Bothalia 14, 2: 283–298 (1983)

Montane plant environments in the Fynbos Biome

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ABSTRACT

Environmental data collected at 507 plots on 22 transects, and soil analytical data from 81 of these plots, have been used to describe the plant environments of the mountains in the Fynbos Biome. Two major regional gradients are recognized: a west-east gradient and a coast-interior gradient. Of particular consequence for fynbos-environment studies is the increase in the proportion of fine soil particles from west to east. At least some aspects of soil fertility also increase towards the east. The edaphic changes are paralleled by climatic changes: chiefly a decrease in the severity of summer drought towards the east. On the coast-interior gradient a major non-climatic variable in the gradient is rock cover. High rock cover is a feature of the interior ranges. Soils with organic horizons or with E horizons are a feature on the coastal mountains, but are generally lacking on the interior mountains.

The other environmental gradients recognized occur on individual transects and all include edaphic variables. The rockiness-soil depth gradient, on which an increase in rockiness is associated with a decrease in soil depth and usually a decrease in clay content, tends to occur in three situations. Firstly, it is associated with local topographic variation; the shallow, rocky soils being a feature of the steeper slopes. Secondly, it is associated with the aspect gradient; the hot, dry northern aspects having shallow, rocky, less developed soils. Thirdly, it tends to be associated with the altitude-rainfall gradient; shallower soils being found at higher altitudes. It is also at higher altitudes that higher rainfall is found. Variation in oxidizable carbon is chiefly accounted for by the altitude-rainfall gradient. Whereas at a biome-wide level, aspects of soil fertility are related to soil texture, it appears that on individual transects fertility is linked to amounts of plant remains in the soil and to rainfall.

Apart from these gradients, which are found on the Table Mountain quartzites, other sources of environmental variation are due to the differences between geological types. The non-quartzitic soils are generally deeper and finer-textured. It is suggested that the nutrient-poor/nutrient-rich distinction must be used with care; at least in the mountains the distinction should not automatically be substituted for the quartzitic/non-quartzitic distinction.

INTRODUCTION

In this paper I describe the variation in plant environments that occur in the mountains within the Fynbos Biome. This work provides the setting for the ecological interpretation of vegetation structural-functional features and vegetation types and, as such, is part of the project aiming at a vegetation classification of the mountains of the Biome. The project and the vegetation-environment interactions are described elsewhere (Campbell, in press a, b, c).

In the present account I limit myself to presenting new environmental data, to unravelling the inter-relationships among environmental variables, and to identifying the major gradients; I do not attempt to review the already well-reviewed topic of fynbos environments (Lambrechts, 1979; Fuggle & Ashton, 1979; Kruger, 1979a). Fire and factors such as grazing are not dealt with here as the vegetation classification was limited to mature vegetation (cf. Campbell, in press a).

METHODS

The study area

The study area consists of all the mountains in the area delimited as the Cape Floristic Region (Goldblatt, 1978), the boundaries of which correspond roughly with the Fynbos Biome (Kruger, 1979b). Also included are the patches of fynbos mapped by Acocks (1953) that occur outside the Cape Floristic Region (Fig. 1). The vegetation of the study area is mostly Mountain Fynbos (*sensu* Taylor, 1978) but also includes forest, grassland and dry non-fynbos shrublands (e.g. Valley Bushveld, Succulent Mountain Scrub, Karroid Broken Veld — Acocks, 1953).

Data recorded

Environmental data have been collected from 507 plots located on 22 transects in the study area (Fig. 1). Each transect spans a mountain. Details of transect and plot location are in Campbell (in press, a, c.). Although plot selection was not random, I have used the plots to describe environmental variation in the study area, and have noted in the text the obvious biases (e.g. precipitous cliffs have not been sampled).

In each plot, 17 easily measured or estimated environmental variables were recorded. For each transect, 3 climatic variables were recorded using the data of Fuggle (1981) which come from climatic stations at or near the base of the transects. The environmental variables collected are summarized in Table 1.

In addition, soil samples were taken from 81 plots. The most detailed soil sampling was done on the Cedarberg transect (29 plots), so as to complement the data becoming available for other regions of the study area (Bond, 1981; Cowling, 1983; Kruger 1974, 1979a; Low, in prep.). The remaining soil samples were located throughout the study area. They have been especially used to check the field estimations of texture, and the field assignment of soils to soil types. The soil samples analysed here were collected from depths of 20–30 cm, except where soils were shallower. The variables assessed and the methods used in the soil analysis are shown in Table 2.

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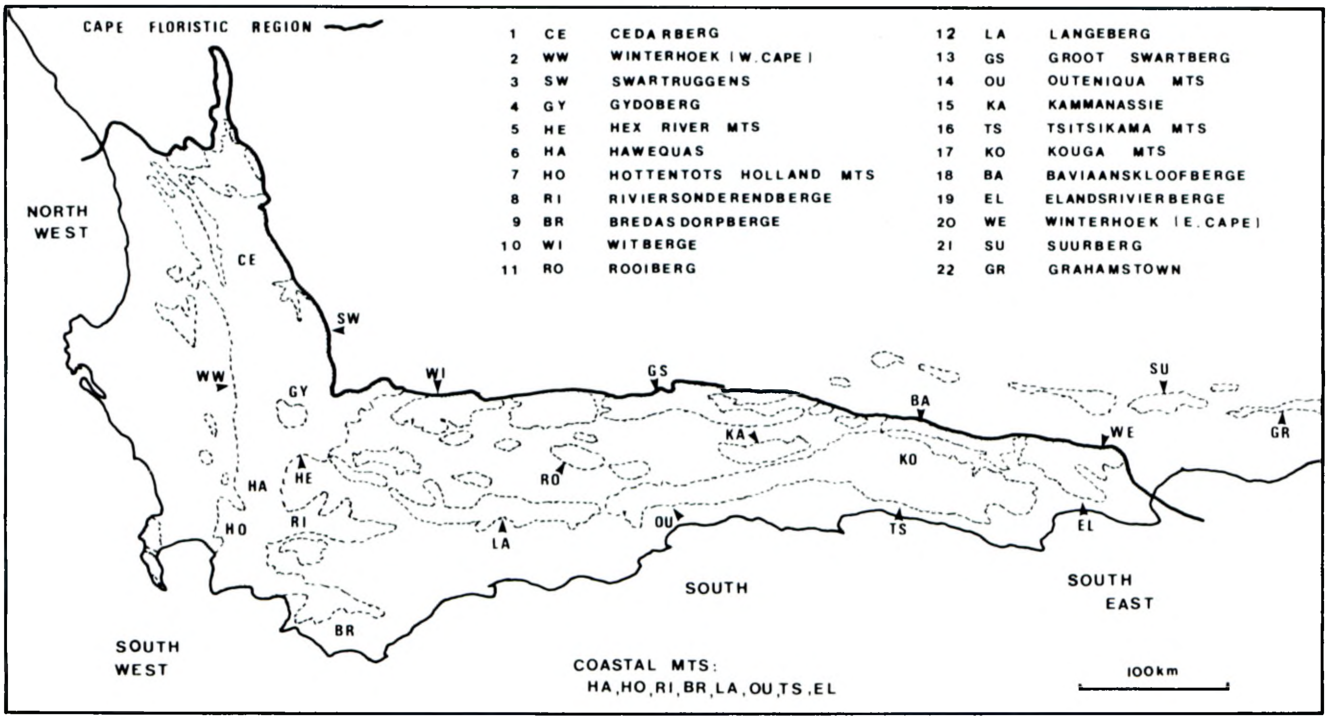

FIG. 1.—The study area and the study transects. Shading indicates fynbos of the mountains (after Acocks, 1953). Transect numbers and abbreviations are given, and the geographical regions referred to in the text are shown.

TABLE 1. — The environmental variables recorded. The abbrevations used in the text and the methods and/or classes used are shown

Abbreviation	Environmental variable recorded in each plot
ALT	ALTITUDE 1:50 000 topographic map.
RAI	ANNUAL RAINFALL 1:250 000 isohyet maps. These maps are not very accurate and many of the patterns represent cartographic interpolation (Fuggle, 1981).
GEO	GEOLOGY Geological maps of various scales.
ASP	ASPECT 1=NE 2=N; 3=E; 4=NW; 5=W; 6=SE; 7=S; 8=SW: a hot to cool gradient (c.f. Whittaker, 1960).
TER	TERRAIN MORPHOLOGICAL UNIT MacVicar *et al.,* 1977: 1=crest; 2=scarp; 3=middleslope; 4=footslope; 5=valley bottom.
TOP	TOPOGRAPHY/DRAINAGE UNIT 1=open slope; 2=protected canyon position; 3=seasonal standing water; 4=seasonal seepage on open slopes; 5=seasonal stream; 6=perennial stream.
SLO	SLOPE INCLINATION
CLA	% CLAY CONTENT Estimated clay content of A horizon (U.S. Dept of Agric., 1951).
TEX	SOIL TEXTURE Estimated soil texture of each horizon (U.S. Dept of Agric., 1951).
SOI	SOIL TYPE Macvicar *et al.*, 1977.
DEP	SOIL DEPTH
RO1..R05, ROT	ROCK COVER (%) BY ROCK SIZE CLASS RO1=rocks with less than 5 cm diameter; R02=5 −50 cm; R03=50−150 cm; R04=greater than 150 cm; R05=bedrock; ROT=total rock cover.
FOR EACH TRANSECT	
EVA	ANNUAL PAN EVAPORATION
TEM	TEMPERATURE RANGE Summer (3 months) mean daily temperature minus winter mean daily temperature (Fuggle, 1981).
WIN	% WINTER RAINFALL Percentage of rain that falls in the 3 winter months (Fuggle, 1981).
NUM	TRANSECT NUMBER Transects are numbered 1 to 22 from the north to the south east (Fig. 1).

Data analysis

To understand the relationships between environmental variables, I have mainly used correlation coefficients. Many relationships are discussed by reference to the correlation matrix of Table 4, which was calculated for the 354 plots of the open slopes (TOP=1)* of the Table Mountain Group. To answer the question whether relationships are similar on each transect, correlation matrices were calculated for each transect, and the correlation coefficients between specified variables were then combined to give a single assessment of the relationship (Table 5). For instance, correlation coefficients between altitude and rainfall for 19 transects are combined to give a single assessment of the trends on all transects. The method of combination is that of Fisher (1970). It combines the p-values corresponding to the correlation coefficients to give a single χ^2 value with d.f. = (n=19) × 2. Poorly sampled transects were excluded from this analysis (GR, BR, KO excluded; cf. Campbell, in press c; therefore n = 19 transects). I use 'combined χ^2' to differentiate the above from other χ^2 tests. The strengths of the relationships between variables as indicated by the above results are reported in the text by using the symbols of Tables 4 & 5 (e.g. +++ and ***). These symbols are given to test statistics with at least p<0,005, and throughout this paper one-sided p-values have been used when appropriate.

I have used principal components analysis (PCA) to summarize correlation matrices. The more easily interpreted rotated factors are reported here (varimax rotation; Morrison, 1976).

*Abbreviations of variables as in Table 1 and abbreviations of transects as in Fig. 1.

TABLE 2.—Soil variables assesed in 81 plots. The abbreviations used in the text and the methods used are shown

Abb.	Soil variable	Method
CL	Clay %	Pipette method (textural classes according to MacVicar *et al.*, 1977)
SI	Silt %	
FS	Fine Sand %	
MS	Medium Sand %	
CS	Coarse Sand %	
	Sodium (Exchangeable cations)	1N NH, acetate leachate
	Potassium (Exchangeable cations)	
	Calcium (Exchangeable cations)	
	Magnesium (Exchangeable cations)	
S	S value	Sum of exchangeable cations
N	Total Nitrogen	Kjeldahl
P	Available Phosphorus	Bray No. 2
C	Oxidisable Carbon	Walkley-Black method
pH	pH	1 N KCI 1:2,5 soln
	Colour	Munsell colour chart
	Stoniness	% by weight of stones > 2 mm

Although plot selection is non-random, I do use statistical methods to explore the data matrices and to describe the strengths of relationships between variables, if only as a labour-saving and page-saving device. The quoted statistical results from Table 4 & 5 would be considered very highly significant in a statistical study; here they must be seen as indicating possible degrees of relationships.

PHYSIOGRAPHY

Geology

The landscape of the Fynbos Biome is dominated by the mountains of the Cape Folded Belt, which consist mainly of hard quartzitic rocks belonging to the Table Mountain (T.M.) Group and Witteberg Group. Of the several mountain chains only the minor interior ranges are of the latter geological type (represented in the sample by transects GY, SW, WI, SU, GR–Fig. 1). Shales, phyllites, slates, conglomerates and granites are mostly restricted to the intermontane valleys (out of the study area) and lower mountain slopes; exceptions to this being the relatively numerous narrow bands of shale in the Witteberg Group and the single high-altitude shaleband (Cedarberg Formation) in the T. M. Group. Table 3 shows the relative abundance of the various geological types encountered in the present study (see Lambrechts, 1979, for a geological map of the Fynbos Biome, and further discussion).

Topographic analysis

Altitudes recorded in the present study (Fig. 2) indicate that average altitudes are generally higher in the interior ranges of the south and in the west (see also Table 4). Maximum altitudes are in the order of 2 000 m.

Slope inclinations recorded range from 0° to over 40° (Fig. 3.) Gentle slopes (≤4°) are significantly associated with transects of the north west (χ^2 = 30,1, d.f. = 16, P<0,025; CE, HE, SW, WW all contributing large values to the χ^2). It is in this

TABLE 3.—Geological types included in the sample. The distribution of plots among geological types gives an indication of the relative abundance of a geological type

Geology	No. of plots	Where sampled
Tertiary to Quaternary		
Alluvium	9	Valleys
Silcrete	4	Plateaux at base of lower slopes (east)
Uitenhage Group (Enon conglomerate)	7	Lower slopes (east
Karoo sequence (Dwyka shale)	2	Lower slopes
Witteberg Group		
Shale, siltstone	2	Interior mountain
Sandstone, quartzite	62	ranges
Bokkeveld Group		
Shale, siltstone	3	Lower slopes
Sandstone	2	
Table Mountain Group		
Quartzite	374	Coastal and interior mountain ranges
Shale	26	High-altitude shaleband
Malmesbury Supergroup (shale)	4	Lower slopes
Cape Granite	12	Lower slopes (west)

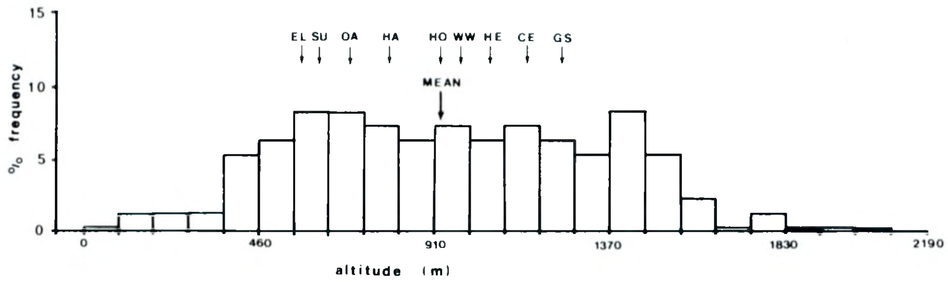

FIG. 2.—Frequency of altitude classes and mean altitude from various transects. For this frequency distribution and those to follow, n = 507 (except in cases of a few missing data values).

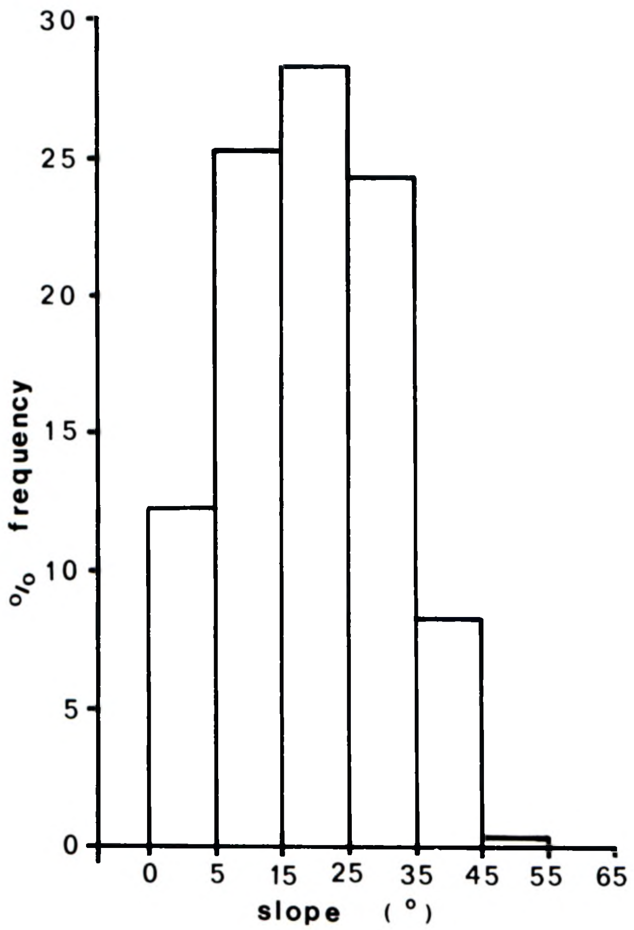

FIG. 3. —Frequency of slope inclination classes. A systematic sample of slope inclinations from 200 points in a small south-western catchment shows a very similar pattern (Kruger, 1974).

region that one gets extensive summit and subsummit plateaux; they are usually lacking elsewhere. The steepest slopes recorded (⩾ 35°) are associated with the more coastal, southern ranges (χ^2 = 23,8, d.f. = 16, p <0, 1; KO, TS, OU, KA all contributing large values to the χ^2). This last association is not the true situation, for my sample reflects vegetated slopes, and does not include precipitous cliffs. It is in the western zone that extremely steep cliffs are found, often with little or no vegetation (e.g. with 60−80% surface rock cover in areas; F. Ellis, pers. comm). Ellis (pers, comm.) records mean slopes of 30° to 42° in the Hex River Mountains whereas my mean slopes for the western area are 15° to 18°. The many steep slopes indicate the considerable relief of the study area. Differences in altitude of 1 000 m in distances of 3 km are not uncommon.

If there is any relationship between slope and altitude, and between slope and aspect, then it is very weak (combined χ^2 < 64,1 in both cases). The altitude/slope/aspect relationships are extremely complex owing to the broken landscape. The relationships are not monotonic on a single transect and they differ from transect to transect. For instance (1) in the west the steeper upper slopes are often broken by subsummit plateaux, and (2) some mountains have steeper south aspects (e.g. RI), whereas other have steeper north aspects (e.g. BA). The combined χ^2 values indicate a slight tendency towards steeper slopes at higher altitudes and on south aspects.

Rockiness

Total rock cover is exceedingly high in the study area (49% mean cover, Fig. 4a). Even if the smaller stones are excluded (< 5 cm diameter) the mean rock cover is high (37%). In the soil samples, stones of less than 5 cm diameter average 31% of a sample (by weight) (n = 52, range 0%−75%).

There is increasing rock cover from coastal to interior ranges (++). Mean rock cover per transect is lowest (40%) on coastal mountains, especially in the south and south east. Most rock is either small (<50 cm in diameter − R01, R02) or is bedrock (R05) (Fig. 4b). The cover or rock within a size class is strongly correlated with total rock cover (*** or **, +++) except in the case of large boulders (over 150 cm diameter − R04) where correlation is weaker (*, +). For each rock size class, rock cover is generally higher in the interior and/or in the west (+'s). High cover (>30%) of large boulders (R04) is more or less restricted to the west whereas high cover (>60%) of bedrock (R05) is a feature of the north west (χ^2 = 4,69, d.f. = 1,p <0, 025 and χ^2 = 22,3, d.f. = 13,p = <0, 05 respectively). Variation in cover of small rocks (R01, R02) tends to be more associated with the coast-interior gradient than the west-east gradient (Table 4).

The sampling is of course biased towards vegetated surfaces. The west-east gradient would be more pronounced if this bias was removed. Ellis (pers. comm.) records mean rock cover values of up to 80% in parts of the Hex River Mountains (though his figures are probably not directly comparable. His figures are based on estimates of large areas, whereas mine are estimates of 10 × 5 m plots).

The correlation coefficients for all plots indicate that total rock cover, bedrock (R05) cover, and

TABLE 4.—Correlation coefficients between the environmental variables collected in each plot. Only plots from open slopes (TOP = 1) and the Table Mountain Group have been included (n = 354 plots). Abbreviations of variables as in Table 1. The symbols indicate strengths of positive and negative correlations. As explained in the text, evaporation (EVA) and temperature range (TEM) decrease from west to east but especially from interior to coast, thus other variables correlated with TEM and EVA tend to show similar geographical patterns. If these other variables are strongly correlated with % winter rainfall (WIN) and transect number (NUM), then their geographical variation is essentially west to east; if uncorrelated with WIN and NUM then their variation is essentially interior to coast

	ALT	RAI	ASP	SLO	DEP	CLA	RO1	R02	R03	R04	R05	ROT	EVA	WIN	TEM
RAI	++														
ASP															
SLO	+														
DEP	-		+	--											
CLA	-	-	+												
R01					-										
R02			-	+	--		+								
R03	+			++	-	-	-	+							
R04									++						
R05	+		-	+	---	--	-								
ROT	+		--	++	---	--	+++	+++	+++	+	+++				
EVA	+++					--	+	+	+		+	+++			
WIN	+	+++				---		-		+	+		+		
TEM	+++					--	+	+			+	++	+++	+	
NUM	--	---				+++		+		-	-		--	---	-

- or + /r/ >0, 14 (p <0,005)
-- or ++ /r/ >0,25
--- or +++ /r/ >0,35

TABLE 5.—χ^2 values between selected environmental variables. The χ^2 value combines the correlation coefficients calculated for 19 transects and thus indicates whether the same trend tends to occur on all transects. The directions of the correlations are the same as in Table 4. In the text these χ^2 values are termed 'combined χ^2'

	ALT	ASP	SLO	DEP	ROT
RAI	***				
SLO	n	n			
DEP	*	*	**		
ROT	n	*	**	***	
RO1	n	n	n	*	**
RO2	n	*	*	**	***
RO3	n	n	**	*	**
RO4	n	n	n	n	*
RO5	*	n	*	***	***
CLA	*	*	n	*	*

n $\chi^2 < 64,1$
* $\chi^2 > 64,1$ (p <0,005)
** $\chi^2 > 100$
*** $\chi^2 > 150$

cover of R03 increase with altitude (+'s), but this reflects the association of rock cover and altitude with continentality rather than a rock cover-altitude relationship within individual transects. On transects it is only bedrock which appears to increase with altitude (*). Steeper slopes have higher rock cover (++,**) and more northerly aspects tend to have higher rock cover : (-,*). Ellis (pers. comm.) reports values of 60–80% cover on north aspects in the Hex River Mountains and 40–60% on the south aspects. Bond (1981) working in the Swartberg and Outeniqua Mountains also records north aspects as being rockier.

CLIMATE

Climatic variation in the Fynbos Biome has been recently reviewed by Kruger (1979a), Fuggle (1981) and Fuggle & Ashton (1979). I have not collected original data and I limit myself to summarizing these reviews in a gradient framework. The dissected topography of the biome makes for complex climate patterns. However, the variability can be summarized by reference to 4 gradients: west-east gradient; coast-interior gradient; altitude gradient and gradient from south to north aspects.

The west to east gradient shows the following trends: (1) a marked summer gradient in receipt of solar radiation (30 to 25 MJ m^{-2} day^{-1} from west to east); (2) greater seasonal temperature ranges in the west; (3) higher annual pan evaporation in the west (1800–2000 mm vs 1300–1700 mm) with greater amounts being evaporated during summer in the west (40% vs 35% in the summer 3 months); (4) a pronounced winter rainfall régime in the west (80% vs 35% rain in the winter 3 months) and (5) higher annual rainfall in the west (over 2500 mm on the high peaks of the south west). The climates of the lower mountain slopes of the west are generally mediterranean (Cs — Köppen system) while those of the east are 'steppe' climates (Bsk) or warm temperate all-year rainfall (Cfb) (Fig. 5). Although it is the west which has marked summer droughts, even the Cfb climate has the dry season in summer as it is then that moisture deficits occur (Bond 1980a, 1981). The west-east gradient is not strictly monotonic with respect to a summer moisture deficit, for it is the southern coastal mountains which have the least moisture deficits, with greater deficits to the west and, to a lesser extent, to the east (e.g. Specht & Moll, 1982).

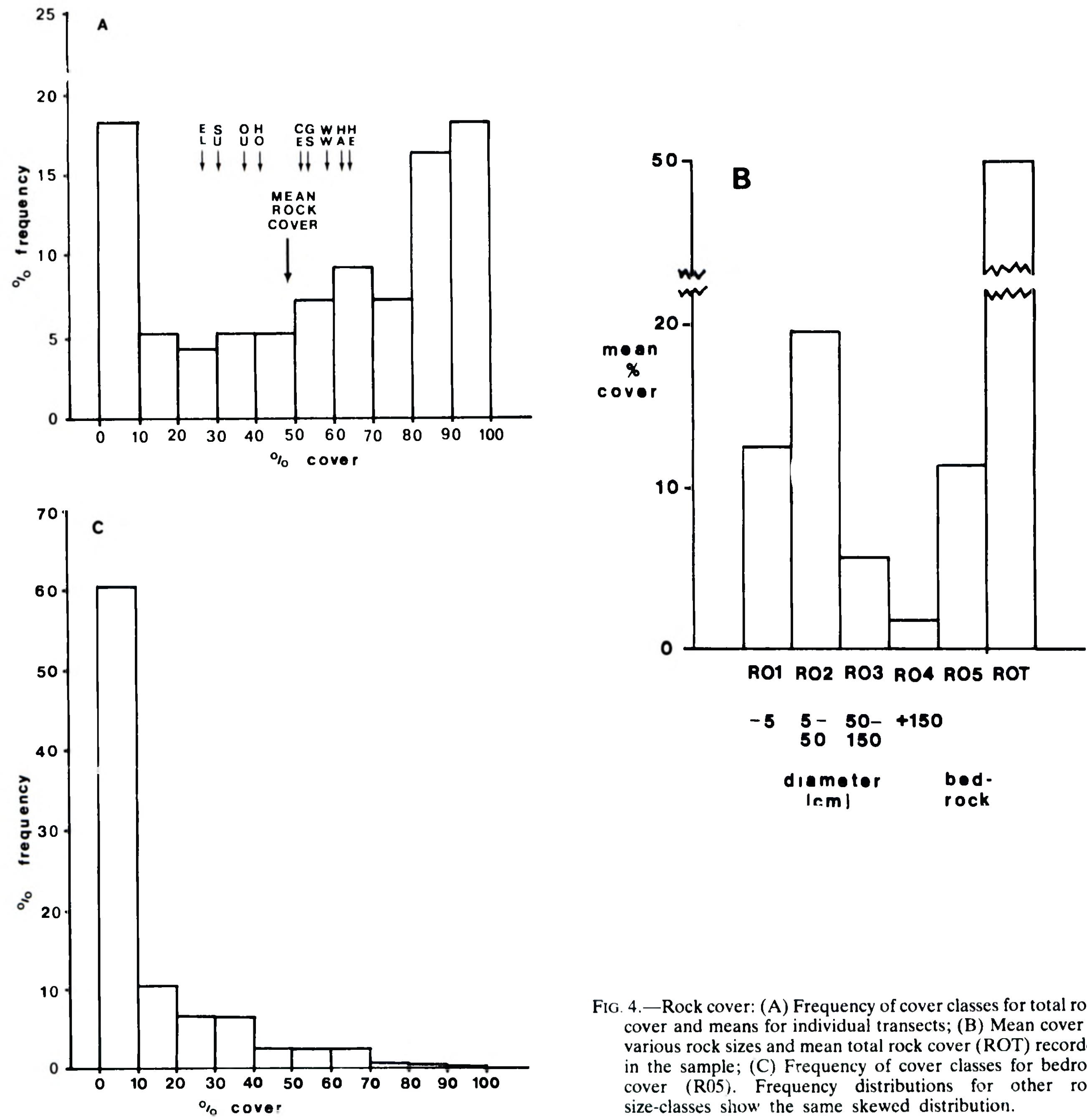

FIG. 4.—Rock cover: (A) Frequency of cover classes for total rock cover and means for individual transects; (B) Mean cover of various rock sizes and mean total rock cover (ROT) recorded in the sample; (C) Frequency of cover classes for bedrock cover (R05). Frequency distributions for other rock size-classes show the same skewed distribution.

Along the coast to interior gradient the following trends can be recognized. On the lower slopes of the coastal mountains there are lower annual temperatures (15°–16°C vs 17°–18°C), smaller seasonal and daily temperature ranges, greater cloudiness, lower pan evaporation (1800 mm vs 2000 mm in the west, 1400 mm vs 2000 mm in the south, and 1300 mm vs 1700 mm in the south-east), and higher rainfall. Considerable summer mists do much to alleviate the summer drought on the high peaks of the coast (e.g. Nagel, 1962). The peaks of the south and south-east coastal ranges, generally lower in altitude, are less prone to snowfall than those of other regions (Bond, 1981; 5,4 snowfalls per annum on average in the study area — Schultz & McGee, 1978). The lowland climates in the west change from cool mediterranean (Csb) at the coast to warm mediterranean (Csa) and eventually in the most interior areas, to 'steppe' and desert climates (Bsk, Bsh). A similar sequence is the rule in the east except that the mediterranean types are not found; they are replaced in the sequence by the all-year rainfall type (Cfb) (Fig. 5).

The altitude gradient tends to have the following characteristics. With increasing altitude, mean annual temperatures decrease (15°–16° to 12°–13° in the south-west), pan evaporation decreases (1800 mm to 1310 mm in the south-west; Kruger, 1974), rainfall increases (from often less than 400 mm to over 1000 mm in the south and to over 2500 mm in the south-west), precipitation from mist increases especially on the coastal ranges, and the likelihood of snow increases. In the south-west there is a change from a Csb climate in the lowlands to a climate which tends to lack a summer drought (Cfb) on the upper peaks (Kruger, 1974; Boucher, 1978). In the more interior ranges, there is a change from a 'steppe' or desert climate in the lowlands to a Cs climate on the upper peaks (Fig. 5).

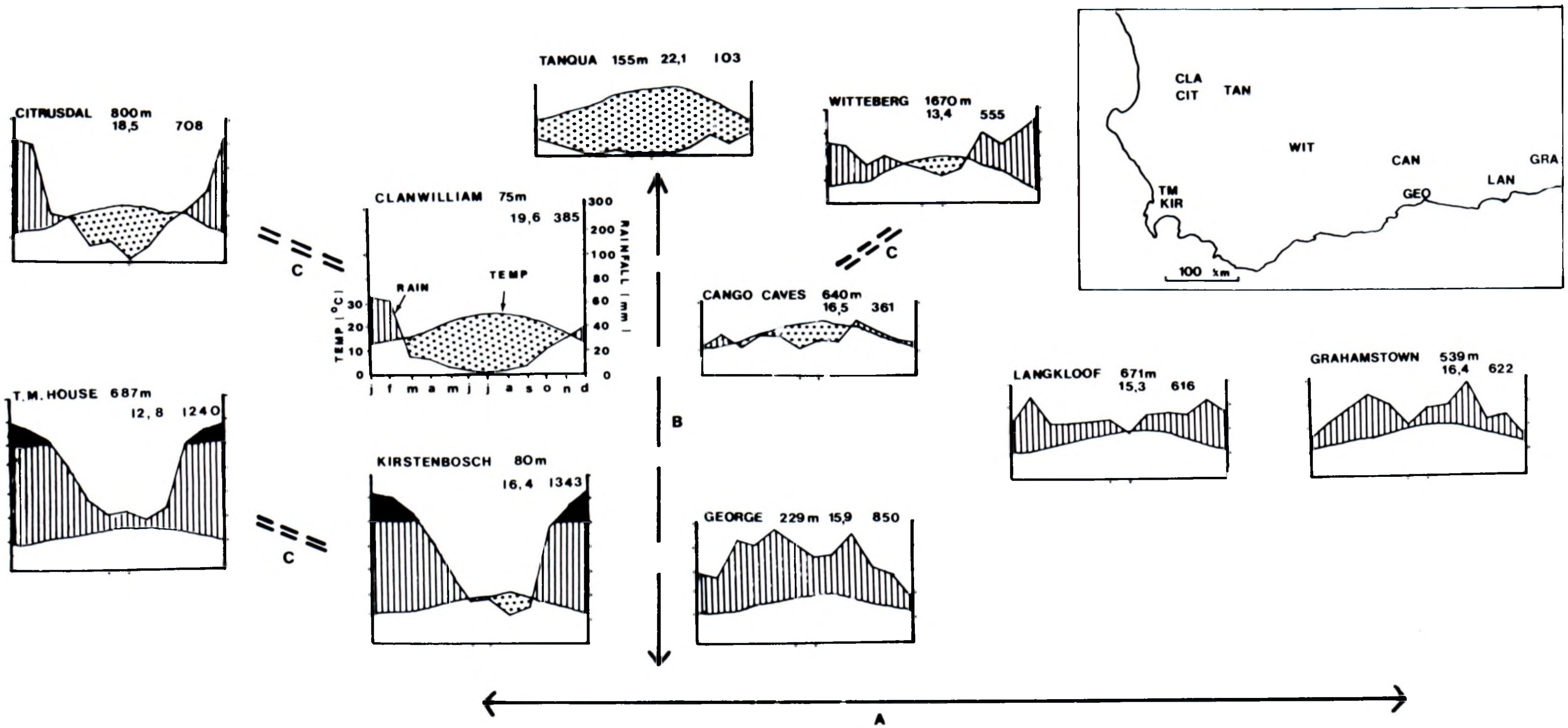

FIG. 5.—Walter-Lieth diagrams for contrasting stations near or in the study area. A, west to east; B, coast to interior; C, low to high altitude. On each climatic diagram the altitude (m) of the climatic station, the mean annual temperature (°C) and the mean annual rainfall (mm) are indicated. The axes are illustrated on the Clanwilliam diagram. The inset indicates the geographical position of climatic stations.

Finally, the fourth gradient is the aspect gradient. There are pronounced differences in receipt of solar radiation between north and south aspects especially in winter. For instance, north aspects of 20° slope receive 4 to 5 times as much energy as the equivalent south aspects during mid-winter. This figure is relevant to the present work, as the average slope recorded is 18°. At least in the southern area, the slopes north of the watershed (generally north aspects) receive less rainfall and less orographic cloud than the slopes south of the watershed (generally south aspects) (Bond 1980b, 1981). Taylor & Van der Meulen (1981) quote 1 year's data showing 50% lower rainfall on the north side of the Rooiberg than on the south side.

In my data set, I have included the following climatic variables: percentage winter rainfall (WIN), pan evaporation (EVA), seasonal range in temperature (TEM) and rainfall (RAI). Transect number (NUM), running from west to east and WIN are strongly correlated (- - -) and are surrogates for the west-east complex gradient. EVA and TEM are strongly correlated (+++) and are surrogates for the continentality gradient. However, they are also correlated to a lesser extent with WIN and NUM (Table 4), and thus the west-east and continentality gradients are not entirely independant. RAI and altitude represent the altitude complex gradient and are highly correlated on individual transects (***). Of the 4 transects which show the weakest altitude-rainfall correlation, 2 were poorly sampled (WI, SU) and 2 were from the southern coastal mountains (OU, TS). In this latter area, there is a strong gradient of rainfall from the coastal slopes to the interior slopes, and therefore the altitude-rainfall relationship is weaker. Altitude and rainfall are also correlated with the regional climatic gradients; higher altitudes tending to be associated with the interior ranges (correlated with EVA and TEM) and higher rainfall being found in the south west (correlated with WIN and NUM—Table 4).

SOILS

Soil depth

Soils in the study area are shallow, a mean depth of 0,5 m being recorded. Only 17% of the recorded depths are over 1 m (Fig. 8) and these are significantly associated with certain geological types especially granite and alluvium and perhaps Malmesbury shales and silcrete (χ^2 = 54,1, d.f. = 10 p<0, 001). Soil depth is highly negatively correlated with total rock cover (- - -,***) and cover of various rock sizes (Tables 4, 5). It therefore shows relationships similar to those shown by rock cover; the shallower (and more rocky) soils being found on steep slopes (- -,**), on the more northerly aspects (+,*) and at higher altitudes (-,*).

Soil texture

In the T. M. Group the strongest relationship shown by percentage clay is the increase in clay content from west to east (+++). The other relationships shown by clay are a decrease in clay content on very rocky sites (++,*), on more northerly slopes (+, *), in shallower soils (*), and with increasing altitude (-,*). The relationships between clay, and aspect and altitude also have support from the soil analytical results from the Cedarberg transect. Of the 29 plots, only 5 had textures finer than loamy sand. Two of these were from the T.M. shaleband, whereas the other three were from low altitudes at the base of the southerly slopes. Bond (1981) also provides support for the occurrence of finer textures on south-facing slopes. He records loamy sands and sandy loams on the north aspects of the Outeniquas and sandy loams and sandy clay loams on the south aspects.

The above correlation analysis showing an east-west gradient in clay content comes from the estimations of clay content in each plot. These results are confirmed by the soil analyses, but the soil analyses also show that other fine-grained soil particles (silt and fine sand) increase towards the east (Table 7). Throughout the western zone, the T.M. quartzites mostly give rise to medium (and some coarse) sands and loamy sands (e.g. means of 5,1% clay, 5,2% silt and 30,5% fine sand; CE, n= 29). In the south east one still finds sands, but textures are mostly fine sandy loams and medium sandy loams (e.g. 9,0% clay, 13,1% silt, 47,8% fine sand; BA, WE & EL, n = 9). On the Witteberg quartzites a similar gradient is apparent. In the west (SW, GY), there are coarse-textured soils, mostly medium sands and medium loamy sands, whereas in the east (SU, GR) the textures are mostly fine sandy loams (e.g. 4,6% clay, 4,6% silt, 49,0% fine sand in the west, n = 4; and 11,1% clay, 15,2% silt, and 54,2% fine sand in the east, n = 8). In general, the Witteberg quartzites appear to be finer textured than the T.M. quartzites, at least from the Witteberg Mountains eastwards.

The soils recorded with the finest texture (sandy clay loams, clay loams, loams, silt loams; in 40 of the 507 plots) are mostly associated with two distinct environmental situations (χ^2 = 136, d.f. = 2, p <0, 001). Sandy clay loams and clay loams are usually found associated with the organic soils of the south-facing slopes of the coastal ranges. The upper shaleband of the T.M. Group usually has sandy clay loams but its texture is very dependant on the amount of quarzitic colluvium present. For example, in the Cedarberg, the two shaleband plots had soils with a higher clay and silt content than other plots on the transect but were nevertheless only medium sandy loams (as opposed to medium loamy sands on the quartzites). The Tchando Formation of the T.M. quartzites appears to sometimes give rise to soils with a texture finer than that of the soils derived from the other quartzitic formations. However, the χ^2 was not significant probably due to insufficient data (the Tchando formation was the recognized quartzite in 19 plots). Fine-textured soils (e.g. sandy clay loams) are also a feature of the Witteberg and T.M. quartzites of the south-east (e.g. BA, WE, GR transects).

Soil types

The only major published works on soil types in the mountains of the Fynbos Biome are those of Lambrechts (1979, and in Boucher, 1978) and

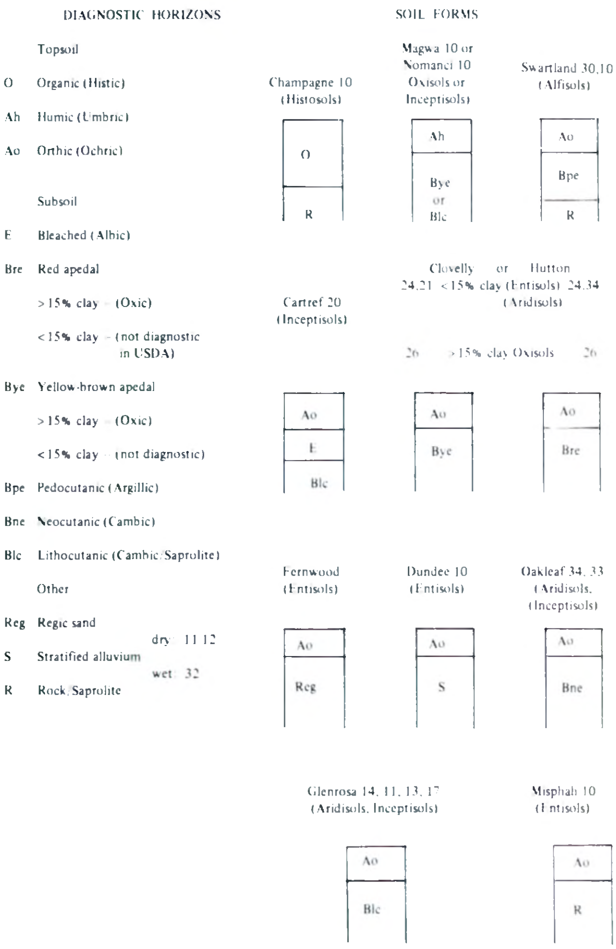

FIG. 6.—The principal soil forms recorded in the study, and their defining characteristics. The South African soil classification system subdivides soils into soil forms on the basis of defined diagnostic soil horizons. Each form is subdivided into series according to texture, base status etc. Approximate U.S. Dept. of Agriculture (1960) equivalents are given in brackets. Some of the major soil series recorded are indicated by their soil series numbers.

Kruger (1979a). In the account below, I discuss the distribution of types identified in the sample of 507 plots. The classification system used (MacVicar *et al.*, 1977) and the diagnostic features of the soil forms identified are shown in Fig. 6. Many plots would probably have been assigned to a rocky-land class by a pedologist, rather than to a soil type, but this does result in an information loss, for plants undoubtedly grow in rocky soils, and classifying soils as incipient Mispahs or Cartrefs does provide some information about different edaphic conditions. I have therefore been generous in assigning very rocky soils to soil types.

The most common forms present (Fig. 7) are Mispah, Glenrosa and Cartref (31%, 18% and 9% occurrence respectively). These three forms are all litholic in the study area, and make up the bulk of the shallower soils (<0, 4 m) that were recorded (Fig. 8). The Cartref form, represented by the series with low clay contents, is especially a feature of the coastal ranges, from the south west (HA, HE, HO) to the extreme east (EL) and is usually found at the higher altitudes. Associated with Cartref, either on the better drained steeper sites, or at lower altitudes on the north aspects, are soils of the Mispah and Glenrosa form. These latter forms are also the dominant forms on the interior ranges including those of Witteberg quartzite.

In the Glenrosa Form it is the coarse-textured series that are the rule in the West (e.g. Oribi Gsll), whereas in the east it is the more medium-textured series that are found (e.g. Kanonkop Gs13, Platt Gs14 and Trevanian Gs17). On the Witteberg quartzites of the south-east (SU and GR) the Mispah form is uncommon and better developed soils are found (e.g. Glenrosa, Oakleaf, Nomanci, the last being a typical mist belt and grassland soil). On three of the ranges comprised of Witteberg quartzite (GR, SU, WI) even the heavy-textured Swartland

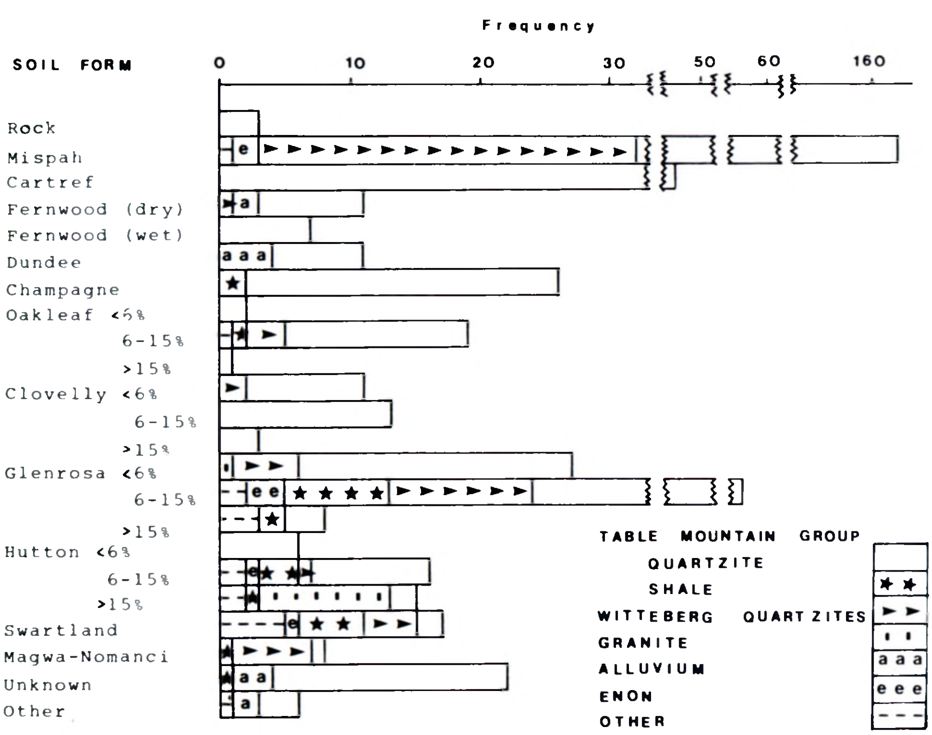

FIG. 7.—Frequency of soil forms and their relationship to geology. Percentages refer to percentage clay content and are the limits recognized in the soil classification system.

form was identified. Its occurrence is probably due to the presence of minor shalebands in the quartzites. Of the Mispah, Glenrosa and Cartref forms, it is only the Glenrosa which occurs to any degree on the non-quartzite geological formations in the study area.

After these three types, the next most common soil forms of the open slopes (TOP = 1) of the quartzites are the relatively deep Clovelly, Hutton and Oakleaf Forms (Figs 7 & 8). These forms are generally found on the lower slopes, on more southerly aspects and on gentler slopes. In the west they are more a feature of the interior ranges. If on north slopes, they are usually restricted to talus slopes, colluvial fans or pediments. The Clovelly Form with its yellow-brown apedal B horizon is more common in the north-west (e.g. Cedarberg), whereas the Hutton Form with its red apedal B horizon is more common in the south (e.g. the deep Hutton's on the south facing-slopes of the southern coastal mountains). However, the red apedal/yellow-brown apedal distinction is not easily correlated with distinct environmental situations (MacVicar *et al.,* 1977, discuss the supposed distinctions). The Hutton and Clovelly Forms are represented mostly by the coarse- and medium-textured mesotrophic series (e.g. Sonneblom Cv21, Springfield Cv24, Clansthal Hu24). The Oakleaf Form is apparently a feature of the south and south-east. However, it is a rather unsatisfactory form, at least as recognized by myself, for it includes very diverse soil profiles.

Of the major soil types mentioned so far those showing more advanced pedogenesis are associated with the more southerly aspects, the gentler slopes and the lower altitudes. As indicated earlier these

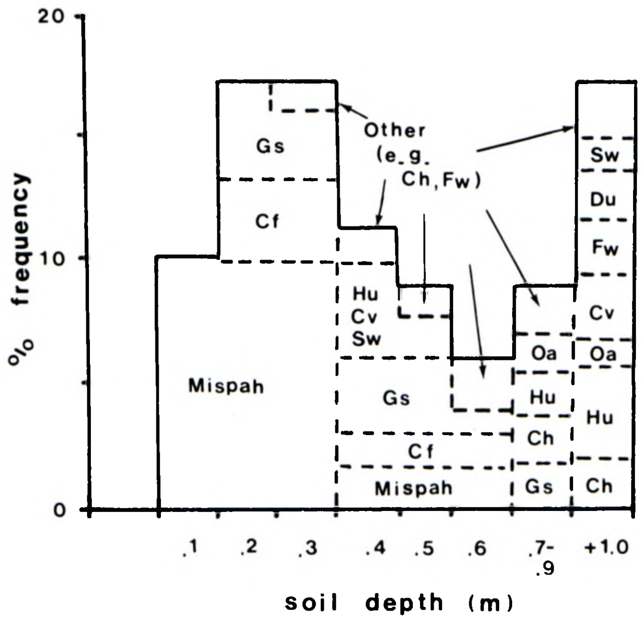

FIG. 8.—Frequency of soil depth and relationships between soil depth and soil form. The soil form distribution among soil depths has been determined for the following depth classes: 0,1–0,3 m, 0,4–0,6 m, 0,7–0,9 m and > 1,0 m. Soil forms abbreviated as follows: Cf., Cartref; Ch, Champagne; Cv, Clovelly; Du, Dundee; Fw, Fernwood; Gs, Glenrosa; Hu, Hutton; Oa, Oakleaf; Sw, Swartland.

situations are also the situations where deeper soils with less rock cover and perhaps higher clay contents occur. The catena that can be expected from situations where soils are least developed to where they are best developed is: [Mispah] [Glenrosa, Cartref] [Hutton, Clovelly, Oakleaf]. Of course, it is not the case that all the forms will be found on a single catena, e.g. the Cartref Form is more or less restricted to the coastal mountains.

The remaining soils that are common on the quartzites are generally not found on the open slopes (i.e. not TOP = 1). Especially common in the west are the deep (often > 1 m) coarse white sands of the dry plateaux. These belong to the Fernwood Form (Fernwood and Sandveld series—Fw11 & Fw12). In the north west where rainfall is lower and soils are richer in iron oxides (Lambrechts, 1979), the Fernwood Form is often replaced on the plateaux by deep, yellow sands of the Clovelly Form. Where the watertable is close to the surface on the plateaux, organic matter accumulates and the soils then belong mostly to the Trafalgar Series (Fw32) of the Fernwood Form. Under situations where profiles are perenially wet, peat-like horizons develop, giving rise to soils of the Champagne Form. These are mostly restricted to the wet south west if on plateaux, to riparian habitats of the coastal mountains, and to the south aspects of the coastal mountains. This last habitat becomes almost zonal, e.g. as on the south aspects of the high peaks of the south-west and as on the lower south slopes of the Tsitsikama Mountains. Associated with the Champagne Form on these south aspects, but also often found on the south aspects of the higher interior peaks, is a 'humic' Mispah. It is a very rocky soil, but it has a high oxidizable carbon content (*c.* 5%) Kruger (1974) and Bond (1981) also note its presence. A humic phace of a Cartref can also be recognized. Alluvial terraces throughout the study area, mostly derived from quartzite, give rise to the Dundee Form.

A different suite of soils, at least at the series level, is associated with the non-quartzitic rocks. On the upper Table Mountain shaleband a common form is Glenrosa represented by the more medium-textured series (e.g. Platt Gs14). On concave shaleband slopes and where the shaleband soils are not mixed with quartzitic colluvium, the Swartland Form is found (e.g. Rosehill Sw30). Other shaleband soil forms include medium-textured Hutton and Oakleaf members, and on the moister sites, Longlands, Estcourt and Magwa (cf. Boucher, 1978). On granites and shales, soils of the Hutton and Swartland forms are common. Most granite soils of the study area belong to the Hutton form (Msinga Series Hu26).

Soil chemistry

The soils of the T.M. quartzites are extremely acidic and have low exchangeable cations (S-value), low total nitrogen and low available phosphorus (Table 6). Oxidizable carbon ranges from less than 1% to over 13%, the high values being recorded in the peat-like Champagne form. These latter soils had the lowest recorded pH values (pH<3,4).

The PCA of soil textural and chemical variables summarizes the variation encountered (Fig. 9). The major gradient that is identified in Fig. 9 (by the first and second principal components) is associated with the west-east gradient (Table 7). In the west, one has course-textured soils with higher available phosphorus, whereas in the east one has finer textured soils (high proportions of clay, silt and fine sand) which have a higher pH and S-value. Nine of the samples from soils of the T.M. quartzites have S-values above 4 me/100 g soil and all of these are found in the eastern and southern Cape. The third principal component identifies the other major gradient in the soil variables. Carbon and nitrogen are strongly positively correlated (Fig. 9) and their variation is chiefly accounted for by altitude and rainfall with which they are positively correlated (Table 7). Carbon and nitrogen are also strongly associated with some variables of the first gradient. Both are positively correlated with S-value (r = 0,35 and r = 0,46 respectively), but carbon is strongly negatively correlated with pH (r= −0,40). Note, however, that S value is primarily associated with clay content (r = 0,66). A PCA using the Cedarberg data indicates independence of texture and soil chemistry (Fig. 10). These quartzitic soils have low clay and silt contents, and the variation in pH, nitrogen, phosphorus and S-value is related to organic content. pH is at the negative pole of the first component and the other variables are at the positive pole. This is mainly a result of a strong negative correlation between pH and carbon (r = −0, 58).

The results above refer to the soils of the T.M. quartzites. The data available (Table 6) are insufficient to provide stringent tests of differences between geological types as the sample sizes for the groups other than the T.M. quartzites are too small. However, F tests between types indicate that textural variables (especially clay and fine sand) are more important in differentiating between geological types than are chemical variables. For instance, clay content is the only variable that differs significantly between T.M. quartzites and non-quartzites ($F = 22{,}9$, df = 1 & 56, $p<0{,}001$). Variables that are nearly significant are S-value (p = 0,07), medium sand (p = 0,13), silt (p = 0,14) and pH (p = 0,16).

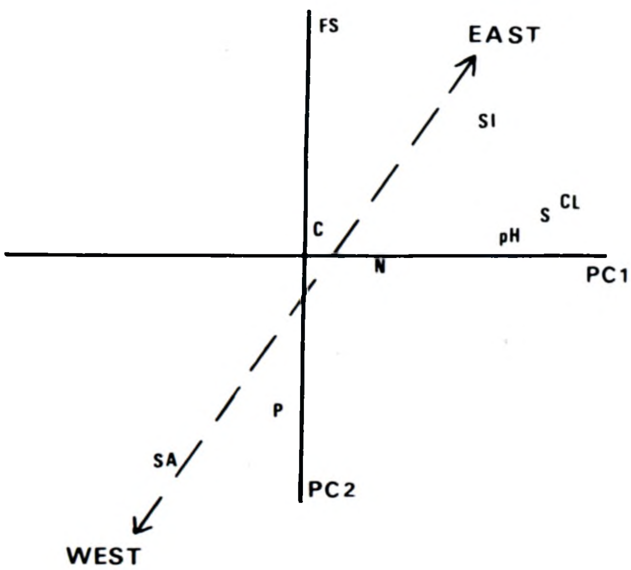

FIG. 9.—The first two principal components (PC) of soil variables. The west-east interpretation of these components is shown. The third component, not shown here, identifies N and C as covarying environmental variables and these are interpreted as being associated with the altitude — rainfall gradient. The analysis was done on the T.M. quartzitic soils (data as for Table 6, n = 51). Results from other subsets of the data from the T.M. quartzites showed almost identical results. The first 3 components account for 69% of the variance (37%, 18%, and 14% respectively). Abbreviations as in Table 2 (SA = MS + CS).

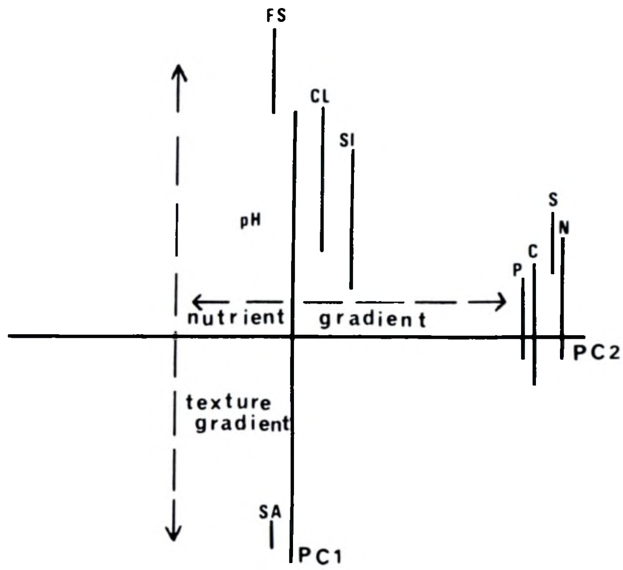

FIG. 10.—The first three principal components (PC) of the PCA of soil variables for the Cedarberg plots (n = 29). The third component is represented by the vertical bars. Results from other subsets of the data from the Cedarberg showed almost identical results. The first three components account for 75% of the variance (39%, 24% and 12% respectively). Abbreviations as in Table 2 (SA = MS + CS).

SYNTHESIS

To synthesize some of the foregoing, PCA was applied. In the PCA with all plots included, the first component represents the rockiness-soil depth gradient (Fig. 11). At the one extreme are the gentle slopes of the foot-hills, plateaux and valley floors with their deep, less rocky soils. At the other extreme are the steep slopes with their litholic soils. The second component represents the regional climatic gradients. It includes both the west-east gradient and the coast-interior gradient, and associated with it are altitude (highest in the interior) and clay (highest in the east). The third component represents a rainfall-rockiness gradient. Because percentage winter rainfall is associated with it, it is regional gradient rather than a gradient representing the altitude-rainfall gradient of individual transects. This PCA may be confounding regional gradients and local gradients and thus further interpretation is difficult.

In the principal components analyses of representative transects an altitude-rainfall gradient is always extracted. Apart from rainfall and altitude, few variables are consistently associated with this gradient. Clay contents are usually higher where

TABLE 6.—Mean values of various soil variables in the different geological types. The peat-like soils (mostly intrazonal, carbon >7,0%) and two outliers from the T. M. quartzites are excluded. The non-quartzitic group includes a range of different geological types: T. M. shaleband (n = 3), Enon conglomerate (n = 2); and two other shale types (n = 2). The samples from the Witteberg quartzite come mainly from the east (8 of 12)

	T. M. quartzites		Witteberg quartzites		Non-quartzites	
	$\bar{x}$	S.D.	$\bar{x}$	S.D.	$\bar{x}$	S. D.
S value (me/100g soil)	2,0	1,62	3,4	1,87	3,2	2,01
Total N (%)	0,07	0,038	0,08	0,049	0,09	0,043
Available P (ppm)	11,9	6,22	10,1	4,26	13,7	10,09
Oxidisable carbon (%)	3,2	1,69	3,5	2,09	3,3	1,81
pH	4,1	0,38	4,3	0,17	4,3	0,39
Coarse sand (%)	13		6		13	
Medium sand (%)	36		20		28	
Fine sand (%)	36		52		32	
Silt (%)	8		12		12	
Clay (%)	7		10		15	
n	**51**		**12**		**7**	

TABLE 7.—Correlation coefficients between soil variables and altitude, annual rainfall, percentage winter rainfall and transect number for the plots of the T. M. quartzites (n = 51, data as for Table 6). The bracketed results are from the Cedarberg (n = 26). The symbols indicate strength of positive and negative correlations. There was insufficient data to do correlations with variables such as aspect

	Annual rainfall	Altitude	% winter rainfall	Transect number
Total nitrogen	+++ (+++)	 (+++)		
Oxidisable carbon	+++ (+++)	 (+++)		
S Value	-		---	+++
pH	--- (--)	- (-)	--	++
Clay	(+)	-	--	++
Silt			---	+++
Fine Sand		---	---	+++
Medium sand		+++ (+)	+++	---
Course sand		+	++	--
Available phosphorus		+++	---	

+ or - p<0,05; r >0,27 (0,38)
++ or -- p<0,01; r >0,35 (0,49)
+++ or --- p<0,001; r >0,44 (0,60)

altitudes and rainfall are lower. The other components represent different aspects of the rockiness-soil depth gradient.

PCA is supposedly a useful tool for summarizing variation of environmental data, for environmental variables are usually linearly related (e.g. Bouxin, 1976; Green, 1979; Orloci, 1975). However, because PCA attempts to summarize variation in as few dimensions as possible, some distortion must occur. This is one reason why I have found that a full understanding of the interrelationships between variables requires the direct examination of correlation matrices, rather than the examination of the principal component summary of the matrix. Another reason why I found PCA unsatisfactory was the absence of a technique to combine PCA's from individual transects into a single statement of the trend within transects. Fisher's (1970) technique for combining correlation matrices was extremely useful for providing this single statement but unlike PCA, it requires direct examination of relationships between variables, In the summary below, I have relied more on the results of the previous sections than on the PCA's reported above.

The variation of environmental variables in the study area can be summarized as follows. One set of gradients in the study area are the regional gradients — the west-east gradient and coast-interior gradient. They are correlated with each other, and although chiefly climatic, also consist of a number of topographic and soil variables (Fig. 12a). The other set of gradients are those within a single transect. The rockiness-soil depth gradient with its often associated variables (rock cover, soil depth, clay

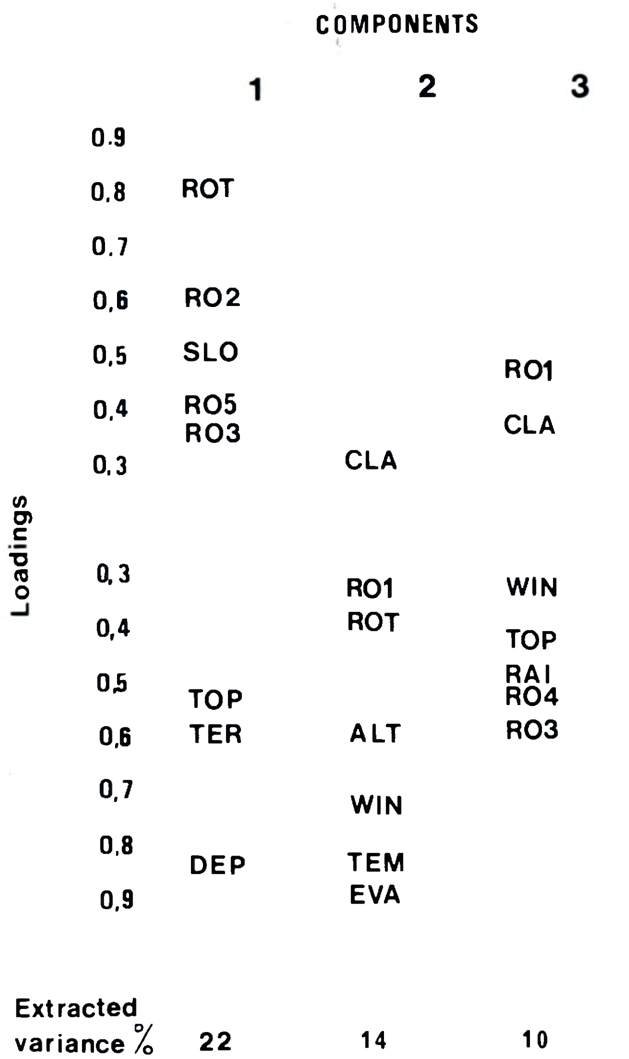

FIG. 11.—Principal components analysis of all plots. Abbreviations as in Table 1. Variables not strongly correlated with a particular component are not shown (− 0,3 < loading < 0,3).

content and slope), is found in three situations, Firstly, it is associated with the altitude-rainfall gradient; secondly, it is associated with the gradient from southerly to northerly aspects and finally, it is associated with local topographic variation (e.g. at any altitude on any aspect it can be found on the gradient from slope to plateau). Fig. 12b summarizes the gradients on a generalized mountain transect. Apart from these gradients there are also the distinctions between geological types. In the quartzitic soils, at least those of the T.M. group, soil depths tend to be shallower than in the non-quartzites, and textures are coarser.

DISCUSSION

Weathering, denudation and pedogenesis

Most of the gradients identified include both climatic and edaphic variables and in most cases the covarying variables are causally related. Perhaps one major exception is the relationship between percentage winter rainfall and soil texture. The texture gradient from west to east is probably a consequence of the manner in which the sediments comprising the quartzites were laid-down (Rust, 1967) and may have little to do with climatic control of pedogenesis, even though one would expect more intense weathering in the summer rainfall regions of the east. The percentage winter rainfall-texture correlation has important implications for vegetation-environment studies: how does one separate the climatic and edaphic effects? Both nutrient conditions (probably related to clay content) and percentage winter rainfall have been implicated as major controlling factors in fynbos structure (Kruger, 1979a). That the soils of the Witteberg quartzites are on average finer textured than those of the T.M. quartzites could also be explained by the manner in which the sediments were laid-down. However, the presence of numerous minor shale-bands in the Witteberg quartzites and the mixing of shale-derived and quartzites-derived material in the soil profile has undoubtedly also resulted in a number of soils of finer textures.

Holland & Steyn (1975) draw attention to the marked vegetation differences on north and south aspects in the Biome and interpret them in terms of differences in soil moisture and ambient temperature and ultimately in terms or radiation loads. Any explanation of the vegetation differences must surely also include the differences in soil development. Because of lower plant cover (Bond, 1981; Campbell, in press b) and lower soil moisture contents on the north aspects one can expect, on the north aspects, lower rates of chemical weathering, a higher degree of sheet erosion and minimal soil development (Bond, 1981; Garland, 1979). These processes probably explain the aspect gradient recorded in this study (Fig 12b). Garland (1979) suggests that a similar scenario has led to the geomorphological asymmetry observed in Drakensberg valleys, where north aspects are less steep than south aspects. As stated earlier there is a slight indication of asymmetry in the present study. However, slope inclination in the present study area is probably more a function of the orogenic processes that have occurred and the extreme resistance of the quartzites to weathering.

Climatic control of the denudation process is indicated by some of the differences between the dry hot interior (e.g. the north-west) and the humid cool coastal mountains (e.g. the south). In the south, especially the south aspects, the slopes are well vegetated and the debris mantle appears to be stable. In the north-west plant cover is low (Campbell, in press b), and there is much evidence of mass wastage, including rock and debris falls, and talus and soil creep. The rocky landscapes of the north west consist of precipitous cliffs and extensive colluvial fans. Prominent cliffs are not a feature of the south.

The importance of summer mists for fynbos has long been recognized (references in Kruger, 1979a). Mists are also important in soil development as is indicated by the location of soils of the Champagne Form on the south aspects of the high peaks of the coast. These slopes are permanently saturated by the winter rains and summer mists thus following an organic horizon to develop.

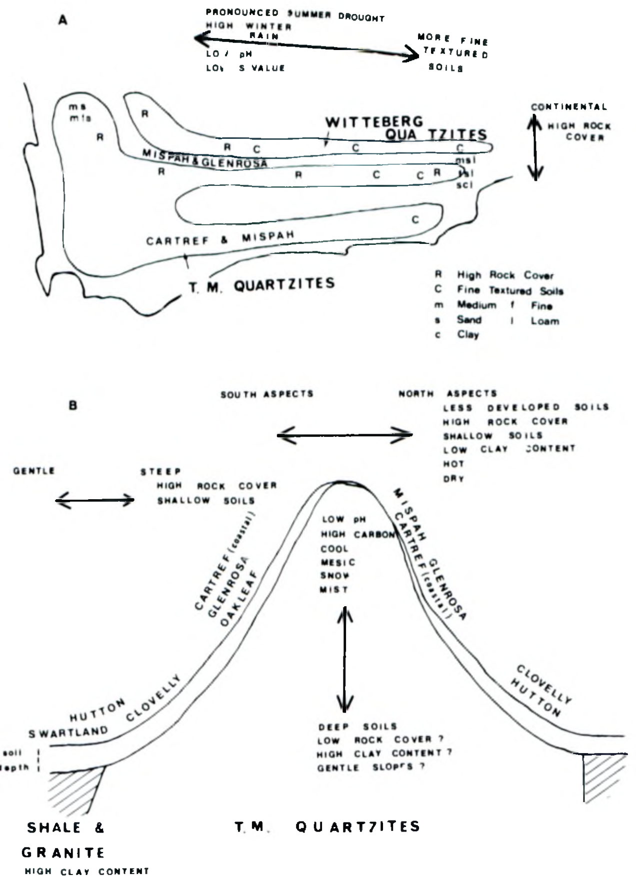

FIG. 12.—Summary of the gradients recognized. A, regional gradients; B, gradients on an idealized mountain. Questionable relationships are indicated.

Nutrient-poor soils

The quartzite/non-quartzite distinction occurring in the Fynbos Biome is often seen as corresponding to a nutrient-poor/nutrient-rich distinction (e.g. Kruger, 1979a; Boucher & Moll 1981; contributions in Day, 1982). The results presented here suggest it is mostly soil textural variables and not chemical variables which distinguish the quartzite-derived soils from the non-quartzitic soils. However, my sample of non-quartzitic soils is small and does include Enon conglomerates which Cowling (1983) records as being of a similar fertility to T.M. quartzites. Low (pers, comm.) and Cowling (1983) have demonstrated very different fertility levels between soils from T.M. quartzites and soils from Malmesbury or Bokkeveld shales. Nevertheless caution should be exercised when substituting the nutrient-poor/nutrient-rich distinction for the quartzite/non-quartzite distinction, at least in the mountains.

The working definition of a nutrient-poor soil at a recent symposium (Day, 1982) included the following: pH less than 6,0; total nitrogen less than 0,12%; and sum of exchangeable cations (S-value) less than 7me/100 g soil. Almost all the soils of the present study (e.g. Table 6) would be classified as nutrient-poor including those of the non-quartzites (a number do not qualify on the total N requirements, but some of these are peat-like soils and would not be regarded as nutrient-rich). Even though the soils would be classified as nutrient-poor, they often support non-fynbos vegetation, a situation which contradicts Specht & Moll's (1982) conception of the contrasting plant communities that are associated with nutrient-poor and nutrient-rich soils. Either the definition of nutrient-poor is at fault or Specht & Moll's (1982) conception is inadequate.

Kruger's (1974) data from a south-west catchment indicate that cation exchange capacity and S-value are strongly correlated with oxidisable carbon and Kruger therefore suggests that fertility in the quartzites depends largely on plant remains in the soil. The result's from the Cedarberg support this finding. However, in the sample as a whole (T.M. quartzites) texture is more important in determining S-value. It is the soils of the east that have the higher clay contents, higher S-value and higher pH values. Therefore, within a transect, soil fertility may be closely tied to plant remains (with organic matter generally higher at higher elevations — this study; Bond 1981; Kruger, 1974), whereas in the Biome as a whole, texture is important in determining fertility, or at least, in determining S-value and pH. pH is consistantly negatively correlated with carbon (this study; Bond, 1981). This is perhaps related to the release of organic acids from organic matter and would definitely be the case in the organic soils. However, carbon does not explain most of the variation of pH in the quartzitic-derived soils; much of the variation, at least at the regional level, is related to soil texture, and ultimately to leaching. Even the carbon-pH correlation may not be casual. Carbon is high and pH is low at high altitudes; the low pH perhaps being determined by higher leaching at high altitudes, and the high carbon probably being determined by lower decomposition rates (Bond, 1981). Available phosphorus as measured by Bray No. 2 is higher in the west and is positively correlated with coarse and medium sand. This pattern has no clear explanation.

Considering the importance placed on nutrients in determining fynbos structure (e.g. Specht & Moll, 1982) it is critical that more work in this direction be undertaken. The present study lacks details with regards to nutrient conditions – too few samples, only one sample per profile and no bulk densities. Bulk densities are especially lacking considering the high degree of rockiness in soil profiles.

Methodology and mythology

A quantitive approach to fynbos environments has been taken by few researchers. Kruger (1974) provides a topographic analysis and some correlations between soil chemical variables and topographic variables for a catchment in the south-west. Bond (1981) in a parallel study to my study, has done a detailed environmental analysis of two of the transect sites that I have studied (OU and GS). Apart from the above the only published account of soils of a specific mountain area is that in Boucher (1978), and that includes no analytical results. The lack of data on Fynbos environments has ensured the development of a number of myths, some of which are discussed below.

Soil depths are usually considered to be extremely shallow (e.g. less than 30 cm — Boucher & Moll, 1981). Average soil depth recorded in this study was 0,5 m. If the soils from non-quartzitic geological types are excluded from the sample then the average depth is still greater than 0,4 m. And even this is an underestimation because of the difficulty of excavating rocky profiles (Bond, 1981). Of the 17 profiles described by Bond (1981), only 40% are less than or equal to 0,5 m in depth.

Kruger (1979b) states that the fynbos soils are mostly lithosols, podzolica and podzols. Lithosols are indeed the case, for as recognized here most of the Cartref, Glenrosa and Mispah Form are litholic. A pedologist would probably map much of the study area as 'Rock/Mispah' complexes (Bond, pers. comm.). The importance of podzolization is apparently overstated. The only dominant soil form which approaches a podzol is the Cartref. It has a bleached E horizon, and it would sometimes be regarded as a true podzol as is evidence by an incipient ferrihumic B horizon (Houwhoek Form). But the Cartref is only a dominant soil form in the coastal mountains. The interior mountains show podzolization very rarely. In the southern Cape, Bond & D. Grey (pers. comm.) almost only find podzolic features on the south aspects of the coastal mountains (e.g. weak accumulation of ferrihumic material even in the deep Hutton soils).

Soil colour is usually considered to be greyish (grey, dark grey, grey brown etc. – e.g. Kruger 1979a, 1979b, Boucher & Moll 1981). 67% of the Cedarberg plots have soils other than greyish (e.g. yellow-brown, brown). The only area where greyish soils predominate are in the coastal mountains especially in the south-west. Even the coastal mountains of the south had a high proportion of non-greyish soils (e.g. many browns, reds and yellows). I would estimate that greyish soils comprise less than 50% of the present sample.

Most of the generalizations about fynbos have been derived from research undertaken in the south-western area and, as shown here, many of the generalizations about soils do not hold in other areas of the biome. The generalizations about soils tend to understate the complexity that occurs within the Biome and may result in the tendency to disregard soils in phytosociological studies of fynbos. Most plant community studies in the Biome have stressed phytosociological relationships to the near exclusion of community-environment relationships. For instance, there are almost no quantitative statements about rock cover. Most studies only include information on altitude, aspect and slope. Bond (1981) and Campbell (in press a) present hypotheses about fynbos vegetation structure which stress the importance of soils.

Bond's (1981) account of environmental gradients provides support for most of my generalizations about trends within transects (as summarized in Fig. 12b). Perhaps the major difference is Bond's stress on the aspect gradient. In his PCA's the aspect gradient is always extracted as the first principal component, i.e. it accounts for most of the variance in the measured variables. My PCA's of individual transects, and all plots, do not usually extract the aspect gradient as the first principal component. This means no more than that Bond's selection of variables for the analyses differed from mine. The importance of the gradients to the plants can only be measured by using biological data; as Mason & Langenheim (1957) state, an environment is only an environment because it is organism-directed.

ACKNOWLEDGEMENTS

I thank William Bond for stimulating discussion; Jeff Morris for giving much of his time in making computer facilities available to me, and B. Low, W. Bond and especially Richard Cowling and Marinus Werger for detailed comments on a draft manuscript.

This study was funded by the Botanical Research Institute and was patiently administered by Dr J. C. Scheepers. Soils were analysed by Mr G. Thompson of the Winter Rainfall Region, Department of Agriculture.

UITTREKSEL

Omgewingsdata versamel op 507 persele op 11 dwars deursnitte, en grond-analise van 81 van hierdie persele is gebruik om die plantomgewings van die berge in die Fynbos-Bioom te beskryf.

Twee hoof- streek gradiënte word herken: 'n wes-oos gradiënt en 'n kus-binnelandse gradiënt. Van besondere belang vir fynbosomgewingstudies is die toename in die verhouding van fyn gronddeeltjies van wes na oos. Minstens sommige aspekte van grondvrugbaarheid vermeerder ook na die ooste toe. Die edafiese veranderinge is parallel aan klimaatsveranderinge: hoofsaaklik 'n afname in die felheid van somerdroogte in 'n oostelike rigting. Op die kus-binnelandse gradiënt is die rotsbedekking 'n belangrike nie-klimatiese veranderlike. Hoë rotsbedekking is 'n kenmerk van die binnelandse reekse. Grond met organiese horisonne of met E-horisonne is 'n kenmerk van die berge van die kus, maar ontbreek dikwels op die binnelandse berge.

Die ander omgewingsgradiënte wat herken is, kom voor op individuele dwars deursnitte en almal sluit edafiese veranderlikes in. Die rotsagtigheid-gronddiepte-gradiënt, waar 'n toename in rotsagtigheid geassosieer word met 'n afname in gronddiepte en gewoonlik 'n afname in klei-inhoud, neig om in drie situasies voor te kom. Eerstens, word dit geassosieer met lokale topografiese variasie; die vlak, rotsagtige grond is 'n kenmerk van die steiler hellings. Tweedens, word dit geassosieer met die hellinggradiënt; die warm, droë noordelike hellings het vlakker, rotsagtige en minder ontwikkelde gronde. Derdens, neig dit om geassosieer te wees met die hoogte-reënvalgradiënt; vlakker gronde word op hoër hoogtes gevind. Dit is ook op hoër hoogtes waar hoër reënval gevind word. Variasies in oksideerbare koolstof word hoofsaaklik toegeskryf aan die hoogte-reënvalgradiënt. Terwyl aspekte van grondvrugbaarheid op 'n bioomwye vlak verband hou met grondtekstuur, blyk dit op individuele dwars deursnitte dat vrugbaarheid verband hou met hoeveelhede plantoorblyfsels teenwoordig in die grond, en met reënval.

Afgesien van hierdie gradiënte, wat op die Tafelberg-kwartsiete gevind is, is ander bronne van omgewingsvariasie die gevolg van verskille tussen geologiese tipes. Die nie-kwartsietiese gronde is oor die algemeen dieper en van fyner tekstuur. Dit word voorgestel dat die voedingstofryke en voedingstofarme onderskeiding met groot omsigtigheid toegepas moet word: die onderskeiding behoort, minstens in die berge, nie outomaties vervang te word deur die kwartsietiese/nie-kwartsietiese onderskeiding nie.

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