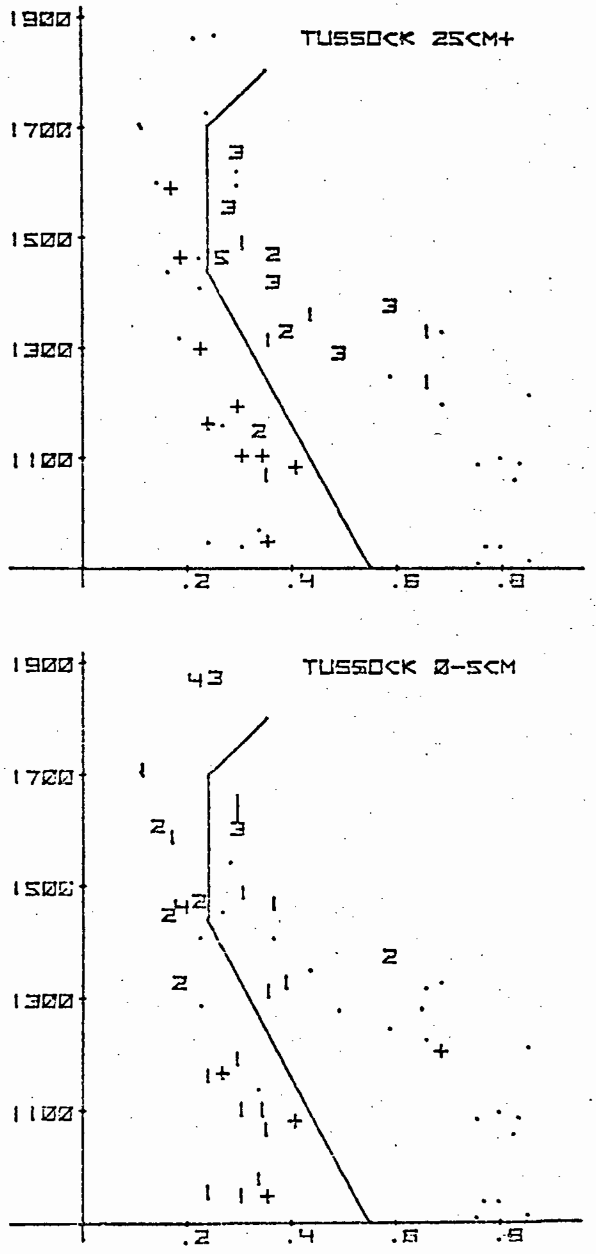


Fig. 7.12 Restio tussock size.

meter $<$ 5 cm) restios are shown in Fig. 7.12). The correlation of tussock size with moisture gradients suggests competition for root space in mesic areas.

(b) Grasses. Total grass cover shows no clear pattern on moisture and altitudinal gradients (Fig. 7.13). If grasses are grouped into temperate genera and subtropical genera, however, a separation is apparent. Temperate genera were taken as Ehrharta, Pentaschistis, Pentameris, Koeleria, Anthoxanthum and Merxmuellera. Subtropical general were taken as Themeda, Heteropogon, Cymbopogon, Aristida, Digitaria and Brachiairia (Fig. 7.14).

The temperate group probably shares the C3 photosynthetic path way and the subtropical group C4 (Hatch and Slack 1971; Vogel et al. 1978; Tieszen et. al. 1979). The subtropical group includes mostly deciduous species whose leaves dieback in summer drought. Many temperate species have long-lived, sclerophyllous, evergreen leaves, e.g. Pentameris dregeana, Penta schistis eriostoma.

The deciduous, perennial strategy is dependent on high nutrient reserves for annual replacement of photosynthetic tissue which probably explains its limitation to base-rich soils in Waboomveld and Succulent Karroid veld. Evergreen species are nutrient conserving but limited by higher moisture loss over summer drought periods. Their cover thus declines with increasing duration and intensity of drought.

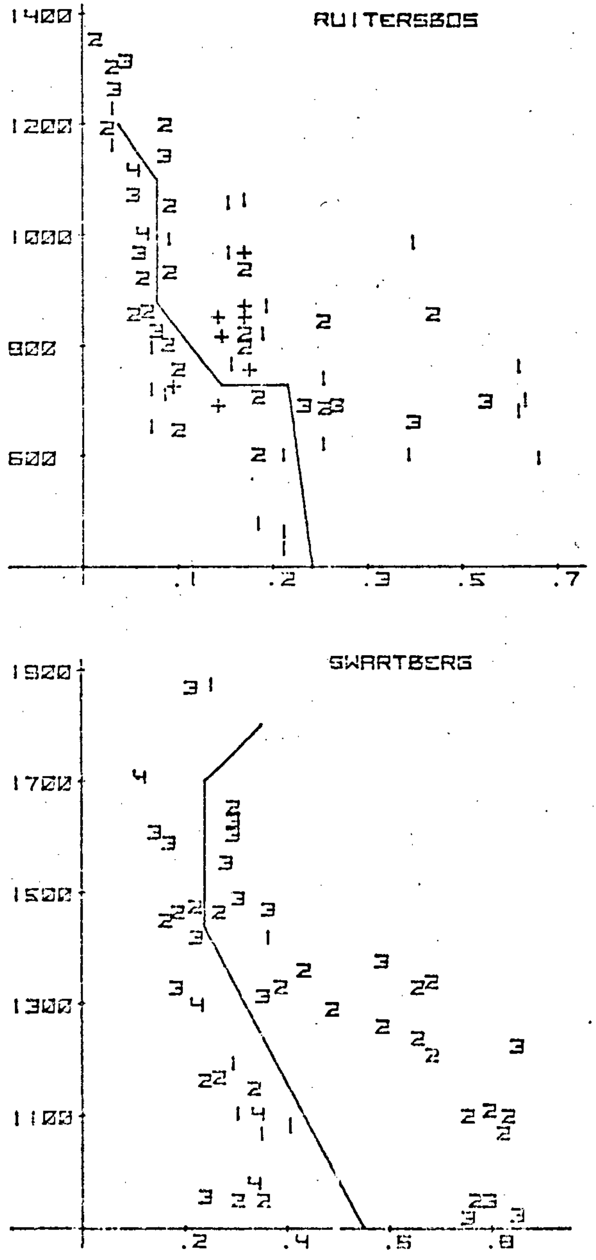


Fig. 7.13 Total Grasses.

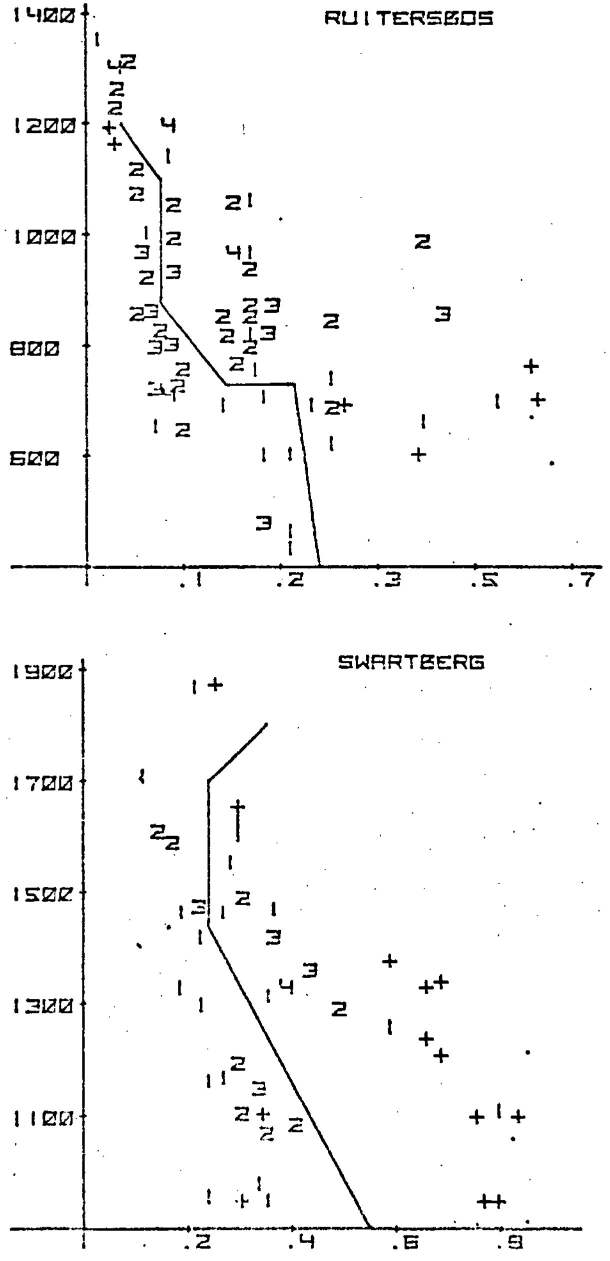


Fig. 7.15 Total Sedges.

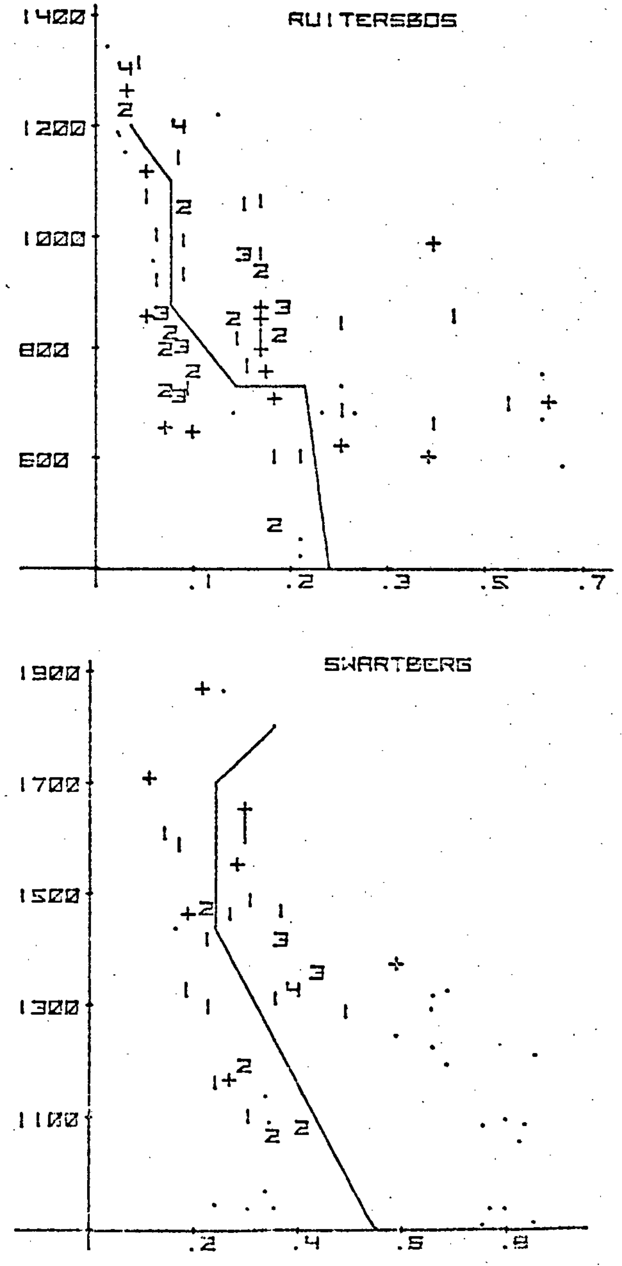


Fig. 7.16 Total grassy sedges.

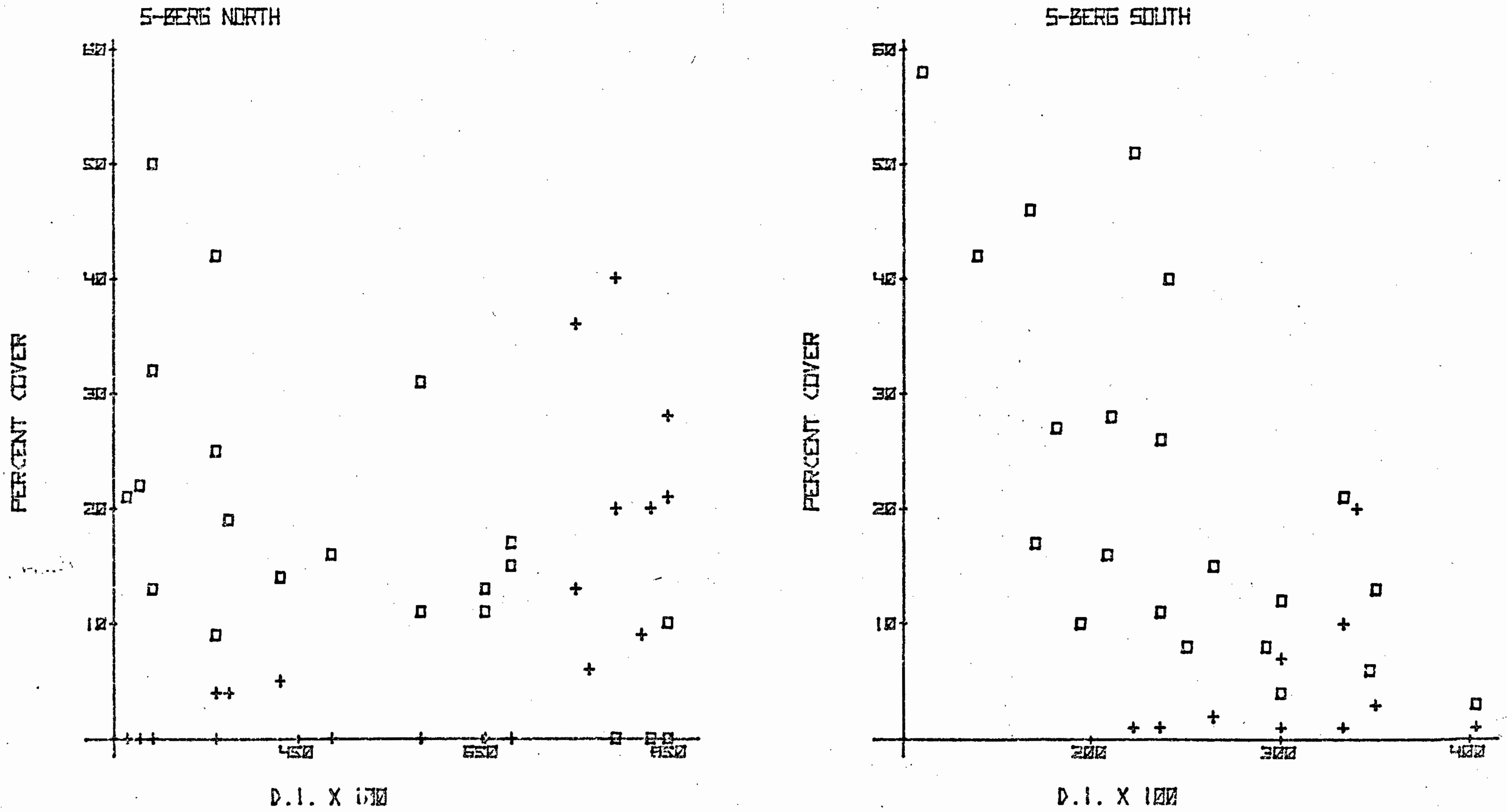


Fig. 7.14 Distribution of C3 and C4 grasses along a moisture gradient on north and south aspects of the Swartberg.
□ = C3, + = C4.

(c) Sedges (Fig. 7.15). Total sedge cover is highest at mid-points on the moisture and altitudinal gradients on Swartberg and Ruitersbos south aspects and on Swartberg north aspects. Sedge cover is high on Ruitersbos north aspects from 800 m to 1 300 m and over medium to peaty, moist soils (D.I. ,01-,2). Sedges are generally more abundant on the Ruitersbos gradient. Their cover distribution generally varies inversely with restioid cover and the two taxocenes are probably antagonistic.

Restioid sedges are widely distributed in the two study areas, but "grassy" leaved sedges are more habitat specific (Fig. 7.16).

7.3.5 Is Fynbos a Savannah? - a Synthesis

Grasses and woody plants are dominant, but antagonistic, growth forms in savannah. The two life forms have different root systems and water economies which are complementary under given climatic/edaphic conditions (Walter 1979). Perennial grasses have an "intensive" root system densely exploiting a small volume of soil. They transpire freely when water is available and die back to dormant buds with negligible moisture loss in the dry seasons. Woody plants have extensive roots penetrating a large volume of soil diffusely. These are particularly successful in stony soils with variable (especially winter) rainfall since moisture can be drawn at depth during drought. Woody plants always require small quantities of moisture to sustain losses from buds and branches and cannot, therefore, survive in low rainfall areas where soil dries out completely (Walter 1979).

Given these assumptions, Walter argues that, dependent on rainfall and soil properties, a balance is maintained between grasses utilising surface water and trees utilizing deep moisture reservoirs. Where available moisture exceeds a threshold, tree canopies close, shade becomes limiting to grasses, and woody plants have the competitive advantage.

Fynbos is also characterised by woody and graminoid elements. The graminoid strategy differs from savannahs in that species are predominantly evergreen, probably to conserve nutrients, so that they do not have the same water-use advantage during the summer drought. Walter's argument can nevertheless be extended as a plausible explanation for major structural types in fynbos.

Three main rooting strategies, with associated characteristics, may be postulated:

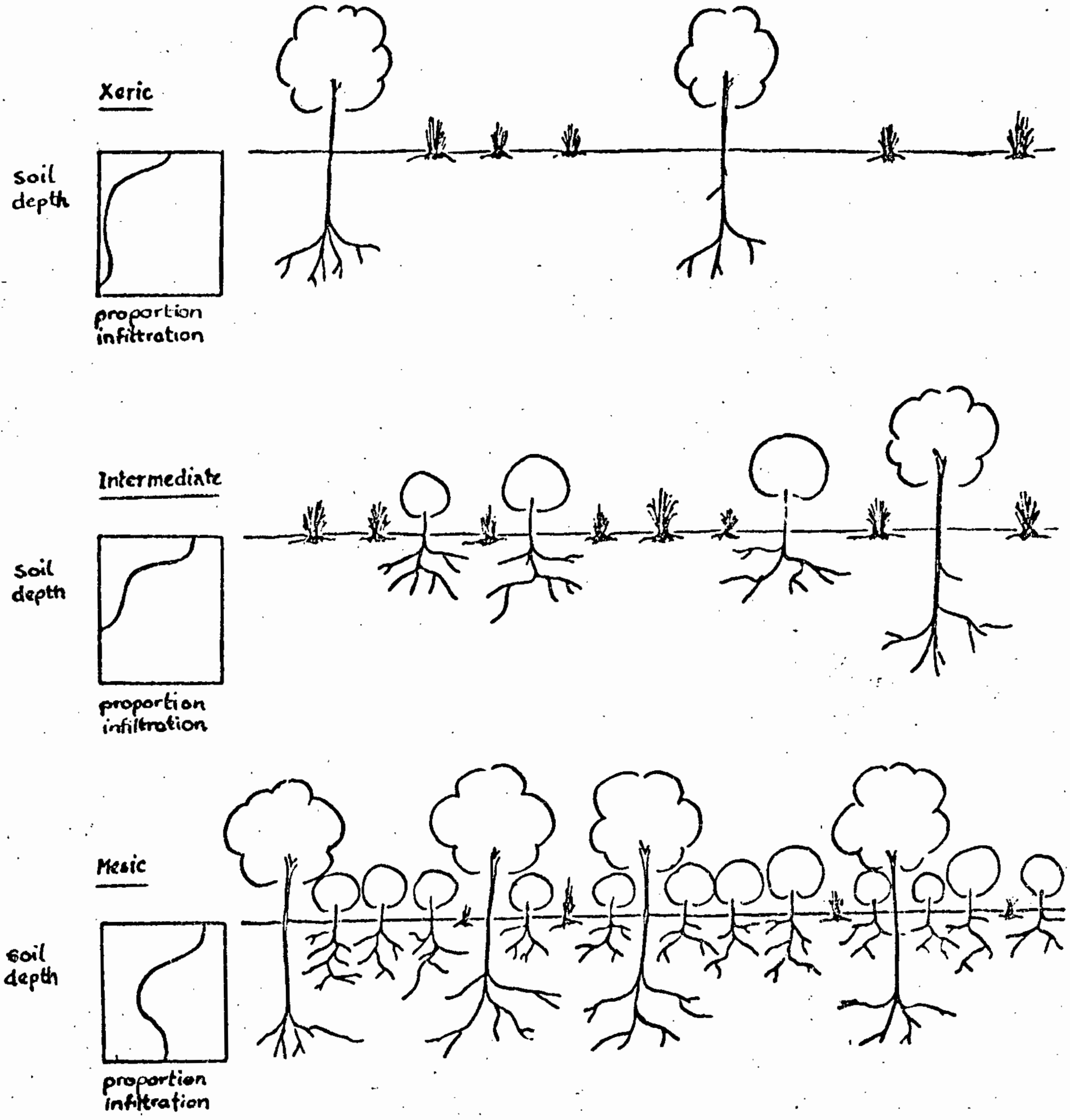
(1) Graminoids - shallow, intensive root systems including rhizomes. Small volumes of soil are intensively exploited near the soil surface. Graminoids are apparently sensitive to shade. Van Wilgen (1980) has reported high graminoid biomass in frequently burnt and senescent stands but low biomass in mature vegetation with closed canopy (see also Campbell and Van der Meulen 1980).

(2) Shallow-rooted (S.R.) Shrubs - shallow, extensive root systems. Larger volumes of soil are exploited over greater, but still shallow, depths than graminoids. These are typically small-leaved understorey shrubs, less sensitive to shading than graminoids, but with cover declining slowly as succession proceeds (e.g. Specht 1981) for shading or other reasons.

(3) <u>Deep-rooted (D.R.) Shrubs</u> - shrubs with deep, extensive root systems and, frequently, water concentrating crowns (Specht 1957). Large volumes of soil are exploited and roots utilise deep soil moisture reserves over summer drought. This relative independence from moisture stress may explain the greater productivity and taller height growth typical of these species which usually form the overstorey. Many Proteaceae are typical examples (cf. Specht 1957, 1981). Succulent and deciduous shrubs and grasses respond to drought in different ways and will be considered only incidentally.

Fynbos soils derived from sandstone are predominantly sandy. Thus variability in soil moisture régime is due primarily to effective rooting depth and rockiness. In broad terms, soils are deep and mesic, shallow and xeric or seasonally or permanently water-logged. Each of the above rooting types occupies a characteristic position on a climatic/edaphic moisture gradient.

Figure 7.18. Suggested distribution of deep-rooted shrubs, shallow-rooted shrubs and graminoids on a moisture gradient on deep, infertile sandy soils.



Explanation of Fig. 7.18

1. All evergreen strategies are limited by moisture in arid areas and cover is low. Deep-rooted species using deep soil reserves can survive. Succulent, semi-succulent and deciduous shrubs show better carbon gain/water loss ratios and increase in cover. Graminoid cover decreases since evergreen graminoids are limited by drought and deciduous species are limited by nutrient supply.

2. Evergreen shallow-rooted graminoids and shrubs are excluded from very arid areas since they cannot survive complete drying out of surface soils. Deep-rooted shrubs persist by drawing on deep soil reserves accumulated from winter surplus drainage. This explains the decline in graminoid cover and increase in shrub cover from restioveld to arid fynbos (Fig. 7.19).

3. Where rainfall is higher, S.R. graminoids and shrubs obtain sufficient moisture to survive summer drought. They utilise a high proportion of available moisture and less is available for deep percolation. D.R. shrubs are consequently excluded. Waboomveld may be an example.

4. Under more mesic conditions, S.R. species cannot use all the winter surplus and deep rooted cover increases drawing on deep soil reserves over summer drought. Growth rates of D.R. species are greater because of reduced drought constraints and these species overtop S.R. species.

5. With sufficient moisture, D.R. species form a closed, or nearly closed canopy and graminoid cover drops sharply, e.g. P1, P2

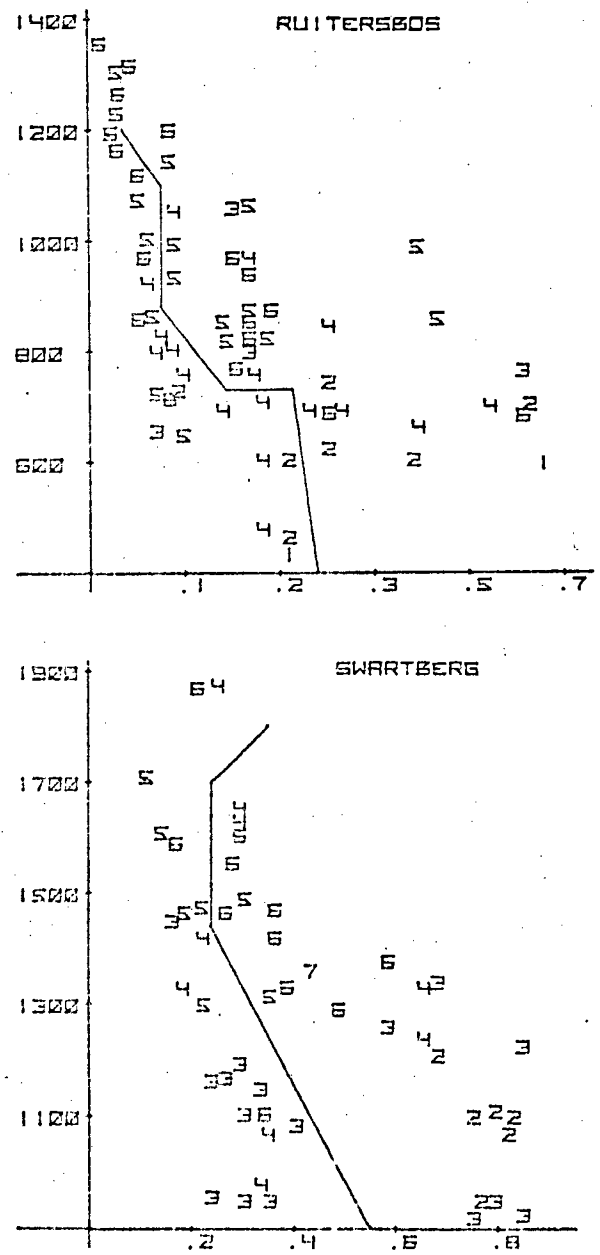


Fig. 7.17 Total graminoids.

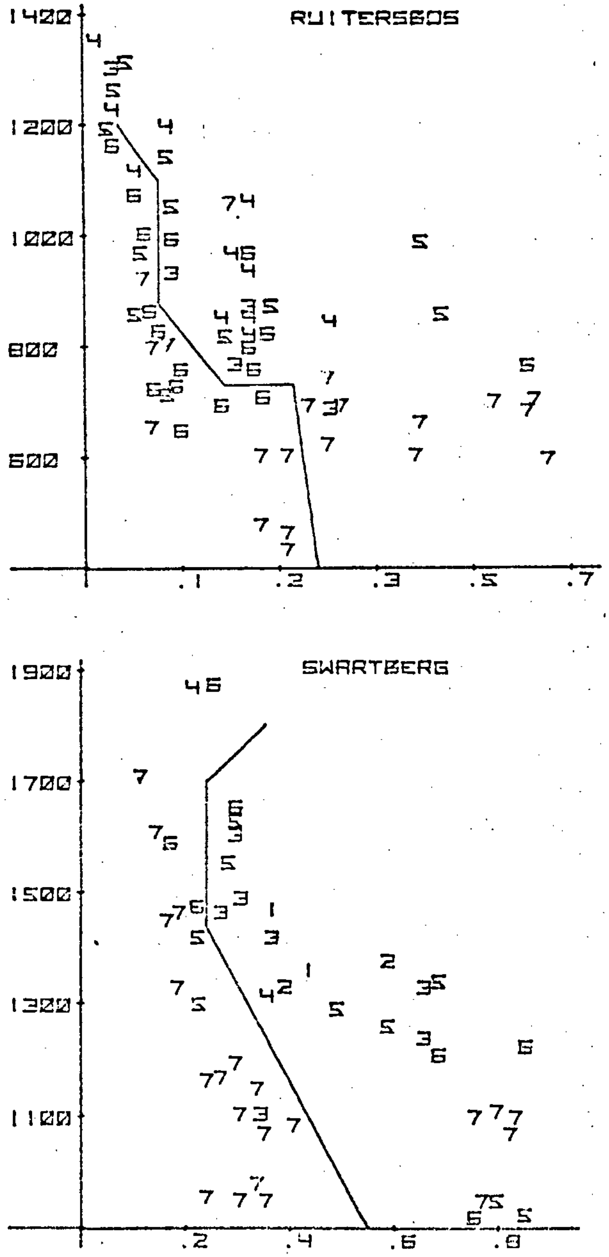
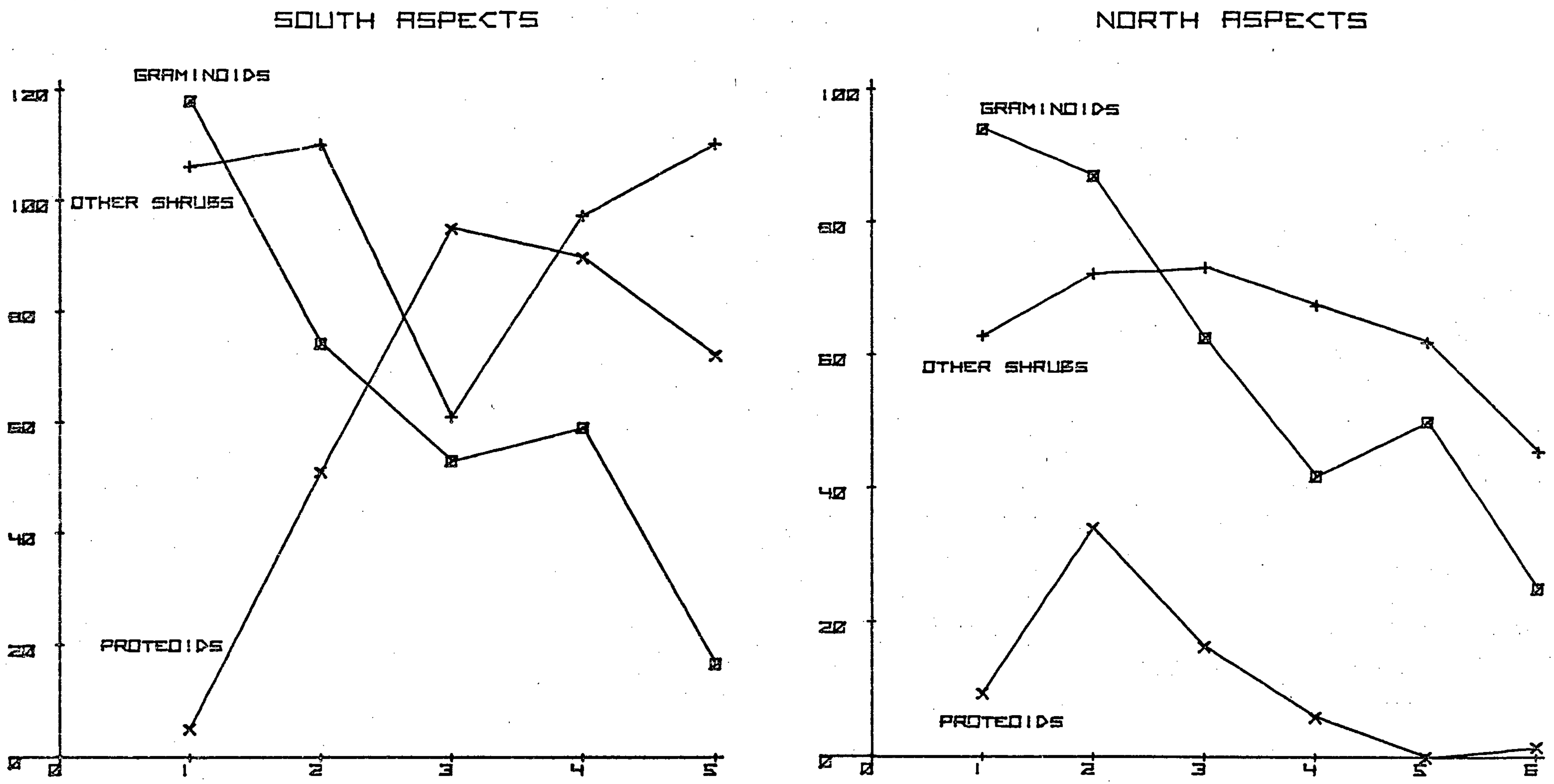


Fig. 7.19 Ratio non-proteoid shrubs/graminoids.



<u>Fig. 7.20a</u> Graminoid, proteoid (±deep-rooted), and other shrub (±shallow-rooted) cover along a moisture gradient (left-mesic, righ xeric), <u>Ruitersbos</u>. Mean cover values within five south and six north aspect D.I. classes are shown. S : 1 = 0-,06, 2 = ,06-,1, 3 = ,1-,15, 4 = ,15-,2, 5 = ,2+. N : 1 = 0-0,1, 2 = ,1-,2, 3 = ,2-,3, 4 = ,3-,4, 5 = ,4-,5, 6 = ,5+.

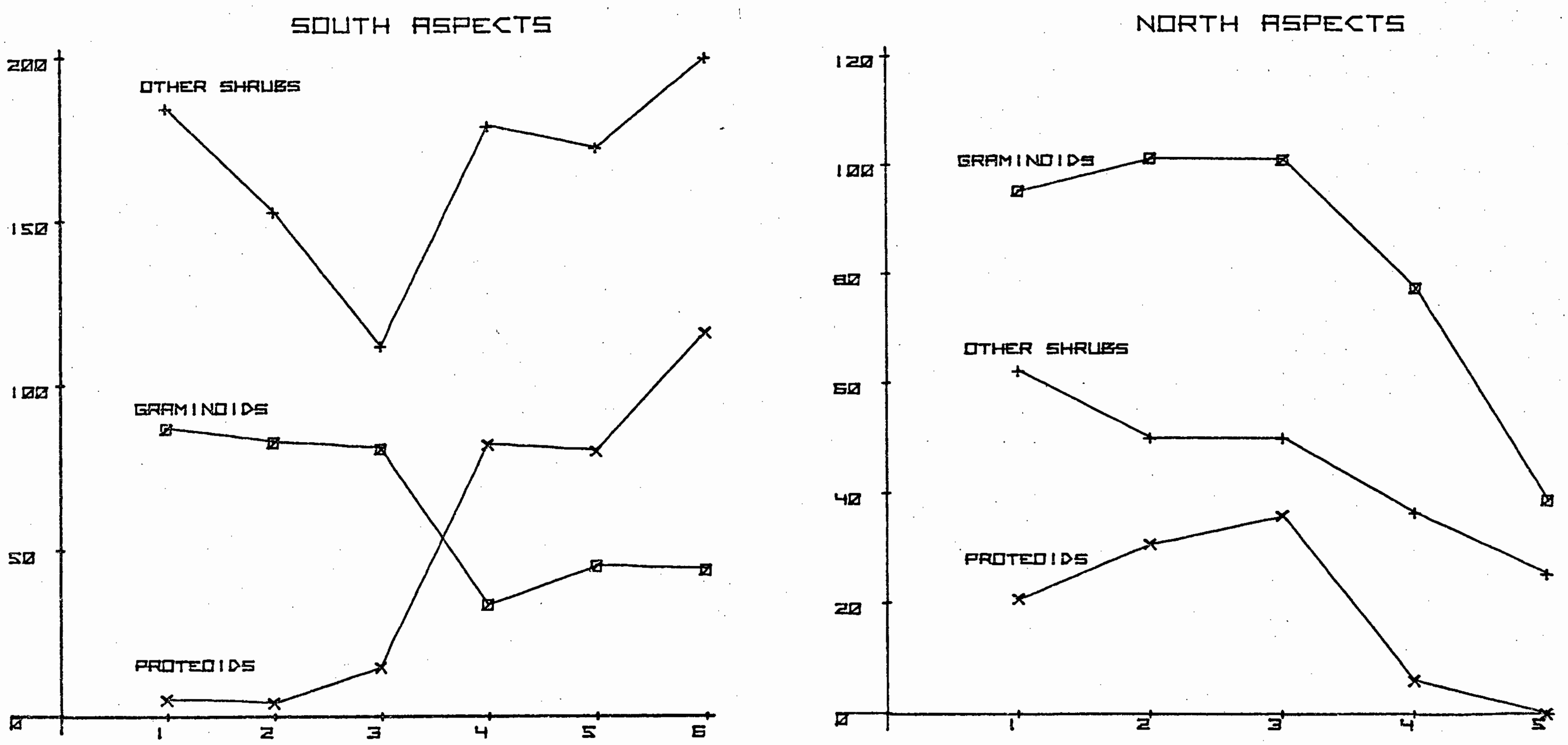
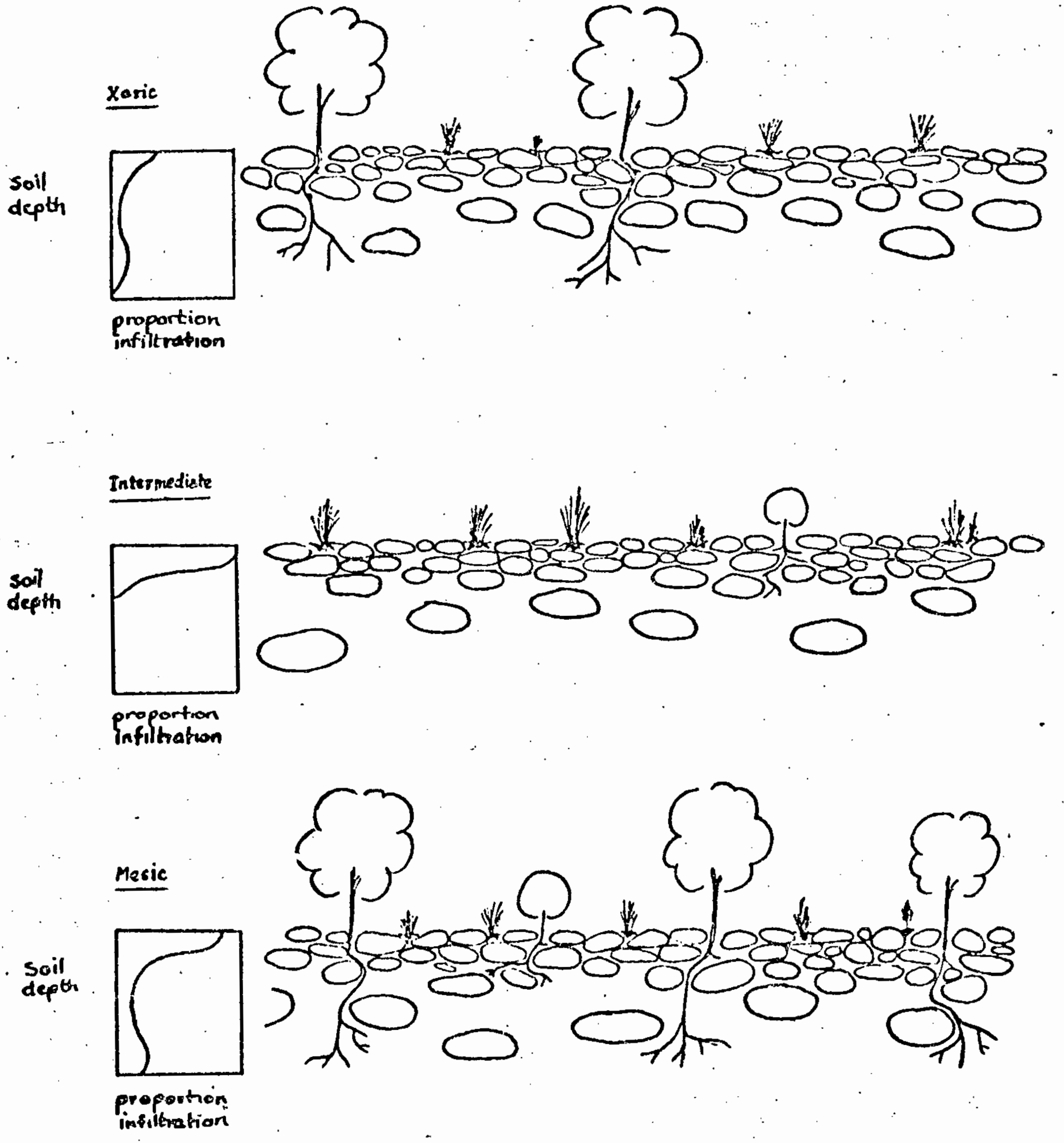


Fig. 7.20b Legend as for 7.20a, SWARTBERG. D.I. classes, S : 1 = ,1-,15, 2 = ,15-,2, 3 = ,2-,25, 4 = ,25-,3, 5 = ,3-,35, 6 = ,35+. N : 1 = ,2-,3, 2 = ,3-,4, 3 = ,4-,5, 4 = ,5-,6, 5 = ,6+. Succulent Karroid plots not included.

in the Swartberg (cf. van Wilgen 1980) (Fig. 7.20). In successional time, S.R. understorey shrub cover may also decline (Specht 1979, 1981).

Figure 7.21. Suggested distribution of D.R. shrubs, S.R. shrubs and graminoids on a moisture gradient on shallow, rocky soils.



Explanation of Fig. 7.21

1. Patterns at the xeric end of the gradient are similar to Fig. 7.18. Graminoid cover may be higher since precipitation is relatively more effective (a large part of the soil volume cannot store moisture) (Fig. 7.19).

2. Under slightly moister conditions, rocks and shallow soil depths favour shallow, intensive rooting systems and graminoids dominate (Fig. 7.22). (Restioid Shrublands of the Swartberg and Outeniquas).

3. At mesic extremes, moisture availability increases and there is sufficient excess for S.R. shrubs to co-exist with restios even in small soil pockets. Deep draining winter surpluses are utilised by D.R. shrubs, but cover is lower than stoneless soils since available rooting volume is less (Fig. 7.20). Cover will seldom be sufficiently closed to limit graminoids by shading (e.g. H3 at Ruitersbos).

7.3.5.3 Waterlogged Soils

On waterlogged soils, deep-rooted species have no advantage and shallow-rooted species predominate. Shallow-rooted species are favoured by greater aeration near the soil surface. All species can potentially grow throughout the year and a tall, deep-rooted overstorey is lacking (Mimetes is a notable exception though it is probably a shallow-rooted proteaceous genus). Consequently graminoid cover is relatively unaffected by shading and cover remains high (e.g. H1, H2, H3 of Ruitersbos). Anaerobic conditions often limit woody plants more than herbaceous species (Walter 1979) and, under extreme conditions, graminoids will probably dominate (cf. Western Cape restioid flats, Taylor 1978).

7.3.5.4 The distribution of structurally and floristically defined communities on altitude and moisture gradients is shown in Fig. 7.23 and 7.24). The units are well described by these two gradients alone, and by differentiating north and south aspects in the middle and upper ranges of the moisture gradient. This aspect division reflects soil rockiness.

Structural types of Chapter 6 are interpreted in terms of the model in Table 7.4, 7.5. It has proved generally useful in interpreting vegetation pattern in the Southern Cape and should also apply in the Western Cape. The absence of restioveld comparable to the north aspects of Southern Cape mountains, for example, can be interpreted as a consequence of geology. Lower slopes of most Western Cape mountains have relatively deep, talus soils of mixed sandstone/granite origin. The model would predict shrub dominated vegetation on these soils. Southern Cape mountains, in contrast, have extensive, shallow, sandstone soils bearing the expected restioveld.

The model would also predict low graminoid cover in the deep, stoneless soils of Australian heathlands!

Alternative Models

The "savannah" hypothesis is based on moisture considerations only. The available nutrient store also varies with soil depth and an alter-

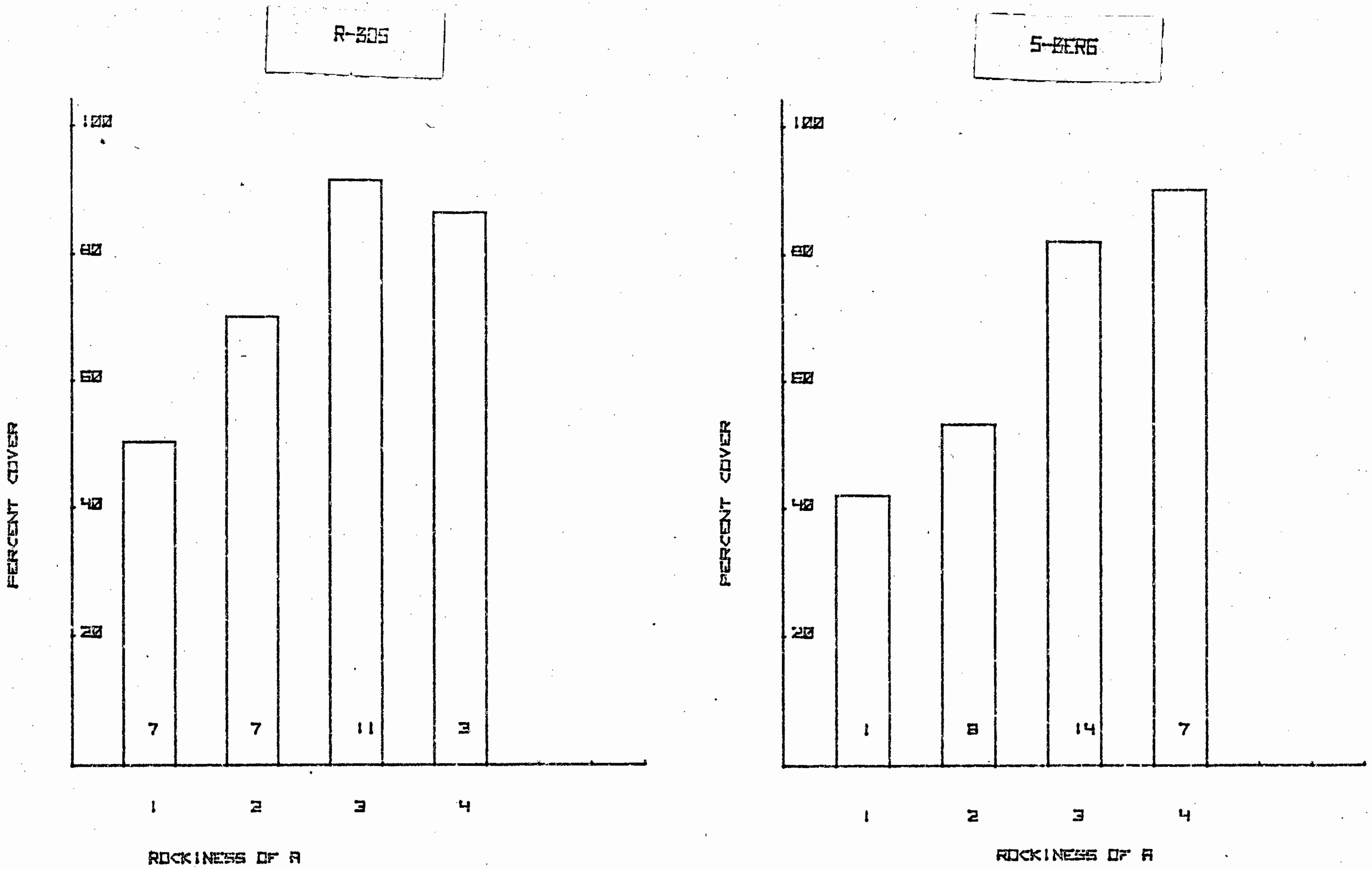


Fig. 7.22 Mean graminoid cover in relation to rockiness of the A horizon. 1 = No rocks, 2 = rare, 3 = frequent, 4 = abundant. Ruitersbos data for relevés in a D.I. range ,8-,21, Swartberg ,1-,4. Plot Numbers used to calculate mean shown in each bar.

native argument could be built on the basis that graminoids are less nutrient demanding than shrubs. A nutrient model, however, fails to explain increased shrub cover on shallow soils in mesic sites and wet peats both of which are poorer in nutrients than shallow stony restioid sites in more arid situations (Appendix 2).

The model is based largely on competition between mature plants. Regeneration strategies may be equally important, for example, the typical resprouting habit of graminoids in contrast to seed reproduction of many DR shrubs may be more significant than rooting depths.

The assumptions and predictions of the model are based largely on supposition and scanty data from Australia and the S.W. Cape. Rooting patterns and methods of measuring effective root depth require particular investigation. Nevertheless it provides a working hypothesis which can be readily tested by field observations and/or experiment.

6.4 CONCLUSIONS

This discussion has concentrated on only a few structural features and their response to montane gradients. Important omissions include flowering and shooting phenology, root systems, dispersal types, and more complete studies of leaf and shoot longevity. I believe the comparative approach to vegetation studies used here is of great utility both in hypothesis generation and testing. It is limited, however, by the covariance of many variables along gradients, for example base status and moisture regime, so that experimental studies are essential to confirm many hypotheses. Direct gradient analysis is analagous to regression techniques with controlled dependent and independent variables. It offers more rigorous tests of hypotheses than ad hoc explanations of a scatter of points on an ordination diagram and is less dependent on assumptions of species distributions (Austin 1980). Kessel 1979, has profitably used both approaches, extracting most variation by direct gradient analysis and then using ordination to generate new direct gradients for unexplained residual variation. His method seems to hold great promise, especially when a large data base (hundreds of relevés) is available.

Objective definition of environmental gradients is a serious problem in direct gradient analysis. The drought index used here provides a relatively explicit measure of climatic moisture, but is based on inaccurate isohyet maps and scanty weather records. More information on mountain climates, especially wind and, temperature variation and physical and chemical properties of mountain soils is essential for intelligent interpretation of fynbos patterns along montane gradients.

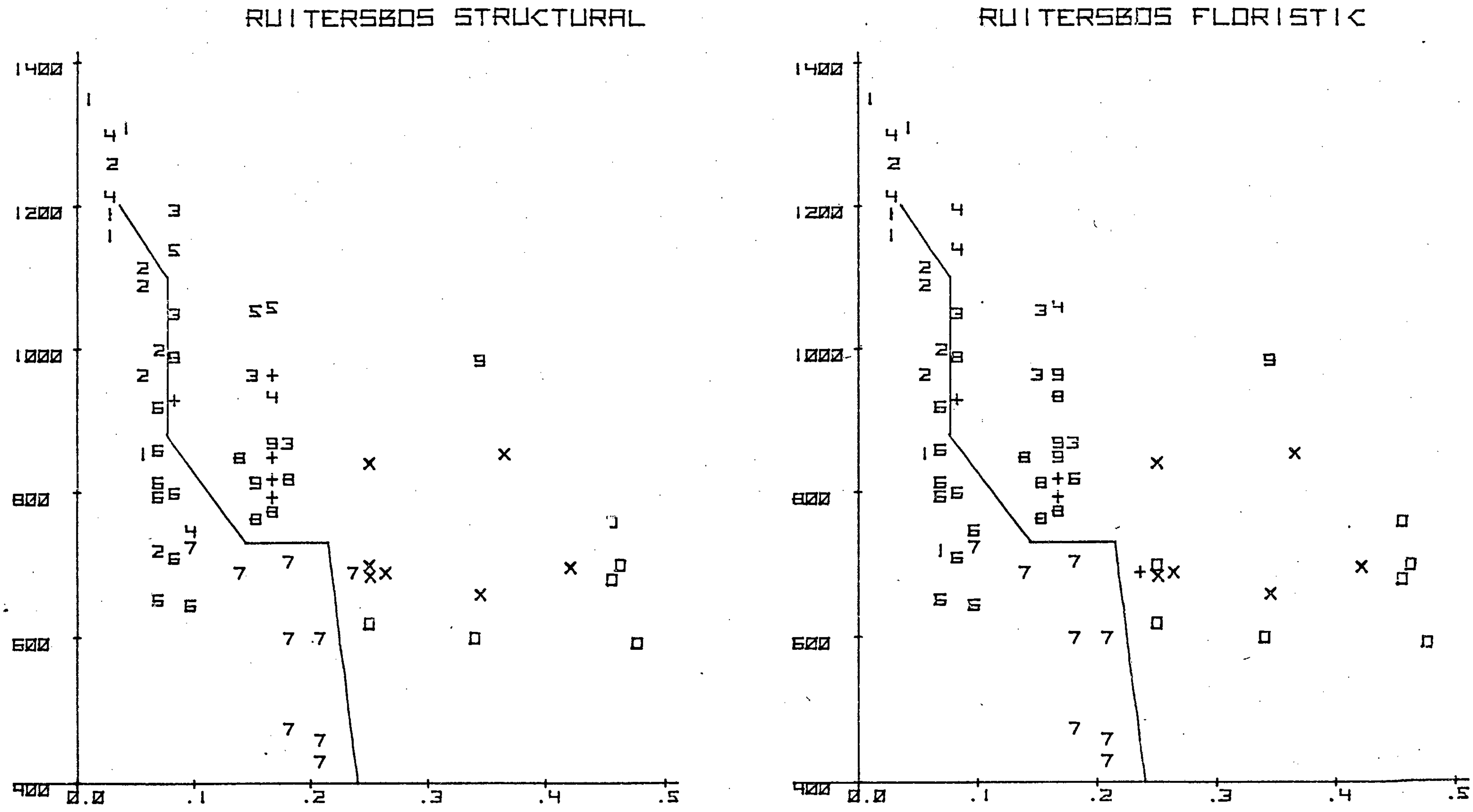


Fig. 7.23 Ruitersbos. Location of Structural and Floristic units on the altitude/moisture gradients. Similar structural and floristic units have been given the same code. Structural type (Ch.6) 1 = H1, 2 = H2, 3 = H3a, 4 = H3b, 5 = H3c, 6 = P1, 7 = P2, 8 = P3, 9 = R1a + = R1b , X = W1, ☐ = A1. Floristic types (Ch. 5) 1 = D1, 2 = D2, 3 = C4a, 4 = C4b, 6 = C3, 7 = C1, 8 = C2, 9 = B3, + = B2, X = B1, ☐ = A.

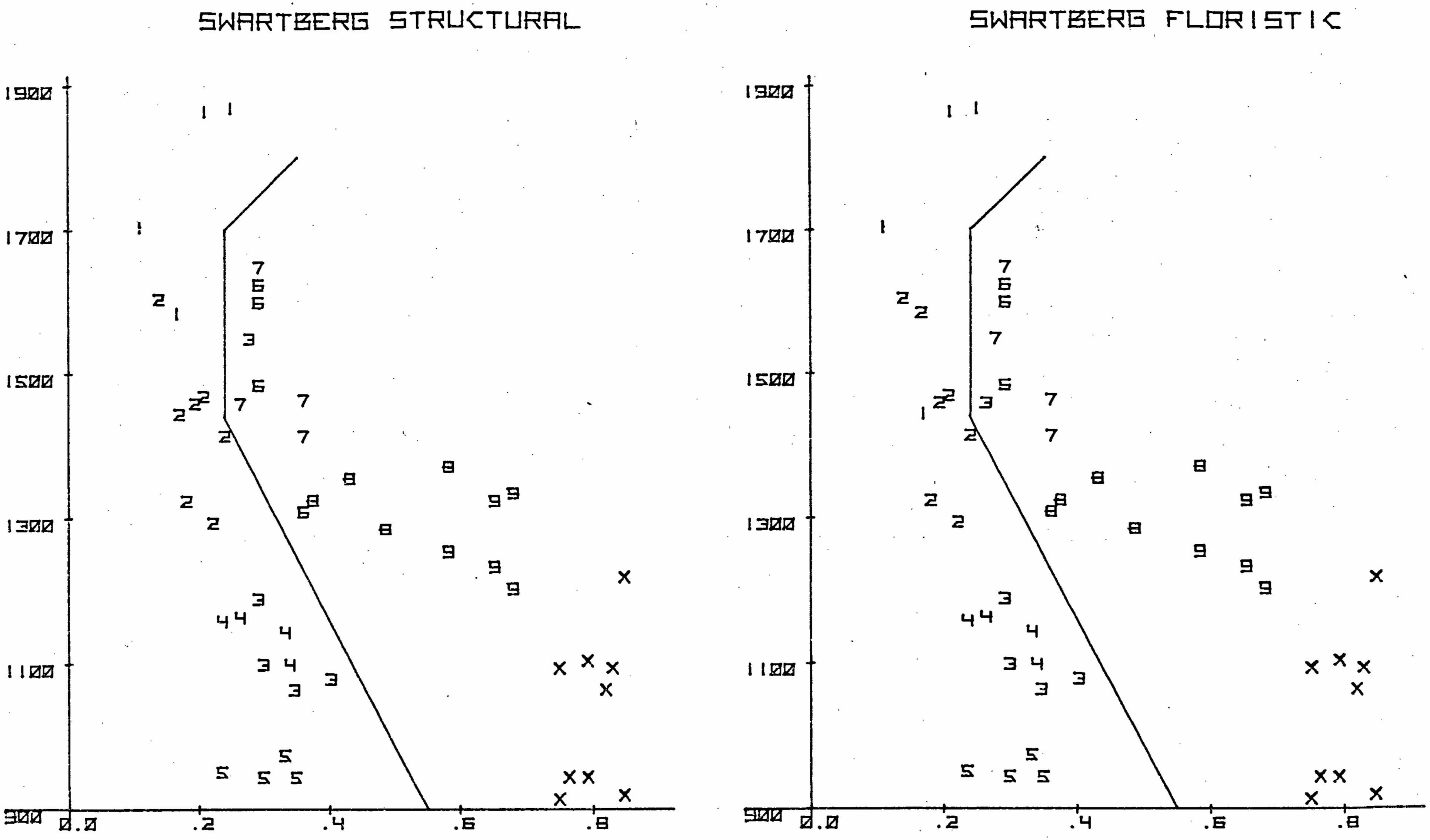


Fig. 7.24 SWARTBERG (See Fig. 7.23). Structural types (Ch.6) - 1 = H1S, 2 = H2S, 3 = P1Sa, 4 = P1Sb, 5 = P2S, 6 = R1Sa, 7 = R1Sb, 8 = R1Sc, 9 = A1S, X = K1. Floristic types (Ch.5) 1 = A1, 2 = A2, 3 = B1, 4 = B2, 5 = B3, 6 = C1a, 7 = C1b, 8 = C2, 9 = D1, X = E1.

CHAPTER 8

CONCLUSIONS

The study has achieved many of its aims. The work on climate confirmed the strong link between vegetation and available moisture. The latter was satisfactorily described by moisture balance equations incorporating slope and aspect effects on incident radiation. Patterns of moisture deficit over the year were synthesised into a drought index measuring the duration and intensity of periods when evapotranspiration exceeds moisture supply. The drought index successfully integrated local bioclimate and may have applications beyond the scope of the study.

Interrelationships of site variables were satisfactorily summarised by principal components analysis. The analysis exposed previously obscure patterns and was useful in developing a hypothetical framework for the interdependence of climate, geology, soils and vegetation. It also provided an environmental summary of variables covarying with altitudinal and moisture gradients used in the direct gradient analysis.

Structural and floristic classifications created very similar groups of relevés and thus provided clear evidence that non-floristic criteria are as effective in detecting small scale variation as species lists. For some purposes at least, structural classifications may free the untrained observer from the tyranny of taxonomy! Indicator species analysis, used in deriving the classifications, is a rapid and promising technique and particularly useful in providing indicator species and a Braun-Blanquet type table. The method grouped relevés well, but early dichotomies sometimes split similar groups and interposed a dissimilar group between them. Species ordering in the final table is not satisfactory and hand manipulation is still required. The results of the method seem better than agglomerative polythetic cluster techniques with which I am familiar, but the algorithms are more complex and the mathematics more difficult.

The scale of both the floristic and non-floristic classifications are too small for practical use in mountain catchment planning, but provide a quantitative base from which more extensive units can be derived. The study has already been beneficial in defining units for catchment planning in the Swartberg (Seydack and Horne 1981).

Direct gradient analysis is a powerful technique for testing and deriving hypotheses on vegetation structure and function. Testing hypothetical predictions against the altitudinal and moisture gradients used in this study provided a theoretical background for attributes used in the structural classification and showed that the approach has predictive value in terms of significant environmental gradients.

Future research should be directed at the technically difficult problem of the role of soil nutrients and water relations in structuring communities. Soil moisture regimes are particularly difficult to categorise in rocky mountain soils yet I have suggested they may be the major determinants of vegetation structure. Rooting patterns and their implications in community organization, leaf and shoot longevity, particularly of graminoids, and the adaptive significance of reproductive mechanisms have been little studied in fynbos but seem fruitful fields for further study.

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LABORATORY METHODS FOR SOIL ANALYSES

(a) pH Determination: pH measurements were made with a glass electrode in the supernatant liquid following agitation of the 2 mm fine earth with 1 N KCl or 0,01 M $CaCl_2$ in the ratio 1 : 2,5 and 1:5,0 respectively.

(b) Conductivity Determination: Electrical conductivity was measured of the saturated soil paste using a Bureau of Soils Cup, with values corrected to 16°C.

(c) Texture Determination: Soil texture was determined by the Bouyoucos particle size method and reported in classes according to the South African Soil Classification System (MacVicar et al. 1977).

(d) Organic Carbon/Matter Determination: Soil organic carbon was determined by the Walkley-Black method using a correction factor of 1,33 for recovery, and organic matter content was calculated by use of the Van Bemmelen factor.

(e) Exchangeable Cation Determination: The determination of exchangeable cations (K, Ca, Mg, Na, Mn, Zn) was made on a 1 N NH_4Cl extract of the 2 mm fine earth by atomic absorption spectrophotometry.

(f) Exchangeable Aluminium: Exchangeable aluminium is determined on a 1 N KCl extract by titration with NaOH and back titration with HCl following the addition of NaF.

(g) Available Phosphorus Determination: Available phosphorus is determined colorimetrically by the molybdenum blue procedure on a Bray No. 2 extract (0,03 N NH_4F + 0,1 N HCl @ 1:7,5 with 40 seconds shaking time).

(h) Total Phosphorus Determination: P determined after perchloric acid digestion.

APPENDIX. Selected Soil Analyses from Swartberg and Ruitersbos. pH was measured in KCl and $CaCl_2$ in Swartberg and in water in Ruitersbos samples. The horizon depth column includes an estimate of effective depth, defined as 80% large rock fragments. Percentage base saturation was calculated as Svalue ÷ Svalue + Exchangeable Acidity. Stones were estimated as 0 absent, r 5% by volume, f 5-20%, c 20-50%, ab 50%+.

No.	Hor.	Depth cm	Alt. m	Aspect		Particle Size					Cond.	pH		Nett extractable cations mg/kg					Svalue m.e./100g cl.	% Base Satu-ration	mg/kg					Bray 2 P	%C	Form	Series	Vegetation and Structure Symbol
						coarse	med.	fine	cl.	silt		KCl or H_2O	$CaCl_2$	K	Ca	Mg	Na	Svalue m.e./100g soil			Mn	Zn	Al.	Total N	Total P					
SW1	A1	0-20	ˈ940	S	f	19	30	51	18	12	,61	3,9	4,2	67	233	87	57	5,18	28,8		4		97	784	75	4	1,9	Glenrosa	Robmore	Proteoid Shrubland
	B21	30-40			f	18	23	59	22	22	,31	4,1	4,4	23	13	28	29	,48	2,2	22		0,7	92	504	98	5				P2
		50																												
SW2	A1	0-35	1150	S	f	8	47	45	18	10	,48	4,05	4,38	47	117	45	17	1,15	6,4	56,1	1	1,9	50	896	129	5	1,7	Hutton	Hutton	Proteoid Shrubland
	B2	35-80			c	16	54	30	18	6	,12																			P2
		80										4,32	4,6	16	18	9	15	,27	1,5	19,7		0,5	63	448	113	4				
SW3	A1	0-22	1220	S	r	13	46	41	20	10	,39	3,9	4,15	43	51	35	21	,74	3,7	18,8	3	1,7	182	1498	191	4		Oakleaf	Leeufontein	Proteoid Shrubland
	B2	35-80			f	16	48	36	8	12	,19	4,34	4,35	23	22	6	17	,29	3,65	20,9	0,5	2,0	63	1204	244	4				P1
		100+																												
SW4	A1	0-25	1600	SE	r	14	49	37	18	10	0,71	3,95	4,22	73	177	63	23	1,69	9,38	33,9	-	1,4	196	1428	138	19	2,3			Heathland
	B21	40-60			f	7	86	7	12	12	,17	3,32	4,52	26	31	9	16	,36	3,04	20,5	-	0,5	83	1176	218	9		Clovelly	Southwold	H2
		110+																												
SW5	A1	0-40	1550	N	f	16	42	42	18	10	,52	4,18	4,60	55	104	38	18	1,04	6,5	44,2	2	0,8	81	1092	119	15	1,9	Oakleaf	Leeufontein	Proteoid Shrubland P2
	B21	40-70			c	33	40	27	18	10	,26	4,32	4,6	36	44	14	16	,5	2,8	35,7	-	1,4	52	700	138	3				
		90+																												
SW6	A1	0-20	1460	N	r	32	56	12	14	8	0,68	3,55	3,95	94	199	81	23	2,0	14,3	40	5	1,4	176	1148	75	13	3,2	Mispah	Mispah	Proteoid/Restioid
		20																												Shrubland R1
SW7	A1	0- 8	1286	NNW	c	24	23	23	20	10	1,04	4,47	4,95	160	718	212	35	5,88	29,4	95	5	0,6	-	246	98	5	2,9	Glenrosa	Robmore	Restioid Shrubland/
	B21	8-60			ab	32	56	12	14	8	,44	4,5	5,0	71	150	107	28	1,93	13,8	95	-	0,7	-			1				Arid Fynbos A1
		10																												
SW9	A1	0-20	900	NNE	c	20	28	52	16	10	,81	4,45	4,88	90	758	102	20	4,94	30,9	98	27	0,7	-	630	169	11	2,3	Hutton	Portsmouth	Succulent Karroid
	B21	20-90			c	17	27	59	10	8	1,04	4,5	5,05	66	546	136	64	4,29	42,9	98	7	0,7	-	350	173	2				Shrubland K1
		90+																												
R^{x}12	A1	0-15	450	S	o	6	6	88	12	14		6,03	4,61	29	116	80	62	1,58	50	64	1		59	2352	56	6	3,6	Hutton	Mangano	Proteoid Shrubland/
	B21	15-60			o	7	7	86	5	20		6,52	4,98	158	7	129	56	1,73	34,6	88,7			13							non-ericaceous under-
		105																												storey P2
R^{x}2	A1	0-35	890	S	r	6	33	60	6	12	,68	4,4	4,14	19	33	69	39	0,95	15,8	24,6	T		[illegible]	1344	6	4	3,9	Houwhoek	Stormsrivier	Wet Heath H1
		35																											"Placaquod"	
R^{x}3	A1	0-35	800	S	r	3	37	60	17	7	,64	4,63	3,24	22	96	69	27	1,23	7,2	41,0	T		100	1302	6	5	3,1	Glenrosa	Williamson	Proteoid Shrubland/
	B21	35-50			c	5	23	21	9	10		4,88	3,42	13	26	24	16	0,43	4,8	19,6	-		104				1,2			ericaceous under-
		50-80																												storey P1
R^{x}4	A1	0-30	890	S	o	6	17	77	9	15	,57	5,15	3,68	22	47	50	61	0,97	10,8	23,6	T		221	756	19	5	1,8	Cartref	Cartref	Transition Proteoid
	A2	30-70			c	17	25	58	6	16		5,38	4,11	12	10	6	15	0,20	3,3	12,4			93				,2			Shrubland/Mesic Heath
		70+																												
R^{x}5	A1	0-20	1015	N	f	12	25	62	5	9	,93	4,62	3,39	36	143	93	31	1,7	34	51,8	1		86	1232	13	5	4,0	Cartref	Grovedale	Graminoid Heath with
	A2	20-70				23	25	52	3	7		5,86	3,92	10	3	6	9	0,13	4,3	35,1			12							Leucadendron
		±25																												uliginosum H3
R^{x}6	A1	0-25	830	N	r	5	21	74	8	8	,96	5,69	3,44	82	149	122	55	2,19	27,4	67,8	1		63	1036	25	5	3,0	Clovelly	Springfield	Proteoid Shrubland
	B21	25-60			f	28	19	53	10	14		6,06	4,71	28	13	32	25	0,5	5,0	48,5			32							P3
		100+																												
R^{x}10	A1	0-20	815	N	c	23	43	34	4	11		6,37	4,95	80	461	134	43	3,79	75,8	97,4	4		5	1064	13	4	1,8	Mispah/	Mispah/	Restioid Shrubland
	B21	20-25/80			ab	35	40	26	7	9		6,91	5,28	16	53	59	25	0,90	12,9	91,8			5					Glenrosa	Paardeberg	R1
		25																												
R^{x}7	A1	0-25	710	N	f	20	34	46	7	8	,64	6,17	4,69	40	303	134	35	2,86	40,9	92,9	2		12	868	31	4	1,7	Oakleaf	Mbanyana	Dry Shrubland/
	B21	25-50			c	35	19	46	3	4		6,35	4,74	22	90	154	55	2,02	67,3	81,1			25							Waboomveld W1
		120+																												
R^{x}8	A1	0-25	585	N	f	41	40	46	9	11	1,67	5,91	4,97	117	646	184	54	5,26	58,4	98,3	5		4	1190	38	6	1,5	Mispah	Mispah	Arid Fynbos
		25																												A1

APPENDIX 3

ENVIRONMENTAL FACTORS

1. Altitude (metres).
2. Slope, percentage.
3. Aspect E.W. (Sine of true north).
4. Aspect N.S. (Cosine of true north).
5. Radiation Index (Frank and Lee 1966).
6. Effective soil depth (Depth to stone/rockline) cms.
7. Depth of A horizon, cms.
8. Soil Colour, Hue of A horizon 5Y/R-1, 7,5Y/R-2, 10Y/R-3.
9. Soil Colour, Value of A horizon.
10. Soil Colour, Chroma of A horizon.
11. Texture of A horizon: sand-1; loamy sand 10% clay-2; loamy sand 10% clay-3; sandy loam-4; sandy clay loam-5; sandy clay-6.
12. Consistence: Soft-1; Very friable-2; friable-3; firm-4.
13. Structure: apedal-1; weak-2; moderate-3. All soils were found to be apedal and this variable was not used in analysis.
14. Stones in A horizon. None-1; rare-2; Frequent-3; Abundant-4.
15. pH in water.

16. Organic matter (%) by weight difference after drying at 105°C and combustion at 475°C for 8 hours.

17. Permeability of A. Very rapid-1; rapid-2; moderate-3; slow-4; very slow-5.

18. Geology. Peninsular-1; Chando-2; Kouga-3; Baviaanskloof-4; Cedarberg-5.

19. Isohyet (from Isohyet map) 1 400 mm; 2-400 to 500 mm; 4-600 to 700 mm; 5-700 to 800 mm; 6-800 to 900 mm; 7-900 to 1000 mm; 8-1000 mm to 1100 mm; 9-1100 to 1200 mm.

20. Distance perpendicular to a line drawn in an east west direction on the southern foothill. This is probably a better reflection of rainfall than an isohyet map in some instances.

21. Total Surface Rock Cover - percentage.

22. Surface Rock Cover of rocks less than or equal to 13 cms in diameter.

23. Surface Rock Cover of rocks from 25-50 cm in diameter.

24. Surface Rock Cover of rocks from 100-200 cm in diameter.

25. Surface Rock Cover of rocks greater than 200 cm in diameter including bedrock.

26. Bare Soil percentage.

27. Litter - percentage cover.

28. Estimated Total Vegetation Cover - percentage.

29. Sum of Cover of each species.

30. Ratio of Estimated Total Cover and Sum of species cover.

31. Wind Exposure. Very exposed-1; Exposed-2; Sheltered-3; Very sheltered-4.

32. Moisture Index. Very droughty-1; Droughty-2; Somewhat Drought-3; Moist-4; Seasonally Waterlogged-5; Waterlogged-6.

33. Erosion. No erosion visible-1; Minimal-2; Very slight-3; Perceptible-4; Distinct-5.

34. Veld age from node counts on Proteaceae plus three years. Succulent Karoo and arid fynbos where fires are unusual are uniformly rated 40 years.

35. Conductivity corrected to 15,8^{0}C.

36. Log. Water Drop Penetration Time (Richardson & Hoyle 1978). This is a measure of soil water repellency.

PHOTOGRAPHS

Photo: Wet heaths (H1-structural (S), D1-floristic (F)) on hard pan podsols, Ruitersbos, Outeniquas.

Photo: Graminoid heath (H3b-S, C4-F), Ruitersbos, Outeniquas.

Photo: Proteoid shrubland with heathy understorey (P1-S, C3-F), Ruitersbos, Outeniquas. Protea neriifolia and Leucadendron eucalyptifolium are prominent proteoid shrubs.

Photo: Proteoid shrubland with a shrubby, mostly non-ericaceous, understorey (P2-S, C1-F), Ruitersbos, Outeniquas. Protea aurea is the dominant proteoid shrub (?).

Photo: Proteoid shrublands transitional from heathy to non-ericaceous understorey (P1S-S, B1-F), Swartberg.

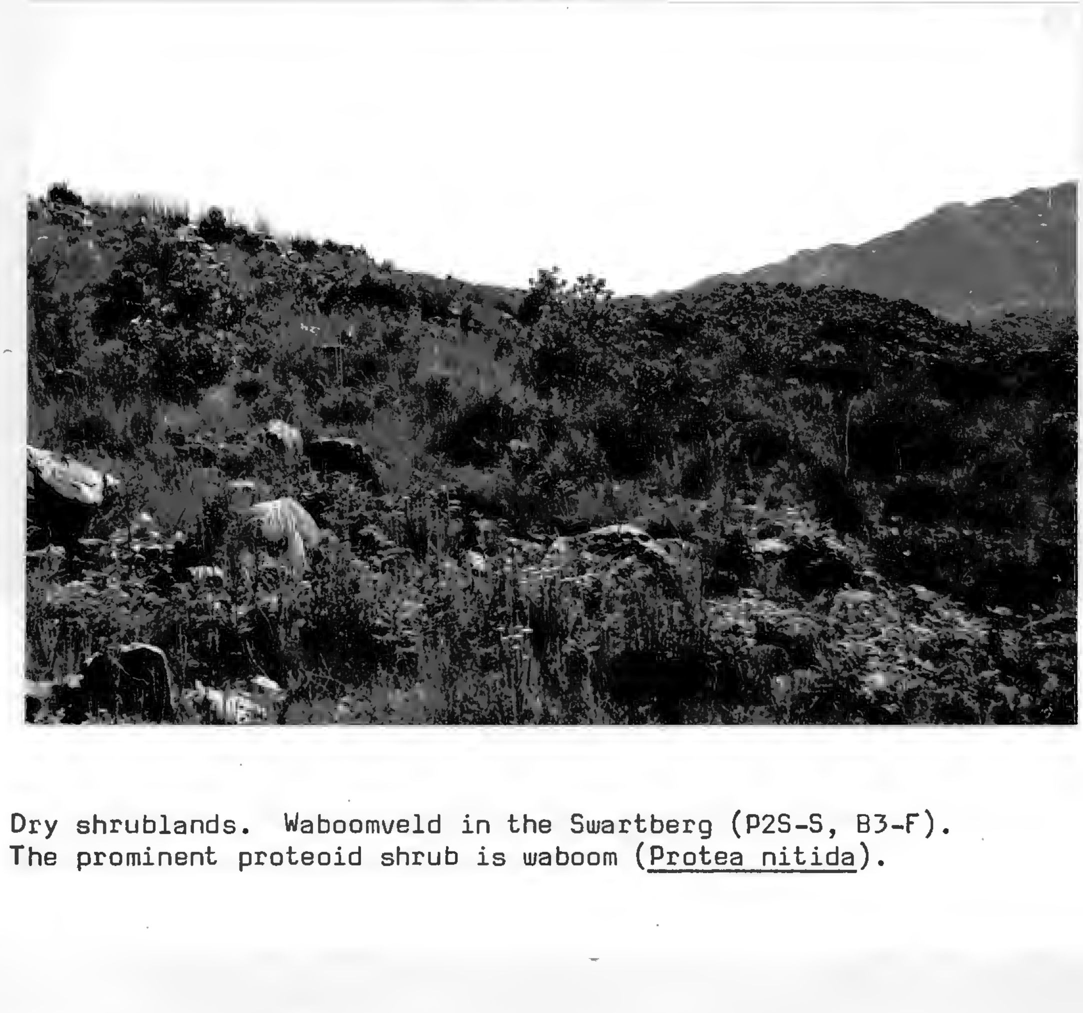

Photo: Dry shrublands. Waboomveld in the Swartberg (P2S-S, B3-F). The prominent proteoid shrub is waboom (Protea nitida).

Photo: Graminoid growth forms: coarse, unbranched restio with broad tussocks > 25 cm - Cannamois dregei.

Photo: Coarse, sclerophyllous grass with broad tussocks, 10-25 cm - Pentaschistis eriostoma.

Photo: Fine, "grassy" sedge with a broad tussock - Tetraria capillacea.

Photo: Medium restioid sedge with a narrow tussock (< 5 cm) - Tetraria cuspidata.