THE DYNAMICS OF THE AFROMONTANE FOREST REMNANTS IN THE SOUTHWESTERN CAPE

by

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ABSTRACT

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This thesis identifies the major forest types present in the southwestern Cape and investigates the floristic and structural changes in vegetation composition across the indigenous forest ecotone. The dynamics of forest-fynbos boundaries of differing post-fire age are compared and patterns of vegetation change from forest to fynbos are related to environmental constraints and disturbance history.

Riparian forest and Scree forest were identified, and differences in the structure and composition of the two forest types and their ecotonal communities were evident at both the recently burnt site of Swartboskloof and the fire-protected catchment of Orange Kloof. Soil moisture, soil depth and the amount of rock cover were key factors influencing the dynamics of the forest-fynbos ecotone, with forest composition and the consequent availability of seed also important. The analysis of post-fire regeneration strategies indicated that seedling production and coppice growth were best represented in the immediate post-fire condition, thus supporting the initial floristic composition (IFC) hypothesis. This implies that coppice production is an immediate, reactionary mode of regeneration following disturbance, and that most seedling establishment and subsequent growth of saplings occurs soon after the disturbance event. The absence of seedlings in scree fynbos areas at Orange Kloof suggests an episodic recruitment strategy which is influenced by local species composition and seed production.

ACKNOWLEDGEMENTS

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INTRODUCTION

In recent years, the study of vegetation science has undergone a progressive shift from qualitative, descriptive accounts of vegetation communities to detailed, quantitative studies of vegetation patterns and processes (West *et al* 1981). In particular, the importance of documenting the change in vegetation structure and composition following disturbance has been recognised from both a theoretical and practical point of view; information of this nature not only enhances our understanding of successional theory in different communities but also provides guidelines for the correct management of vegetation types.

Although post-disturbance changes in forest structure and composition have been well documented elsewhere, a considerable lack of information exists on forest dynamics in South Africa. Past studies on forest dynamics have been largely limited to descriptive accounts of post-fire regeneration (Pammenter *et al* 1985; Everard 1986; van Daalen *et al* 1986) and studies on long-term changes in forest composition (Phillips 1931; Granger 1976; Weisser and Marques 1979) with little quantitative data recorded.

In the southwestern Cape, the efforts of the Fynbos Biome Project in the late 1970s greatly enhanced the understanding of the effects of fire on the growth and development of fynbos vegetation in the region, but little attention was paid to the plight of forest patches present in deep kloofs and on boulder screes. In 1979, the inception of an informal Forest Task Group led to the development of the Indigenous Forest Research Programme (Jarman and Geldenhuys 1984) and key objectives and hypotheses were formulated to provide a framework for forest research in South Africa. Of major importance in the formulation of research priorities in the forest biome was the effect of disturbance on the conservation and management of indigenous forest. In addition, the scattered nature of the forest biome provides a large ratio of forest margin to forest area, and an understanding of the dynamics of the forest ecotone was considered important for effective conservation and management (Jarman and Geldenhuys 1984).

Although earlier references to the forest-grassland ecotone were made by Granger

(1976), the first detailed account of the forest-fynbos ecotone and the environmental factors affecting the distribution of the two vegetation types was carried out by van Daalen (1981) in the southern Cape. A similar study by Meadows and Dewey (1986) reported on environmental differences between forest and grass-heathland communities in the southeastern Cape and Masson and Moll (1987) investigated differences in forest-fynbos environments following a long period of fire protection on the Cape Peninsula.

Although environmental constraints on vegetation dynamics are undoubtedly important (Kruger 1984), no clear indication of the potential for vegetation change can be guaged unless structural information is recorded. To date, no study has yet reported on structural changes in vegetation composition across the forest-fynbos boundary. This study was therefore initiated through the CSIR Forest Biome Research Programme to provide information on the structure and dynamics of the indigenous forest ecotone in the southwestern Cape. The key objectives identified were:

1. To understand the dynamic nature of forest remnants in the face of recurrent disturbance and determine whether they are regressing, expanding or static entities
2. To compare forest development at Orange Kloof on the Cape Peninsula with forest development at Wynand Louwsbos in the Kogelberg Nature Reserve. Both sites have not been burnt for many years thus providing an opportunity to compare marginal dynamics of forests in two different localities
3. To determine the mechanisms involved in post-disturbance recovery

In order to facilitate the immediate dissemination of information to current journals, the thesis has been written in paper form, with each section providing a detailed account of relevant literature and research carried out both locally and abroad.

In **Chapter 1**, the results detail the immediate post-fire response along the forest-fynbos ecotone and previous floristic classifications of forest communities at Swartboskloof are compared with structural information collected in the study. The identification of different forest types using vegetation structure, along with obvious differences in substrate composition provided a framework for later comparisons (Chapters 3 and 4) and enabled new methods in determining soil-vegetation relationships to be tested.

In **Chapter 2**, the effect of long-term protection from fire on the forest-fynbos boundary is investigated and findings are discussed in the light of previous investigations conducted in fire-protected areas in South Africa and similar studies carried out in Australia.

The results presented in **Chapter 3** provide a comparison of four scree forest boundaries representing different stages in post-fire development. A comparison of scree forest environments is made and the apparent abrupt transition from forest to fynbos in these areas is discussed with respect to substrate specificity and length of fire protection.

A similar comparison of riverine forest margins is carried out in **Chapter 4** with a detailed discussion of the role of soil moisture in determining the extent of the forest-fynbos ecotone. Integrated in this section is the comparison of riverine forest at Orange Kloof and the two communities sampled on the Kogelberg, thus providing information of relevance to Objective 2.

The final chapter of an analytical nature is a written account of a paper presented at a symposium on the biogeography of southern African indigenous forests and is not limited to data collected in this study. In **Chapter 5**, the floristic composition, species-area relationships and phytogeographical relationships of six different forest patches are assessed using both floristic and structural information, and similarities between forest patches are noted.

In conclusion, a brief summary of the major findings of the study is given, key questions are answered and areas in which further information is required are identified.

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SECTION 1

THE EARLY POST-FIRE CONDITION

CHAPTER ONE

FOREST TYPES AT SWARTBOSKLOOF AND THEIR RELATION TO ENVIRONMENT

ABSTRACT

Differences in forest types at Swartboskloof have previously been identified using floristic classification. This study was undertaken to determine floristic and structural differences between forest types and to investigate the effects of environment on forest regeneration following fire.

Riparian forests located in the upper and lower regions of the valley were similar both floristically and structurally but differed substantially from forests found on boulder screes. Post-fire regeneration patterns of forest species on the margin and in the fynbos differed between scree and riparian forests, with initial colonizing species differing in composition and structure.

Soil moisture, slope, soil depth and rock cover were identified as major factors affecting forest colonizing patterns.

INTRODUCTION

The Swartboskloof catchment area in the Jonkershoek valley near Stellenbosch has been used extensively in the study of mountain fynbos ecosystems. In March 1987, the area was burnt as part of the normal management policy of fynbos catchment areas. Vegetation studies previously carried out in the area were initially concerned with the response of fynbos to fire (van der Merwe 1966) with further work relating to this theme being carried out by van Wilgen (1981). Current studies conducted in the study area are detailed in Van Wilgen *et al* (1986).

The first phytosociological survey of Swartboskloof was carried out by Werger *et al* (1972). Eleven years later, a more extensive survey was carried out by McDonald (1983,1985) with the objectives of reclassifying the vegetation and relating the plant communities to the environment (McDonald 1987).

Although fynbos is the dominant vegetation type in the area, small patches of Afromontane forest vegetation are present along stream banks and in boulder screes. Werger *et al* (1972) recognised three forest communities; the *Brabejum stellatifolium* community which was termed a dense scrub and found in the lower reaches of the valley; the *Rapanea melanophloeos* community which occurred at higher altitudes on steep slopes, and the *Heeria argentea* community which was found in small patches on loose screes. Similarities in species composition between the last two communities were noted.

McDonald (1983,1985) identified two major forest divisions: the *Hartogiella schinoides-Diospyros glabra* riparian forest communities, which included the *Brabejum* community of Werger *et al* (1972) and the *Diospyros glabra-Rapanea melanophloeos* forest communities. The second forest division was further divided into the *Rapanea melanophloeos-Cunonia capensis* High forest and the *Rapanea melanophloeos-Heeria argentea* Short forest. These two forest types were floristically similar (distinguished only by the presence or absence of *Heeria argentea*) and corresponded with the *Rapanea* community and the *Heeria* community of Werger *et al* (1972). No reference to structural similarities among the forest types present in the area has been made in either work. The separation of Afromontane forest communities into three types was queried by McDonald and the need for further testing of Swartboskloof forest data noted.

The aim of this paper therefore, is to determine the floristic and structural similarities of the forest communities at Swartboskloof. In addition, comparisons of the species-environment relationships in the forest margin and adjacent fynbos areas were undertaken to determine whether the regeneration potential in these areas differed substantially between forest types and what environmental variables were responsible for the differences. This study forms part of a more extensive investigation in which ecotonal communities of differing post-fire ages are described and compared.

STUDY AREA

Swartboskloof (34°00'S 18°57'E) is situated in the Jonkershoek Forest Reserve some 15 kilometres from Stellenbosch and is approximately 375 ha in extent. It is a steep, fan-shaped valley, with the head of the valley forming the widest part of the fan at 1200 m. The valley narrows with decreasing altitude to reach its lowest point at 285 m. Slope varies from less than 5° to 45° with steep slopes averaging 30°.

Porphyritic Cape granite forms the floor of the valley while the surrounding steep cliffs and rugged mountains are composed of quartzitic sandstones of the Table Mountain group. Debris from these cliffs, together with granite boulders form a colluvium covering most parts of the granite floor. Loose sandstone boulder screes in the higher reaches of the valley are present immediately below the steep cliffs.

The two main streams present in the valley follow fault lines and join at the lower end of the valley before joining the Eerste River which drains the Jonkershoek valley.

The climate is mediterranean, conforming to Koppen's (1931) humid-mesothermal (type Csb). Mean annual rainfall is 1475mm, 67% of which falls during the period May to September. Precipitation is usually associated with strong cyclonic winds from the north-west. In summer, strong anti-cyclonic winds from the south-east may also bring moisture to the region but usually they are hot and dry. Summer temperatures (December to February) are high, with a mean maximum and minimum for February 27.3°C and 14.5°C respectively. Winter temperatures (June to August) are cool ranging from a mean maximum for July of 16.8°C and a mean minimum of 6.2°C.

METHODS

Forest types and location of plots

Three forest types were recognised on the basis of forest structure and substrate type. In the lower part of the valley (Figure 1), short, riverine forest dominated by *Brabejum stellatifolium*, *Ilex mitis* and *Rapanea melanophloeos* was found. This forest type

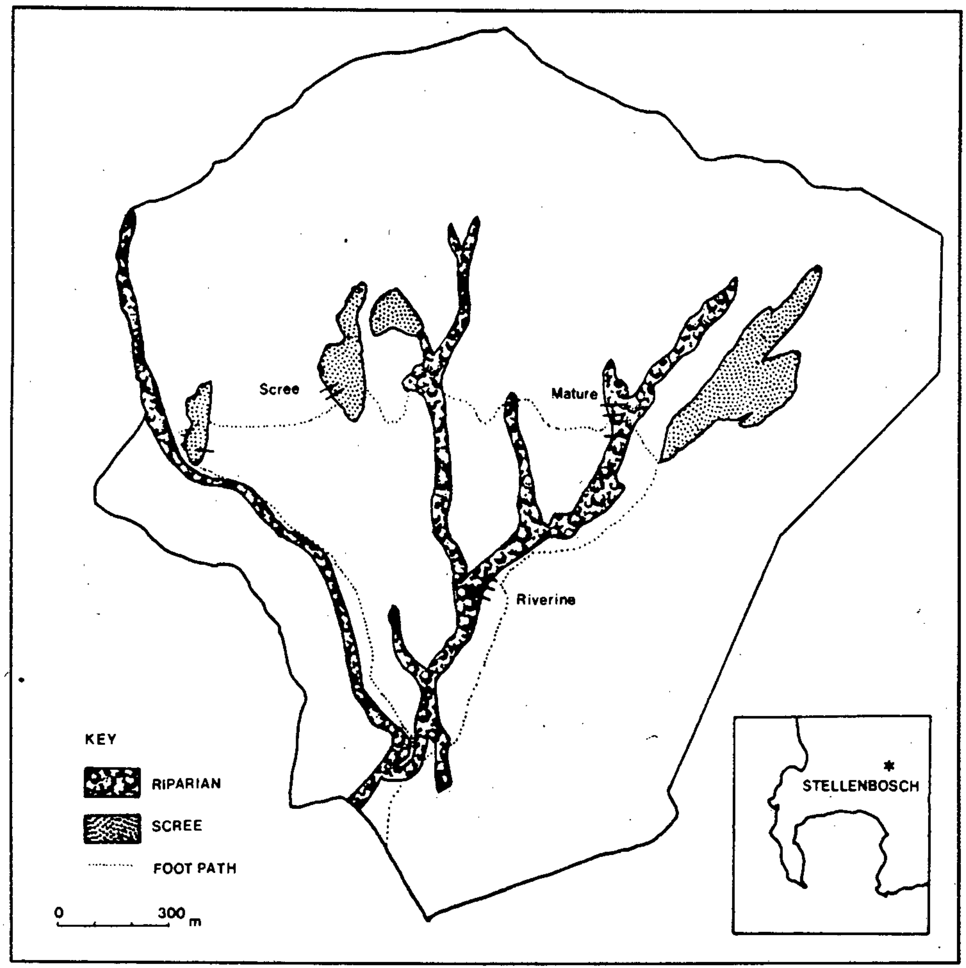

Figure 1. Map of Swartboskloof showing approximate locations of forests.

corresponds with the *Halleria elliptica-Brabejum stellatifolium* Short forest of McDonald (1987) and is referred to as Riverine forest in this study. Further up the valley, the forest became taller with a more open understorey. Within the forest, the substrate was substantially more rocky than the low-lying riverine forest and *Rapanea melanophloeos, Olea europaea* subsp *africana* and *Hartogiella schinoides* were dominants. This forest type was identified as the *Rapanea melanophloeos-Cunonia capensis* High forest by McDonald (1987) and is referred to as Mature forest in this study. The third forest type present at Swartboskloof was relatively short in stature and was confined to sandstone boulder screes. These were termed Scree forests and corresponded with McDonald's *Rapanea melanophloeos - Heeria argentea* Short forest.

In each forest type, three transects were laid out perpendicular to the forest edge, each transect consisting of a 5 m x 10 m plot located within the forest, a 5 m x 10 m plot spanning the forest margin and a 5 m x 10 m plot located in the adjacent fynbos.

Data Collection

In each plot, the type of species present, its height and DBH (if greater than 1.3 m tall) were recorded. Information on aspect, slope, position on slope, percentage rock cover and soil depth was recorded for each plot. Soil samples were collected from the forest, margin and fynbos localities of each transect and the percentage soil moisture, soil particle composition and soil nutrient status determined for each sample.

Data Analysis

The woody species composition of the three forest types was examined and comparisons were made of all forest plots, all marginal plots and all fynbos plots.

Using the structural information obtained from each plot, the relative densities of species in six different height classes were calculated for the plots located within the forest, the marginal plots and the fynbos plots. These height classes were arbitrarily chosen to illustrate structural changes within the vegetation, especially in the lower height classes. This was repeated for each forest type and the results obtained were then compared graphically in order to identify structural similarities between the three forest types. In addition, the contribution of species to the total recorded basal area in forest, margin and fynbos plots was also determined and compared with relative density patterns.

Soil moisture, depth, particle size and nutrient analyses were analysed using two-way analysis of variance. Significant differences in soil properties between forest, margin and fynbos areas were determined using the SNK multiple range test (SAS.1985) and were related to changes in vegetation structure along the forest-fynbos gradient.

Vegetation-environment relationships were determined by canonical correspondance analysis (CCA). This is a multivariate direct gradient analysis technique in which community composition is related to known variation in the environment. Unlike other reciprocal averaging techniques in which environmental interpretation of the ordination axes is carried out only after the ordination has been completed, CCA incorporates the environmental variables into the analysis by specifying that the ordination axes are linear combinations of environmental variables (Ter Braak 1987).

In view of the large environmental data set, two separate analyses were carried out. The environmental data set used in the first analysis was made up of macroenvironmental variables such as soil moisture, soil depth, percentage rock cover, position on slope, angle of slope and aspect. An arbitrary coding system designed for distinguishing between environmental variables was used in the construction of the matrix (Table 1). In the second analysis, the vegetation data was related to microenvironmental data obtained from the soil nutrient analyses.

Table 1. Codings used to compile macro-environmental data set.

ASPECT: NW=1 N=2 W=3 E=4 SW=5 NE=6 SE=7 S=8
SLOPE: Level=1 Gentle=2 Moderate=3 Steep=4 VerySteep=5
POSITION ON SLOPE: Top=1 Middle=2 Bottom=3
SOIL DEPTH: 0-100mm=1 101-200mm=2 201-300mm=3 301-400mm=4 401-500mm=5
% ROCK COVER: 0-20=1 21-40=2 41-60=3 61-80=4 80+ =5
% SOIL MOISTURE: 0-10=1 11-20=2 21-30=3 31-40=4 40+ =5

RESULTS

Vegetation data

Table 2 reflects the number of woody species shared between the forests in the forest, margin and fynbos localities and indicates the number of species which are found exclusively in one or other locality.

Table 2. Species richness of Riverine, Mature and Scree forests a) irrespective of position along transects and b) in one of three localities along the transect.

	a)	Within b)forest	Forest margin	Fynbos area
Number of species shared by all 3 forest types	11	6	7	5
Number of species found only in Riverine and Mature forests	4	3	4	3
Number of species found only in Mature and Scree forests	2	2	1	3
Number of species found only in Riverine and Scree forests	1	1	-	-
Number of species found only in Mature forests	1	2	-	2
Number of species found only in Scree forests	1	1	4	-
Number of species found only in Riverine forests	3	1	2	1
Total number of species occurring in all 3 forest types	23	16	18	14

Species richness in the forests was low, with only 23 woody species recorded in the study area. Of this total, *Brabejum stellatifolium, Platylophus trifoliatus* and *Agathosma crenulata* occurred exclusively in the riverine transects, *Diospyros whyteana* was found only in mature forests and *Heeria argentea* was confined to scree forests.

A comparison of the number of species present in each area along the forest-fynbos transect showed high numbers of woody species on the margin, followed by the forested plots and then the fynbos plots. This may be due to the presence of a distinct marginal flora composed of species such as *Rhus tomentosa, Rhus angustifolia, Myrsine africana* and *Diospyros glabra*. These species do not attain great heights and yet play an important role in the establishment and growth of forest precursors. The presence of species along the transects was not always clear cut with a number of species occurring in more than one locality. For example, although four species found on the scree margin did not occur on the riverine or mature margin, three of these species were also found within the scree forest. Similarly, of the four species common to riverine and mature margins, all were also represented in the adjacent fynbos.

Relative densities of species occurring in plots located within the three forests declined with an increase in height class for both riverine and mature forests, producing a characteristic reverse J shaped curve (Figure 2a). *Kiggelaria africana* and *Rapanea melanophloeos* were major contributors to densities in all height classes in both riverine and mature forests. Relative densities in scree forests however, showed an initial decline followed by an increase in height class 2. A gradual decline from height class 2 to height class 4 was followed by an increase in height class 5, with *Podocarpus latifolius* and *Myrsine africana* contributing initially to densities in the lower height classes, followed by *Maytenus acuminata, Hartogiella schinoides* and *Olinia ventosa* in the higher height classes. Although seedling densities in scree forests were much lower than in the other two forest types, scree forest densities exceeded those of the riverine and mature forests in higher height classes. This pattern was also reflected in the margin and fynbos plots.

A comparison of the relative densities of species found in marginal areas showed an initial decline in densities in riverine and mature margins. Relative densities increased in height class 2 and then gradually declined in the higher height classes (Figure 2b).

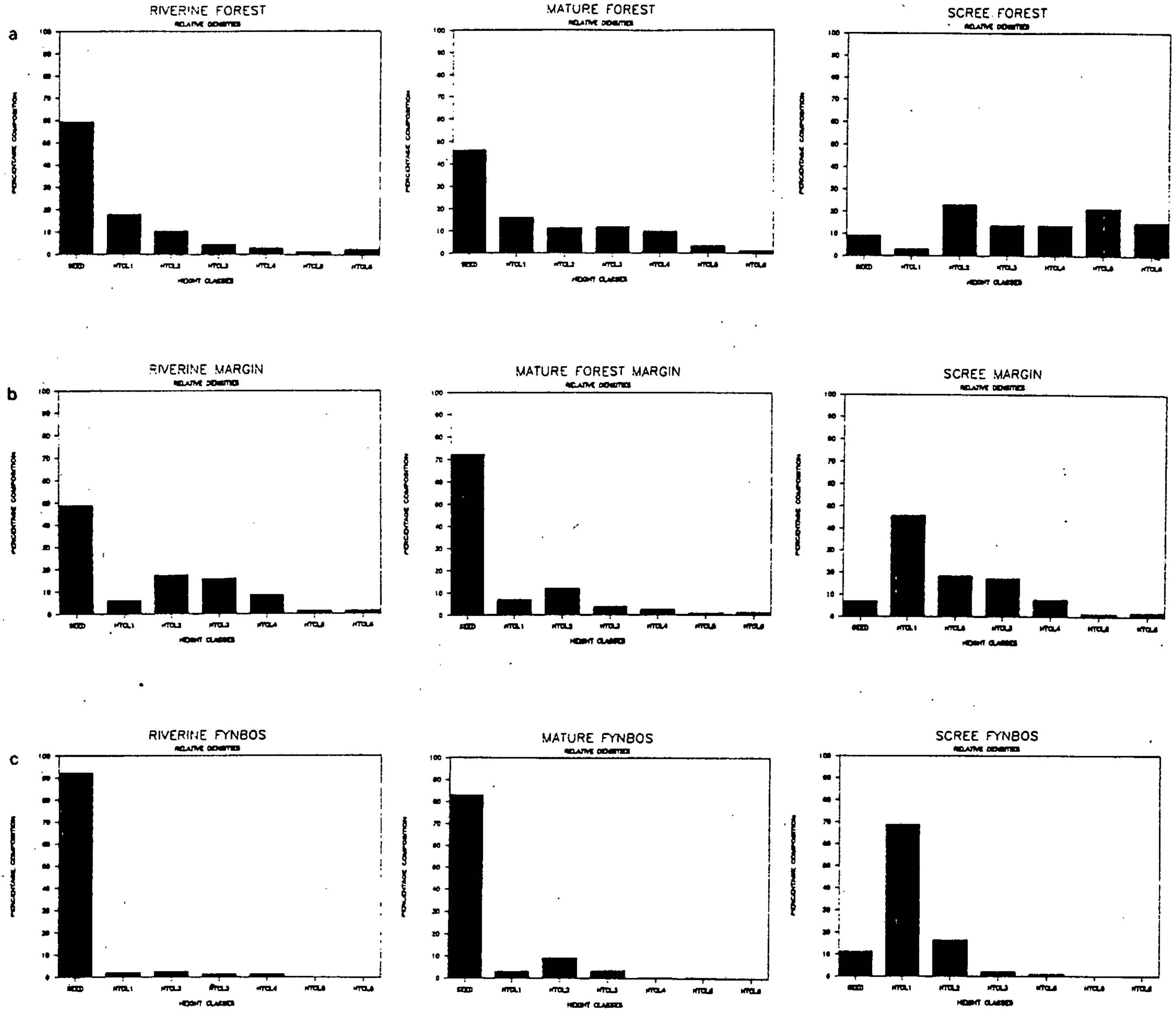
a
RIVERINE FOREST
MATURE FOREST
SCREE FOREST
b
RIVERINE MARGIN
MATURE FOREST MARGIN
SCREE MARGIN
c
RIVERINE FYNBOS
MATURE FYNBOS
SCREE FYNBOS

Figure 2. Relative density contributions in six different height classes of plots located a) within the forest, b) on the margin and c) in the fynbos of the three forest types studied.
Height class 1 = 0.1-0.2m;Height class 2 = 0.21-0.5m;
Height class 3 = 0.51-1.0m; Height class 4 = 1.1-3.0m;
Height class 5 = 3.1-5.0m;Height class 6 = 5.1m+.

Species dominant in the lower height classes in both the riverine and mature margins were *Podalyria calyptrata, Cliffortia cuneata, Kiggelaria africana* and *Rapanea melanophloeos,* with continued dominance of *Rapanea melanophloeos* in the higher height classes on the riverine margin. Densities on the scree margin were initially very low but increased in the first height class mainly due to the presence of *Myrsine africana* and *Olea europaea* subsp *africana.* This was followed by a gradual decline with an increase in height class.

Density profiles in fynbos plots in both the riverine and mature transects were the same as the marginal plots, namely an initial decline in densities followed by an increase in height class 2 and then a decline in the higher height classes (Figure 2c). Here, *Podalyria calyptrata* and *Cliffortia cuneata* dominated the seedling category with *Hartogiella schinoides, Myrsine africana* and *Olea europaea* subsp *africana* assuming importance in the higher height classes. Fynbos plots located adjacent to the scree forest reflected the same pattern in species densities as the marginal plots; densities peaked in height class 1 and then declined with increase in height. Seedling densities were much lower than in the fynbos plots lying adjacent to the riverine and mature forests, thus indicating a lower recruitment potential. Unlike the riverine and mature fynbos plots where *Cliffortia cuneata* was dominant only at the seedling level, in fynbos plots adjacent to the scree forest, *Cliffortia cuneata* persisted in dominance up to a height of 0,5m after which *Maytenus oleoides* became dominant.

Owing to the large number of seedlings and saplings present in the plots whose basal areas were negligible, a comparison of basal areas recorded in forest, margin and fynbos plots using graphing techniques was not informative. Instead, basal area totals from the forest, margin and fynbos regions of the three forest types were calculated (Table 3), the major contributors were noted and their corresponding density contributions listed.

Basal area estimates of 126.42 m^2/ha and 124 m^2/ha were recorded from within riverine and scree forests respectively. These are unexpectedly high when compared to the 40-50 m^2/ha recorded by Geldenhuys (1980) for the southern Cape forests. The high values may however be a reflection of small plot size (an area of only 150m^2 in each area along the transect) and the presence of a few large individuals (in riverine forest, *Brabejum stellatifolium* and *Ilex mitis* and in scree forest, *Olinia ventosa* and *Podocarpus latifolius*).

Table 3. Basal area expressed in m^2/ha- for the three forest types.

Area along Transect	Forest Type RIVERINE	MATURE	SCREE
Forest	126.42	26.09	124.35
Margin	7.35	5.52	44.45
Fynbos	0.29	1.54	0.61

Although *Rapanea melanophloeos* and *Kiggelaria africana* made significant contributions to relative densities inside both the riverine and mature forest, their basal area contribution was low (Table 4). Conversely, *Cunonia capensis* and *Olea europaea* subsp *africana* were major contributors to basal area inside the mature forest but did not feature in density contributions.

On the forest margin, *Podalyria calyptrata* and *Cliffortia cuneata* made similar contributions to density and basal area in both the riverine and mature forests but had negligible effect on the scree margin composition.

In the fynbos, densities of *Cliffortia cuneata* and *Podalyria calyptrata* were high adjacent to all three forest types although their contribution to basal area was negligible in mature and scree areas. Instead, *Maytenus oleoides* and *Protea nitida* had the highest basal areas in the riverine and scree areas, with *Olea europaea* subsp *africana* and *Kiggelaria africana* contributing significantly in the mature fynbos areas.

Table 4. Major contributors to relative density (D) and relative basal area (BA) in plots located a) within the forest b) on the margin and c) in the fynbos of Riverine, Mature and Scree forests. Where no value is indicated, the contribution of that species to the overall density or basal area in the region is negligible. Low values have been entered where the corresponding basal area or density of the same species in other localities has been high.

	RIVERINE		MATURE		SCREE	
a)Within Forest	**D**	**BA**	**D**	**BA**	**D**	**BA**
Rapanea melanophleoes	26.48	2.15	40.87	4.50	6.02	0.04
Kiggelaria africana	53.70	-	35.52	0.47	4.81	9.68
Olea africana	7.25	-	7.34	28.61	2.41	0.58
Maytenus acuminata	6.66	2.02	5.75	8.46	10.84	26.04
Cunonia capensis	0.29	5.10	0.40	48.86	-	-
Ilex mitis	0.75	79.36	1.39	0.10	-	-
Brabejum stellatifolium	2.96	10.52	-	-	-	-
Hartogiella schinoides	1.63	0.5	2.38	4.68	-	3.20
Podocarpus latifolius	0.15	0.35	-	-	14.46	18.22
Myrsine africana	-	-	0.99	-	18.07	-
Zantedeschia aethiopica	-	-	-	-	13.25	-
Knowltonia vesicatora	-	-	-	-	8.43	-
b) Margin						
Olea africana	7.67	27.16	0.46	0.94	9.83	23.56
Rapanea melanophloeos	7.91	16.42	10.19	78.76	-	-
Kiggelaria africana	10.07	5.99	4.93	12.59	1.45	0.02
Podalyria calyptrata	30.21	11.79	29.16	6.28	-	-
Cliffortia cuneata	11.27	-	18.84	-	-	-
Maytenus oleoides	1.44	-	0.13	-	2.60	56.76
Olinia ventosa	-	-	-	-	1.73	13.55
Rhus angustifolia	8.63	0.02	2.66	-	-	-
Maytenus acuminata	4.08	0.07	0.27	-	1.16	1.45
Myrsine africana	4.08	-	6.86	-	57.51	-
Othonna spp	-	-	8.19	-	-	-
Zantedeschia aethiopica	-	-	-	-	6.07	-
Solanum nigrum	-	-	-	-	5.49	-
c)Fynbos						
Cliffortia cuneata	28.24	11.99	31.09	-	21.79	-
Podalyria calyptrata	6.07	-	21.17	-	-	-
Maytenus oleoides	0.24	26.20	0.28	19.45	8.97	50.0
Protea nitida	0.16	57.30	-	-	1.60	50.0
Rapanea melanophloeos	0.08	4.52	0.05	-	-	-
Kiggelaria africana	0.48	-	1.57	44.67	-	-
Olea europea	-	-	1.48	25.96	0.32	-
Myrsine africana	1.86	-	4.89	-	51.60	-
Fynbos seedling	33.74	-	1.24	-	-	-
Agathosma crenulata	8.9	-	-	-	-	-
Unknown seedling	8.33	-	4.34	-	-	-
Othonnaspp	-	-	21.91	-	-	-

Soil Analyses

The percentage soil moisture determined from soil samples collected along the transects is illustrated in Figure 3. Although forest soils generally had a higher soil moisture content than their margin and fynbos plots, the only significant differences between forest and fynbos plots was recorded along riverine and scree transects (Table 5). In the vicinity of the scree forest, a significant difference was apparent between the wetter, forest soils and the drier, margin and fynbos soils.

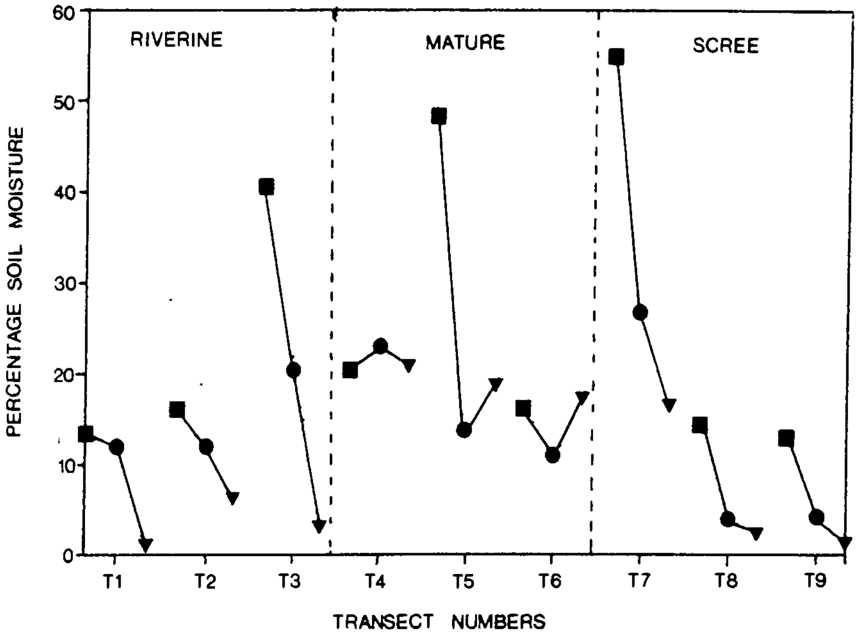

Figure 3. Percentage soil moisture of samples collected from the forest (■), margin (●) and fynbos (▼) regions of each transect from the three forest types.

Soil depth measurements did not differ significantly along mature and scree transects although fynbos plots adjacent to riverine forest were significantly shallower than the forest and marginal plots in that vicinity. A marked difference was noted when comparing the overall soil depths recorded from each forest type, with soil depth measurements recorded from the scree area approximately half that of those measurements obtained from mature plots.

The soils in the study area were predominantly sandy, with highest levels of sand recorded from plots located within the forest. Silt levels tended to be lowest inside the forest with higher levels found in the margin and fynbos localities. Although clay content

Table 5. Two way analysis of variance showing differences across the forest-fynbos ecotone. Mean values from three transects in each forest type are represented. D.F. for vegetation type = 2,8 P.05 *.

RIVERINE	**Forest**	**Margin**	**Fynbos**	**F**	**P**
Soil moisture	28.21a	22.44ab	10.47b	8.39	*
Soil depth	16.03a	16.12a	12.78b	9.33	*
% Sand	72.73	73.08	76.34	5.69	N.S.
% Clay	10.53	10.40	2.71	4.39	N.S.
% Silt	14.05	14.27	13.53	0.08	N.S.
Organic matter	21.64	20.02	13.08	1.97	N.S.
pH	5.65	5.17	4.84	1.67	N.S.
% Carbon	16.23	14.97	9.87	1.93	N.S.
K	225.33	115.00	25.67	3.81	N.S.
Na	69.00	54.67	16.33	1.26	N.S.
EA	0.19	0.87	0.44	1.32	N.S.
S Value	16.65	11.50	2.99	1.72	N.S.
MATURE					
Soil moisture	31.51	23.33	25.89	1.09	N.S.
Soil depth	20.78	22.28	24.07	0.55	N.S.
% Sand	77.93	67.88	68.84	7.04	N.S.
% Clay	11.32	13.76	12.92	2.24	N.S.
% Silt	15.66	18.42	17.75	4.75	N.S.
Organic matter	23.56	26.57	27.88	1.64	N.S.
pH	5.96a	4.86b	4.84b	16.91	*
% Carbon	17.64	19.89	20.76	1.64	N.S.
K	160.00a	55.33b	89.67ab	8.64	*
Na	79.33	53.33	42.0	3.77	N.S.
EA	0.12	1.61	1.62	5.93	N.S.
S Value	21.12	6.75	5.34	4.21	N.S.
SCREE					
Soil moisture	30.42a	18.09b	13.33b	26.38	*
Soil depth	12.70	13.73	12.00	0.35	N.S.
% Sand	51.53	76.50	72.74	0.83	N.S.
% Clay	10.49ab	7.95b	12.46a	6.69	*
% Silt	9.08	13.16	14.51	3.87	N.S.
Organic matter	25.52a	20.17ab	15.21b	13.22	*
pH	5.89	5.86	5.39	3.01	N.S.
% Carbon	19.13a	15.14ab	11.45b	12.34	*
K	291.67	126.67	51.67	4.10	N.S.
Na	112.0	50.33	32.67	3.80	N.S.
EA	0.21	0.10	0.26	2.42	N.S.
S Value	26.19a	10.56ab	4.04b	7.38	N.S.

Table 6. Swartboskloof forest vegetation and macroenvironmental variables. Canonical coefficients and correlations with the first two axes of CCA.

Axis Variable	Correlation Coefficient		Canonical Coefficient	
	1	2	1	2
ASPECT	-0.122	+0.067	-0.215	+0.106
SLOPE	+0.119	-0.689	-0.060	-0.702
POSITION ON SLOPE	+0.028	+0.333	+0.251	-0.019
SOIL DEPTH	-0.584	-0.122	-0.247	+0.308
ROCK COVER	+0.839	-0.093	+0.881	+0.296
SOIL MOISTURE	+0.084	+0.381	+0.003	+0.338

was highest in the marginal plots of two mature transects, lowest levels of clay were found in the scree marginal plots. The shallower soils in this region in conjunction with the lower clay content and hence lower water holding capacity, may account for the low soil moisture levels recorded in the area and the lower seedling densities present in the scree margin. Differences in soil nutrient status along the forest-fynbos gradient were generally not significant in riverine or mature forests although levels of carbon, organic matter and S values were significantly higher in scree forests than in adjacent fynbos plots. Although differences were not significant, a similar decrease in Na levels and K levels was noted from forest to fynbos in riverine transects. This supports Meadows and Dewey's (1986) findings in the eastern Cape where forest soils had significantly higher levels of K within the forest than in the ecotonal area or grassland-heath region.

Vegetation-environment relationships

The ordination diagrams obtained from CCA to determine macroenvironmental and microenvironmental vegetation relationships are shown in Figures 4 and 5 respectively. From the first ordination, it is apparent from the species distribution pattern that there exists a vertical separation of forest, margin and fynbos plots along Axis 2. A second separation between scree forests to the right of the diagram and riverine and mature forest plots on the lefthand side is evident along Axis 1. This separation is also shown by marginal and fynbos plots located adjacent to the scree forests and those of the other two forest types. This tends to support the theory that scree forests are recognisably different from mature and riverine forests. The close associations of mature and riverine forest plots does not however support the observations of Werger *et al* (1972) and McDonald (1983,1985,1987) in which the *Rapanea melanophloeos -Cunonia capensis* High forest was closely related to the *Rapanea melanophloeos-Heeria argentea* Short forest.

Since the importance of an environmental variable is determined by the length of the biplot arrow (Ter Braak 1987), it can be inferred from the diagram that rock cover, soil depth, soil moisture and slope are important in determining vegetation composition. This is supported by Table 6 in which Axis 1 has the highest and lowest correlation coefficients for rock cover and soil depth respectively. Similarly, soil moisture and slope were both

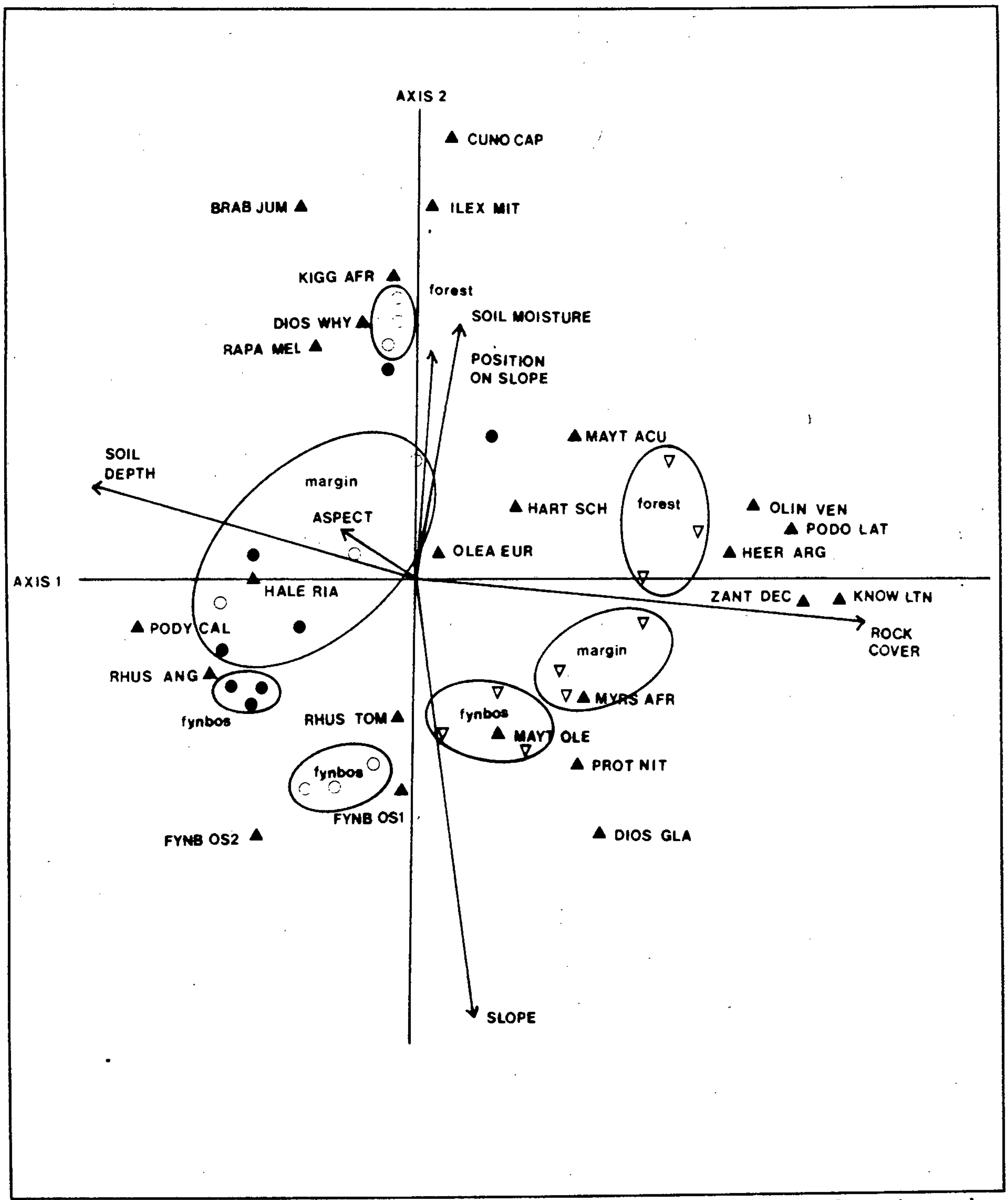

Figure 4. Ordination diagram obtained from CCA, using relative densities of species and macro-environmental variables.The environmental variables are represented by arrows; scree transect plots by ∇ ; mature transect plots by ● and riverine transect plots by ○ . The abbreviated species names used in the diagram are explained in full in Appendix A.

positively and negatively correlated with Axis 2. Plots located within the riverine and mature forests therefore had the highest soil moisture content, whereas those located in

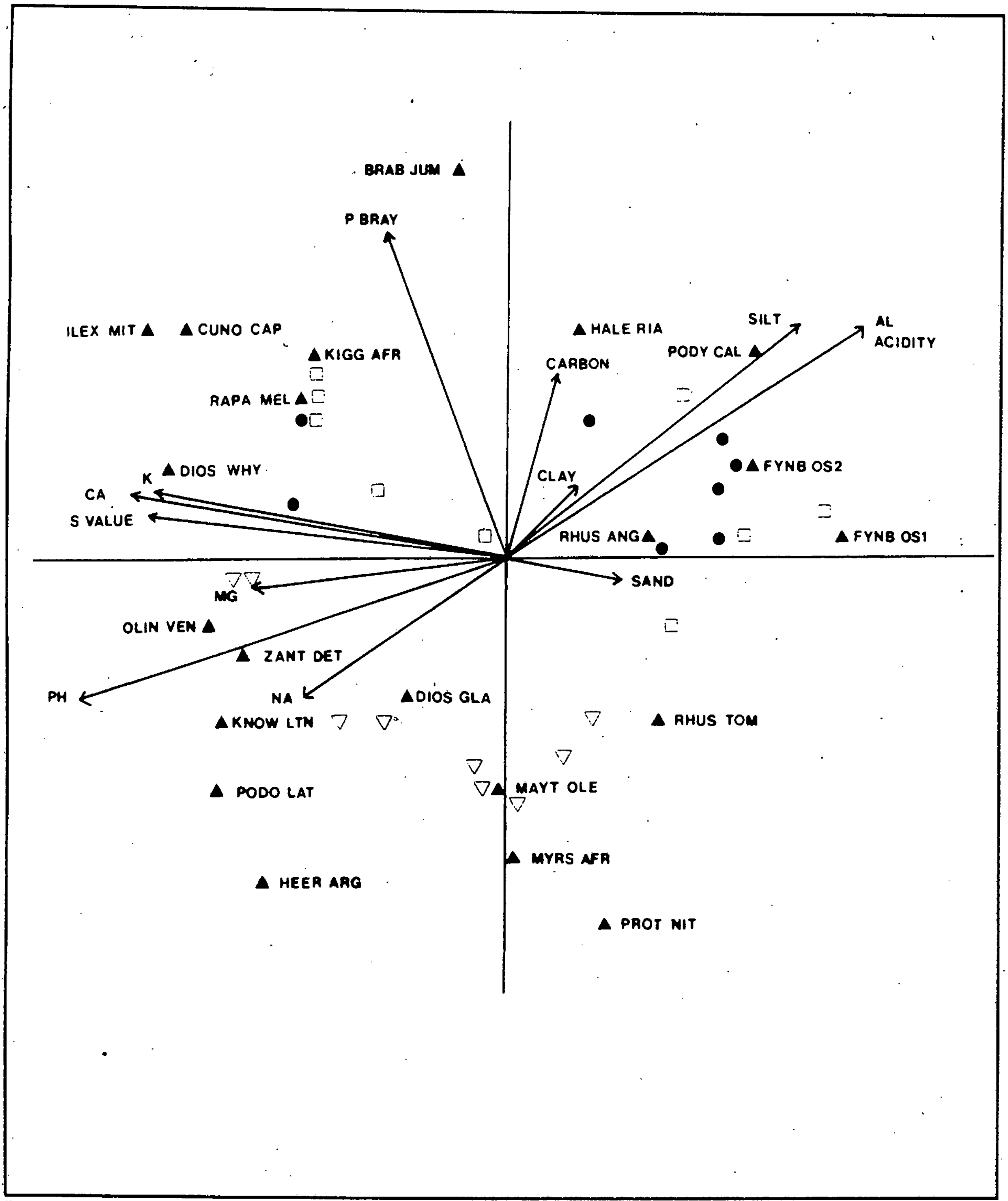

Figure 5. Ordination diagram obtained from CCA, using relative densities of species and micro-environmental variables. The woody species used in this analysis are same as those used in Figure 4.

the fynbos plots had the lowest soil moisture values. Conversely, fynbos plots were usually found on steep slopes which became less severe to finally level out within the forests.

The second ordination diagram relating micro-environmental data to vegetation (Figure 5) showed a similar distinction between the scree forest and the riverine and mature forests although in this instance the separation was vertically orientated along Axis 2. Environmental biplot interpretation indicated that pH levels, acidity and aluminium levels were related to Axis 1, whereas P levels and carbon levels were correlated with Axis 2. Levels of Na were highest in the scree forest environment, declining to its lowest levels in the mature fynbos. Silt levels on the other hand, showed a reverse trend, being highest in the mature fynbos and lowest in the scree forest.

DISCUSSION

In view of the above results, the classification of remnant Afromontane forests at Swartboskloof into three communities is not justified. Although scree forests are noticeably different from riverine and mature forests, the latter two forest types are similar in both species composition (Figure 4) and density composition (Figures 2a-c). A distinction is thus made between scree forests found on rocky boulder screes and riparian forests confined to moist river banks. This latter forest type includes the riverine and mature forests sampled in this study. This dichotomy does not support the findings of Werger *et al* (1972) and McDonald (1987) who recognised similarities between the *Rapanea melanophloeos-Cunonia capensis* High forest and the *Rapanea melanophloeos-Heeria argentea* Short forest. This may be due to a greater emphasis being placed on the structural composition and woody species present in the three forests in this study which contrasts with the overall general species analyses of Werger *et al* (1972) and McDonald (1987) who made little reference to structure.

Vegetation structure and composition

The decline in densities with increasing height is a feature of both riverine and mature forests at Swartboskloof. Childes and Walker (1987) reported a similar pattern of a large number of small individuals and fewer tall representatives in two dominant species found in the disturbed scrub and woodlands of Zimbabwe. The use of diameter distributions in the analysis of past disturbance history has been discussed by Lorimer (1985). Although a reverse J shaped curve is characteristically produced by monospecific all-aged stands, the steeply descending diameter distribution is also a feature of any mixed species even-aged stand if data from all the species are pooled (Lorimer 1985). The results therefore indicate that age structure is relatively constant within the riverine and mature forests at Swartboskloof.

The presence of *Rapanea melanophloeos* and *Kiggelaria africana* in all height classes was noted in both the riverine and mature forests. These two species have been identified as forest precursors capable of colonization and growth in the surrounding fynbos (van Wilgen 1981; Kruger 1984; Masson and Moll 1987). *Kiggelaria africana* is usually found close to disturbed sites or in moribund vegetation (Masson and Moll 1987) whereas *Rapanea melanophloeos* prefers a more moist environment. The seeds of both species are bird dispersed.

The low seedling numbers within the scree forest coupled with higher numbers of large individuals differs substantially from the two previous forest types. This suggests that a static state exists within the scree forest in which older individuals are no longer replaced by younger saplings. The lack of seedling recruitment within the scree forest may be due to the rocky nature of the terrain, the lack of available soil and the consequent low soil nutrient availability.

In contrast with the riverine and mature marginal communities where *Kiggelaria africana* and *Rapanea melanophloeos* were once again major contributors to height class composition, the scree marginal flora was dominated by *Myrsine africana* and *Olea europaea* subsp *africana*. *Myrsine africana* is found throughout the Southern African Afromontane region and is a small shrub, commonly occurring on the margins of evergreen forest (Coates-Palgrave 1977). It is often considered a pioneer species and contributed significantly to the ground coppice category of all three marginal types. *Olea europaea* subsp *africana* or the wild olive, is found in a variety of habitats, ranging from moist riverine fringes to open woodland and rocky outcrops (Coates-Palgrave 1977). The fruit, although bitter, is widely used as a food source and the speckled mouse bird, Cape bulbul, Olive thrush, redwinged starling and Cape white eye have all been observed feeding on the fruit at Swartboskloof (Richardson and Fraser, in press). This high potential for dispersal, together with the ubiquitous habitat preferences of the species, explains the existence of *Olea europaea* subsp *africana* in all three forest areas and its presence in the adjacent marginal and fynbos areas.

Although not strictly a tree species, the presence of *Podalyria calyptrata* and *Cliffortia cuneata* along the transects was recorded in view of the high number of seedlings present in the areas adjacent to the riverine and mature forests. This was not the case in the margin and fynbos plots adjacent to the scree forest, where *Podalyria calyptrata* and *Cliffortia cuneata* densities were negligible on the margin, with only *Cliffortia cuneata* persisting in the fynbos adjacent to the scree. This again illustrates a difference in the post-fire regeneration strategies of the communities adjacent to the three forests studied, with the communities adjacent to the scree forest differing markedly in both structure and composition from those adjacent to the riverine and mature forests. The effect of differences in forest structure on subsequent regeneration processes has been noted by Stewart (1986) in the valley floor forests of New Zealand. Regeneration was infrequent in landslide and windthrown forests having high basal areas, dense canopies and a lack of suitable establishment sites, whereas regeneration levels were high in the more open, frequently disturbed forests where ample sites for seedling establishment were available. The same may be said for the forests at Swartboskloof where structural differences between the three forests studied and along the forest-fynbos transect can be related to species compositional differences which in turn, affect regeneration processes.

Determinants of vegetation composition

Recently, the forest-fynbos boundary and the factors affecting its composition and dynamics have been the subject of investigation. In the southern Cape, van Daalen (1981) found forests on all soil types except those derived from granites and the Enon conglomerates. In limited areas only was soil moisture related to the forest-fynbos ecotone and the location of forests was indirectly affected by topography and aspect through their influence on soil moisture and the spread of fires.

In the southeastern Cape, Meadows and Dewey (1986) found there to be a clear difference in the characteristics of soils collected from within forests and from the grassland-heath communities.

Although not directly related to the forest-fynbos boundary theme, van Wilgen (1981) concluded from a study on the effects of fire frequency on fynbos composition and structure, that sites having the same soil type, geology and fire history do not necessarily have the same vegetation composition. The appearance of tree species in certain areas of Jonkershoek suggested that forest expansion could occur but was considered unlikely in view of the shallow soils and summer drought in the study area.

At Swartboskloof, McDonald (1987) found it difficult to isolate one factor that had an overriding effect on vegetation pattern, and Masson and Moll (1987) suggested a combination of soil type, degree of rockiness and soil nutrient status were responsible for determining the location of forest and fynbos species at Orange Kloof on the Cape Peninsula. That no single factor but rather the interaction of various environmental variables is responsible for determining the location of rainforest boundaries in north eastern Queensland is also proposed by Ash (1988).

In contrast to McDonald's (1987) findings in which the interpretation of the vegetation-environment data proved difficult, the use of canonical correspondance analysis provided a clear indication of which environmental factors were important in determining forest types and the forest-fynbos boundary.

The separation between scree forests on the right of the diagram and riverine and mature forests on the left for example, can be related to rock cover and soil depth respectively. Rock cover is highest in the scree forest plots on the right of the diagram and declines towards the left. Conversely, soil depth measurements were greatest in the plots located on the extreme left of the diagram, declining towards the scree forest plots located on the right. Campbell and Moll (1977) found a similar association between vegetation type and rock cover on Table Mountain where a *Maytenus oleoides* sub association was commonly found in areas with shallow sandy soils and a high rock cover.

Factors responsible for determining the vertical separation of forest, margin and fynbos were soil moisture and slope. Soil moisture levels were highest in the forest plots, declining to their lowest levels in the fynbos plots. This agrees with the pattern detected in Figure 3 although differences were not always statistically significant. The implication that soil moisture availablity controls the distribution of forest has been stated by Craib (1929), Glyphis *et al* (1978) and Marker and Russell (1984). Van Daalen (1981) found this to be the case in the foothills of the Outeniqua Mountains, where forests were found only on the moister southern slopes. Contrary to their expectations, Meadows and Dewey (1986) found soil moisture levels were lower inside the Beggarsbush Sate Forest than in the surrounding grassland-fynbos. Weather conditions prior to soil sampling, higher evapo-transpirative losses and leaf canopy interception of rainfall were suggested as possible explanations for this anomaly.

Although soil moisture played an important role in determining forest types in the Transkei, the influence of slope and aspect on floristic composition of forests was not considered to be important (Cawe and McKenzie 1989). At Swartboskloof, slope was related to differences in composition of forest and fynbos communities (indicated by species distribution patterns along Axis 2) but was not associated with differences in forest composition. Similarly, aspect does not appear to be an important determinant of forest composition at Swartboskloof although aspect and geological substrate were related to fynbos community composition in the earlier study of Werger *et al* (1972).

The importance of geological substrate on fynbos community distribution and composition was also supported by McDonald (1987). Its effect on forest community distribution was less obvious but nevertheless was thought to be more important than soil moisture.

Owing to the lack of adequate soil data, no conclusive testing of the effects of soil nutrient status on forest distribution and composition could be made by McDonald (1987). Results from this study indicate that pH levels and Na are highest within scree forests, declining to their lowest levels in mature margin and fynbos plots. The reverse trend was shown by Al levels, acidity and silt content, with lowest levels apparent in scree forests and highest in the margin and fynbos plots. Although not as important, S values, Ca, K and Mg were highest within forests and lowest in fynbos plots. This supports the findings of Meadows and Dewey (1986) and Granger (1976) that levels of K, Mg and Ca increased from grassland to forest.

CONCLUSIONS

It may be concluded that the forest communities at Swartboskloof can be identified as distinct types on the basis of forest structure and composition. Two major forest types were identified; the riparian forests associated with the riverine courses and streambanks in the lower and upper part of the valley and the scree forests associated with boulder scree outcrops in the upper reaches of Swartboskloof.

Post-fire regeneration patterns in the margin and fynbos did appear to differ between scree and riparian forests, with initial colonization differing in species composition and structure.

Soil moisture, slope soil depth and rock cover may influence the ability of an area to be colonized by woody species.

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SECTION 2

THE FIRE-PROTECTED CONDITION

CHAPTER TWO

THE DYNAMICS OF THE FOREST-FYNBOS ECOTONE IN A FIRE-PROTECTED AREA ON TABLE MOUNTAIN, CAPE PROVINCE, SOUTH AFRICA.

ABSTRACT

The composition, structure and regenerative strategies of woody species along the forest-fynbos ecotone at three forest sites are documented following fifty-five years of fire protection. Similarities in site conditions are identified using one-way analysis of variance (ANOVA) and soil-vegetation relationships determined using canonical correspondance analysis (CANOCO). The long-term protection of an area from fire and the effects of fire frequency on the stability of forest boundaries are discussed.

Regenerative strategies and density patterns along the forest-fynbos ecotones were influenced by species composition and the suitability of local environmental conditions. The structure of the scree forest ecotone differed markedly from patterns exhibited by riverine and mature ecotones and were attributed to differences in slope, soil moisture and soil depth.

Distinct species replacement patterns were evident in riverine and mature forest localities but not in the scree locality. In riverine fynbos, *Apodytes dimidiata* dominated the higher height classes but was replaced by *Olea capensis* in the lower height classes. In mature fynbos, dominant saplings were *Podocarpus latifolius* and *Rhus tomentosa* whilst *Kiggelaria africana* was a major contributor to seedling numbers.

The presence of woody species in fynbos areas adjacent to forests implies that forest expansion is occurring in the absence of disturbance. The rate at which colonisation is proceeding is influenced by species composition and local edaphic conditions.

INTRODUCTION

In recent years, many studies have been conducted on vegetation changes and forest succession in northern temperate forests. Studies vary from the immediate post-disturbance response (Anderson and Brown 1986) to long-term studies in which the changes in vegetation are monitored over a long period of time (e.g. Hibbs 1983; Clebsch and Busing 1989; Hartnett and Krofta 1989; Peet and Christensen 1980).

Considerably less information exists however, on forest dynamics and vegetation change in the southern hemisphere, with most studies conducted in Australia and New Zealand. Hill and Read (1984) for example, discussed early post-fire regeneration of forest communities and more recently (Read and Hill 1988) have documented changes in regeneration ecology of selected species on undisturbed forest sites. Brown and Podger (1982) quantified floristic differences between communities of different ages as measured by the time since the last fire and Ellis (1985) investigated the relationships among vegetation types in northeastern Tasmania. Studies relating to boundary stability and ecotonal dynamics are described by Ash (1988) in northern Queensland and Norton (1989) in South Island, New Zealand.

Despite its importance in understanding community interactions and vegetation changes following disturbance, the study of forest dynamics is poorly researched in South Africa. The earliest study documenting changes in forest composition with time was by Phillips (1931) in the Knysna region. Killick (1963), Granger (1976) and Everard (1986) have described vegetation changes in the Natal Drakensberg, and Pammenter *et al* (1985) and van Daalen *et al* (1986) have investigated the post-fire regeneration and structural changes in a Natal coastal dune forest. In the southern Cape, a study by van Daalen (1981) tested the hypothesis that indigenous forest colonises suitable fynbos sites in the absence of disturbance and in the southeastern Cape, Meadows and Dewey (1986) investigated soil-vegetation relationships across a forest/grass-heathland ecotone.

In the southwestern Cape, most indigenous forest studies have been descriptive (McKenzie *et al* 1976; Campbell and Moll 1977; McDonald 1983;1985). In recent years, widespread attention has been focused on the effects of fire frequency on fynbos regeneration and composition (van Wilgen 1981), but little recorded information exists on the response of indigenous forests and their marginal communities to periodic burning. In particular, the long-term protection of an area from fire and the concomitant changes in structure and composition of the forest boundary have not been documented.

In contrast to most fynbos areas which are frequently subjected to wildfires, the catchment area of Orange Kloof has not been burnt since 1933 and thus provides an opportunity to test the forest colonisation hypothesis outlined by van Daalen (1981). In this study, the composition and structure of three forest ecotones were examined and compared; significant differences in environmental conditions at each of the three areas sampled were noted and conditions suitable for the establishment and survival of forest species were identified.

STUDY AREA

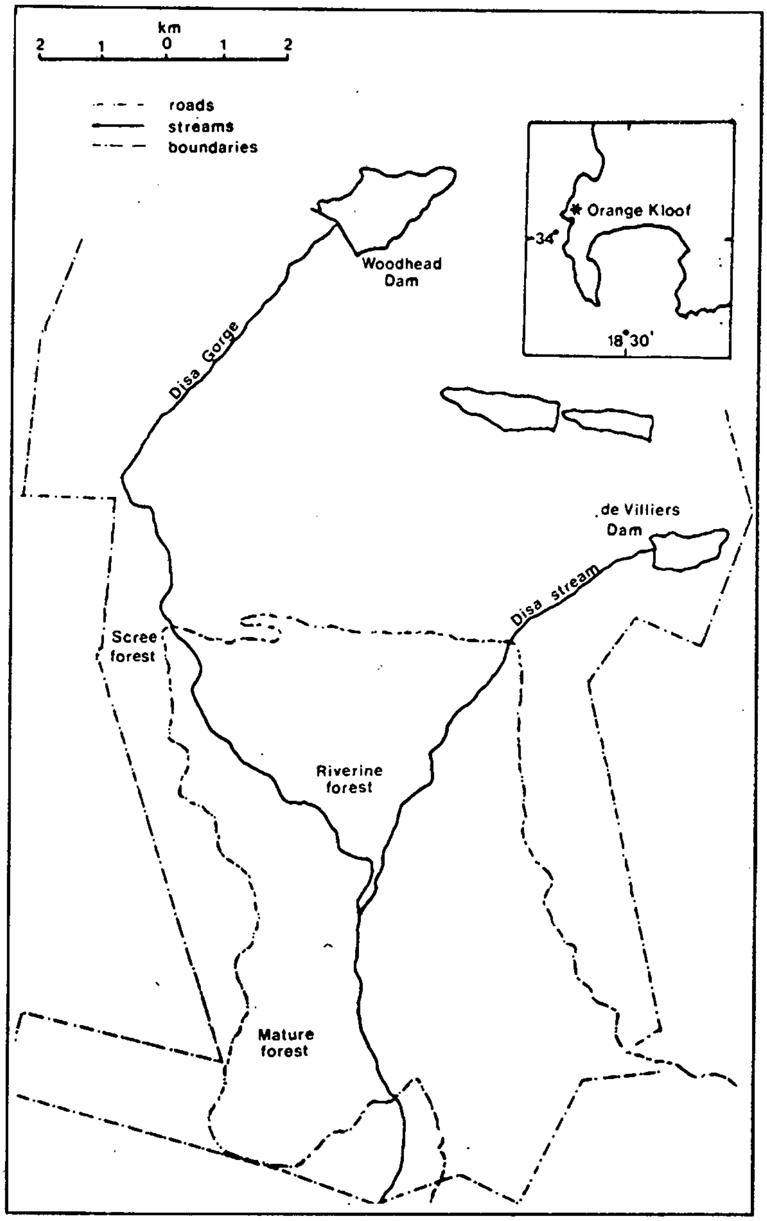
Orange Kloof (18°25'W and 34°5'S) is a water catchment area at the southern end of the Table Mountain massif and falls within the Table Mountain Nature Reserve (Figure 1). Public access to the area is restricted, with management and control of the area administered by the Parks and Forestry Branch of the Cape Town Engineers Department (McKenzie *et al* 1977).

Altitude ranges from 140 m in the south to 600 m in the north- east and west. Slope varies from a gently undulating valley floor to steep, scree-covered slopes above the circular access road. Basement granite overlain by colluvial deposits derived from Table Mountain Group Quartzites (TMGQ) forms the valley floor with mountain slopes composed of TMG shale and TMGQ. Two main streams are present in the area; the Disa Gorge stream which drains from the Woodhead dam on the Table Mountain plateau and the Disa stream which discharges from the de Villiers dam.

The climate is typically mediterranean, with hot, dry summers and cool, wet winters.

Mean annual rainfall is 1227 mm, 68% of which falls between May and September. Precipitation is usually accompanied by strong northwesterly winds in winter, with southeasterly winds occasionally bringing mists in summer. Summer temperatures taken from the Kirstenbosch weather station on Table Mountain range from a mean maximum of 33-34°C and mean summer minimum of 10,7°C. Winter temperatures are cool, with a mean maximum and minimum of 25°C and 5°C respectively.

Figure 1. Map of Orange Kloof showing approximate locations of forest types (after McKenzie *et al* 1977)



METHODS

Forest types and location of plots

Using the same criteria as those described in Chapter 1, three forest types were identified in the Orange Kloof catchment area. In the central region of the valley, short, riverine forest was found along the banks of the Disa stream. Dominant species in the area were *Olea capensis* subsp *capensis*, *Rapanea melanophloeos* and *Apodytes dimidiata*.

Immediately above the circular road and below Frustration Buttress, scree forest was identified on loose boulder scree (Figure 2). Trees were generally taller than those in the riverine forest and *Olea capensis, Diospyros whyteana* and *Rapanea melanophloeos* were dominant.

Figure 2. Forested ravines at Orange Kloof. The abrupt scree margin is illustrated on the far right of the photograph.

The third type of forest found in the study area was termed mature forest and was found in the low-lying part of the valley. This forest type possessed characteristics of both riverine and scree forests, with a high canopy and generally rocky substrate reflecting scree forest affinities, whilst the presence of a perennial riverbed suggested riparian origins. *Rapanea melanophloeos, Cassine peragua* and *Olea capensis* were dominants inside the forest.

In each forest type, three transects were laid out perpendicular to the forest edge, with each transect made up of a 5m x 10m plot located within the forest, a 5m x10m plot spanning the forest margin, and a 5m x 10m plot located in the adjacent fynbos.

Data collection

Vegetation structure

In each plot, woody species present were identified, their heights estimated and DBH measured for individuals taller than 1,3m in height. The regenerative capabilities of the different forest types was assessed by categorising individuals as seedlings (s) if they were less than 0,1m in height; saplings (category 1) if their heights ranged between 0,1 and 1,3m; saplings (category 2) for heights in the greater than 1,3m - 5m category and adults (I) for individuals exceeding 5m in height. Individuals showing signs of above ground coppicing or resprouting from ground level were assigned to the (C) and (G) categories respectively.

Environmental Data

Environmental information recorded for each plot included aspect, slope, position on slope, percentage rock cover and soil depth. Soil samples were collected from forest, margin and fynbos localities along each transect, and the percentage soil moisture and soil particle composition determined gravimetrically for each sample. A soil textural analysis was carried out using methods outlined by Day (1965), and organic matter and percentage carbon were determined using the Walkley-Black method (1934). Na and K levels were determined using flame photometry.

Data analysis

The woody species composition of each forest type, its margin and adjacent fynbos area was examined. Similarities in species composition of the three forest types were noted and dominant species identified.

Using the structural information obtained from the forest, margin and fynbos localities, relative densities of species in six different height classes were calculated. These height classes were arbitrarily chosen to illustrate structural changes within the vegetation, especially in the lower height classes. This was repeated for each forest type and the results obtained were then compared graphically to illustrate structural similarities and differences between the three forests studied.

The total basal area of each plot along the forest-fynbos transect was calculated and the relative contribution of individual species to basal area determined. DBH classes were not used as a measure of stand structure because of the high number of saplings present in the area which have negligible basal area (the exclusion of these individuals from the analysis would have resulted in an incomplete and distorted account of vegetation structure in the area). The relative percentage composition of the six different regenerative categories was calculated for forest, margin and fynbos localities of each forest type and key contributors in each area identified.

In order to assess the environmental similarity of the catchment area, all macro-environmental variables from each plot were ordinated using correspondence analysis. In this way, an impression of the overall site similarity could be gained, with dissimilar plots represented as outliers in the ordination.

An investigation of soil properties along the forest-fynbos transect using two-way analysis of variance showed there to be little significant difference between forest, margin and fynbos soils at each forest site sampled. For this reason, a comparison of all forest soils, all margin soils and all fynbos soils was undertaken using one-way analysis of variance and significant F ratios determined at the 0.05 level. Significant differences in soil moisture, depth and soil nutrient status of the three forest types were noted and related to the composition and structure of the overlying woody vegetation in each area.

The relationship between forest type and the environment was also investigated using canonical correspondence analysis. This is an ordination technique in which patterns of community variation are related to known variation in the environment (Ter Braak 1986). Two separate analyses were carried out; the first analysis used relative densities of species as an indication of vegetation composition, whilst the second analysis related the relative basal area contribution of species to the environment. In both cases, the environmental data set used was composed of macro-environmental variables. Coding procedures and the construction of the environmental matrix are outlined in Chapter 1.

RESULTS

Environmental Data Analysis

Results from a one way ANOVA using environmental data are presented in Table 1. In general, soils collected from within the three forest types were not appreciably different from each other, with only soil depth and percentage silt content differing significantly. This was not the case for plots located on the margin where most variables tested revealed significant differences between the three areas.

In fynbos areas, differences were again apparent, with fynbos plots located adjacent to the scree forest significantly drier than those fynbos plots adjacent to the mature forest. In addition, silt and clay levels in fynbos plots near the scree forest were significantly lower than in fynbos areas adjacent to riverine and mature forests, but sand content was significantly higher. No significant difference in soil depth was recorded between the three fynbos areas. In contrast, soil depth measurements taken from within the scree forest and on the scree margin were significantly lower than those recorded from mature and riverine forests. This may not however, be a true reflection of conditions owing to the overall rocky nature of the terrain.

Organic matter and percentage carbon did not differ appreciably in any of the areas sampled, but the riverine margin possessed significantly lower levels of K and Na than the mature margin. Similarly, pH levels were significantly lower on riverine margins and in the fynbos adjacent to the river than in similar areas adjacent to the scree forest.

TABLE 1.One-way analysis of variance on environmental variables measured in riverine, mature and scree forest localities. Mean values from three transects in each forest type are represented. D.F. for vegetation type = 2,8 P.05 *; P.01 **; P.001 *.**

FOREST	**Riverine**	**Mature**	**Scree**	**F**	**P**
% Soil moisture	21.50	22.50	35.84	4.79	N.S.
Soil depth	35.45b	30.75b	15.57a	23.39	*
% Sand	67.31	71.23	73.12	1.62	N.S.
% Clay	15.26	12.74	12.81	0.65	N.S.
% Silt	19.67b	14.43a	13.34a	13.43	**
Organic matter	5.72	15.66	13.40	3.94	N.S.
pH	5.42	4.86	4.74	0.94	N.S.
% Carbon	12.09	17.33	16.11	3.28	N.S.
K	206.50	231.50	404.96	0.84	N.S.
Na	118.40	173.73	268.33	1.26	N.S.
MARGIN					
% Soil moisture	21.84	17.96	21.84	0.74	N.S.
Soil depth	33.00b	21.41ab	17.16a	6.67	*
% Sand	68.57a	73.49b	76.77b	13.39	**
% Clay	13.27b	12.92b	9.36a	8.73	*
% Silt	19.32b	13.76a	13.16a	8.73	*
Organic matter	7.22	12.21	11.65	1.56	N.S.
pH	5.01a	5.56ab	6.69b	7.43	*
% Carbon	14.36	15.18	14.87	0.05	N.S.
K	80.73a	280.27b	207.17ab	5.16	*
Na	64.36a	211.13b	166.26ab	5.53	*
FYNBOS					
% Soil moisture	22.88ab	25.46b	18.99a	5.80	*
Soil depth	33.87	38.58	21.71	3.56	N.S.
% Sand	67.90a	70.09a	79.33b	27.06	***
% Clay	16.21b	12.88ab	9.36a	6.94	*
% Silt	18.72b	18.42b	11.02a	45.44	***
Organic matter	8.48	8.36	10.62	0.34	N.S.
pH	5.13a	6.03b	6.72c	25.56	**
% Carbon	12.79	12.58	13.97	0.26	N.S.
K	120.90	85.63	63.43	0.98	N.S.
Na	85.76	66.10	45.87	0.68	N.S.

the fynbos adjacent to the river than in similar areas adjacent to the scree forest.

All forests were located on southeast facing slopes, with angle of slope varying from gentle in mature forests to very steep in scree forests. Rock cover was predictably high within the scree forest, declining to lowest values within the riverine forest.

In summary, it appears that whilst environmental conditions remain the same within the three forest types, marginal areas and fynbos areas adjacent to the forest types do not possess the same characteristics. In marginal areas, scree margins differed significantly from riverine and mature margins with mature margins representing the intermediate condition between the two extremes. In fynbos areas, a similar pattern was reflected by soil moisture and percentage clay content, but closer affinities between mature fynbos plots and riverine fynbos areas were indicated by sand and silt content of the soils. Fynbos soils adjacent to mature and riverine forests were deeper than scree fynbos soils although differences were not significant.

Vegetation analysis

Table 2 reflects the total number of species present in each forest area and gives a breakdown of the distribution characteristics of species. Although the total number of species present in all three forest types showed little variation, the number of species present in any one area differed with forest type. Marginal plots alongside the mature forest for example, had the highest number of site-specific species, with eight of the 29 species present in the area found only on the mature margin. Similarly, seven of the total of 28 species found in the scree forest and surrounding environment were confined to margin and fynbos areas, contrasting with the two and three species found exclusively in the same areas of riverine and mature forests.

TABLE 2. Total number of species present in each forest type.

	RIVERINE	MATURE	SCREE
Species found only in the forest	4	3	2
Species found only on the margin	4	8	2
Species found only in the fynbos	3	1	2
Forest and margin location	6	7	8
Margin and fynbos location	2	3	7
Fynbos and forest location	1	1	0
Species occurring in all three areas along the transect	12	6	7
TOTAL number of species	**32**	**29**	**28**

Although the number of species present in all three areas along the transect was similarly low in both mature and scree transects, species distribution along riverine transects were more widespread with 12 of the total of 32 species present in the area found in all three areas of the transect. The presence of species capable of exploiting more than one environment, together with favourable environmental conditions is a clear indication that forest expansion is occurring in this part of the valley.

A comparison of forest, marginal and woody fynbos species numbers is outlined in Table 3. In this analysis, the species distribution patterns were not confined to one forest type as in Table 2, but rather all marginal flora was examined for shared species between the three forest types. In the same way, all forest and fynbos checklists were analysed for similarities in species composition.

An interesting feature of this analysis is the high number of marginal species present in the catchment area. Of the 40 species recorded in total, 36 were recorded in marginal plots with *Halleria lucida, Ilex mitis, Virgilia oroboides* and *Colpoon compressum* found only in the forest or in the fynbos. This contrasts with forest and fynbos areas where only 26 species were recorded in each area. Although half the number of species found inside forests was shared by all three forest types, this proportion declined in marginal plots and fynbos areas. Instead site specificity became apparent with six species confined to only fynbos plots in riverine areas and marginal plots in scree areas.

Table 3. Number of species shared a) regardless of position along transect, and b) in three different areas along the transect.

Number of species shared	a)	b)WITHIN	MARGIN	FYNBOS
by all three forest types	21	13	14	5
by Riverine and Mature forest	4	1	4	3
by Mature and Scree forest	1	2	2	2
by Riverine and Scree forest	2	3	2	4
Species found only in				
Mature forest	3	2	4	1
Scree forest	4	0	6	5
Riverine forest	5	4	4	6
TOTAL	**40**	**26**	**36**	**26**

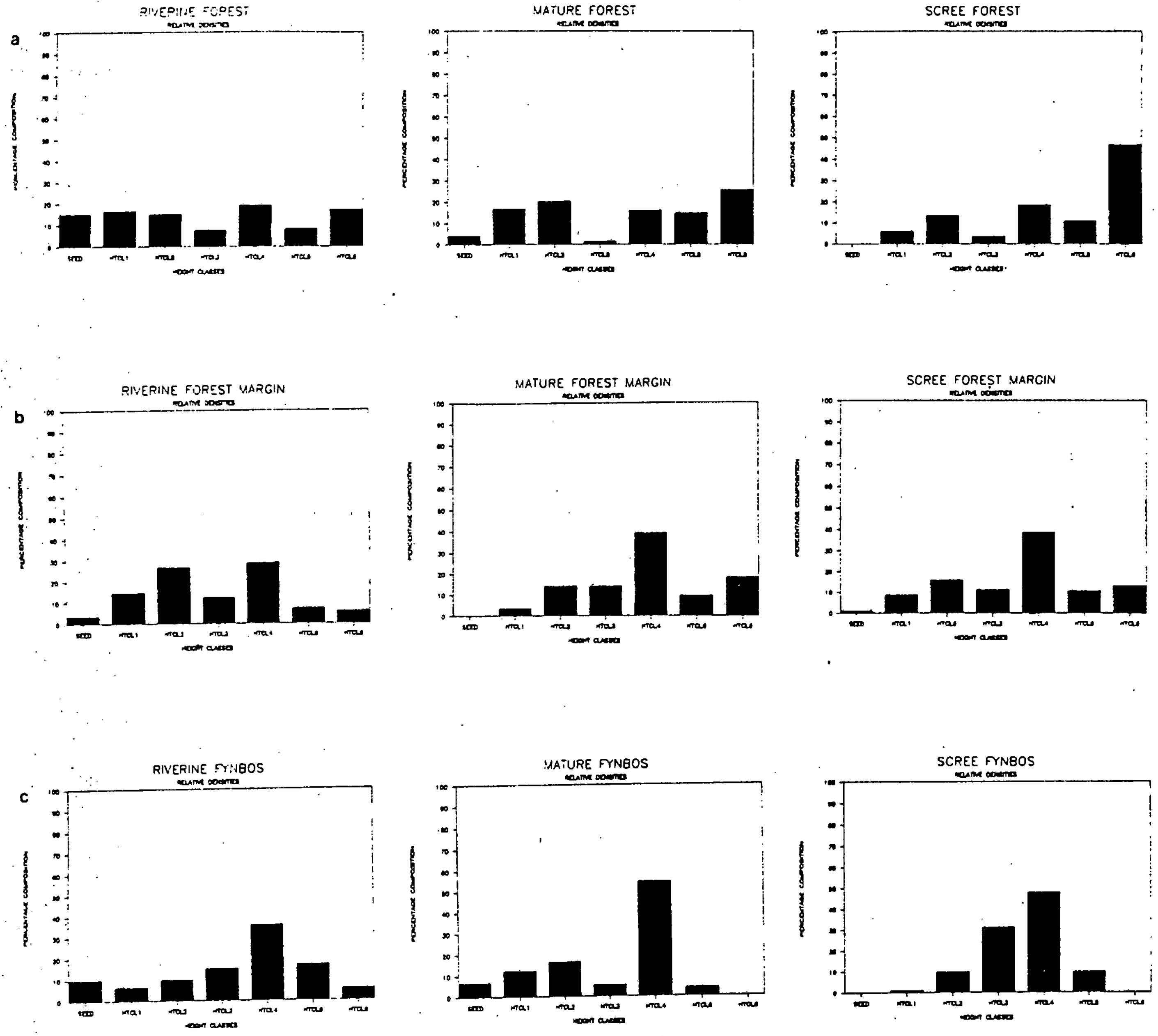


Figure 3. Relative density contributions in six different height classes of plots located in forest, margin and fynbos localities of the three forests studied.

Graphing of relative densities showed similar patterns for plots located within riverine and mature forests (Figure 3a). With the exception of height class 3 and 5 in riverine forest plots and the seedling category and height class 3 in mature forest, densities ranged from 15 to 25 % in all other height classes. In contrast, scree forest plots showed a less evenly distributed vegetation structure, with a gradual increase in densities with height. The reduced densities exhibited in height class 3 and 5 by riverine forests was also evident in scree forests, implicating possible disturbance events leading to phasic regeneration. Similarities between riverine forest and mature forest was also indicated by species composition in which *Kiggelaria africana* dominated the seedling category in both forest types and lower height classes of both forest types were dominated by *Apodytes dimidiata, Diospyros whyteana* and *Chionanthus foveolatus.*

Although *Diospyros whyteana* was only present in the lower height classes of riverine forests, its dominance in higher height classes was a feature of both mature and scree forests. A similar phenomenon was illustrated by *Olea capensis* which dominated the highest height class of both riverine and scree forests. Although adult individuals of *Olea capensis* were present in mature forest, this species dominated the lower height classes of the forest. A distinguishing feature of scree forest was the dominance of *Podocarpus latifolius* in all height classes. This species was not prominent in riverine or mature forest.

Marginal density profiles were similar in all three areas sampled although greatest resemblance was shown between riverine and scree margins(Figure 3b). In both cases, a gradual increase was followed by a decline in height class 3, the decline in this height class again implies a past disturbance event. The dominant species in riverine margins was *Rapanea melanophloeos* in all height classes except the seedling category which was dominated by *Cassine peragua* and *Kiggelaria africana.* Mature margins were dominated by *Canthium mundianum* and *Chionanthus foveolatus* in the lower height classes and *Cassine peragua* in the higher height classes. Although *Diospyros whyteana* was the most common species in the lower height classes of scree margins, an assortment of species present in the higher height classes detracted from the single species dominance shown by riverine and mature margins.

Relative densities in fynbos plots of all three areas reflected a similar trend of highest representation of individuals in height class 4 (Figure 3c). Unlike scree fynbos which had high densities in the high height classes with few individuals in lower height classes, riverine and mature fynbos were better represented in lower height classes. A distinct suite of species replacements was evident in these two forest types; in riverine fynbos, domination of lower height classes by *Olea capensis* was followed by *Apodytes dimidiata* in the higher height classes. In mature fynbos, *Kiggelaria africana* was prominent in lower height classes but was replaced by *Podocarpus latifolius* and *Rhus tomentosa* in the higher height categories.

An analysis of basal area data identified *Cassine peragua* as a major contributor towards basal area totals in all areas excepting riverine fynbos and mature fynbos (Table 4). In the riverine fynbos, *Apodytes dimidiata, Cunonia capensis* and *Rapanea melanophloeos* contributed significantly towards the basal area totals whilst *Rhus tomentosa, Podocarpus latifolius* and *Clutia pulchella* were dominant contributors in mature fynbos.

Another species which made significant basal area contributions in forest and marginal areas of all three types was *Olea capensis*. In the riverine locality, *Rapanea melanophloeos* was a major contributor in marginal and fynbos areas whilst scree marginal plots and fynbos areas were dominated by *Maytenus oleoides.*

A comparison of density data and basal area information indicated that the relative contributions of species to either category was not necessarily linked (Table 4). Although a major contributor to basal area in all three forests, relative densities of *Cassine peragua* were not always high. Conversely *Chionanthus foveolatus* and *Diospyros whyteana* exhibited relatively high densities in riverine and mature forest with correspondingly low basal areas.

By assigning individuals to different growth form categories, the following trends became apparent (Figure 4). Coppicing individuals were generally poorly represented in all forest types, with the only significant contributions occurring in scree forest. Species commonly showing signs of epicormic or ground level resprouting were *Olea capensis* inside the

TABLE 4. Major contributors to relative densities (D) and relative basal areas (BA) of three forest types at Orange Kloof.

FOREST	**RIVERINE**		**MATURE**		**SCREE**	
	D	**BA**	**D**	**BA**	**D**	**BA**
Olea capensis	11.11	16.28	14.03	8.79	13.33	52.94
Rapanea melanophloeos	11.43	9.16	12.22	24.58	5.55	1.20
Diospyros whyteana	8.57	1.33	12.67	2.35	15.55	8.04
Chionanthus foveolatus	8.57	1.07	17.65	1.38	3.33	----
Apodytes dimidiata	11.43	0.84	1.81	1.04	3.33	----
Kiggelaria africana	7.62	----	4.98	0.02	4.44	0.79
Cassine peragua	4.44	44.76	9.95	20.84	5.55	16.27
Canthium mundianum	----	17.73	14.03	3.93	1.11	----
Podocarpus latifolius	0.63	0.02	0.91	----	21.11	7.83
Olinia ventosa	----	----	0.91	25.93	5.55	----
Secamone alpini	14.60	----	0.45	----	7.77	----
MARGIN						
Apodytes dimidiata	10.50	5.78	1.13	----	5.65	2.61
Rapanea melanophloeos	30.67	33.60	1.88	0.18	9.04	1.13
Cassine peragua	10.92	35.21	16.16	57.91	7.91	65.23
Olea capensis	15.55	----	12.03	7.79	4.52	4.85
Rhus tomentosa	4.62	4.50	3.38	3.14	1.69	0.61
Myrsine africana	6.30	----	2.63	----	11.30	----
Canthium mundianum	0.42	----	14.66	8.16	0.56	----
Chionanthus foveolatus	0.42	----	23.68	5.66	1.69	0.04
Knowltonia vesicatora	2.94	----	4.13	----	9.04	----
Maytenus acuminata	0.42	----	2.63	1.55	8.47	5.33
Clutia pulchella	0.84	0.20	1.50	0.17	5.08	0.64
Cussonia thyrsiflora	----	----	----	----	4.52	----
Diospyros whyteana	2.52	----	5.64	1.70	12.43	1.56
Kiggelaria africana	2.52	19.99	----	-----	1.13	0.65
FYNBOS						
Apodytes dimidiata	19.88	45.90	----	----	----	----
Rapanea melanophloeos	13.04	10.99	16.44	----	----	----
Olea capensis	22.98	6.86	2.74	----	1.10	----
Myrsine africana	18.01	----	1.37	----	17.58	----
Cassine peragua	4.9 7	----	----	----	19.78	11.65
Podocarpus latifolius	----	----	10.96	16.31	1.10	----
Rhus tomentosa	6.83	3.75	31.51	66.36	2.20	----
Diospyros whyteana	1.24	0.26	9.59	----	3.30	----
Kiggelaria africana	1.86	----	15.07	----	----	----
Maytenus oleoides	3.11	0.77	----	----	19.78	15.51
Widdringtonia nodiflora	----	----	----	----	9.89	62.10
Maytenus acuminata	----	----	1.37	----	8.79	10.74
Cunonia capensis	0.62	19.61	----	----	----	----
Clutia pulchella	1.24	5.34	4.11	10.87	2.20	----

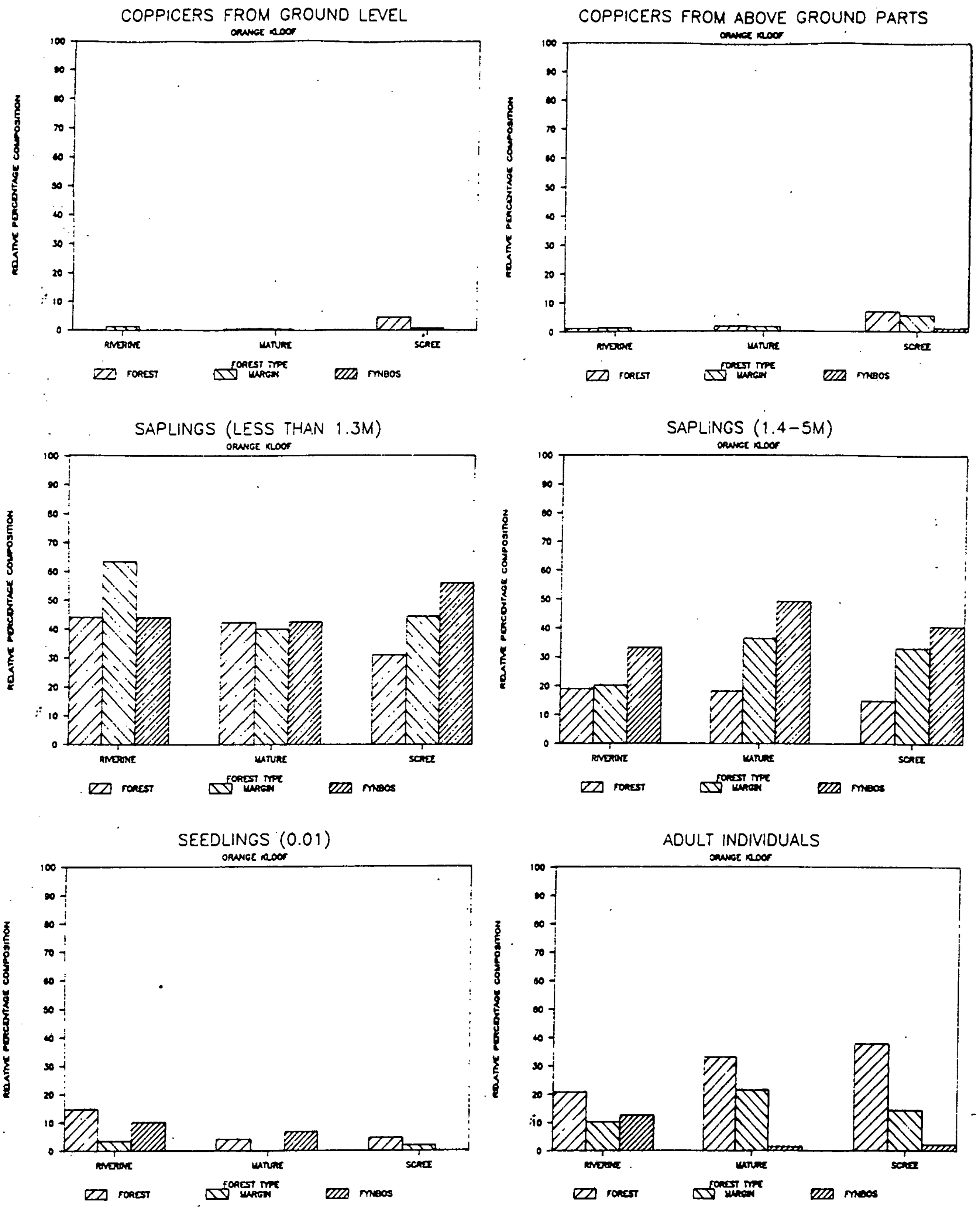


Figure 4. Percentage contribution of individuals to growth form categories.

forest and *Cassine peragua* on the scree margin.

Saplings in the 1,4-5m height category were well represented in all forests and identical trends of high sapling numbers in fynbos plots was exhibited by all three forest types. The riverine forest-fynbos transect was consistently dominated by *Apodytes dimidiata* and *Rapanea melanophloeos;* this contrasts with the scree transect composition in which no single species dominated throughout.

In the lower sapling height category, the percentage composition of forest, margin and fynbos areas did not show the same trend for each forest type. Although sapling composition in scree forest areas was similar to the pattern shown by the higher sapling category with high representation in the fynbos, along the riverine transect, sapling numbers were highest on the margin. Mature forests on the other hand, showed equal representation of sapling numbers in all three localities along the transect, suggesting similar recruitment strategies exist throughout the area.

Seedling numbers were most prevalent in riverine and mature forest localities, with seedling recruitment occurring in fynbos plots of both areas. *Kiggelaria africana* was the dominant seedling in both mature and riverine forest plots, although the most common seedling in riverine fynbos was *Olea capensis*. This is not surprising since *Olea capensis* is also the most common tree canopy species inside the riverine forest.

Although adult numbers were understandably higher inside the three forests than in the margin or fynbos areas, the number of tall individuals present in riverine fynbos was significantly higher than in mature or scree fynbos areas. This factor, together with the high level of seedling recruitment and the relatively high composition of saplings on the margin and in the fynbos, suggests that forest expansion is more prevalent adjacent to riverine forest than in other areas of Orange Kloof.

The results obtained from an analysis of the vegetation-environment relationships using CCA are depicted in Figure 5 and Figure 6. The ordination produced using relative density data identifies a clear distinction between scree fynbos plots on the one side of the diagram and mature fynbos on the other. An amalgamation of forest and marginal plots, along with riverine fynbos plots is found in the central region of the diagram, although a further separation of scree forest and scree marginal plots is possible along the horizontal axis.

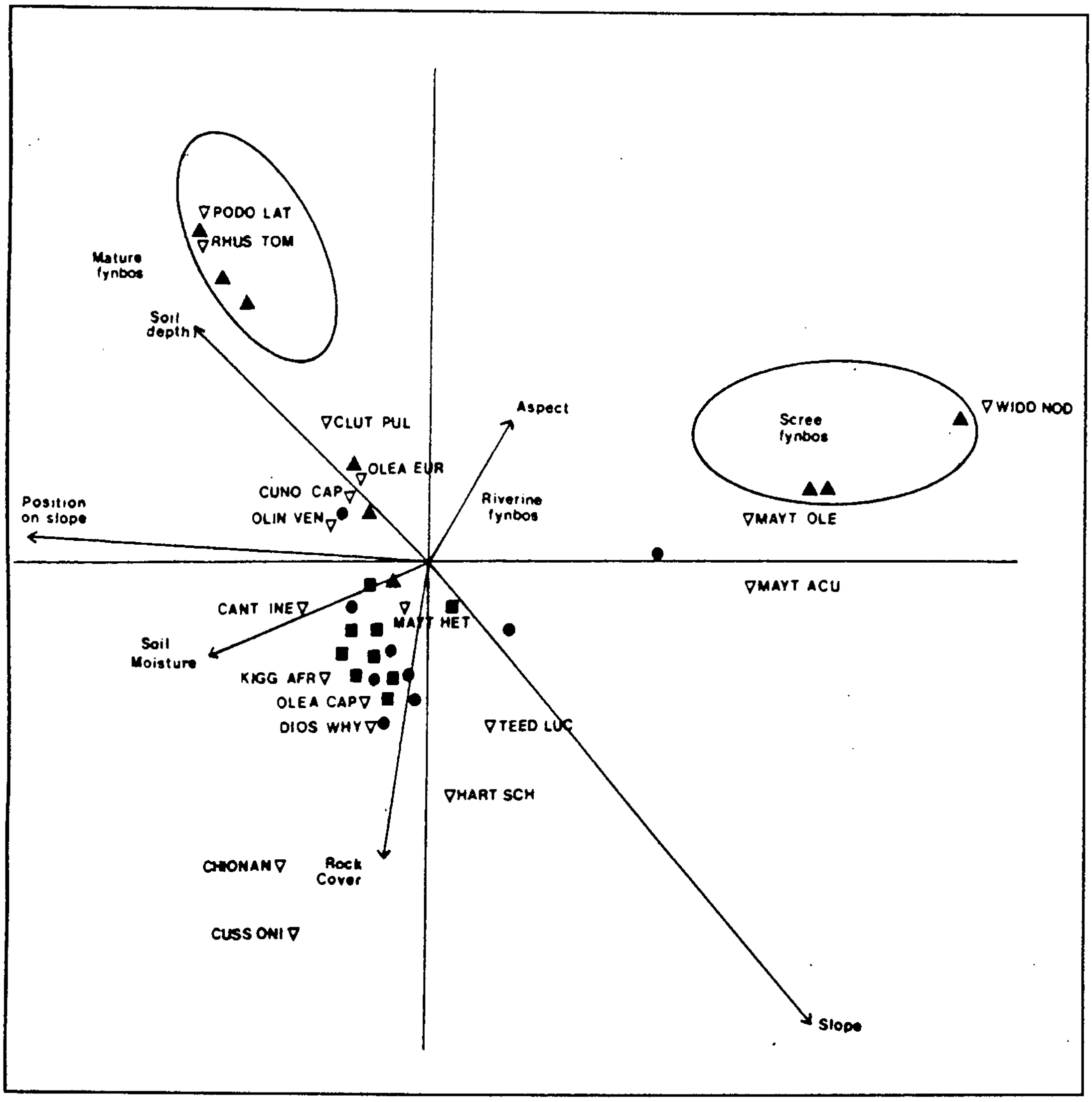


Figure 5. Canonical correspondence analysis using relative density data and macro-environmental variables. Forest plots are represented by ■ margin plots by ● and fynbos plots by ▲

A similar pattern emphasizing mature fynbos and scree fynbos differences with other vegetation was also shown by basal area data. In this analysis however, scree marginal plots and riverine fynbos plots were not as closely associated with other forest and marginal areas.

Since the length of the environmental biplot arrow is related to the importance of that variable, slope, soil moisture and soil depth were identified as key factors influencing vegetation distribution in both density and basal area analyses. In the first analysis, soils of mature fynbos were deepest and had the highest soil moisture content whereas scree fynbos plots showed the opposite trend of having relatively shallow, drier soils. In the second analysis, orientation of environmental arrows was approximately the same as for the relative density data, although rock cover was given more importance and the altered orientation of the soil moisture arrow implied higher soil moisture levels were found in forested plots and marginal areas. In both analyses, scree fynbos plots were found on the steepest slopes.

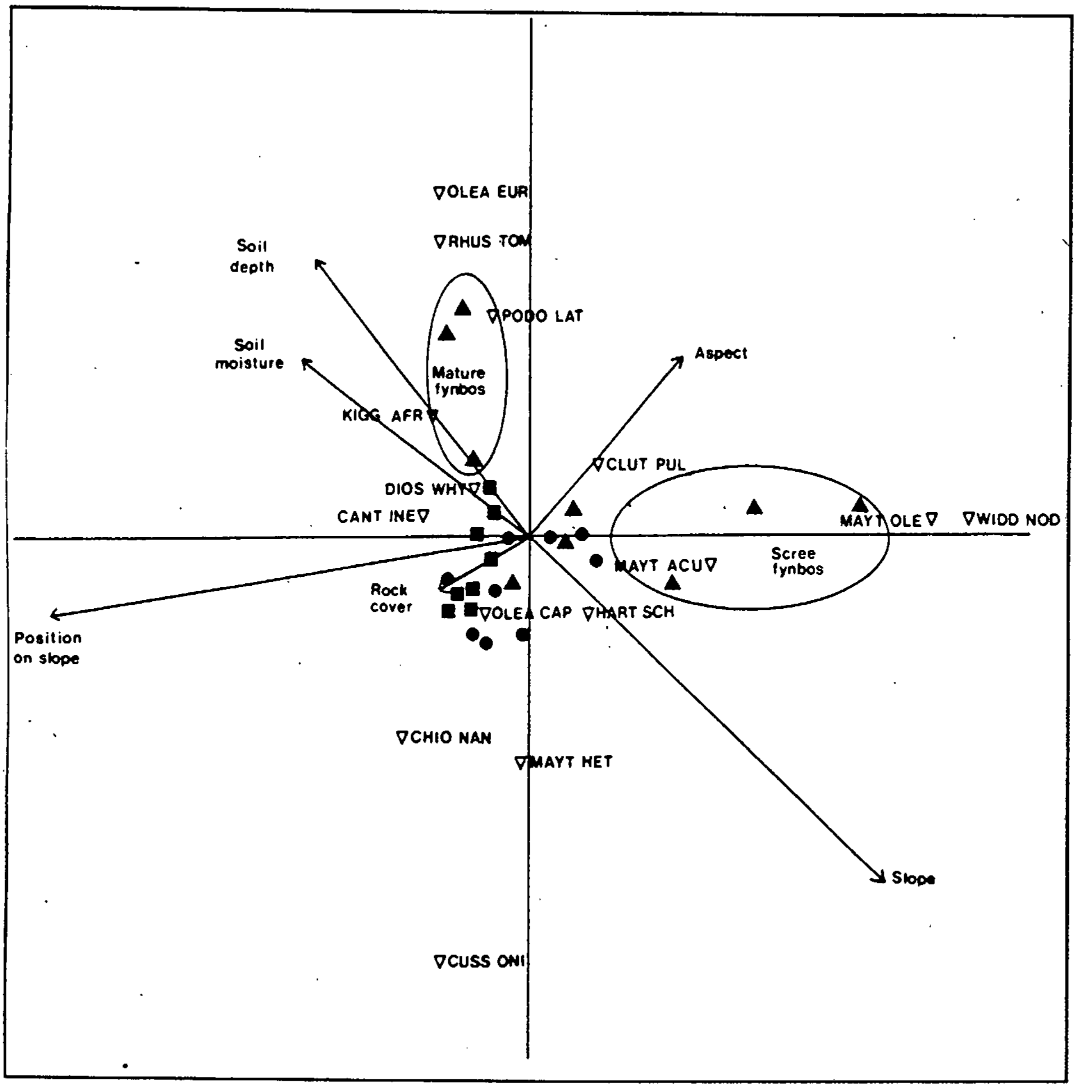


Figure 6. Canonical correspondence analysis using basal area data and macro-environmental variables.An explanation of the symbols is provided in Figure 5.

DISCUSSION

The presence of woody species in fynbos areas of Orange Kloof, together with the high representation of individuals in marginal areas, suggests that in certain areas of Orange Kloof, forest boundaries are not limited by environmental constraints and in the absence of fire, forest development will occur. The rate of expansion differs however in accordance with forest location, and is influenced by topography, edaphic factors and species composition. These factors will now be discussed with regard to the stability of forest boundaries.

A similar phenomenon of inter-fire invasion of sclerophyll vegetation by adjacent rainforest taxa following a long period of fire protection has been reported by Ash (1988). However, subsequent burning resulted in the retreat of the advanced margin to its original position. Rainforest boundaries invariably coincided with geological substrates and soils supporting rainforest or pyrophytic vegetation differed in both chemical and physical properties. Soils were generally deeper and wetter on lower slopes whilst fires burned more rapidly on upper slopes. Although differences between forest and fynbos soils were not significant at Orange Kloof, the deeper, more moist soils of the low-lying region of the valley is consistent with Ash's results. The modified behaviour of fire on upper slopes as reported by Ash, together with the location of scree forest on steep slopes, may have resulted in the development of differences in post-fire environmental conditions.This may explain the subsequent differences in species replacement patterns shown by the riverine and mature forests located in the lower region of the catchment, and the more exposed, high-lying scree forest.

The ebb and flow situation reported by Ash (1988) complies with the fire model proposed by Jackson (1968) in which vegetation distribution and the existence of rainforest, eucalypt forest or grassland is determined by differential fire frequencies amongst vegetation communities. Mount (1979) proposed an alternative model in which the interaction of vegetation and fire produces stable fire cycles, dependant on the levels of fuel accumulation of different vegetation types. These fire cycles reinforce environmental boundaries, resulting in the existence of stable vegetation boundaries

(Brown and Podger 1982).

In Tasmania, investigations by Ellis (1985) indicated that the distribution of eucalypts and mature rainforest on the Mount Maurice plateau was consistently correlated with topographic position whilst the distribution of types on Paradise Plains was determined primarily by the occurrence and intensity of fire. Brown and Podger (1982) found that whilst regular burning was an important determinant of major vegetation differences, edaphic factors, vegetation type and the total fire regime were important in determining local vegetation changes. In addition, fire boundaries were not maintained by vegetation type, with shifts from sedgeland-heath to scrub vegetation occurring. Norton (1989) on the other hand, suggested that structural boundaries observed in mire-forest ecotones in New Zealand may represent old fire boundaries and concluded that the position of the present ecotone was determined by underlying sediments and was relatively stable. The structure and composition of the ecotone was dynamic, however, and changed in response to disturbances.

In South Africa, ecotonal dynamics in the absence of disturbance has been investigated by Granger (1976) and van Daalen (1981). Meadows and Dewey (1986) examined environmental differences between forest and fynbos vegetation in the eastern Cape whilst Masson and Moll (1987) related the rate of forest colonization to differences in edaphic factors.

The importance of determining physical controls on vegetation prior to investigating the effect of fire regime on vegetation dynamics has been noted by Kruger (1984). Although Granger (1976) found there to be differences between forest soils and grassland soils in the Natal Drakensberg, and Meadows and Dewey (1986) reported significant differences between forest and fynbos environments in the eastern Cape, van Daalen (1981) found no marked difference between forest and fynbos soils in the southern Cape. Results from this study are consistent with van Daalen's findings although in a previous study conducted at Orange Kloof by Masson and Moll (1987), environmental differences between the two vegetation types were apparent but not significant.

The close association between soil type and vegetation composition in the eastern Cape supported the existence of a stable forest/grass-heath boundary which was maintained by a periodic burning regime (Meadows and Dewey 1986). In the southern Cape, however, certain forest-fynbos ecotones were not characterised by physiographic or edaphic boundaries and were presumably fire induced (van Daalen 1981). The inability of forest precursor species to establish in the adjacent fynbos areas was attributed to nutrient deficiencies in fynbos sites and unfavourable microclimatic conditions. The seasonal moisture deficit in particular, was identified as a major factor preventing the colonization and growth of forest species. The importance of physiographic patterns in determining forest boundary location was also stressed by Phillips (1931).

Although differences in soil depth, sand content, silt content and soil moisture of forest and fynbos soils were reported by Masson and Moll (1987), the large variation shown between the forests located in the lower part of the valley and the upper scree forest made a general comparison of forest-fynbos soils difficult, and each forest-fynbos boundary was assessed separately. On the whole, significant differences were not recorded between forest and fynbos soils although scree forest soils were significantly shallower than fynbos soils and mature marginal areas were significantly drier and had a higher silt content than adjacent fynbos areas.

The presence of forest species on the forest margin and in the fynbos, together with the lack of variation shown between forest, margin and fynbos soils implies that although differences between forest types are apparent, local differences at each site are not significant to preclude forest expansion.

The identification of three different forest types and their separate analysis follows the findings at Swartboskloof (McDonald 1987; Chapter 1) in which marked differences between riparian forest and scree forest were noted. At Orange Kloof, a previous phytosociological survey by McKenzie *et al* (1977) identified eight different forest communities. Sample plots located near or within riverine forest were classified as the *Cunonia-Ilex-Rapanea* community by McKenzie *et al* (1977) and were typically moist sites adjacent to annual streams. The *Olea europaea-Podocarpus* forest community was analogous with the scree forest classification of this study and was found on shallow, dry soils. Species richness was reportedly low. The third forest type identified in this study, the mature forest, was classified as the *Scutia myrtina* community by McKenzie *et al* (1977) and was considered the most characteristic forest community at Orange Kloof. Species dominant were *Cassine peragua* and *Chionanthus foveolatus*.

The recognised floristic differences between these communities together with differences in topographic location and edaphic conditions supports the separate analysis of vegetation change across forest boundaries. Indeed, the marked differences between the margin and fynbos plots located adjacent to scree forest and those located adjacent to the lower riparian forests were illustrated not only by the CCA distribution patterns and one-way ANOVAS, but also by seedling recruitment levels and species regeneration patterns.

Species regeneration following disturbance may take one of several forms, depending on the severity of the disturbance and the attributes of the species present in the area (Stewart 1986). This feature was also reported by Granger (1984) who noted that post-fire changes in the structure and dynamics of forest and forest marginal communities were determined by the adaptive responses of plants to fire. In the absence of disturbance, the relative proportions of the different modes of regeneration may change. Hibbs (1983) for example, found that ten years after a hurricane, species regeneration patterns in the Harvard Forest were diverse, with most species displaying more than one method of regeneration. Species present forty years later were present either before or immediately after the disturbance with stand structure determined by species life spans and relative growth rates. Although information on the early post-fire responses of individuals at Orange Kloof is not available, and the severity of disturbance throughout the area was presumed equal, the different regenerative strategies exhibited by the three forest types and their adjacent communities can be related to species composition and substrate availability.

A common feature of a number of woody species is the production of sprouts or coppices, the incidence of which is influenced by the frequency and severity of disturbance

(Granger 1984). At Orange Kloof, the incidence of resprouters was low, with most representation occurring in the vicinity of the scree forest. This may be related to forest location, with the low-lying more mesic riverine and mature forests experiencing fires of less intensity than the upper scree forests where steep slopes may have enhanced fire intensity.

The two most common coppicers in the scree forest area, *Olea capensis* and *Cassine peragua,* were also present in riverine and mature forests but showed little evidence of coppicing in those two vicinities. Instead, *Olea capensis* contributed significantly to sapling numbers in the riverine and mature forest areas whilst *Cassine peragua* was an important contributor towards riverine seedling numbers.

The generally high representation of saplings together with low seedling densities evident in certain areas of Orange Kloof suggests that species establishment has already taken place. This complies with the findings of Hibbs (1983) and Read and Hill (1988) in which canopy composition of stands is determined soon after disturbance, through seedling recruitment with the structure of the community dependent on differential growth rates.

Although the contribution of seedlings towards growth form was relatively low, the underlying difference between scree forest and the other two forests is also illustrated by seedling numbers and again may be explained in terms of environmental conditions. The rocky, dry substrate in the vicinity of the scree is clearly unsuitable for seedling establishment whereas the gently undulating, more moist environment of the valley basin provides a more equable climate for species establishment.

The influence of substrate type and availability on seedling densities has been noted by Read and Hill (1988), Stewart (1986) and Kruger (1984). Kruger (1984) suggested that in the absence of fire, a mixed forest precursor stand composed of *Widdringtonia nodiflora, Kiggelaria africana, Erica hispidula* and *Watsonia pyramidata* could develop in fynbos areas, although this was not always the case and was largely dependent on edaphic conditions. Similarly, the presence of certain forest precursors such as *Kiggelaria africana* was variable, despite the seemingly uniform conditions of the surrounding areas, with most individuals found in close proximity to nearby streams. At Orange Kloof, this species was a major contributor to seedling numbers in both riverine and mature forests, but was not well represented in fynbos areas.

The characteristic reverse J-shaped size distribution pattern reported by Read and Hill (1988) was not a feature of relative density profiles at Orange Kloof. Although relative densities showed similar patterns of distribution in both riverine and mature forest types, relative densities increased with height in the scree forest. This pattern was also evident in scree forests at Swartboskloof (Chapter 1).

Observations that species richness increases with increase in soil moisture and fertility (Hartnett 1988) is supported by this study in which 32 species were found in the more moist environment in contrast to the 28 of the less favourable scree area.

CONCLUSION

An investigation of forest structure, composition and the associated environmental conditions present at Orange Kloof provides a clear indication that forest expansion is occurring in the absence of disturbance. The similarities in soil properties across the forest-fynbos ecotone, together with the presence of forest species in marginal and fynbos areas strongly suggest that local differences in environmental conditions are not sufficient to prevent forest expansion in the absence of fire. The rate at which forest colonization proceeds does, however differ with respect to forest location and is influenced by soil depth, soil moisture availability and forest composition. Results from canonical correspondence analysis and the analysis of regenerative strategies identify floristic differences between the three forest types with regenerative patterns influenced by forest location and associated microclimatic conditions.

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SECTION 3

SCREE FOREST ECOTONES OF DIFFERING POST-FIRE AGE

CHAPTER THREE

SCREE FORESTS, FIRE AND THE POST-FIRE REGENERATION OF ECOTONAL COMMUNITIES IN THE SOUTHWESTERN CAPE, SOUTH AFRICA

ABSTRACT

The dynamics of ecotonal vegetation of four scree forests representing different post-fire ages was investigated. Environmental differences between sites indicated that post-fire age was not the sole determinant of vegetation dynamics along the forest-fynbos ecotone, and parameters such as soil depth, soil moisture and rock cover contributed to differences in forest seedling establishment in adjacent fynbos areas.

The effects of fire protection on vegetation structure and composition is nevertheless important; the high numbers of saplings recorded in the fire-protected environments of Betty's Bay and Orange Kloof indicates that forest expansion beyond the confines of the boulder scree is possible. However, the lack of seedlings recorded in scree fynbos areas at Orange Kloof suggests that recruitment in the area is episodic.

The mode of regeneration adopted by ecotonal vegetation is influenced by the time elapsed since the last fire. The immediate post-fire condition of vegetation revealed high levels of coppicing and increased seedling production in contrast to the lower levels recorded in fire-protected environments and greater sapling production.

INTRODUCTION

The southwestern Cape region is dominated by a sclerophyllous heathland called fynbos, with isolated forest patches restricted to streambanks, kloofs and boulder screes (McKenzie 1978). Although recent research has centred on the post-fire responses of fynbos communities in the southwestern Cape (Van Wilgen 1981), very little is known about the regeneration capabilities of forests in the region.

The ability of forests to expand into the adjacent fynbos in the absence of fire has been questioned and differences in soil-vegetation relationships of forests and their adjacent communities have been investigated by van Daalen (1981), Meadows and Dewey (1986) and Masson and Moll (1987). In the eastern Cape, Meadows and Dewey (1986) concluded that the forest/grass-heath mosaic was in a state of equilibrium with the underlying soils and that a periodic burning regime maintained a stable ecotonal boundary. In the absence of fire, Masson and Moll (1987) found that certain areas of fynbos were colonised by forest species if soil moisture, slope, soil depth and rock cover provided a suitable environment for establishment.

Scree forests provide an interesting area for research in that there exists an abrupt transition between scree forest and fynbos which usually coincides with the scree substrate boundary (Figure 1). It is not known whether the abrupt scree margin is simply due to substrate specificity in which scree forest species are unable to colonise other areas, or if it is a fire-induced phenomenon in which frequent fires limit the expansion of the forest.

A study was therefore undertaken of scree forests, their substrates and the regeneration capabilities of their margins of differing post-fire age. Provided scree forest environments are similar at all sites in the study area, and that the forest species composition is similar, it was assumed that each forest margin represents a different stage in post-fire succession. If this were not the case, then differences in forest marginal behaviour should be determined by differences in local environmental conditions. This paper compares

Figure 1. Example of scree forest edge at Orange Kloof.

environmental conditions at a number of sites representing different post-fire ages; similarities and differences in species composition and structure between sites were noted, and the regeneration capabilities of woody species in forest, margin and fynbos areas at each site were determined.

STUDY AREA

Scree forests selected for study were limited to those occurring within a 200km radius of the Cape Peninsula. Sites were situated at Orange Kloof on the Cape Peninsula, Swartboskloof in the Jonkershoek valley near Stellenbosch, on scree slopes above Betty's Bay and in the Vogelgat Nature Reserve near Hermanus (Figure 2). Both Orange Kloof and Swartboskloof are protected water catchment areas, whereas the scree forests at Betty's Bay and Vogelgat are found on steep, unprotected slopes in close proximity to the sea.

The study area is situated in a winter rainfall area, with mean annual rainfall varying from 1227 mm at Orange Kloof to 648 mm at Hermanus. Precipitation is usually associated with strong cyclonic winds from the northwest. In summer, additional moisture may be introduced into the area by strong anti-cyclonic winds from the southeast.

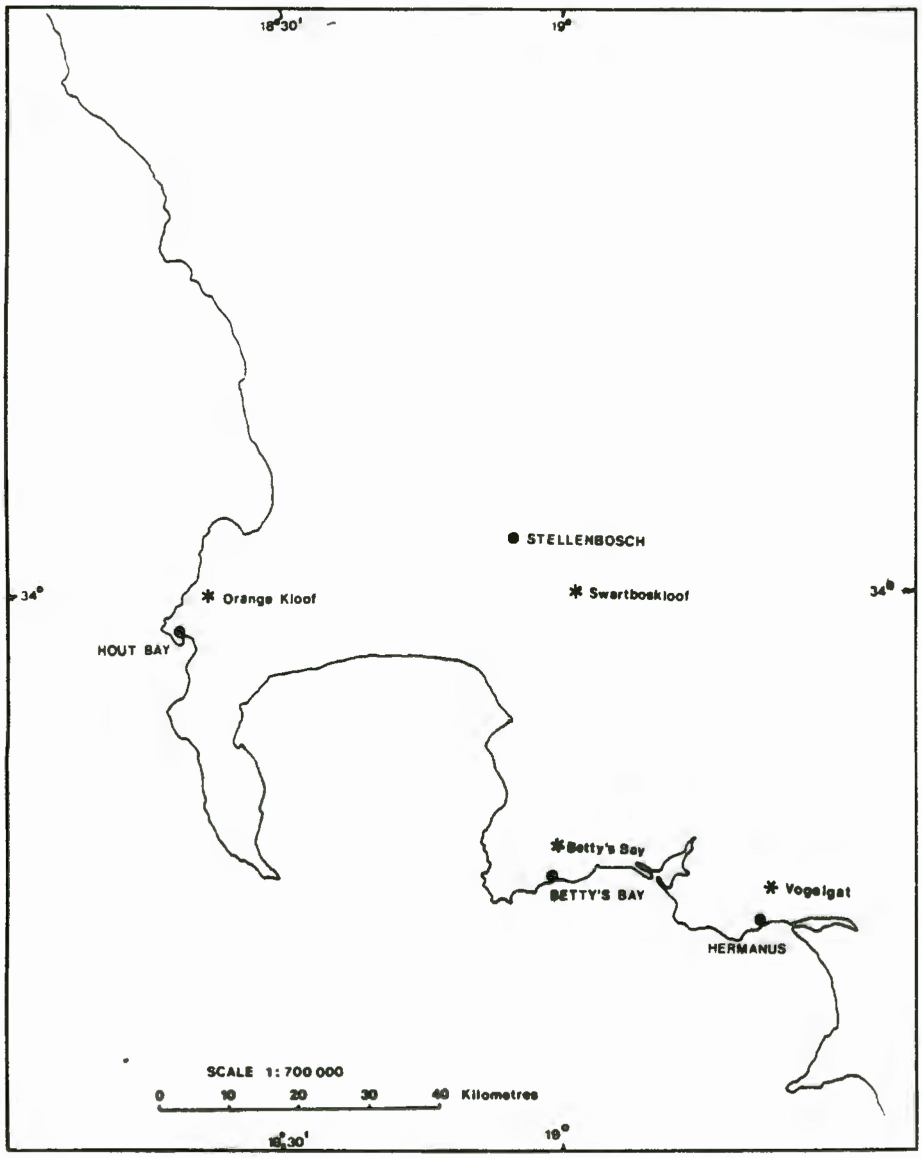

Figure 2. Map showing approximate locations of scree forests studied.

Vegetation types at each site consisted of Afromontane forest vegetation (White 1983) confined to sandstone boulder screes, and Cape fynbos. The plant communities at Orange Kloof have been described by Campbell and Moll (1977), those at Swartboskloof by McDonald (1988), and Betty's Bay by Boucher (1977). No published information is available on the forests of Vogelgat.

Soils in the study are nutrient-poor and little soil development was noted inside the scree forests.

METHODS

Selection of sites and the location of plots

Forested areas were identified using aerial photography and 1:10 000 orthophoto maps. Selected areas were then visited, and the forests were subjectively classified into riverine or scree forests, on the basis of forest structure and substrate type (outlined in Chapter 1).

Four scree forests were selected for study, with each forest located in an area representing a different post-fire age. At Swartboskloof for example, the surrounding fynbos was burnt six months prior to sampling whilst Vogelgat represents a two year post-fire community. The last known major disturbance at Betty's Bay occurred in 1970 when a wild fire swept through the area (R. Attwell pers comm 1988), placing the age of the surrounding fynbos at eighteen years at the time of sampling. Orange Kloof represents the oldest post-fire vegetation type in the study area, and has not been burnt since 1933.

By recording information from within the forest, an indication of the available seed source and potential for recruitment was obtained. Similarly, plots located in the fynbos provided an indication of seedling survival and establishment success outside the forest environment.

At each forest site, three transects were laid out perpendicular to the forest edge, each transect comprising of a 5 m x 10 m plot located within the forest, a 5 m x 10 m plot spanning the forest margin and a 5 m x 10 m plot located in the adjacent fynbos.

Data collection

In each plot, species name, its height and dbh (if greater than 1.3m tall) were recorded. Information on the regeneration strategies of different species was obtained by categorising each individual as seedling (s), sapling (S) or adult (I) according to their heights. In addition, individuals showing signs of epicormic coppicing or resprouting from ground level were assigned to the (c) and (g) categories respectively.

Environmental parameters such as aspect, slope, position on slope, percentage rock cover, and soil depth were recorded for each plot. Soil samples were collected from the forest, margin and fynbos localities along each transect and the percentage soil moisture, soil particle composition and soil nutrient status were determined for each sample. Mean annual rainfall was determined for each locality and related to the mean soil moisture values obtained along each transect.

Data analysis

All soil moisture measurements taken from within the four scree forests were analysed using one-way analysis of variance (ANOVA) and significant F-ratios determined at the 0.05 level. Similarly, soil depth estimates, soil nutrient data and information obtained from a soil particle analysis were compared and significant differences between the four forests noted. This procedure was repeated for marginal and fynbos plots. Differences in soil properties across the forest-fynbos gradient were also investigated using two-way analysis of variance and significant differences were related to vegetation distribution.

Another method of determining similarities between scree forest environments entailed the ordination of macro-environmental variables, using correspondance analysis. Macro-environmental variables such as aspect, slope, position on slope, percentage rock cover, soil depth and soil moisture were assigned values obtained from an arbitrary coding system which were then used in the construction of a data matrix (see Chapter 1 for coding system). In the event of there being no major difference in environmental conditions between the sites, no real partitioning of sites would be evident and an integration of sites on the ordination diagram was expected.

The woody species composition of the forest, marginal and fynbos plots in each locality was examined and compared. Similarities and differences in the composition of the four scree forests, their margins and fynbos plots were noted and dominant species in each area identified.

At each locality, the relative densities and relative basal area contributions of each species in six different height classes were calculated for forest, margin and fynbos plots. The results obtained were then compared graphically and related to post-fire age. The height of individuals was used in preference to dbh as an indication of stand structure because of the high number of saplings in the plots with negligible basal area and the low number of adult individuals having significant basal areas. The percentage contribution of individual species to each height class was calculated for selected species and shifts in height class dominance were related to post-fire age.

The percentage contribution of the five different growth forms identified were calculated for each forest site and comparisons were made of forest plots, margin plots and fynbos plots of differing post-fire age.

The relationship between scree forest composition and environment was investigated using canonical correspondance analysis. This is a recently developed technique in which community composition is related to known variation in the environment (Ter Braak 1986). The relative densities of species present in the forest, margin and fynbos plots were used as an indication of vegetation composition and formed the basis of the vegetation matrix whilst the environmental matrix was composed of macro-environmental variables.

RESULTS

Environmental Data

An ordination of macroenvironmental variables revealed no clear grouping of sites, although Swartboskloof plots tended to dominate the right hand side of the graph (Figure 3). This suggests an overall similarity in environmental conditions, although on closer scrutiny, differences do become apparent.

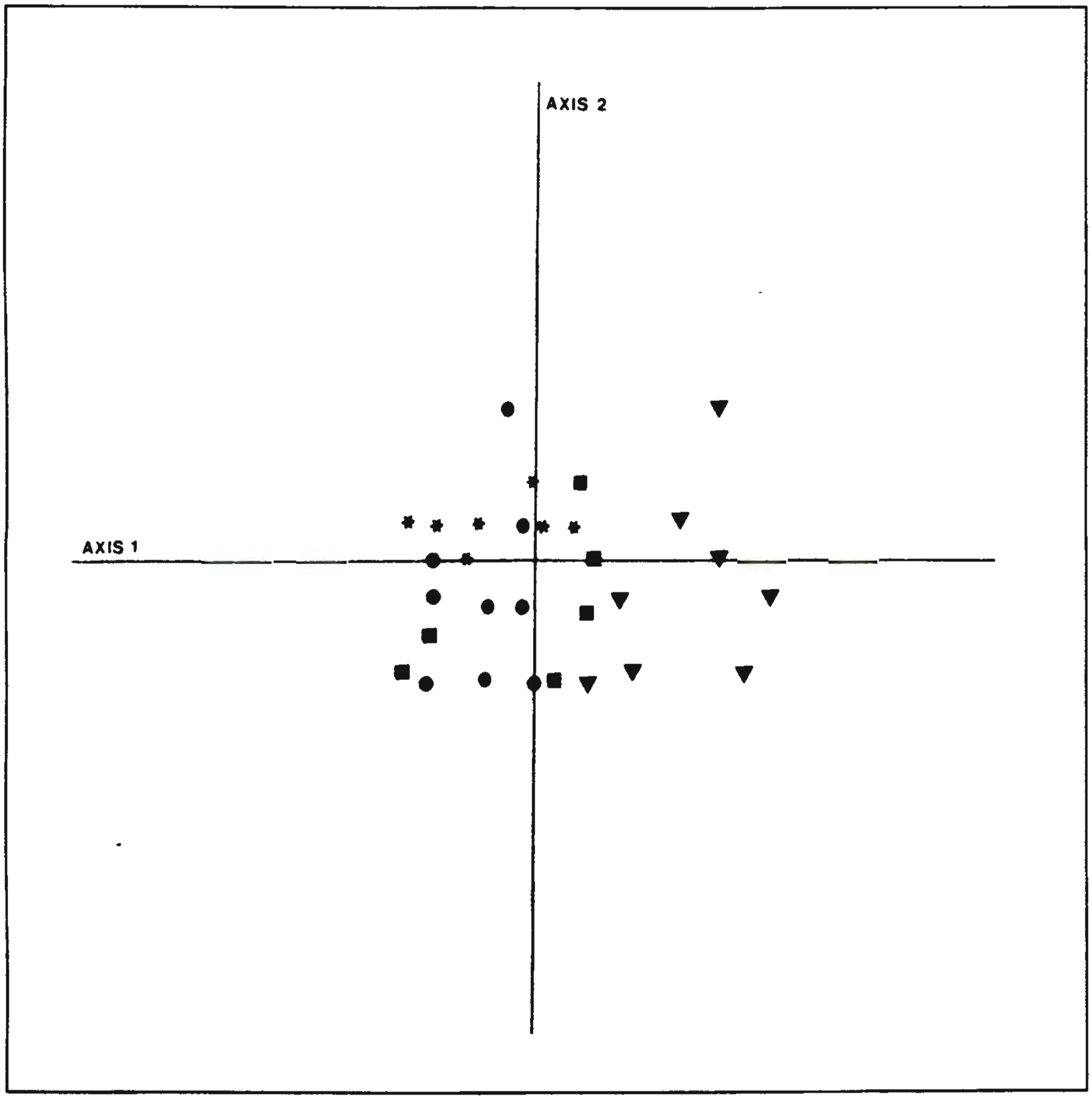

Figure 3. Ordination of macro-environmental variables using correspondence analysis. Swartboskloof plots are represented by▼; Orange Kloof by■; Betty's Bay by✱; and Vogelgat by●.

Despite the variation in rainfall, the mean soil moisture values recorded from within each forest remained constant and showed no significant difference between the four localities. (Figure 4). Similarly, marginal moisture values were not significantly different from each other but fynbos plots at Betty's Bay were significantly more moist than those soils at other localities (Table 1). At each site, moisture values recorded from fynbos soils were consistently lower than those values recorded from within the forest and on the margin.

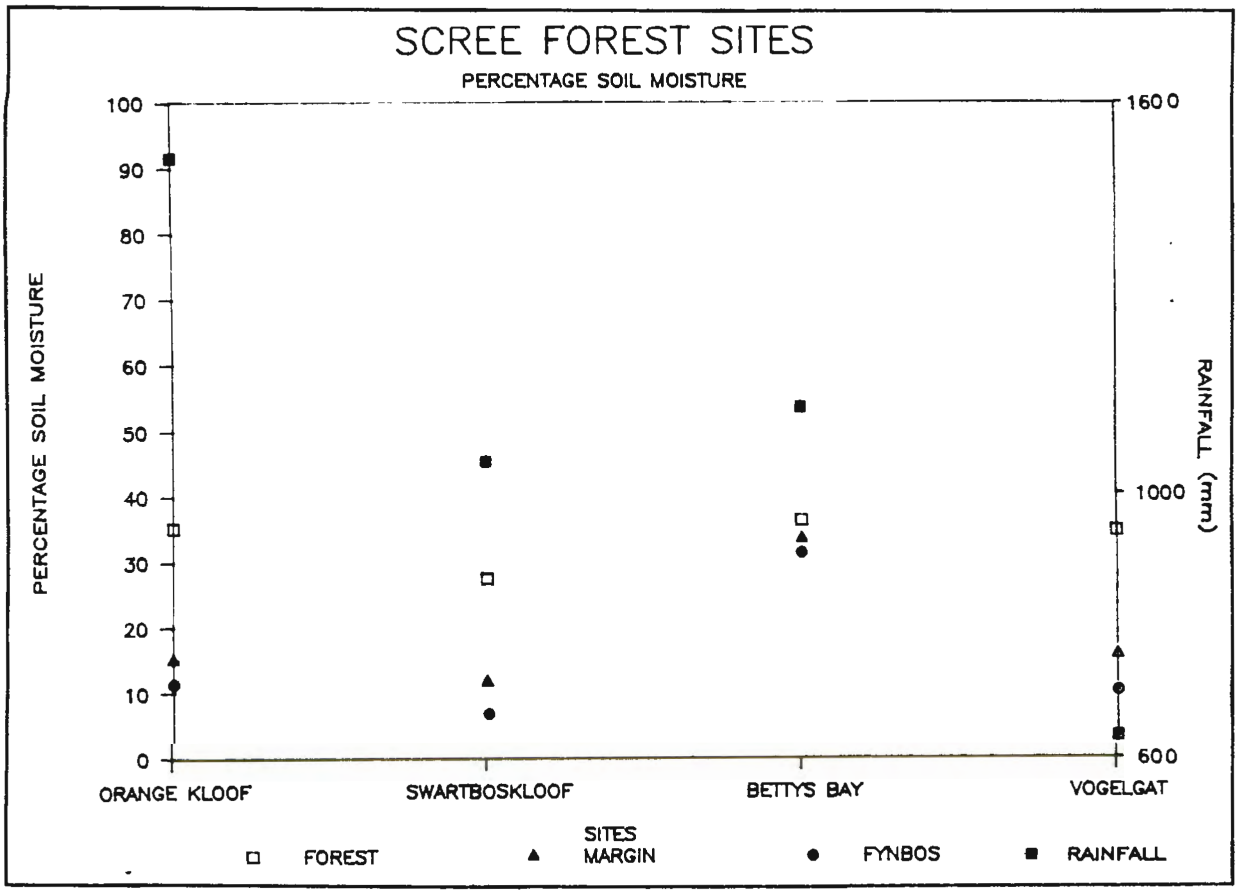

Figure 4. Percentage soil moisture recorded in forest, margin, and fynbos plots at each forest site. Mean annual rainfall for each locality is also represented.

Soil depths recorded from within forests did not differ significantly, but marginal soil depths showed a significant difference between the deeper soils of Betty's Bay and Orange Kloof and the shallower soils of Vogelgat (Table 1). The fynbos soils at Orange Kloof and Betty's Bay were significantly deeper than those at Swartboskloof and Vogelgat.

A comparison of soil particle size data showed no significant difference in marginal soil composition although soils at Vogelgat possessed higher levels of silt than soils collected from Swartboskloof and Betty's Bay. Differences were also noted in clay and silt content of fynbos soils with considerably lower levels recorded at Betty's Bay than at the other sites sampled.

TABLE 1. One way analysis of variance showing differences in environmental parameters measured at each site sampled. SWB = Swartboskloof; VOG = Vogelgat; BB = Bettys Bay; OK = Orange Kloof. Mean values from three transects in each forest are represented. D.F. for forest site =2,8 P <.05 *. Significant differences between sites are indicated by the symbols a, b, and c.

FOREST	**SWB**	**VOG**	**BB**	**OK**	**F**	**P**
% Soil moisture	30.42	36.06	36.99	35.84	0.29	NS
Soil depth	12.70	11.58	15.43	15.57	0.86	NS
% Sand	77.30	68.44	76.57	73.12	0.72	NS
% Clay	10.49	12.74	10.40	12.81	0.74	NS
% Silt	9.08a	17.81b	10.40a	13.34ab	5.59	*
Organic Matter	25.52ab	29.34b	----	7.16a	7.25	*
PH	5.89	5.20	----	4.75	3.23	NS
% Carbon	19.13ab	21.90b	----	5.37a	7.20	*
K	291.66	390.26	----	404.96	0.23	NS
Na	112.00	360.96	----	268.33	2.51	NS
MARGIN						
% Soil Moisture	18.09	23.25	35.03	22.20	3.02	NS
Soil depth	13.73ab	9.53a	18.27b	17.16b	11.24	*
% Sand	76.50	70.45	77.31	76.77	4.23	NS
% Clay	7.95	12.42	8.47	9.36	2.92	NS
% Silt	9.08	17.81	10.40	13.34	3.68	NS
Organic Matter	20.14	20.88	----	18.80	0.44	NS
PH	5.86	5.95	----	6.69	1.40	NS
% Carbon	19.13	21.90	----	16.11	0.11	NS
K	126.60	96.10	----	207.16	3.93	NS
Na	50.33a	90.46a	----	166.26b	17.41	*
FYNBOS						
% Soil Moisture	13.33a	18.37a	34.15b	18.99a	8.18	*
Soil Depth	12.00a	13.30a	23.66b	21.71b	14.50	*
% Sand	72.74ab	70.82a	80.49c	79.33bc	10.12	*
% Clay	12.46b	11.48b	3.83a	9.36b	11.97	*
% Silt	14.51ab	19.54b	5.74a	11.02ab	7.45	*
Organic Matter	15.21	16.65	----	18.77	0.62	NS
PH	5.39a	5.35a	----	6.72b	13.42	*
% Carbon	11.45	12.25	----	13.97	0.52	NS
K	112.00	360.96	----	268.33	1.23	NS
Na	32.66a	70.26b	----	45.86ab	5.49	*

An investigation of percentage rock cover showed Swartboskloof and Orange Kloof to have the highest rock cover in both the forest and the margin. Rock cover continued to dominate fynbos plots at Swartboskloof but dwindled to negligible cover at Orange Kloof. Betty's Bay had a high percentage rock cover within the forest but this dropped sharply when passing from the margin to the fynbos.

In summary, it appears that whilst most scree forests are generally found on steep slopes, usually below a slip face, the soil depth, soil moisture and extent of rock cover are not always the same. This means that vegetation differences at each of the four sites studied may not be solely a reflection of post-fire age and environmental influences must be considered in addition to disturbance history.

Vegetation Data

The total number of woody species present at each site is reflected in Table 2. The number of species found exclusively in either forested plots, marginal plots or fynbos plots is listed, along with the number of species which are not confined to one area along the transect.

TABLE 2. Number of species a) with restricted distributions and b) found in more than one area along the forest-fynbos transect at each study site.

	SWB	VOG	BB	OK
TOTAL	**23**	**29**	**13**	**28**
a) Found only inside forest	2	4	1	2
Found only on the margin	3	3	1	2
Found only in the fynbos	4	4	1	2
b) Forests and other areas	10	14	8	15
Margins and other areas	13	17	10	22
Fynbos and other areas	9	12	6	14

Although species numbers were highest at Vogelgat and Orange Kloof, all forests showed a similar pattern of having few species confined to one area along the forest-fynbos transect. On the whole the number of species found on the forest margin, but which were not necessarily confined to that region was higher than forest and fynbos numbers which tended to be equal (Table 2). Despite this similarity, the number of species shared between all four sites was low, with only four species found inside the forests at all four scree sites (Table 3). At the other end of the spectrum, seventeen species present in the fynbos were found only at one site. A comparison of distribution patterns along the forest-fynbos ecotone was therefore limited to four species which were well represented in three or more sites (Table 4).

TABLE 3 Number of species found in forest, margin and fynbos areas a) at four sites b) three sites, c) two sites and d) one site only.

	a)	b)	c)	d)
FOREST	4	5	6	11
MARGIN	1	9	11	16
FYNBOS	0	2	14	17

Within forests, *Maytenus acuminata* showed the same pattern of change in percentage contribution with increase in height class at both Swartboskloof and Orange Kloof. This similarity extended to the marginal contribution where a similar increase in densities with increase in height class was noted for both areas (Table 4). Similar trends were not apparent. in fynbos areas however, where *Maytenus acuminata* was present in intermediate height classes at Orange Kloof. No individuals were present in the fynbos at Swartboskloof. This suggests that *Maytenus acuminata* is capable of colonising adjacent fynbos communities only in the absence of fire.

Although present at both Swartboskloof and Orange Kloof, *Rapanea melanophloeos* was best represented at Vogelgat and Betty's Bay. On the margin, the percentage contribution of *Rapanea melanophloeos* to the total woody flora of the intermediate

Table 4. Percentage contribution of individual species to height classes.

	PERCENTAGE CONTRIBUTION TO EACH HEIGHT CLASS						
	SEED	HTCL1	HTCL2	HTCL3	HTCL4	HTCL5	HTCL6
MAYTENUS ACUMINATA							
FOREST							
Swartboskloof	----	----	6.67	----	22.22	35.71	10.0
Vogelgat	17.49	----	----	----	----	25.0	11.11
Orange Kloof	----	----	9.09	----	6.67	11.11	2.63
MARGIN							
Swartboskloof	----	----	1.92	2.08	4.55	25.0	----
Vogelgat	35.56	9.52	4.55	4.65	6.98	9.09	15.0
Orange Kloof	----	7.14	4.00	5.56	8.20	17.65	19.05
FYNBOS							
Swartboskloof	----	----	----	----	----	----	----
Vogelgat	----	----	----	----	----	----	----
Orange Kloof	----	----	----	3.57	13.95	11.11	----
RAPANEA MELANOPHLOEOS							
FOREST							
Swartboskloof	----	----	13.33	11.11	11.11	----	10.0
Vogelgat	60.11	21.88	30.19	20.0	15.0	25.0	22.22
Bettys Bay	----	85.71	85.71	75.0	65.71	----	35.48
Orange Kloof	----	----	9.09	----	13.33	----	5.26
MARGIN							
Swartboskloof	----	----	----	----	----	----	----
Vogelgat	48.89	14.29	18.18	20.93	18.60	9.09	15.0
Bettys Bay	40.0	84.6	77.27	57.14	60.0	50.0	20.0
Orange Kloof	----	7.14	12.0	----	14.75	11.76	4.76
FYNBOS							
Swartboskloof	----	----	----	----	----	----	----
Vogelgat	----	----	----	----	----	----	----
Bettys Bay	43.75	----	----	----	----	----	----
Orange Kloof	----	----	----	----	----	----	----
KIGGELARIA AFRICANA							
FOREST							
Swartboskloof	----	----	6.67	----	11.11	7.14	10.0
Bettys Bay	100.0	----	----	----	5.71	----	----
Orange Kloof	----	----	9.09	----	----	----	----
MARGIN							
Swartboskloof	15.0	0.78	----	----	4.55	----	----
Bettys Bay	40.0	3.85	9.09	----	----	6.25	----
Orange Kloof	----	7.14	----	----	----	----	4.76
FYNBOS							
Swartboskloof	----	----	----	----	----	----	----
Bettys Bay	31.25	14.29	----	----	----	----	----
Orange Kloof	----	----	----	----	----	----	----
HARTOGIELLA SCHINOIDES							
FOREST							
Swartboskloof	----	----	----	----	----	7.14	30.0
Vogelgat	4.37	----	----	2.86	25.0	----	14.81
Bettys Bay	----	7.14	7.14	----	----	20.0	3.23
Orange Kloof	----	----	----	----	13.33	----	----
MARGIN							
Swartboskloof	----	----	3.85	----	31.82	25.0	----
Vogelgat	----	----	----	----	13.95	----	25.0
Bettys Bay	----	7.69	4.55	----	----	25.0	30.0
Orange Kloof	----	----	----	----	1.64	----	----
FYNBOS							
Swartboskloof	----	----	----	16.67	----	----	----
Vogelgat	----	----	----	11.43	----	----	----
Bettys Bay	----	----	----	----	----	----	----
Orange Kloof	----	----	----	3.57	----	----	----

height classes remained constant, indicating a stable replacement cycle. The presence of *Rapanea melanophloeos* in the fynbos was not noted except at Betty's Bay where approximately half the woody seedlings in the fynbos were *Rapanea melanophloeos.*

On the margin, *Kiggelaria africana* was well represented in the seedling category at both Swartboskloof and Betty's Bay, with larger individuals present in height classes 4 and 5 respectively. *Kiggelaria africana* was also present in the fynbos at Betty's Bay, a factor which may be attributed to higher soil moisture availability in the area.

Hartogiella schinoides was well represented in higher height classes at all sites in the forest and on the margin. In the fynbos, its presence was noted in height class 3 only at Swartboskloof, Vogelgat and Orange Kloof. This indicates a similar growth strategy at all sites irrespective of post-fire age.

Composite relative densities within the scree forest at Swartboskloof were lower in the lower height classes, increasing gradually with height (Figure 5). Dominance shifted from *Podocarpus latifolius* and *Rapanea melanophloeos* in the lower height classes to *Olinia ventosa* in the higher height classes. A similar pattern of increasing densities with increase in height classes was reflected at Betty's Bay and Orange Kloof although sporadic fall-offs in densities were evident in height class 3 and 5 at both localities. Reasons for the lower numbers of individuals in these two height classes at both sites are not known, but may be linked to some disturbance event other than fire. Dominant species throughout the profiles were *Kiggelaria africana* and *Rapanea melanophloeos* at Betty's Bay and *Podocarpus latifolius* at Orange Kloof.

Marginal densities at Swartboskloof and Betty's Bay showed a similar trend of a decline in densities with height, except for height class 4 which was best represented in both areas (Figure 5). Vogelgat and Orange Kloof showed a similar gradual increase in densities with height, with the highest contribution being in height class 4. In both cases, this was attributed to high numbers of *Rapanea melanophloeos* individuals.

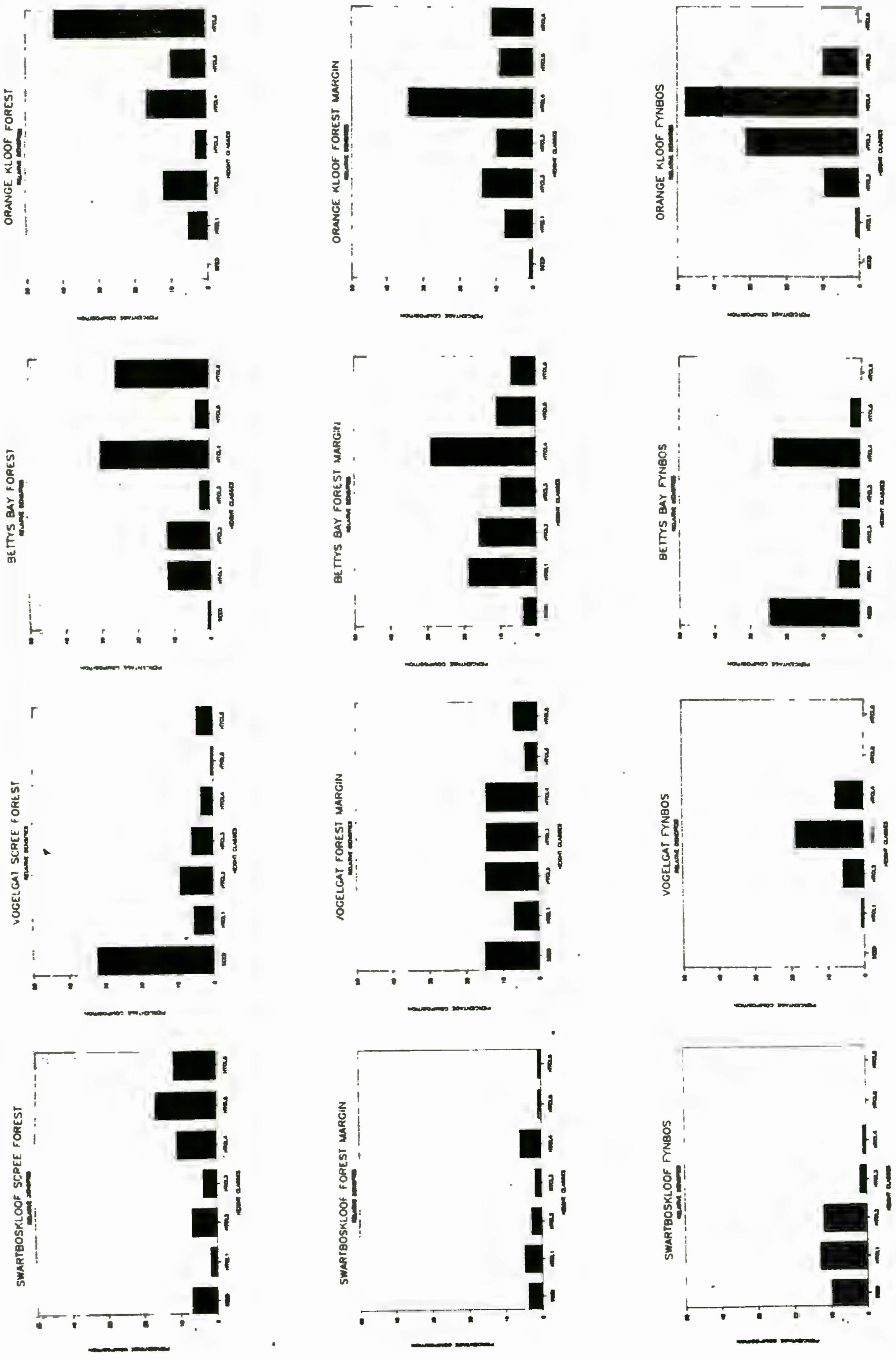

Figure 5. **Relative densities of individuals present in forest, margin and fynbos areas. Height class categories are as follows:**
Height class 1 = 0.1-0.2m;Height class 2 = 0.21-0.5m;
Height class 3 = 0.51-1.0m;Height class 4 = 1.1-3.0m;
Height class 5 = 3.1-5.0m;Height class 6 = 5.1m+.

TABLE 5 Major contributors to relative densities (D) and relative basal areas (BA) at four scree forests.

	SWB		VOG		BB		OK	
Within forest	D	BA	D	BA	D	BA	D	BA
Rapanea melanophloeos	6.02	0.04	26.55	19.44	51.69	43.53	5.55	1.20
Podocarpus latifolius	14.46	18.22	----	----	----	----	21.11	7.83
Kiggelaria africana	4.81	9.68	0.18	0.09	13.56	18.45	4.44	1.64
Olinia ventosa	12.05	41.34	0.35	----	----	----	5.55	----
Olea capensis	----	----	9.73	29.44	----	----	13.33	52.94
Maytenus acuminata	10.84	26.04	6.37	10.93	----	----	4.44	1.17
Cassine peragua	----	----	3.54	----	----	----	5.55	16.27
Cunonia capensis	----	----	----	----	5.08	33.21	----	----
Knowltonia vesicatora	8.43	----	2.48	----	6.78	----	2.22	----
Zantedetchia aethiopica	13.25	----	----	----	5.08	----	----	----
Myrsine africana	18.07	----	0.18	----	----	----	----	----
Secamone alpini	----	----	33.98	----	----	----	7.77	----
Cussonia spp	----	----	----	----	8.47	0.22	----	----
Diospyros whyteana	----	----	----	----	----	----	15.55	8.04
Hartogiella schinoides	4.82	3.20	3.19	23.10	3.39	1.13	2.22	----
Margin								
Rapanea melanophloeos	----	----	17.76	6.02	60.14	22.67	9.04	1.13
Maytenus acuminata	1.20	1.45	9.54	2.76	----	----	8.47	3.36
Kiggelaria africana	1.66	0.02	----	----	4.35	0.57	1.13	----
Cassine peragua	----	----	9.54	5.87	----	----	7.91	65.23
Olea europaea	11.29	23.56	----	----	----	----	0.56	----
Olea capensis	----	----	7.89	34.47	----	----	4.52	4.85
Hartogiella schinoides	2.89	3.31	3.62	39.69	7.25	24.70	1.13	0.14
Maytenus oleoides	2.99	56.76	----	----	----	----	2.82	14.22
Cunonia capensis	----	----	----	----	4.35	46.25	----	----
Chionanthus foveolatus	----	----	4.61	10.37	----	----	1.69	0.04
Myrsine africana	57.51	----	----	----	----	----	11.30	----
Zantdetchia aethiopica	6.07	----	----	----	0.72	----	----	----
Solanum nigrum	6.36	----	----	----	----	----	----	----
Secamone alpini	----	----	16.78	----	----	----	1.13	----
Laurophyllus capensis	----	----	0.66	----	5.07	1.05	----	----
Halleria lucida	0.29	----	0.33	----	7.97	4.38	----	----
Knowltonia vesicatora	1.16	----	6.58	----	4.35	----	9.04	----
Diospyros whyteana	----	----	----	----	----	----	12.43	1.56
Apodytes dimidiata	----	----	----	----	----	----	5.65	2.60
Cussonia spp	----	----	----	----	4.35	0.36	4.52	----
Clutia pulchella	----	----	----	----	----	----	5.08	0.64
Fynbos								
Rapanea melanophloeos	----	----	0.58	----	11.11	----	----	----
Maytenus oleoides	8.97	----	----	----	----	----	19.78	15.51
Laurophyllus capensis	----	----	1.17	----	17.46	12.20	----	----
Cunonia capensis	----	----	----	----	1.59	63.43	----	----
Leucadendron spp	----	----	0.58	----	22.22	24.28	----	----
Cassine peragua	----	----	5.26	----	----	----	19.78	11.65
Widdringtonia nodiflora	----	----	4.09	----	----	----	9.89	62.10
Myrsine africana	51.60	----	15.20	----	----	----	17.58	----
Cliffortia cuneata	21.79	----	----	----	----	----	----	----
Osmitopsis spp	6.09	----	----	----	----	----	----	----
Chrysanthemoides spp	----	----	30.99	----	----	----	----	----
Arctotis semipapposa	----	----	14.04	----	----	----	----	----
Rhus lucida	----	----	10.53	----	----	----	3.30	----
Myrica serrata	----	----	4.09	----	30.16	----	----	----
Protea spp	1.60	----	0.58	----	6.35	----	----	----
Kiggelaria africana	----	----	----	----	9.52	----	----	----
Maytenus acuminata	0.32	----	----	----	----	----	8.79	10.74

In fynbos areas, relative densities shifted from a dominance in low height classes at Swartboskloof through intermediate height classes at Vogelgat to higher height classes at Orange Kloof (Figure 5). *Maytenus oleoides* dominated both the lower height classes at Swartboskloof and the higher height classes at Orange Kloof. Similarly, *Cassine peragua* was present in the fynbos at Vogelgat and persisted in higher height classes at Orange Kloof. This suggests that *Maytenus oleoides* and *Cassine peragua* have good colonizing capabilites if protected from fire and environmental conditions are suitable for colonization.

Although basal area contributions to height classes showed a predictable pattern of highest values in the highest height class followed by a steep decline with decrease in height class, the species contributing to basal area differed markedly between forests (Table 5). Although *Rapanea melanophloeos* was a major contributor to basal area within the scree forests at Vogelgat and Betty's Bay, its contribution towards basal area at Swartboskloof and Orange Kloof was negligible. Instead, *Olinia ventosa* and *Maytenus acuminata* were dominant contributors at Swartboskloof whilst *Olea capensis* contributed just over half of the total basal area inside the Orange Kloof scree forest.

On the margin, major contributors to basal area at Swartboskloof, Vogelgat, Betty's Bay and Orange Kloof were *Maytenus oleoides, Olea capensis, Cunonia capensis* and *Cassine peragua* respectively.

No basal areas were recorded in the fynbos plots for Swartboskloof and Vogelgat but *Cunonia capensis* continued to dominate fynbos plots at Betty's Bay. Although not a major contributor to basal area on the margin, *Maytenus oleoides* and *Cassine peragua* made modest contributions towards basal area totals in the fynbos at Orange Kloof. The major contributor however, was the fynbos 'tree' *Widdringtonia nodiflora,* whilst another fynbos species, *Leucadendron spp.* made a significant contribution at Betty's Bay. The lack of large individuals in the older fynbos plots at Betty's Bay and Orange Kloof, suggests that fire is not the only cause for forest confinement to rocky screes. This is supported by figures reflecting the total basal area data for forest, margin and fynbos areas (Table 6) where even in the absence of fire, basal area totals were considerably lower in fynbos plots than in forested and marginal plots.

TABLE 6. Total basal area of forest, margin and fynbos areas adjacent to scree forests. Values are expressed in m^2/hectare.

	Swartboskloof	Vogelgat	Betty's Bay	Orange Kloof
FOREST	124.35	26.69	111.55	99.48
MARGIN	44.41	19.29	37.05	46.81
FYNBOS	-	-	2.03	2.91

Regeneration

An investigation of post-fire regeneration strategies indicated a high proportion of ground coppicing in fynbos plots at Swartboskloof and Vogelgat (Figure 6a). Ground coppicers were not evident in fynbos plots at Betty's Bay or Orange Kloof but were present inside both forests.

Epicormic resprouters were most prevalent at Swartboskloof on the margin (Figure 6b). Although evident in forest, margin and fynbos areas at Orange Kloof, their contribution to the overall composition of each area of the transect was negligible. A similar pattern of increased coppice regrowth following disturbance was reported by Childes and Walker (1987) in the Hwange National Park where most of the regeneration in the lower size classes of the *Baikaia plurijuga* woodland was due to coppicing.

Although the relatively low sapling numbers in forest and marginal plots at Swartboskloof and Vogelgat differed markedly to the higher proportions at Betty's Bay and Orange Kloof, a trend of increasing sapling representation with increase in post-fire age was noted in fynbos plots (Figure 6c). Although *Rapanea melanophloeos* saplings dominated the marginal regions of both Betty's Bay and Orange Kloof, no saplings were present in the adjacent fynbos areas. Instead, *Laurophyllus capensis* was the dominant woody species in fynbos sites at Betty's Bay and *Cassine peragua* and *Maytenus oleoides* at Orange Kloof.

Seedlings were well represented in the forest and marginal communities of the younger post-fire forests, but numbers were non-existent to negligible within forests at Betty's Bay

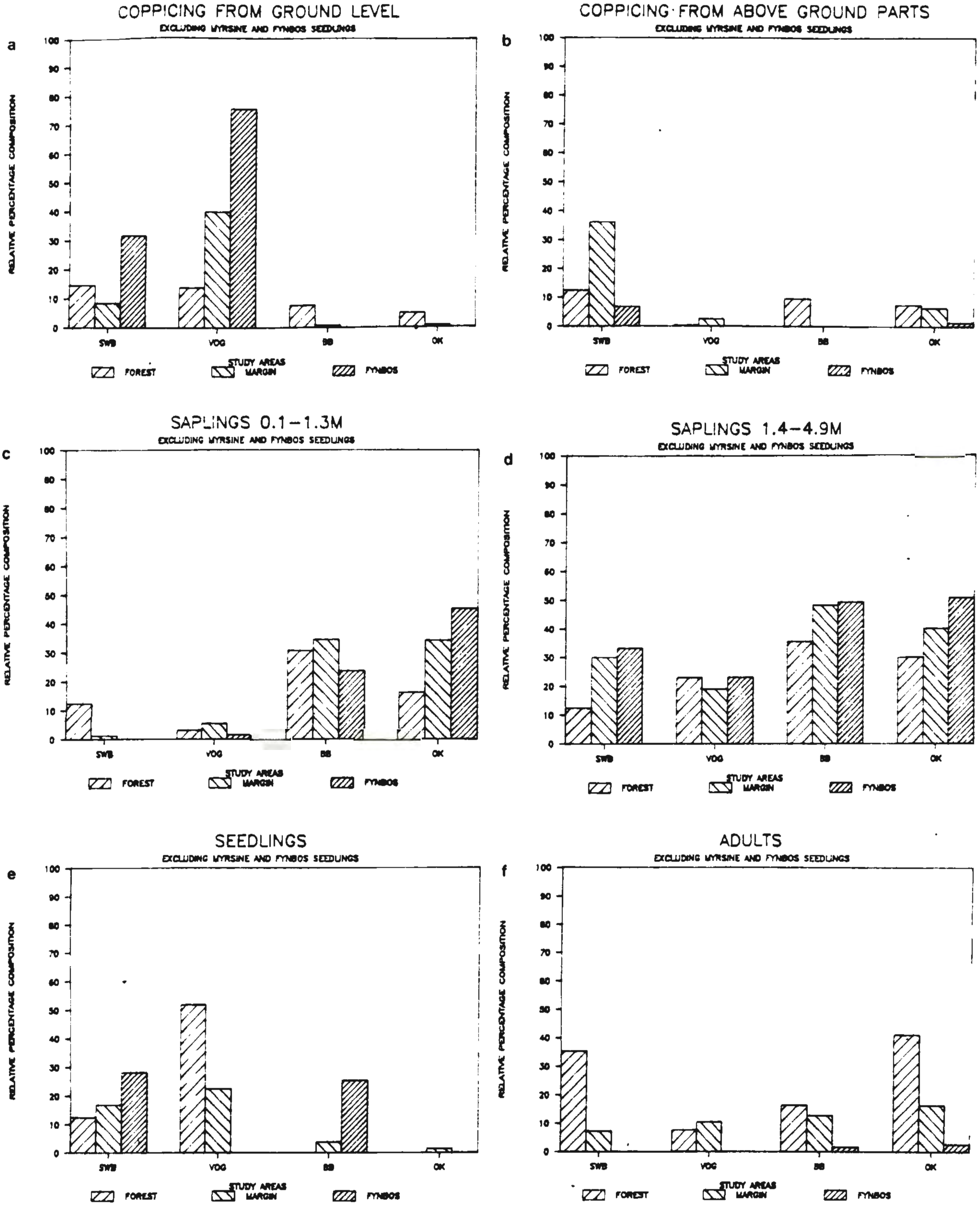

Figure 6. Categorization of individuals into different growth forms.

and Orange Kloof (Figure 6e). The only fynbos area in which seedlings of woody species were found was at Betty's Bay. This may be attributed to the higher soil moisture availability in the area and deeper soils.

The analysis of vegetation-environment relationships using CCA indicated a similar graphing pattern as that produced by correspondance analysis (Figure 3). Plots located at Swartboskloof and Orange Kloof occurred in discrete clusters on the right of the graph whilst those of Betty's Bay and Vogelgat appeared on the left (Figure 7).

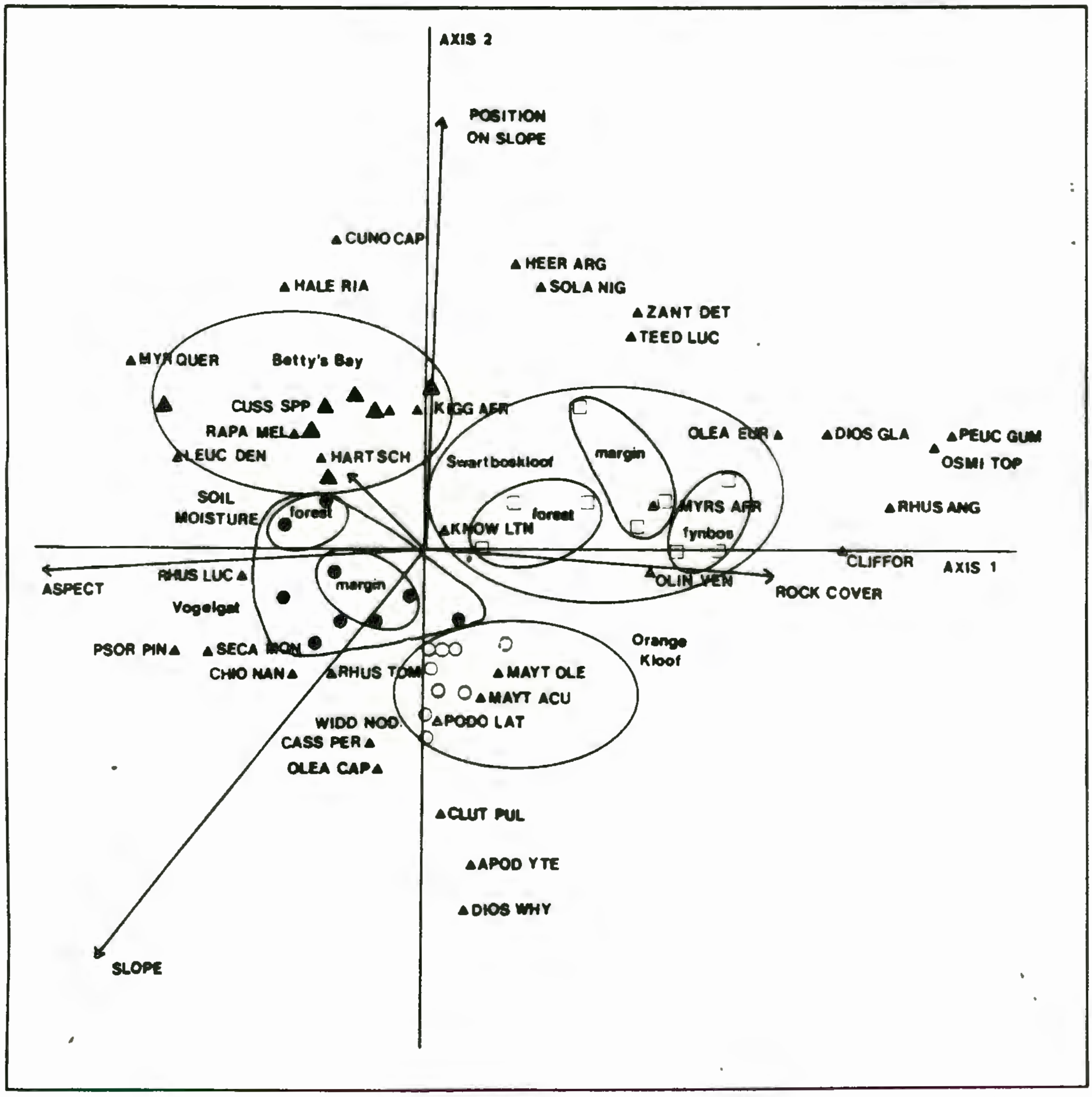

Figure 7. Canonical correspondance analysis of data using relative density data and macro-environmental variables.

Although the younger forests of Swartboskloof and Vogelgat showed a distinction between forest, margin and fynbos plots, this was not the case at Betty's Bay and Orange Kloof. This suggests a less rigid partitioning of communities with increasing time since fire.

The importance of environmental variables is depicted by the length of the associated arrow and points in the direction of maximum variation. Figure 7 indicates that much of the variation along axis 1 is accounted for by rock cover and aspect whilst axis 2 is related to position on slope and slope. A subjective appraisal of environmental data showed little variation in position on slope or steepness of slope between sites, but did indicate a decline in rock cover from plots on the right hand side of the graph to those on the left.

DISCUSSION

Very little information exists concerning post-fire regeneration of forests in southern Africa (Granger 1984; Kruger 1984). An early study by Phillips (1931) documents forest succession and ecology in the Knysna region and more recent studies by Pammenter *et al* (1985) and Everard (1986) refer to the short-term regeneration of a coastal forest and an inland forest respectively. Studies dealing with long-term protection of areas from fire have been carried out by Granger (1976) and Masson and Moll (1987). No studies document the immediate post-fire changes in structure and composition of an ecotonal community or detail intermediate stages of vegetation changes across a vegetation boundary.

The presence of forest-edge boundaries and the factors controlling their distribution have been discussed by Meadows and Dewey (1986) in the eastern Cape, by Ash (1988) in northeastern Queensland, and by Anderson and Brown (1986) in the forest/prairie edge communities of Illinois. In all three studies, fire was implicated as an important stabilizing influence on the forest edge community. Brown and Podger (1982) however, found that rainforest boundaries in Tasmania were not strictly maintained by fire frequency and their extent was influenced by a number of other factors, including local edaphic conditions and floristic composition. This tended to support Jackson's (1968) concept of succession in which vegetation boundaries are essentially stable and that chance events may create new boundaries or ebb and flow situations across existing boundaries (Brown and Podger 1982). Although fire is not discounted as being an important factor in affecting species distribution, results from this study suggest environmental conditions and species composition are the overriding factors affecting forest boundary movement.

Soil moisture values show that although fynbos soils were generally drier than forest and marginal soils, where soil moisture was sufficiently high, at Betty's Bay for example, seedling establishment was possible. This factor, together with the deeper soils, and lower rock cover indicates a possible gradation of the adjacent area to scrub-forest, if protection from fire is maintained. A similar situation was found in Tasmania (Brown and Podger 1982) where forest regeneration was in progress following 12 years of fire protection.

At Orange Kloof, where vegetation has not been burnt for fifty years, sapling regeneration in the fynbos is dominated by *Cassine peragua* and *Maytenus oleoides* and there was no evidence of seedling recruitment. This is surprising in view of the length of time passed since the last disturbance and the relatively deep, moist soils of the area. A possible explanation may lie in the species composition of the forest. Although species numbers were generally higher at Orange Kloof than at other sites, only 7 species were found exclusively in the area. The low seedling recruitment levels found along the forest-fynbos transect suggests that either common seed generators are absent from the area or recruitment is episodic. Alternatively, environmental conditions may not be optimal for seedling establishment. Major contributors to lower height classes in the earlier post-burn localities were *Maytenus oleoides* at Swartboskloof and *Cassine peragua* at Vogelgat. The same two species dominated the higher height classes at Orange Kloof which suggests that in the past, conditions were suitable for seedling establishment and implies that species recruitment in the area is episodic.

Species composition and structure has been cited as having a profound affect on the post-fire regeneration capabilities of vegetation. Stewart (1986) found that the type of disturbance affects the expression of life history attributes which results in differences in regeneration strategies and consequent changes in vegetation structure; frequent minor disturbances produced abundant seedlings and saplings of *Nothofagus menziesii* whereas infrequent disturbances had little effect on seedling regeneration. Scree forest regeneration patterns indicated that soon after disturbance, coppicing from above ground parts and from ground level were the most common forms of regeneration on the margin and in the fynbos respectively. In areas protected from fire, saplings were the dominant growth form, with relatively low levels of coppicing. Although seedling production was relatively high in recently burnt areas, it was low in fire-protected margins. This supports Stewart's findings in which the mode of regeneration adopted by vegetation is determined by the type of disturbance and frequency of occurrence. Morgan (1988) attributed the low densities of seedlings in British lowland forests to variations in light regime and the presence of dense stands of *Ilex aquifolium*, a common component of the understorey and contributor to shade. Read and Hill (1988) found that seedling densities were affected by substrate availability and Stewart (1986) reported significant differences in seedling frequencies on different substrates in frequently disturbed forests. Although no suppressive effect by understory species on seedling regeneration was noted in this study, variations in seedling numbers could be attributed to variations in substrate; the scree forest at Vogelgat had the lowest rock cover of all sites whilst fynbos areas at Betty's Bay recorded the highest moisture values.

Anderson and Brown (1986) found that prairie-edge seedling numbers almost doubled immediately following a burn, but returned to preburn levels after five years. Sapling numbers decreased initially and then returned to preburn levels. Although preburn levels of sapling numbers in the study area are not known, the higher proportions of saplings present in the older post-burn vegetation suggests that there is a gradual increase in numbers with time.

Pammenter *et al* (1985) found that three years after a fire, the regenerating forest consisted almost entirely of *Trema orientalis*, with most of the regeneration derived from seed. This monospecific dominance was not a feature of scree forest regeneration and seedling production was not the most common form of regeneration.

The relationship between relative density and basal area in burnt and unburnt forest communities has been mentioned by Pammenter *et al* (1985). Whereas plant densities remained relatively constant, basal area was considerably reduced in post-fire communities. Although a similar reduction in basal area following fire was noted in fynbos plots at Swartboskloof and Vogelgat, this was not the case in marginal plots where similar patterns were evident in both recently burnt communities and fire-protected areas.

Despite the similarities shown in overall densities within forests, individual species profiles bore no relation to the general density patten reflected by each forest. This underlines the importance of identifying individual species attributes and their response to disturbance.

CONCLUSION

Although initially the scree forest environment was considered to be similar in all four study sites, this was not the case, with soil moisture, soil depth and the extent of rock cover varying between sites. This factor, in conjunction with the varied species composition of the forests, precluded the use of the chronosequence approach to studying vegetation changes in which vegetation of differing ages are taken to represent differing stages in succession. The regeneration strategies employed by different species following disturbance was nevertheless informative and highlighted the need for further information of this type.

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SECTION 4

RIVERINE FOREST ECOTONES OF DIFFERING POST-FIRE AGE

CHAPTER FOUR

FIRE AND THE ECOTONAL DYNAMICS OF RIVERINE FOREST IN THE SOUTHWESTERN CAPE, CAPE PROVINCE, SOUTH AFRICA

ABSTRACT

The relationship between forest boundary dynamics, the environment and post-fire age of four riparian forests were investigated. Environmental differences along the forest-fynbos gradient and between sites were identified using analysis of variance and soil-vegetation relationships determined using canonical correspondance analysis. Relative densities, basal area and growth form characterisation were used to obtain a structural profile along the forest-fynbos ecotone.

Environmental differences were generally not detected along the forest-fynbos gradient at each site, but significant differences were noted between the younger, more recently disturbed ecotones of Swartboskloof and Platbos and the older fire-protected ecotones of Orange Kloof and Wynand Louwsbos.

A comparison of vegetation composition and structure along each forest-fynbos gradient revealed no consistent trends although density patterns within the forest and regeneration strategies at Swartboskloof were markedly different from the other localities sampled. Fluctuations in marginal density patterns were identical at the two fire-protected sites and were attributed to episodic seed production and the differential growth of species.

INTRODUCTION

The southwestern Cape region of the Cape Province is one of five mediterranean-type ecosystems supporting a heath or shrubland vegetation (Kruger 1979). The dominant vegetation is fynbos, a low sclerophyllous heathland in which members of the families Ericaceae, Restionaceae and Proteaceae are common. Forest communities present in the area can be categorised as either scree forest or riparian forest depending on substrate type and availability of water (Chapter 1).

The importance of soil moisture in determining the forest-fynbos balance was first suggested by Phillips (1931) and later supported by Taylor (1978) who identified hygrophilous fynbos sites as being seral to forest in the absence of fire. This was supported by Masson and Moll (1987) who found that forest colonization of fynbos was possible in the absence of fire, although other local environmental factors such as soil depth, slope and degree of rockiness also affected the rate at which colonization proceeded. In the southern Cape, van Daalen (1981) found no evidence of forest precursors in fire-protected fynbos 'islands', although the limits of a natural forest-fynbos boundary in the Ysternek Nature Reserve was determined by soil moisture and the presence of deep alluvial soils.

Owing to the highly flammable nature of fynbos vegetation, disturbance in the form of summer wildfires is common throughout the region. Although fire rarely penetrates forest, substantial damage to the marginal flora may result, thus reducing the extent of the ecotonal boundary and limiting forest expansion. It is not known whether the restricted nature of the southwestern Cape forests is simply due to limited water availability or is a product of frequent burning practices. A study of riparian forest vegetation was therefore undertaken determine to the environmental variables that could be correlated with the forest-fynbos boundary. This paper examines the role of soil moisture and other environmental variables in determining the ecotonal boundary. The effect of fire protection on forest marginal dynamics is investigated and forest precursor species extending beyond the confines of the forest are identified. In addition, the question is asked whether areas protected from fire for the same period of time exhibit similar patterns in vegetation dynamics.

STUDY AREA

Locality

The study was limited to four riverine forests located within 200 km of the Cape Peninsula and for which reliable information on past disturbance was available. Swartboskloof lies within the Jonkershoek State Forest area near Stellenbosch and has been used extensively as a mountain fynbos research site (Van Wilgen *et al* 1986). The Orange Kloof water catchment is situated on the back of Table Mountain in close proximity to the sea, above Hout Bay. The remaining two study sites, namely Platbos and Wynand Louwsbos, are located in the Kogelberg State Forest area where access is restricted and compartmentalised burning of fynbos is enforced (Figure 1).

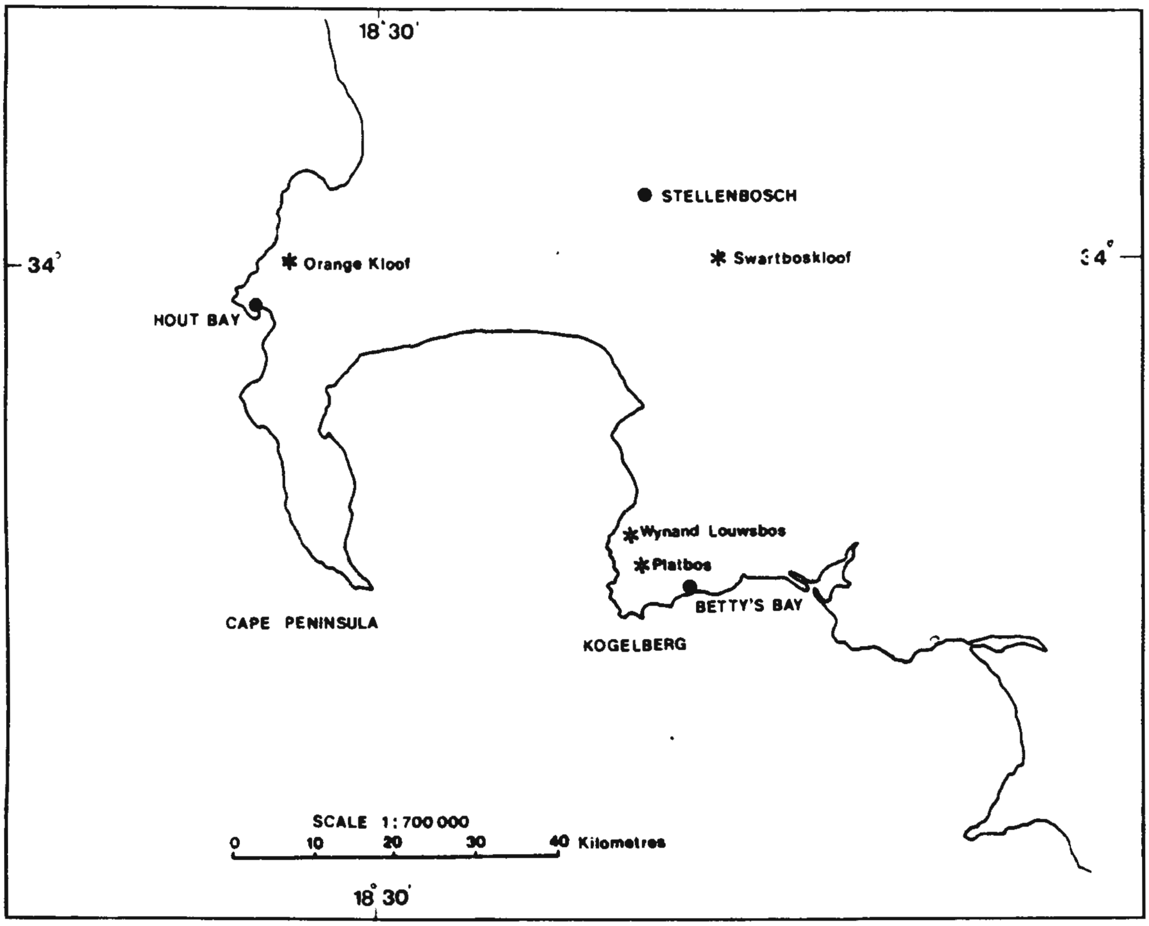

Figure 1. Map showing the approximate location of riverine forests sampled in the study.

Climate and soils

The climate of the southwestern Cape region is characteristically mediterranean with hot, dry summers and cool, wet winters. Mean annual rainfall ranges from 1475 mm at Swartboskloof to 1208 mm at Oudebosch which is situated at the entrance to the Kogelberg State Forest. Rainfall is greatly influenced by orographic features and much of the variation in the region can be directly attributed to topography. In summer, low rainfall may be supplemented by precipitation from mist brought in by light southeasterly winds. These winds may reach gale-force and when associated with rains, are generally referred to as the 'black southeaster'. In winter, precipitation is brought to the area by strong northwesterly winds and take the form of a succession of eastward-moving fronts (Jackson and Tyson 1971).

Temperatures recorded on the Cape Peninsula range from 10.7° to 33°C in summer and from 5° to 25°C in winter. Temperatures are slightly lower at Jonkershoek, varying from between 14.5° and 27.3°C in summer and 6.2° and 16.8°C in winter.

Soils in the vicinity of the forest sites sampled are generally correlated with the underlying parent rock. Most are acidic, nutrient-poor and are derived from quartzitic sandstone. Colluvial drift covers much of the floor of the Swartboskloof and Orange Kloof catchments and it is on this substrate that forests are most likely to be found (McKenzie 1978).

METHODS

Site selection and the location of plots

Using aerial photography and 1:10 000 orthophoto maps, forest patches were identified, visited and then classified as riverine or scree forests on the basis of forest structure and substrate type (Chapter 1). Riverine forests for example, were generally densely stocked and were confined to perennial streams or watercourses in contrast with the more open nature of scree forests found on loose, unconsolidated boulder scree. Further information on scree forest structure and composition is outlined in Chapter 3.

Since information on past disturbance events was not readily available for all forests in the study area, the study was confined to those areas in which previous fire management practices had been documented. Four forest sites were sampled; the Swartboskloof catchment area at Jonkershoek was burnt in March 1987 and represents the most recently disturbed site. In contrast, Orange Kloof on the Cape Peninsula has not been disturbed for more than fifty years and is representative of a fire-protected environment. The two other forests sampled, Platbos and Wynand Louwsbos, were last burnt in 1983 and 1945 respectively. The long period of fire protection afforded to both Orange Kloof and Wynand Louwsbos enabled a comparison to be made of fire-free marginal dynamics in two different localities. In addition, the influence of *Protea mundii* on forest expansion was recorded at Platbos and Wynand Louwsbos. *Protea mundii* is endemic to the Kogelberg and is found in dense stands along the forest margin (Rourke 1980).

At each forest site, three transects were set out perpendicular to the forest edge. Each transect consisted of a 5m x 10m plot located within the forest, a 5m x 10m plot spanning the forest margin and a 5m x 10m plot located in the adjacent fynbos.

Data collection

In each plot, the species name, height and dbh (if greater than 1.3m in height) of woody individuals were recorded. Post-fire regenerative capabilities were assessed by assigning individuals to the seedling category if they were less than 0.1m in height, sapling categories 1 and 2 if their heights ranged from 0.1-1.3m and > 1..3-5m respectively and the adult category if individuals exceeded 5m in height. Regeneration through epicormic resprouting or coppicing from ground level was also noted and individuals displaying regenerative strategies of this nature were assigned to the C and G categories respectively.

Environmental data recorded from each plot included aspect, slope, position on slope, percentage rock cover and soil depth. Soil samples collected from within the forest, on the margin and in the fynbos were tested for differences in soil moisture, soil nutrient composition and soil particle size.

Data analysis

The differences in environmental conditions of forest, margin and fynbos plots along transects were assessed for each site using two-way analysis of variance and significant F ratios determined at the 0.05 level. This comparison was carried out in order to determine which factors differed significantly between those areas supporting forest and those not and which would therefore be likely candidates for limiting fynbos expansion. To determine the similarities in environmental conditions between sites, a further comparison of all forested plots , all marginal plots and all fynbos plots was performed using one-way analysis of variance and significant differences noted at the 0.05 level.

Another method of investigating similarities between riverine environments involved the ordination of environmental variables using correspondance analysis. Similarities between sites were indicated through plot location, with clumping of plots indicative of similar site conditions.

The woody species composition of each of the four forest sites was examined and comparisons made of woody species numbers in forested plots, marginal plots and fynbos plots.

By assigning individuals to different height classes, the relative density of each height class was assessed for each area along the transect. Height class categories were arbitrarily chosen and were used in preference to the more commonly used dbh classes so that the large number of saplings of negligible basal area present at each site could be included in the analysis.

Using dbh measurements, basal area estimates were calculated for each region along the forest-fynbos transect and values obtained for each site related to post-fire age.

The contributions of individual species to density and basal area were calculated and dominant contributors identified at each site.

The number of individuals in each growth form category was determined for forest, margin and fynbos areas, and expressed as a percentage of the total woody flora in that region. These percentages were then graphed and comparisons made between sites.

Vegetation-environment relationships were investigated using canonical correspondance analysis (CANOCO). This technique is an extension of DECORANA and relates community composition to known variation in environment (Ter Braak, 1986). Two separate analyses were carried out; the first using macro-environmental variables as the environmental data set, whilst the second data set reflected particle size and soil nutrient composition. In both cases, relative densities of species were used as an indication of vegetation composition.

RESULTS

Environmental data

An examination of macro-environmental variables at each site revealed little variation in conditions at Platbos, Wynand Louwsbos and Orange Kloof. Forests were generally found on moderately sloping terrain, in areas having low rock cover and relatively deep soils. In contrast, riverine forest at Swartboskloof differed from the other forests sampled, being found on steeper slopes, with shallow soils and a more rocky terrain.

Two way analysis of variance determining differences along transects showed that, with the exception of the Wynand Louwsbos transects where significant differences in soil depth, sand content and K levels were found, there was no significant difference between forest, margin and fynbos plots at each site for the rest of the variables measured (Table 1). This suggests that conditions along the forest-fynbos transect are not sufficiently different to preclude forest expansion, and other factors such as species composition and disturbance history may be determinants of present patterns of vegetation dynamics.

TABLE 1. Two way analysis of variance showing differences in environmental variables along transect.
D.F. = 2,8 P < 0.05.
Significant differences along the transect are indicated by the symbols a, b, and c.

Soil depth (cm)	FOREST	MARGIN	FYNBOS	F	P
Swartboskloof	16.03a	16.12a	12.78b	9.33	.05
Platbos	23.73	19.73	16.93	0.88	N.S.
Wynand Louwsbos	37.03a	36.37a	23.72b	18.76	.05
Orange Kloof	35.46	32.99	33.75	0.39	N.S.
Soil moisture (%)					
Swartboskloof	28.21a	22.44ab	10.47b	5.41	.07
Platbos	31.31	27.64	34.39	1.07	N.S.
Wynand Louwsbos	25.41	20.30	26.24	2.83	N.S.
Orange Kloof	21.50	21.84	22.88	0.79	N.S.
Sand content (%)					
Swartboskloof	72.73	73.08	76.34	5.69	N.S.
Platbos	60.64	58.60	58.72	1.36	N.S.
Wynand Louwsbos	70.43	69.49	76.11	17.89	.05
Orange Kloof	67.31	68.57	67.90	0.36	N.S.
Clay content (%)					
Swartboskloof	10.53	10.40	2.71	4.39	N.S.
Platbos	17.65	18.66	17.22	1.13	N.S.
Wynand Louwsbos	14.76	14.91	12.42	2.25	N.S.
Orange Kloof	21.50	21.84	22.88	0.79	N.S.
Silt content (%)					
Swartboskloof	14.05	14.27	13.53	0.08	N.S.
Platbos	24.11	25.97	26.74	1.18	N.S.
Wynand Louwsbos	17.63	17.55	15.56	3.26	N.S.
Orange Kloof	19.67	19.32	18.72	0.28	N.S.
Organic matter (%)					
Swartboskloof	21.64	20.02	13.08	1.97	N.S.
Platbos	19.49	20.27	21.27	0.08	N.S.
Wynand Louwsbos	18.10	16.84	15.00	1.15	N.S.
Orange Kloof	13.85	15.51	16.95	0.27	N.S.
Carbon (%)					
Swartboskloof	16.23	14.97	9.87	1.93	N.S.
Platbos	14.64	18.42	15.99	2.64	N.S.
Wynand Louwsbos	13.65	12.70	11.39	1.58	N.S.
Orange Kloof	12.09	14.36	12.79	0.61	N.S.
K Levels (ppm)					
Swartboskloof	225.33	115.00	25.67	3.81	N.S.
Platbos	129.60	88.70	89.53	0.34	N.S.
Wynand Louwsbos	121.80a	66.60b	45.90b	11.03	0.05
Orange Kloof	206.50	80.70	120.90	0.65	N.S.
Na Levels (ppm)					
Swartboskloof	69.00	54.67	16.33	1.26	N.S.
Platbos	135.43	102.20	88.97	0.85	N.S.
Wynand Louwsbos	94.43	53.83	41.07	3.64	N.S.
Orange Kloof	118.40	64.37	85.77	0.38	N.S.
PH Value					
Swartboskloof	5.65	5.17	4.84	1.67	N.S.
Platbos	4.13	4.18	3.76	1.03	N.S.
Wynand Louwsbos	4.62	4.50	4.36	2.17	N.S.
Orange Kloof	5.42	5.01	5.13	0.88	N.S.

Despite uniformity of conditions along the forest-fynbos transect, a comparison of all fynbos plots revealed that significantly higher percentages of carbon, silt and soil moisture and lower levels of pH and sand content were recorded in the vicinity of Platbos when compared with other fynbos sites sampled. In contrast, fynbos soils at Swartboskloof were generally shallower and had lower percentages of clay and soil moisture. A comparison of all marginal plots sampled again distinguished Platbos from the other sites by having the highest percentage silt, soil moisture and lowest percentage sand (Table 1). Inside forests, significant differences were not so apparent and most differences were again reflected by Platbos and Swartboskloof. Forest soils collected from Platbos for example, had significantly lower levels of sand and pH values than other forested sites, whilst shallow soils with a high sand content and high pH were collected from the riverine forest at Swartboskloof.

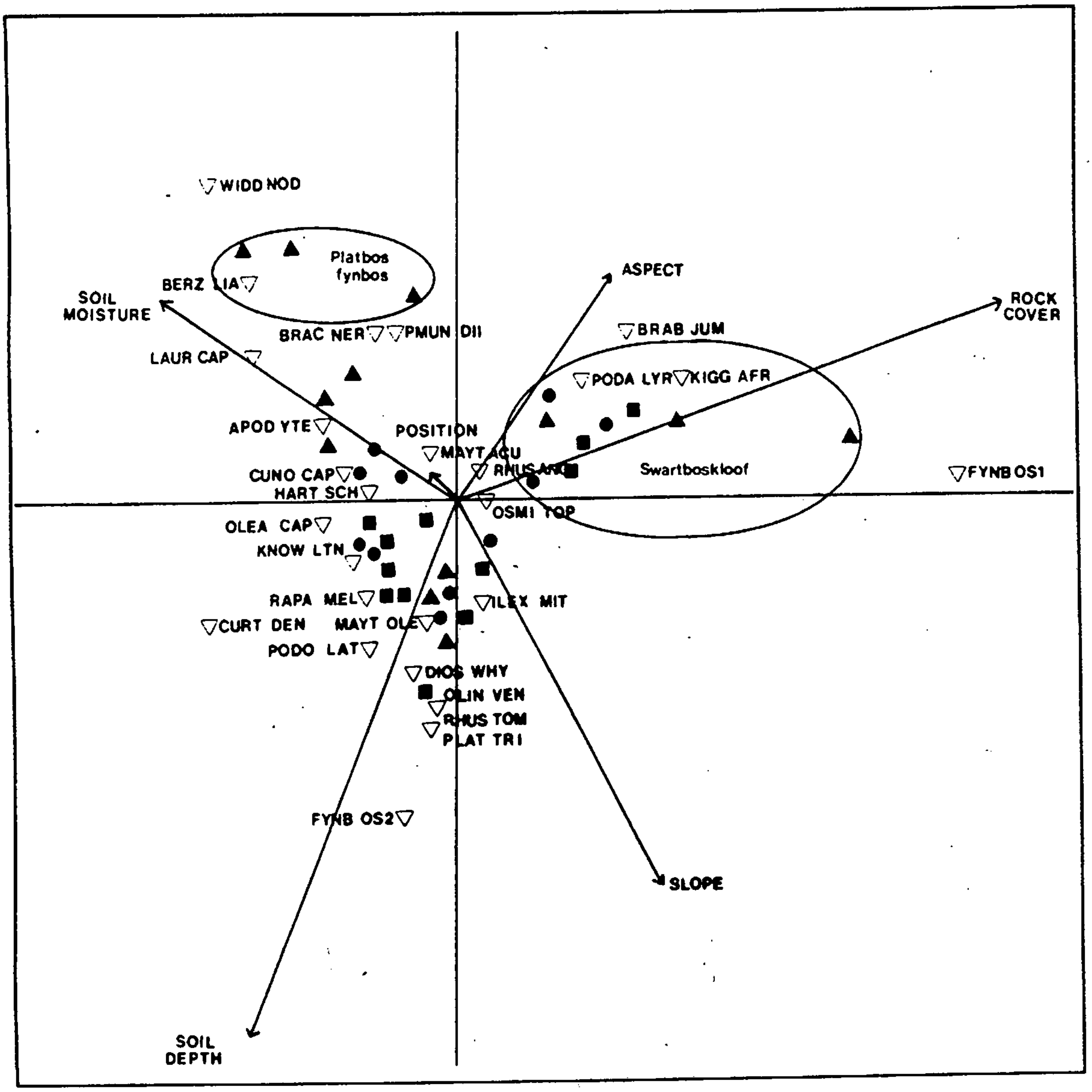

Figure 2. Canonical correspondence analysis using relative density data and macro-environmental variables. Forest plots are represented by ■; marginal plots by ●; and fynbos plots by ▲.

The differences noted between the more recently disturbed forests of Platbos and Swartboskloof, and the older, protected sites of Wynand Louwsbos and Orange Kloof were also illustrated by sample plot ordination patterns produced using CANOCO (Figure 2 and 3). In Figure 2, plots sampled at Swartboskloof appeared on the right of the ordination diagram in contrast to the interspersed nature of the plots located on the left. In Figure 3, a clear separation of forest, margin and fynbos plots was illustrated by the younger sites of Swartboskloof and Platbos. The distinction made between Platbos fynbos plots and other fynbos sites is also reflected by its isolation at the top left of

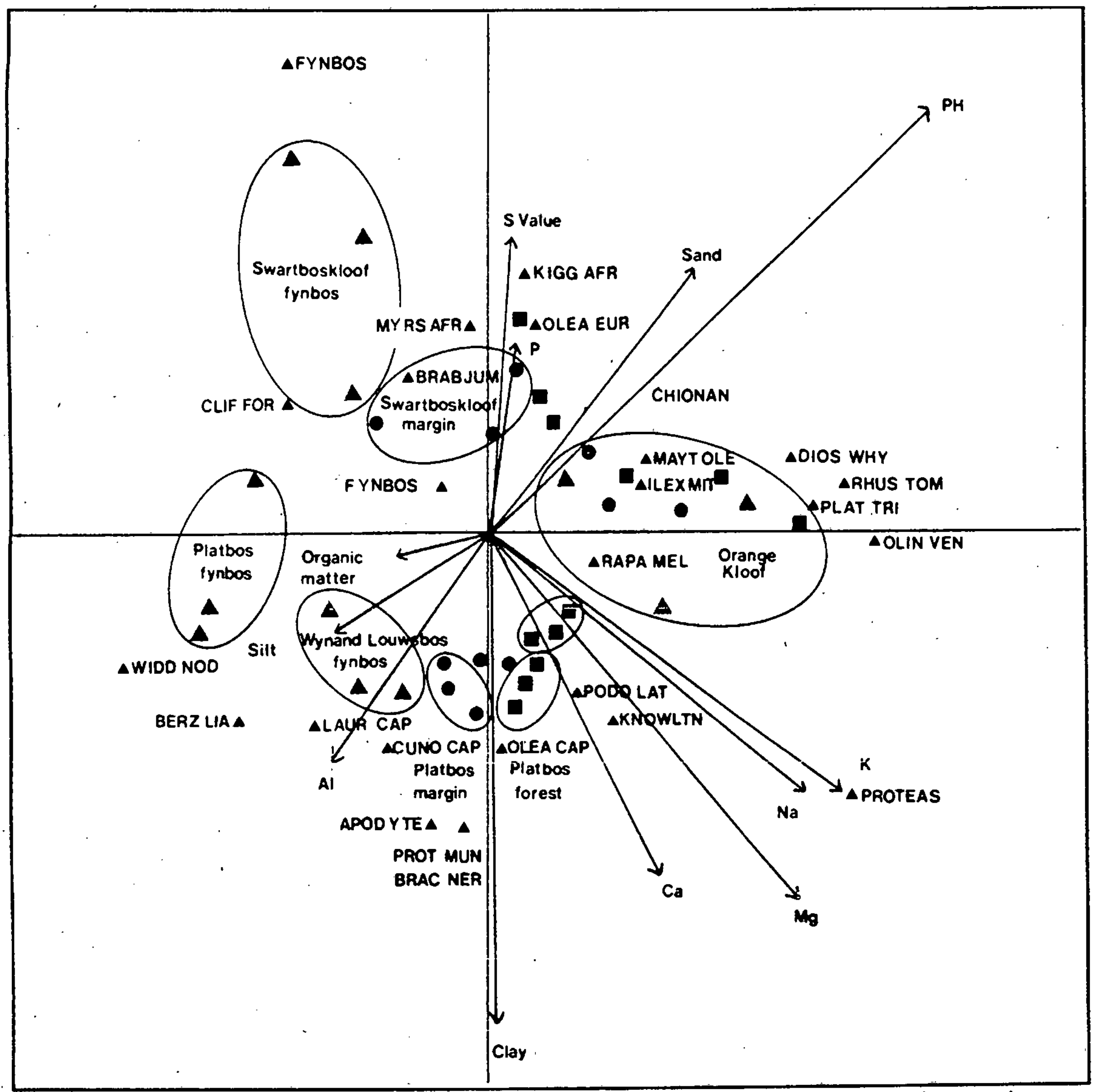

Figure 3. Canonical correspondence analysis using relative density data and of micro-environmental variables

Figure 2.

In summary, although conditions along the forest-fynbos transect did not differ substantially at each site and appeared superficially to be the same, significant differences between sites were noted. This therefore precluded the adoption of a chronosequence approach to studying succession in which similar sites supporting vegetation of different ages are compared. Despite this, an investigation of soil-vegetation relationships at each site and the analysis of vegetation structure was considered meaningful.

Vegetation data

Species richness

The number of species present in each site studied and a breakdown of distribution patterns is reflected in Table 2. In total, 42 species were found in all four areas, with Swartboskloof and Orange Kloof contributing the lowest and highest numbers respectively. Of the 18 species present at Swartboskloof in the riverine site, 10 were found inside the forest, 13 were found on the margin and 9 were found in the fynbos. Values expressed as percentages of the total found in each area revealed a high percentage of the total woody flora were present on the margin at Platbos and Wynand Louwsbos (82.61% and 90.91% respectively). This contrasts with the relatively low levels of 72.22% and 73.33% recorded for Swartboskloof and Orange Kloof and illustrates a difference in vegetation behaviour between those sites found on the Kogelberg and those located elsewhere.

TABLE 2. Species richness at each site. SWB = Swartboskloof WLB = Wynand Louwsbos OK = Orange Kloof

	TOTAL	SWB	PLATBOS	WLB	OK
	42	18	23	22	30
Number of species found in					
forested area		10	15	12	23
marginal area		13	19	20	22
fynbos area		9	5	13	18

Relative Densities

An investigation of relative densities showed that within forests, Platbos, Wynand Louwsbos and Orange Kloof showed similar patterns of alternating high and low densities in the larger height classes (Figure 4). Swartboskloof on the other hand, produced a sharply descending J-shaped curve which is reportedly a reflection of an even-aged mixed species stand (Lorimer 1985). Major contributors to height classes varied at each site, with *Curtisia dentata, Podocarpus latifolius* and *Rapanea melanophloeos* dominating higher height classes at Platbos, *Curtisia dentata* and *Hartogiella schinoides* dominant adults at Wynand Louwsbos and *Olea capensis* and *Rapanea melanophloeos* the common adult form at Orange Kloof. *Rapanea melanophloeos* was generally well represented in all height classes at each of the four sites sampled, although adult representatives of *Ilex mitis* and *Brabejum stellatifolium* were also found at Swartboskloof. *Kiggelaria africana* was a major seedling producer within forests at Swartboskloof and Orange Kloof although in both instances, no adult individuals were recorded. Similarly, *Podocarpus latifolius* was a major contributor to lower height class densities and seedling numbers, but was not well represented in the higher height classes at Wynand Louwsbos. In contrast, *Maytenus acuminata* was a major contributor to all height classes at Platbos and contributed significantly to seedling numbers in that forest.

Height class densities on the margin were identical in the two fire protected forest sites, with both Wynand Louwsbos and Orange Kloof showing high representations in height class two and four (Figure 4). These fluctuations could not be attributed to any one species but may be caused by episodic seed production or may be simply a reflection of differential growth patterns among species. *Rapanea melanophloeos, Curtisia dentata* and *Hartogiella schinoides* were again well represented in all height classes at Wynand Louwsbos although at Orange Kloof, *Olea capensis* was replaced by *Apodytes dimidiata* as an important contributor to adult marginal densities. Slightly better representation of lower and intermediate height classes was reflected by density patterns at Platbos and Swartboskloof. *Maytenus acuminata* continued to dominate seedling numbers at Platbos

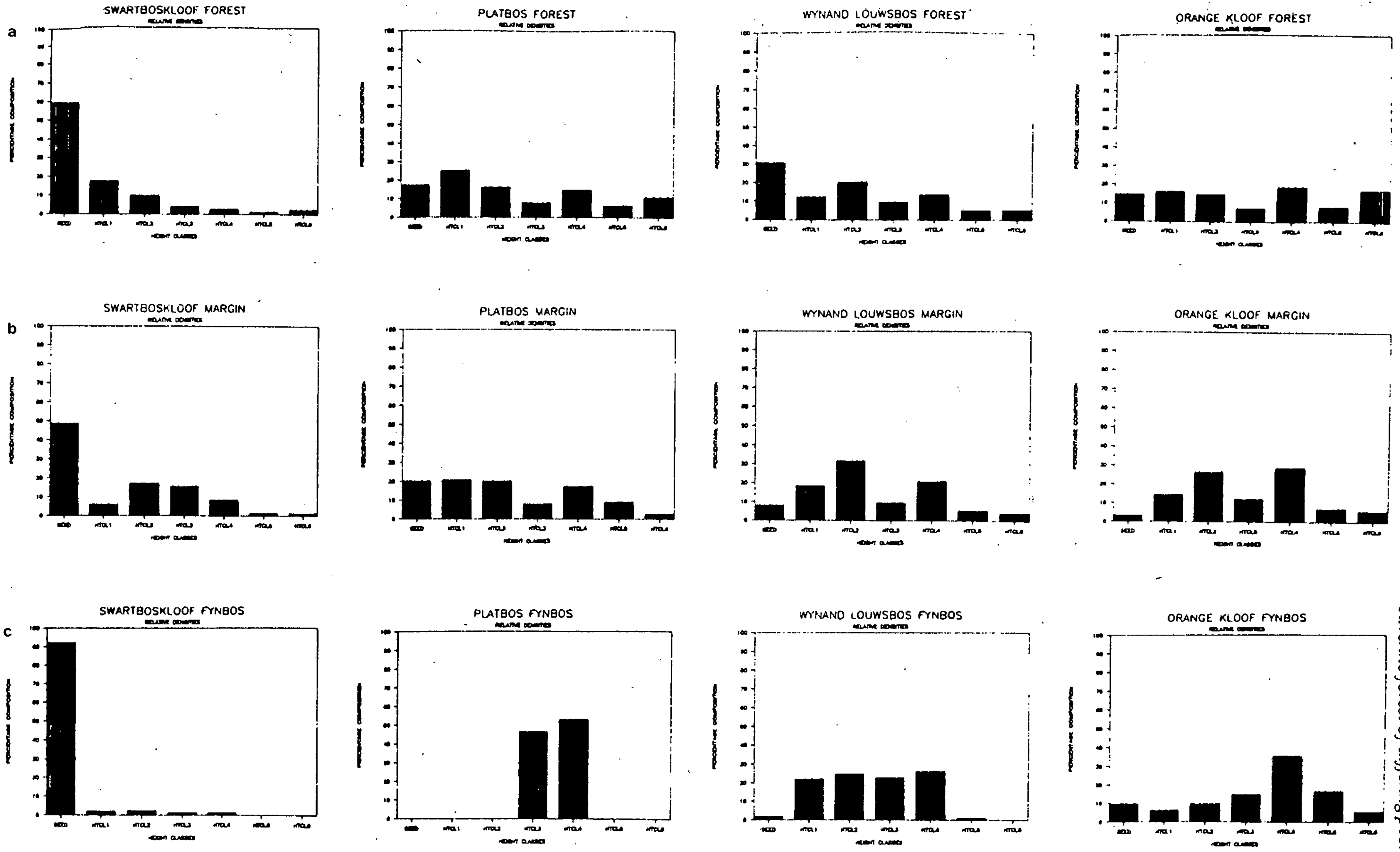

Figure 4. Relative densities of individuals in forest, margin and fynbos areas. Height class categories are as follows
Height class 1 = 0.1-0.2m;Height class 2 = 0.21-0.5m;
Height class 3 = 0.51-1.0m;Height class 4 = 1.1-3.0m;
Height class 5 = 3.1-5.0m;Height class 6 = 5.1m +.

and along with *Olea capensis* and *Hartogiella schinoides,* was well represented in all height classes. In contrast to the high numbers of *Curtisia dentata* and *Podocarpus latifolius* present within the forest at Platbos, *Curtisia dentata* was poorly represented on the margin with *Podocarpus latifolius* present only in the lower height classes at Platbos. At Swartboskloof, *Kiggelaria africana* continued to produce many seedlings on the forest margin but adult species common within the forest were not represented on the margin. Instead *Rhus angustifolia* and *Rapanea melanophloeos* dominated the intermediate height classes.

Plots located some 20m away from the forest edge in the adjacent fynbos showed no seedling recruitment of woody species at Platbos and very low representation at Wynand Louwsbos. Although seedling numbers were high at Swartboskloof, major contributors were fynbos elements such as *Cliffortia cuneata, Podalyria calyptrata* and *Agathosma* spp. The persistence of these species with time has not been noted although a few adult individuals were recorded on the forest edge. The production of many seedlings immediately following fire is a common regeneration strategy in fynbos plants, although few individuals persist to adulthood. At Orange Kloof, the presence of *Olea capensis* in both the lowest height class and the highest suggests that in the absence of fire, certain species are capable of exploiting fynbos environments. Another species commonly found in fynbos plots at Orange Kloof was *Apodytes dimidiata.* Although represented in lower height classes within the forest and in higher height classes in the fynbos, seedling production in both areas was low. This therefore suggests an episodic recruitment strategy.

Basal areas

Figures for basal area determinations for forest, margin and fynbos plots sampled at each site are given in Table 3. With the exception of the Swartboskloof site, basal area estimates for forested plots ranged from 55m^2/ha at Platbos to 65.45 m^2/ha at Wynand Louwsbos. This is slightly more than estimates calculated from the Knysna forests in the Southern Cape (Geldenhuys 1980), and may be due to the small plot size used in this study. The inordinately large basal area estimate obtained for the Swartboskloof riverine

TABLE 3. Basal areas expressed in m^2/hectare. SWB = Swartboskloof WLB = Wynand Louwsbos

	SWB	PLATBOS	WLB	ORANGE KLOOF
FOREST	126.42	55.52	65.45	59.09
MARGIN	7.35	16.01	14.91	17.11
FYNBOS	0.29	0.06	0.95	5.79

forest plots is probably due to the presence of large individuals of *Brabejum stellatifolium* and *Ilex mitis* which contributed 10% and 79% respectively of the total basal area recorded within the forest. These species were not present at the other sites where major contributors were *Olea capensis, Olinia ventosa, Hartogiella schinoides* and *Cassine peragua.*

The total basal area recorded on the forest margin ranged from 14.91 m^2/ha at Wynand Louwsbos to 17.11 m^2/ha at Orange Kloof. The figure recorded from Swartboskloof was very much lower than the other three areas sampled, possibly due to the more recent disturbance.

Woody basal areas recorded in fynbos plots were low at all sites except Orange Kloof where a figure of 5.79m^2/ha was calculated. Although still relatively low, the presence of water loving species such as *Apodytes dimidiata* and *Cunonia capensis* in the fynbos suggest that given adequate protection from fire and provided soil moisture is not limiting, selected species are capable of establishment and growth beyond the confines of the forest.

The contribution of certain species to the structure and dynamics of forests and their margins can be guaged by relative density estimates and basal area measurements (Table 4). *Rapanea melanophloeos* for example, was well represented in all height classes of all four forests sampled. Densities of *Kiggelaria africana* on the other hand, were high at Swartboskloof (mostly in the seedling category) but were not as prominent at other sites. Similarly, *Cunonia capensis* was a major contributor to basal area in forested plots at Wynand Louwsbos but was not important at other sites.

Major contributors to basal area in the forest were generally not well represented on the

TABLE 4. Relative densities (D) and relative basal areas (BA) of species within the forest, on the margin and in the fynbos at four sites.

FOREST	**SWB**		**PLATBOS**		**WLB**		**OK**	
	RD	**BA**	**RD**	**BA**	**RD**	**BA**	**RD**	**BA**
Rapanea melanophloeos	26.48	2.15	16.71	8.62	47.33	1.15	11.43	9.16
Kiggelaria africana	53.70	---	1.17	---	0.46	0.59	7.62	---
Maytenus acuminata	6.66	2.02	27.57	3.07	3.94	0.33	---	---
Cunonia capensis	0.29	5.10	1.46	0.77	1.86	36.56	0.32	0.52
Ilex mitis	0.75	79.36	0.29	2.20	---	---	---	---
Brabejum stellatifolium	2.96	10.52	---	---	---	---	---	---
Hartogiella schinoides	1.63	0.50	8.50	8.39	5.10	17.74	0.63	---
Podocarpus latifolius	0.15	0.35	12.61	6.81	22.27	21.59	0.63	0.02
Curtisia dentata	---	---	2.05	22.92	6.03	4.75	1.27	0.39
Olea capensis	---	---	16.13	32.25	9.98	17.24	11.11	16.28
Halleria lucida	0.15	---	---	---	0.93	0.06	0.32	0.09
Cassine peragua	---	---	---	---	---	---	4.44	44.76
Canthium mundianum	---	---	---	---	---	---	3.17	17.73
Apodytes dimidiata	---	---	0.88	0.01	0.23	---	11.43	0.84
Secamone alpini	---	---	---	---	---	---	14.60	---
Chionanthus foveolatus	---	---	---	---	---	---	8.57	1.07
Diospyros whyteana	---	---	---	---	---	---	8.57	1.33
MARGIN								
Curtisia dentata	---	---	0.24	---	11.71	8.54	1.68	0.05
Hartogiella schinoides	3.36	---	17.58	29.84	28.53	64.41	1.68	0.45
Olea capensis	---	---	13.06	0.33	9.69	3.96	15.55	---
Rapanea melanophloeos	7.91	16.42	20.43	0.27	22.34	4.72	30.67	33.60
Podocarpus latifolius	---	---	1.42	---	12.52	0.13	0.84	---
Protea mundii	---	---	2.85	9.99	0.27	7.27	---	---
Cunonia capensis	---	---	0.48	---	5.65	4.73	0.42	---
Cassine peragua	---	---	---	---	---	---	10.92	35.21
Kiggelaria africana	10.07	5.99	---	---	---	---	2.52	19.99
Olea europaea	7.67	27.16	---	---	---	---	---	---
Podalyria calyptrata	30.21	11.79	---	---	0.13	1.28	0.84	---
Cliffortia cuneata	11.27	1.82	3.56	5.88	0.27	2.30	---	---
Rhus spp	8.63	0.02	---	---	---	---	4.62	4.50
Brachylaena nerifolia	---	---	4.04	20.70	---	---	---	---
Maytenus acuminata	4.08	0.07	16.39	8.59	1.21	0.26	0.42	---
Berzelia spp	---	---	7.36	9.82	0.54	0.58	---	---
Apodytes dimidiata	---	---	1.42	---	---	---	10.50	5.78
Maytenus oleoides	1.44	32.02	---	---	---	---	---	---
FYNBOS								
Apodytes dimidiata	---	---	---	---	---	---	19.87	45.91
Olea capensis	---	---	---	---	0.43	---	22.98	6.86
Cunonia capensis	---	---	---	---	25.21	15.24	0.62	19.61
Curtisia dentata	---	---	---	---	---	---	0.62	5.06
Clutia pulchella	---	---	---	---	---	---	1.24	0.27
Rapanea melanophloeos	0.08	4.52	---	---	5.56	2.75	13.04	10.99
Rhus tomentosa	---	---	---	---	---	---	6.83	3.75
Cliffortia cuneata	28.24	11.99	34.78	100.0	2.99	26.03	---	---
Berzelia spp	---	---	18.48	---	16.24	38.09	---	---
Protea spp	0.16	57.30	---	---	0.43	---	---	---
Maytenus oleoides	0.24	26.20	---	---	---	---	3.10	0.77
Fynbos seedling	33.74	---	---	---	11.11	---	---	---
Podalyria calyptrata	6.07	---	---	---	---	---	---	---
Agathosma spp	8.90	---	---	---	---	---	---	---
Leucadendron spp	---	---	42.39	---	13.25	1.70	---	---
Myrsine africana	1.86	---	---	---	---	---	18.01	---
Cassine peragua	---	---	---	---	---	---	---	---
Hartogiella schinoides	---	---	---	---	14.53	---	4.97	---

margin. Conversely, species such as *Olea europaea* subsp *africana* and *Maytenus oleoides* were important marginal species at Swartboskloof but were not well represented in the forest. This was also reflected at Platbos where *Curtisia dentata* and *Olea capensis* were replaced by *Hartogiella schinoides* and *Brachylaena nerifolia* on the margin. At Wynand Louwsbos, dominance shifted from *Cunonia capensis, Podocarpus latifolius* and *Hartogiella schinoides* to *Hartogiella schinoides, Curtisia dentata* and *Protea mundii.* At Wynand Louwsbos and Orange Kloof however, *Hartogiella schinoides* and *Cassine peragua* dominated the margins but were also well represented within the forest. This implies that marginal microclimatic conditions created through protection from fire provide a suitable environment for the establishment and growth of species previously confined to the forest.

Growth form analysis

Categorisation of individuals into different growth forms revealed some marked differences in structure and growth form between Swartboskloof and the other forests sampled (Figure 5). Although coppicing was not well documented at any of the sites, ground-level coppicing was generally more evident at Swartboskloof, particularly on the margin. Small and large saplings were well represented at Platbos, Wynand Louwsbos and Orange Kloof but not abundant at Swartboskloof. Similarly, adult representation was lower at Swartboskloof than at other sites but seedling numbers were considerably higher. The high representation of seedlings in fynbos plots at Swartboskloof may however be distorted by the presence of many seedlings of *Cliffortia spp* and *Podalyria spp.*

Vegetation-soil relationships

Patterns relating vegetation to environment are reflected in Figures 2 and 3. The first analysis related sampled vegetation to macro environmental variables such as aspect, slope, position on slope, soil moisture, rock cover and soil depth. Variables important in determining vegetation composition were soil depth which was deepest in the Orange kloof/Platbos/Wynand Louwsbos forests declining to lowest levels at Swartboskloof, and

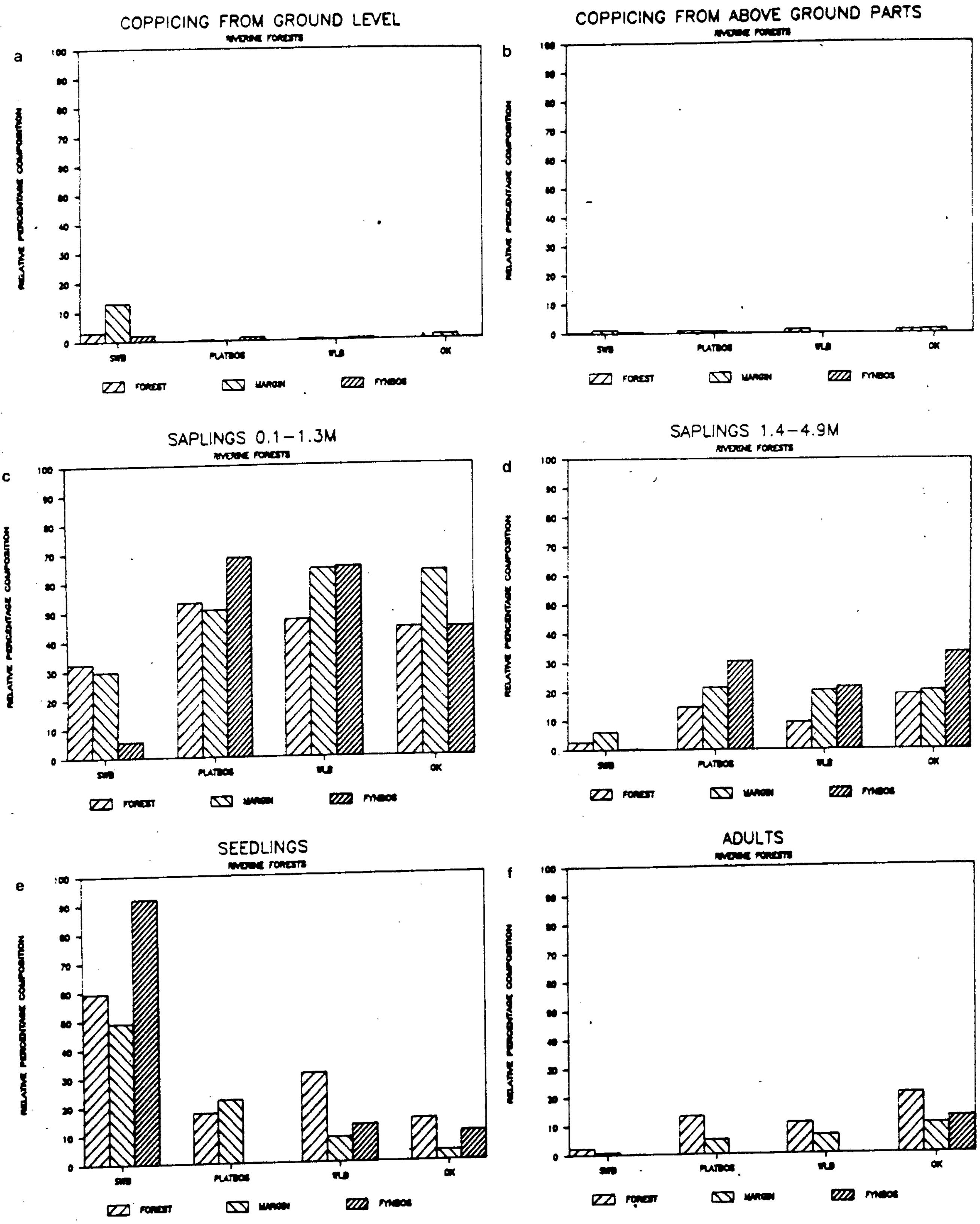

Figure 5. Percentage contribution of individuals to different growth forms.

rock cover which showed the reverse trend of being high at Swartboskloof and low at the other sites. The high levels of soil moisture recorded at Platbos were reflected by the direction of the arrow in the ordination diagram and was also found to be significantly higher than other fynbos areas sampled in the study.

An ordination using soil nutrient data and results from a soil particle analysis produced a distinct clumping pattern in which plots located in forest, margin and fynbos areas at Swartboskloof, Platbos and Wynand Louwsbos were separated out into discrete units. Orange Kloof did not show the same pattern, thus indicating a similarity in soil nutrient conditions along the forest-fynbos transect. Lowest nutrient levels were indicated in soils located in the fynbos at Swartboskloof which supports the generally held belief that fynbos soils are nutrient-poor.

DISCUSSION

Environmental trends

Many studies have attributed the success of fynbos vegetation in the southwestern Cape to its ability to survive summer drought on infertile, leached soils (Kruger 1979; Van Wilgen *et al* 1986). Indeed, the lack of soil nutrients in the surrounding fynbos, together with the more efficient nutrient cycling regime within forests was suggested by Van Daalen (1981) as one probable explanation for the absence of forest precursors in fynbos islands in the southern Cape. Although the effects of soil moisture availability on community distribution has long been recognised (Schimper 1903; Craib 1929; Phillips 1931), more recent investigations on the forest-fynbos boundary have produced conflicting results. In the southeastern Cape, Meadows and Dewey (1986) found there to be a clear distinction between soils collected from within the forest and those collected from grassland-heathland communities. Although there was no evidence of forest precursors in the surrounding fynbos, soil moisture levels were significantly higher outside the forest than within. This is consistent with results obtained from Platbos and may be related to the weather conditions at the time of soil collection (Meadows and

Dewey 1986) or may reflect a frequent burning regime.

In the southern Cape, colonisation of fynbos 'islands' by forest species was not reported by Van Daalen (1981) and the forest-fynbos boundary was thought to be fire-induced. The more natural boundary at Ysternek Nature Reserve did however coincide with differences in soil moisture, which was indirectly affected by topography and aspect. The claim by Phillips (1931) that fynbos was seral to forest in the absence of fire was refuted by Van Daalen who considered forest and fynbos to be two distinct vegetation types, with the extent of fynbos favoured by the present climate.

A recent study by Masson and Moll (1987) in a fire-protected environment on the Cape Peninsula found that forest expansion was determined by a composite effect of soil moisture, parent rock material, degree of rockiness and soil nutrient status.

This study showed very little difference between forest, margin and fynbos soils at each site. On the other hand, the high levels of soil moisture recorded in fynbos plots at Platbos, Wynand Louwsbos and Orange Kloof, together with the presence of hygrophilous forest species such as *Cunonia capensis* in fynbos areas at Wynand Louwsbos, provides a clear indication that forest expansion in the southwestern Cape is dependant on moisture availability. However, the absence of forest species in fynbos areas at Platbos and Swartboskloof suggests that the time elapsed since disturbance is an important contributory factor influencing the rate of forest expansion.

Although significant differences were generally not detected along forest-fynbos transects at each site, the differences noted between sites, together with a knowledge of disturbance history can be used to explain differences in vegetation structure and dynamics at each site sampled. For example, although both Wynand Louwsbos and Orange Kloof have been protected for comparable periods of time, the different patterns in species densities recorded in fynbos plots can be ascribed to differences in soil particle composition, pH levels, K levels, and Na levels (Table 1). These differences were also detected in the CANOCO plot where pH levels and sand content were higher in Orange Kloof soils than in soils collected from Wynand Louwsbos.

In view of the shallow soil depths and low levels of soil moisture recorded in fynbos plots at Swartboskloof, it is unlikely that forest expansion will occur in the vicinity of the riverine forest even if protected from fire (this is not the case for other forested areas sampled at Swartboskloof, see Chapter 1). In contrast, similarities in soil moisture, clay content, percentage carbon, K and Na levels recorded at Platbos, Wynand Louwsbos and Orange Kloof suggest that forest advancement into fynbos areas at Platbos may occur, given adequate fire protection.

Other investigations of vegetation changes and the effects of fire on forest boundary dynamics in southern Africa have been carried out by Granger (1976) and Everard (1986) in the Natal Drakensberg. Granger (1976) found that soil nutrient status differed between grassland and forest areas and that fire exclusion resulted in the development of a more mesic environment, usually associated with the invasion of woody species such as *Phillipia evansii* and *Leucosidea sericea.* A comparison of burnt and unburnt margins of *Podocarpus latifolius* forests in the Drakensberg (Everard 1986) showed clear differences in vegetation composition and abundance between sites but little variation in soil properties were detected.

Comparable overseas studies relating forest boundary dynamics to environment have been carried out in Tasmania by Ellis (1985), Ellis and Graley (1987) and Gilfedder (1988) and in northern Queensland by Ash (1988). Investigations by Ellis and Graley (1987) showed that soil properties did not affect the distribution of vegetation types and any differences in soils of the grassland/eucalypt-rainforest successional sequence were probably influenced by vegetation. A progressive decrease in pH, total P and Mg was noted from grassland to rainforest, with pH providing the most consistent index of change during succession.

Another study by Ellis (1985) found that rainforest distribution was correlated with topography and establishment of rainforest was most rapid on moist sites and/or southern aspects. Soil moisture was also identified by Gilfedder (1988) as an important determinant of *Eucalyptus coccifera* distributions on the Mount Wellington Plateau in Tasmania.

On mainland Australia, the location of rainforest boundaries was determined by an interaction between rainforest, substrate, topography and fire. Successional changes resulted from changes in fire regime and the survival of tree species some distance away from rainforest was limited, occurring only in most favourable fire-protected sites (Ash 1988).

Vegetation trends

The need for detailed, quantitative data is essential if the dynamics of ecotones is to be discussed (Norton 1989). In South Africa, studies on vegetation change following disturbance have been limited to floristic descriptions with little quantitative data reported. More recently, the usefulness of assessing the utilization potential of forests in South Africa through a structural classification has been identified. In particular, the identification of structural changes following disturbance is considered important in understanding underlying processes involved in vegetation recovery.

Composite density patterns in forested plots at Platbos, Wynand Louwsbos and Orange Kloof reflected alternating high and low densities with increase in size. A similar pattern of discontinuous size structure has been shown by Read and Hill (1988) for *Antherotaxis selaginoides* in Tasmanian rainforests and was attributed to a phasic regeneration strategy. At Swartboskloof, density levels were high in small height classes and declined with increase in height. This reverse J-shaped curve has been reported by Read and Hill (1988) in Tasmania, Saldarriaga et al (1988) in the Amazon basin and Parker (1986) in ecotonal forests in the Sierra Nevada.

With the exception of *Rapanea melanophloeos* which was well represented in each of the four forests studied, the importance of species (as measured by their relative densities) varied both with height and between sites. For example, although *Podocarpus latifolius* was well represented in lower height classes and by seedling numbers inside forest at Wynand Louwsbos, it was commonly found in the adult form at Platbos. Similarly, *Olea capensis* dominated the lower height classes at Platbos but was present in higher height classes at Orange Kloof. These patterns do not appear to be related to fire history and imply that conditions within forest are not affected by past fire disturbance.

In contrast, marginal density profiles were identical for Orange Kloof and Wynand Louwsbos although similarities were not apparent between the two more recently disturbed ecotones. This suggests that forest ecotonal communities in the southwestern Cape are affected by disturbances such as fire and their state of recovery is influenced by time since disturbance.

The density fluctuations in higher height classes at Wynand Louwsbos and Orange Kloof could not be attributed to the dominance of any single species and is thought to be a composite effect of episodic seed production and the differential growth of species. Although *Apodytes dimidiata* was a dominant sapling in fynbos plots at Orange Kloof, seedlings were poorly represented within the forest and not recorded on the margin. This suggests that recruitment of *Apodytes dimidiata* is not continuous and occurs in pulses. On the other hand, the many seedlings produced by *Curtisia dentata* and *Hartogiella schinoides* at Wynand Louwsbos, together with the high marginal densities recorded in the adult height class suggest that recruitment of these two species is continuous.

Another feature noted was that dominant adults within the forest at each site were not necessarily well represented on the margin or in the fynbos. This was illustrated by *Podocarpus latifolius* and *Curtisia dentata* at Platbos where they were dominant adults within the forest but were poorly represented in lower height classes only on the margin. This change in form with change in position along transect has been noted by Norton (1989) who linked structural changes to changes in substrate composition.

In New Zealand beechwood/hardwood forests, the differential response of species to major and minor disturbances produced significant differences in forest structure which influenced subsequent regeneration processes (Stewart 1986). The importance of regeneration studies in understanding vegetation dynamics has also been noted by Read and Hill (1988) and Hibbs (1983). In this study, the effects of disturbance on vegetation structure were clearly indicated by an analysis of regeneration strategies at each site. The slightly higher incidence of vegetative regeneration, together with the low incidence of adults and saplings and high seedling production was representative of a recently disturbed site, in contrast to the high numbers of established individuals at Orange Kloof and Wynand Louwsbos. The similarities in sapling numbers and adult abundance between Platbos and Wynand Louwsbos were not expected, but may be explained by the presence of a dense protective margin of *Protea mundii* and *Berzelia spp.*

Although structural similarities were noted between the forests of Orange Kloof and Wynand Louwsbos, species composition was not the same. This implies that different species adopt similar roles in different localities according to their abundance. Conversely, the importance of the same species may vary with locality.

Variation in species numbers may also be explained in terms of forest location. Although the higher numbers of species found at Orange Kloof can be attributed to a long period of fire protection, the lower species numbers recorded at Platbos and Wynand Louwsbos suggest that some other factor besides fire history may influence species numbers. The proximity of Orange Kloof to forest communities above Kirstenbosch is in direct contrast to the isolated nature of Wynand Louwsbos and Platbos and may be responsible for differences in species numbers.

CONCLUSION

The identification of soil moisture as an important determinant of forest boundary dynamics is upheld by the findings of this study in which the high levels of soil moisture recorded in fynbos plots at Orange Kloof and Wynand Louwsbos were usually accompanied by the presence of large, hygrophilous forest species such as *Cunonia capensis* and *Apodytes dimidiata.*

The importance of disturbance history cannot be discounted, and although soil moisture values recorded in fynbos plots at Platbos were high, the absence of individuals was attributed to the short period elapsed since the last disturbance. It is predicted that forest expansion will proceed in this locality, given adequate protection. In contrast, the shallow, dry soils of fynbos plots at Swartboskloof, coupled with steep, rocky slopes do not provide a suitable environment for forest colonisation, and in the absence of disturbance, forest expansion is not envisaged in the lower reaches of the Swartboskloof valley.

The identical patterns produced by marginal densities at Orange Kloof and Wynand Louwsbos indicates that ecotonal communities are affected by fire and the state of recovery is influenced by the time since disturbance. However, differences in fynbos density profiles are attributed to differences in soil nutrient status and species composition. The lower numbers of species recorded in the Kogelberg forests compared with Orange Kloof may be influenced by distance from a 'mainland' seed source; the isolated nature of Wynand Louwsbos and Platbos is in direct contrast to the location of Orange Kloof which is situated in close proximity to the Kirstenbosch forest communities on Table Mountain. Further biogeographical relationships of southwestern Cape forests are discussed in the following section.

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SECTION 5

BIOGEOGRAPHICAL RELATIONSHIPS

CHAPTER FIVE

THE PHYTOGEOGRAPHY AND FLORISTICS OF SOUTHWESTERN CAPE FORESTS

ABSTRACT

Species-area relationships of eight forested areas in the Cape Province were investigated. A phytochorological analysis of six southwestern Cape forests using floristic and structural information identified similarities between the Stanford forests and forests on the Cape Peninsula.

Differences between the coastal forests and inland forests were substantiated by a decline in the Tongaland-Pondoland elements from Stanford to Swartboskloof. The change in phytochorological composition of the two forests is possibly related to a change from a dry, coastal habitat to a wetter, more mountainous environment.

INTRODUCTION

The vegetation of the southwestern Cape region is dominated by low, sclerophyllous shrubland with forest patches restricted to sheltered valleys, southern slopes and rock screes (McKenzie 1978). Owing to their small size, these forests rarely appear marked on maps, giving the impression that no forests exist west of Knysna.

Initially, the southwestern Cape forests were either thought to have Cape affinities or were excluded from phytochorological examinations (White 1978). Later, forest species were identified as having tropical affinities in contrast to the more temperate Cape flora and similarities between the southwestern Cape forests and the larger Southern Cape forest complex were alluded to by Sim (1907), Laughton (1937), von Breitenbach (1974) and Taylor (1978).

Although floristic information is available on the forests of the Riversdale area (Muir 1929), Grootvadersbos (Taylor 1955), Stanford (Taylor 1961) and the forests of Table Mountain (Adamson 1927; Campbell and Moll 1977; Masson and Moll 1987), the phytochorological relationships of the southwestern Cape forests remains poorly documented. White (1978) compared the species compositions of forests west of Knysna with those of Knysna, the Eastern Cape, and Natal-Transkei. He considered the forests west of Knysna to be forest outliers largely composed of Afromontane elements. Where forests graded into scrub forest or thicket, the Afromontane element was diluted by the occurence of Tongaland-Pondoland or Cape species. McKenzie (1978) divided the area west of Knysna into seven forest complexes and noted a decline in species numbers from the Jonkersberg complex in the east to the Cape Peninsula complex in the west. Slight differences in species composition were noted in the three most westerly complexes of the Cape Peninsula, Hottentots-Holland and Riviersondereind mountains. No attempt was made to assign the seven complexes to chorological groups. McKenzie and Moll (in press) have recently examined the phytochorological affinities of the Stanford forests and have found them to be strongly influenced by Tongaland-Pondoland species.

The aim of this paper is to examine the floristic composition of six forest patches in the southwestern Cape and compare their phytogeographic affinities, noting significant differences where they occur. These results are then compared with a separate assessment using basal area data. The species-area relationship of small forest patches is also investigated to determine whether forest size does affect floristic composition.

STUDY AREA

The study area was limited to forest patches within a 200 km radius of the Cape Peninsula, with the majority of forests considered in the study rarely being more than 50 kms away from each other. Because information on the structure and size of the Swellendam/Riviersonderend forests was not available at the time of writing, these forests were not included in the study. The number of forest patches included in the study was limited by the number of available checklists. Forest patches included in the study and their check list source are listed in Table 1. These checklists were supplemented with checklists compiled by the authors and by reference to the National list of Indigenous Trees (von Breitenbach 1986).

Table 1. Southwestern Cape forest patches and their checklist sources.

Cape Peninsula (PEN)	- Campbell and Moll (1977) - McKenzie *et al* (1977) - Masson and Moll (1987)
Swartboskloof (SWB)	- McDonald (1984)
Cederberg (CED)	- Taylor (unpubl)
Kogelberg (KOG)	- Boucher (unpubl)
Hermanus (HER)	- Knight (unpubl)
Stanford (STN)	- Taylor (1955) - McKenzie and Moll (in prep)

The southwestern Cape region is characterised by high mountain ranges rising up from coastal forelands and aeolian plains. In the west, the ranges strike in a north-south direction whilst further east, beyond the study area, the direction switches to an east-west direction. Ranges present in the region include the Cedarberg Mountains, the Cape Peninsula Mountain chain (including Table Mountain of 1090m a.s.l.), the Hottentots-Holland Mountain range of over 2000m a.s.l. and the lower Klein River range of 630m a.s.l.(McKenzie 1978). The ranges are composed mainly of quartzites and shales of the Table Mountain Series with lowland areas of either loose, unconsolidated sands or shales. The rivers present in the study area are generally small with flow restricted to the winter months. In general, the southwestern Cape forests are found in close proximity to rivers or seepage areas; this is particularly true in the Cedarberg where tree species are confined to river banks and streams. In the Betty's Bay-Hermanus vicinity, forests are found in protected steep-sided valleys, either bordering river banks or on filled-in screes. Similarly, the Table Mountain, Kogelberg and Swartboskloof forests are confined to river banks and rock screes, but unlike the Hermanus area, the terrain is not as steep and is more open. Forests in the Stanford region are found on the relatively open coastal lowland where the topography provides little protection against the desiccating summer southeasterly winds and the rain-bearing northwesterly winds in winter (McKenzie and Moll, in prep).

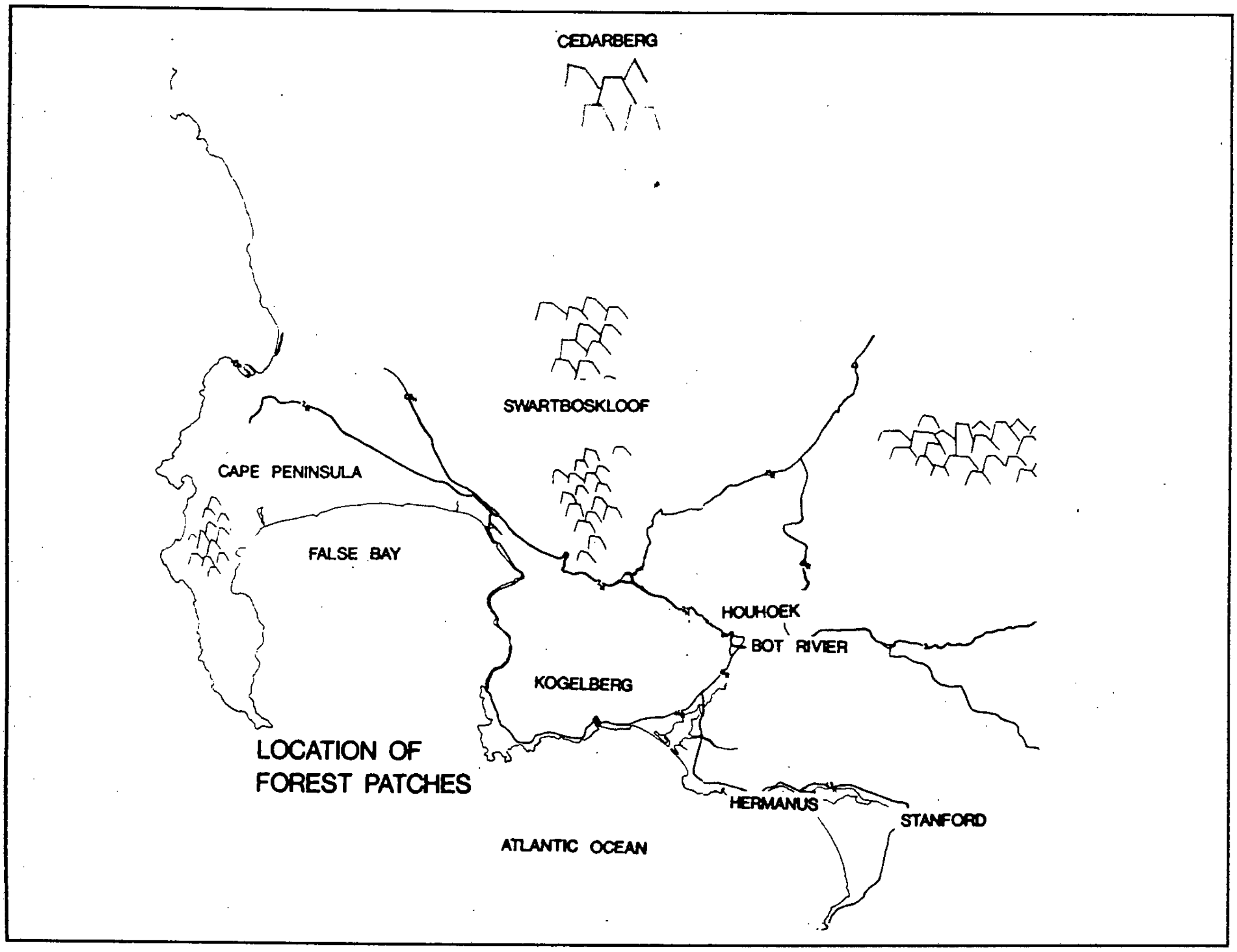

Figure 1. Map showing the approximate localities of forest patches sampled in the study.

METHODS

Woody species were allocated to Afromontane, Tongaland-Pondoland or Cape categories on the basis of their distribution patterns ie Cape species were those woody species confined to the Cape region; Tongaland-Pondoland species included species which are found in the Tongaland-Pondoland forests of Natal-Transkei (Moll pers comm). Transgressor species having both Afromontane and Tongaland-Pondoland affinities were assigned to both categories. Similarly, those Afromontane species confined to the Cape Fynbos region were assigned to both the Afromontane and Cape categories.

A comparative phytogeographic division was made using basal area data from Swartboskloof, the Kogelberg, Hermanus and Stanford (Masson unpubl; McKenzie and Moll in press).

The sizes of forest patches in each area was determined using a summagraphics IB digitizer with an AO table. The digitizer was linked up to a tektronix 4051 graphic computer and a log-log graph of species versus area was produced. Where forest patches were in close proximity to one another and could be recognised as a distinct group, the species checklists of both forests were pooled and considered as one entity ie Betty's Bay (Leopards Kloof and Dasbos) and Stanford (Grootbos, Steynsbos, Kleinbos and Platbos).

RESULTS

Species - area relationship.

Figure 2 represents the relationship between the logs of species number and forest area. A clear distinction is evident between the larger, species-rich southern Cape forests and the smaller, depauperate southwestern Cape forests. Although the forests of this latter region are rarely more than 20 hectares in size, (the one exception being the Cape Peninsula forests where a forest cover of 150 hectares was estimated) species number nevertheless appears to be correlated with forest size. The forests of Swartboskloof and

Stanford for example (of approx 17 ha and 14 ha respectively) have a larger complement of species than those forests at Betty's Bay and Hermanus where forest size is 4.5 ha and 5.62 ha respectively. This supports the theory proposed by McArthur and Wilson (1967) that the number of species is related to area.

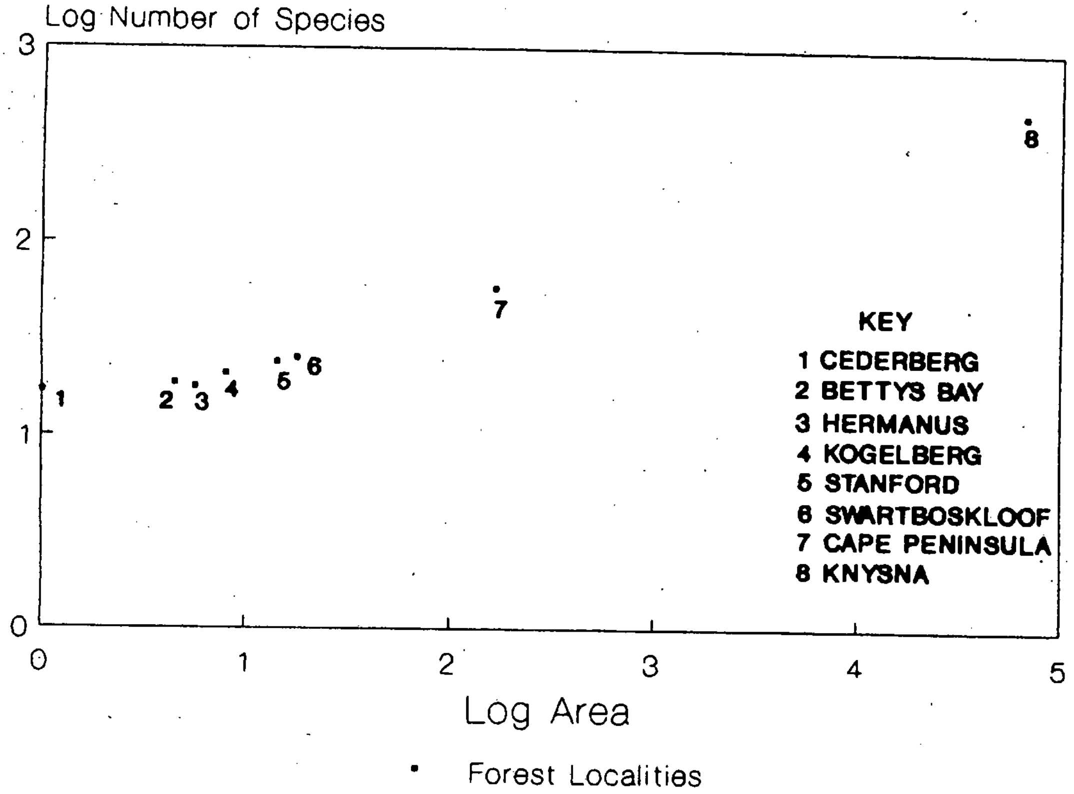

Figure 2. Species-area relationship of western Cape forest patches.

Within the southwestern Cape region, a further less obvious distinction is apparent at both ends of the spectrum, with the larger, species-rich forests of the Cape Peninsula being situated some distance away from the central body of forests and the smaller, depauperate Cedarberg forests being similarly removed from the rest. This suggests that these two forested areas are substantially different from the other southwestern Cape forests.

Species relationships.

Species were re-ordered according to their distribution pattern along an east-west gradient (Figure 3). Of the total number of species existing in the study area, 31,25% had a continuous distribution, 18,75% were narrowly disjunct and 25% were widely disjunct. Of the 25% making up the endemic category, three quarters were found on the Cape Peninsula. A closer examination of the widely disjunct species category indicated that half the species present in this category were found only on the Cape Peninsula and at Stanford. This similarity between the two areas is illustrated again in later analyses.

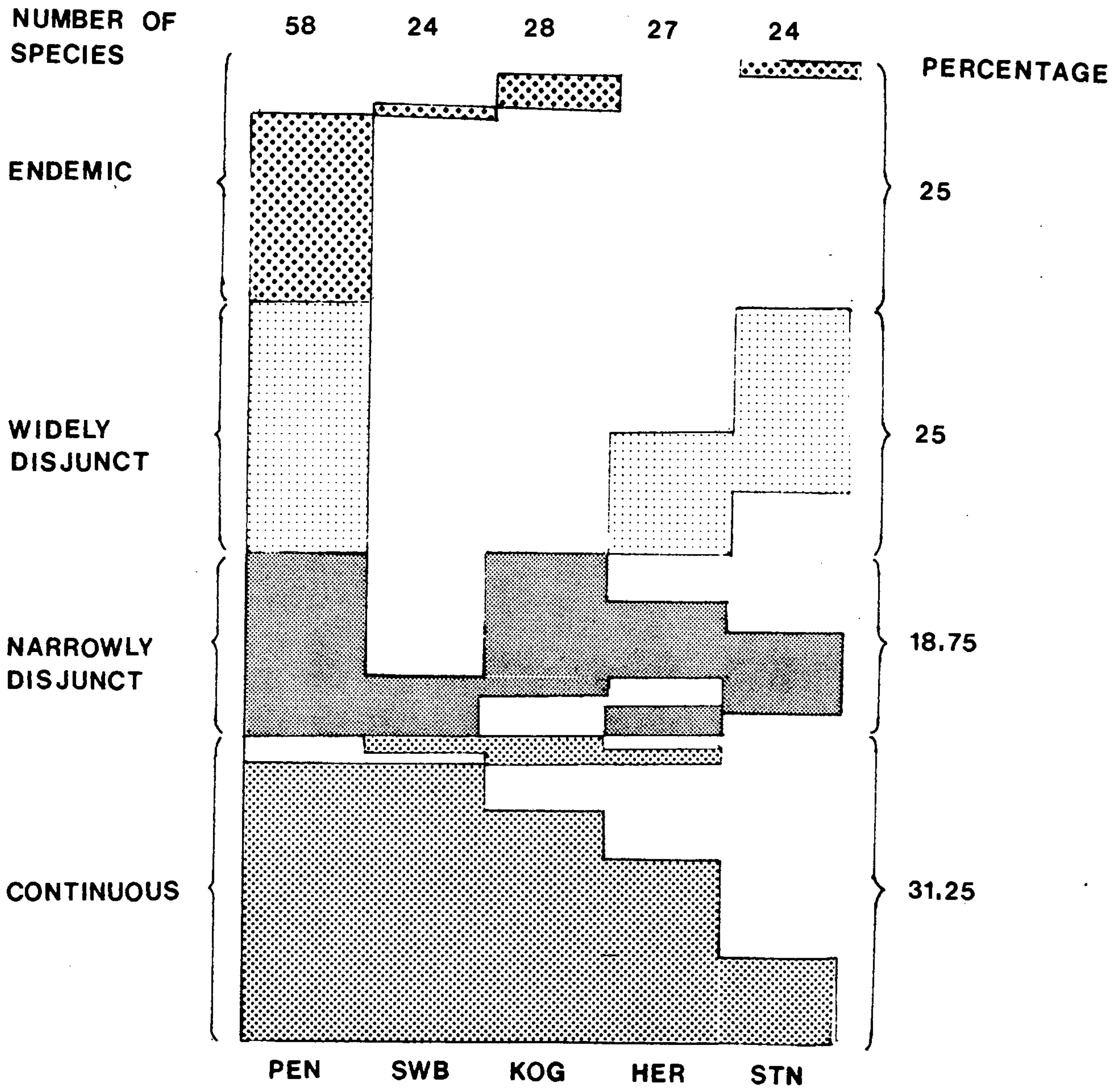

Figure 3. Distribution patterns of western Cape forest species.

Family associations.

The number of species represented in each family was determined for each study area and those families having three or more species present in one or more locality were singled out for further examination. This reduced the number of families available to seven, with the families Celastraceae, Oleaceae, Ebenaceae and Anacardiaceae being well represented in all the forests studied (Table 2). The families Celastraceae and Oleaceae were well represented in both the Cape Peninsula forests and the Stanford forests, indicating a further similarity between the two areas. The two most common families on the Cape Peninsula were Celastraceae and Anacardiaceae and together they represented almost a third of the total woody species present in the area. A similar pattern was reflected in the Hermanus and Stanford forests with figures of 30% and 29% respectively.

TABLE 2. Families having three or more species represented in one or more localities.PEN = Cape Peninsula; SWB = Swartboskloof; KOG = Kogelberg; CED = Cederberg; HER = Hermanus and STN = Stanford.

FAMILY	PEN	SWB	KOG	CED	HER	STN
Anacardiaceae	8	1	1	2	3	2
Asteraceae	2	2	2	1	3	1
Celastraceae	9	3	4	2	5	5
Ebenaceae	3	2	1	3	1	2
Flacourtiaceae	3	1	1	1	1	1
Myrsinaceae	3	2	2	1	2	1
Oleaceae	5	1	2	1	2	3
Number of *spp* belonging to Anacardiaceae and Celastraceae (% of all *spp* present in each area)	29	16	18	23	30	29

Divisive Information Analysis (DIA).

This technique determines the differences between entities based on presence-absence data. An analysis of the southwestern Cape forest data showed the Cape Peninsula forests to be most different from the others, followed by Stanford, Hermanus, the Kogelberg and Swartboskloof (Figure 4). The number of species responsible for dictating the division between forests remained relatively constant with ten species being present in the Cape Peninsula forests and not at Stanford, nine species distinguishing Stanford from Hermanus, eight species separating Hermanus from the Kogelberg and nine species present on the Kogelberg and not found at Swartboskloof. Of the nine species dividing the Kogelberg forests from Swartboskloof, one was endemic to the Kogelberg, three species were found in all other localities, two were present at Hermanus and on the Peninsula and three species were found only on the Cape Peninsula and the Kogelberg.

Species were then categorised as either Afromontane, Tongaland- Pondoland or Cape and the relative contributions of the different phytochoria to each division calculated. Of the ten species distinguishing the Cape Peninsula from the rest, half were classified as Afromontane followed by Tongaland-Pondoland and then Cape species. The proportions changed slightly at Hermanus in that of the eight species distinguishing Hermanus from the Kogelberg and Swartboskloof, half were classified as Tongaland-Pondoland, followed by Afromontane and then Cape. Four of these species are found only at Hermanus and on the Cape Peninsula, in contrast to the other four species which are also found in the Stanford forests. Of the nine species separating Stanford from the rest, one was endemic and eight were only found on the Cape Peninsula and at Stanford.

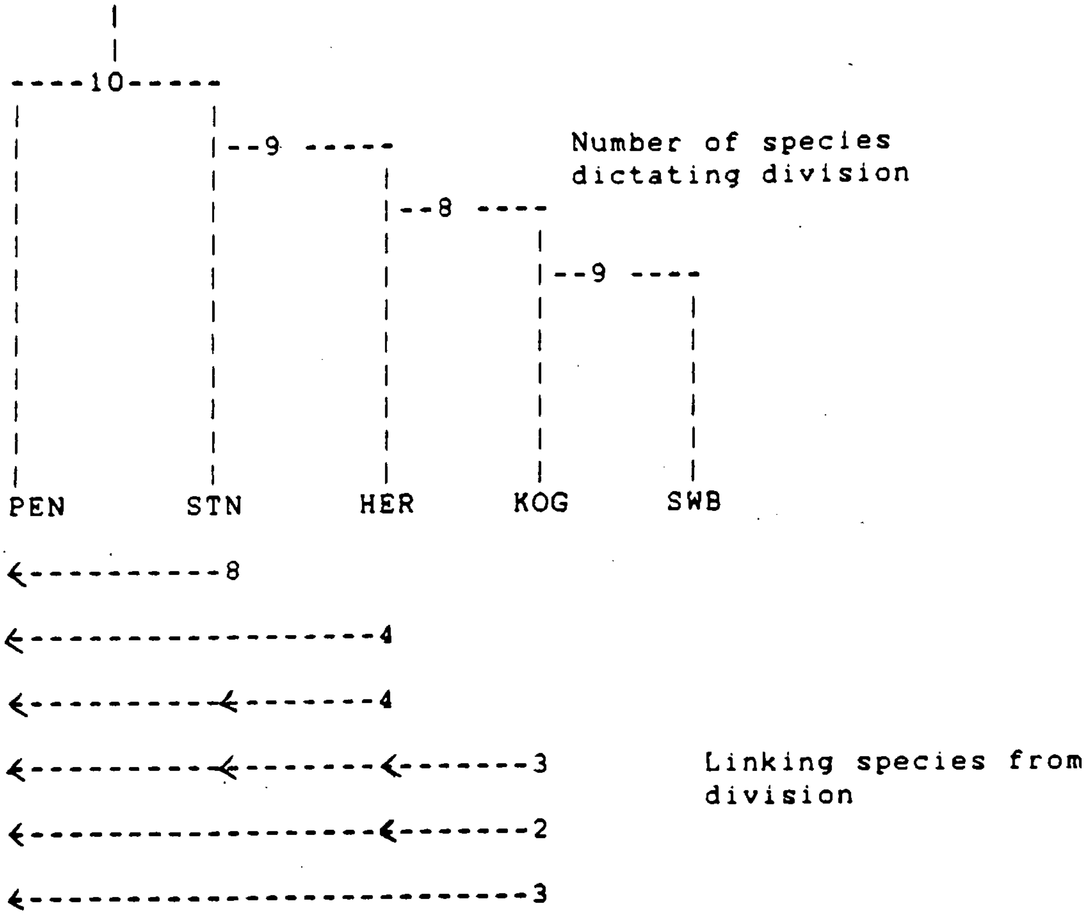

Figure 4. **Division of southwestern Cape forests based on the distribution of 62 species using divisive information analysis.**

By calculating the average contributions of the phytochorological elements to the divisions, it was found that the greatest contribution was made by Afromontane species (42.25%) followed by Tongaland-Pondoland species(31.5%), Cape species (17%) and finally those species categorised as transgressors (9.25%).

Phytochorological relationships using species composition and basal area data.

The species present in each area were assigned to one of three categories, each category was then totalled and expressed as a percentage of the whole. The results from each area were then graphed and arranged in the order determined from the DIA. The same procedure was repeated using basal area data and the resultant patterns are illustrated in Figure 5.

Species composition.

If it is accepted that the Peninsula forests and the Cedarberg forests are substantially different from the others present in the study area and limit the analysis to the four central areas present on the graph, then the following trends become apparent. In all areas, the Afromontane element is dominant, the Tongaland-Pondoland contribution decreases from Stanford to Swartboskloof whereas the Cape element shows the reverse trend of increasing in this direction. We suggest that this could be linked to a change from a dry, coastal habitat to a wetter, more mountainous terrain.

Basal area

Analysis of available basal area data indicated a distinct difference between the Stanford forests and the others. A large contribution of Tongaland-Pondoland elements was evident at Stanford although the number of Cape elements was relatively small. In general, the Afromontane contribution was highest at Swartboskloof and then declined towards Stanford whilst Cape elements declined from Hermanus to Swartboskloof.

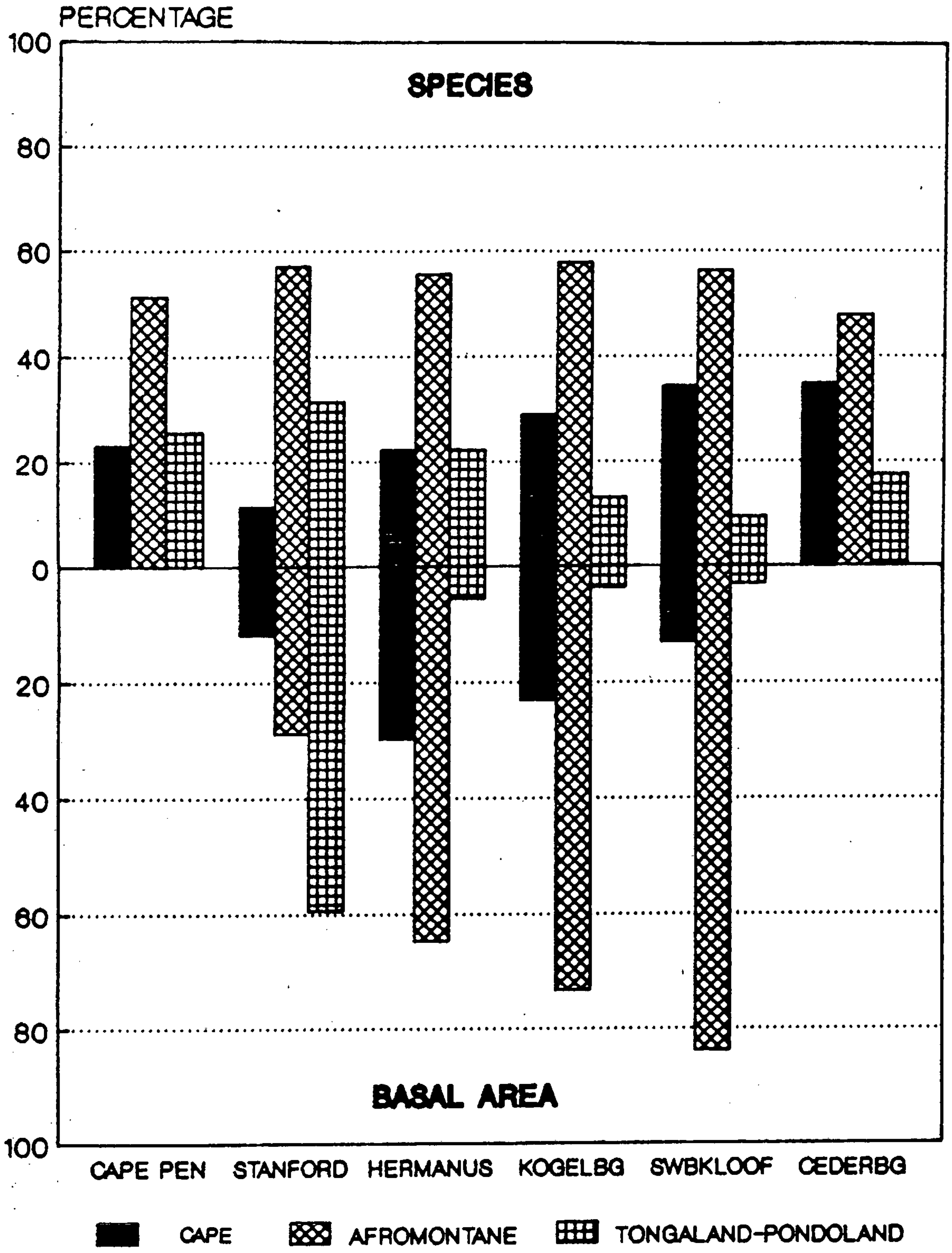

Figure 5. Phytochorological relationships of southwestern Cape forest patches using basal area data and species composition.

DISCUSSION

The predominance of Afromontane elements in the southwestern Cape forests illustrated by divisive information analysis and the phytochorological grouping of species data supports the findings of White (1978) in which a strong Afromontane component of forests west of Knysna was identified. Numbers of Tongaland-Pondoland species were high in the Stanford forests, thus confirming the results of McKenzie and Moll (in press), who found these forests to be strongly influenced by Tongaland-Pondoland taxa.

A distinction between the coastal forests of the Cape Peninsula, Stanford and Hermanus areas and the inland forests on the Kogelberg and at Swartboskloof was illustrated by divisive information analysis with Tongaland-Pondoland taxa being relatively important in this division. A subsequent analysis of phytochorological affinities using species data showed a decline in Tongaland-Pondoland elements from Stanford to Swartboskloof and a reverse trend of an increase in Cape elements in the same direction. This change in phytochorological composition is possibly linked to the change from a dry, coastal habitat to a wetter, more mountainous terrain. This pattern is not displayed for the Cape Peninsula forests possibly because the analysis for this area is based on data from many small forests. Individual forests may either occur on wet or dry habitats and/or on coastal sites or mountainous terrain.

A comparative analysis of phytochorological composition using basal area information identified a difference between the forests at Stanford and those located elsewhere. Tongaland-Pondoland elements made the largest contribution to basal area at Stanford, with a decrease in representation towards Swartboskloof. The trend of an increase in Cape species from Stanford to Swartboskloof was not illustrated by basal area information in which the basal areas of species belonging to the Cape category was highest at Hermanus with lower levels recorded in the inland forests of the Kogelberg and Swartboskloof. McKenzie and Moll (in press) argued that the use of quantitative data such as basal area was important for phytochorological determinations and classified the Stanford forests as belonging to the Tongaland-Pondoland phytochorion despite the fact that there were more Afromontane than Tongaland-Pondoland elements. All other forests besides Stanford in the analysis would be classified as Afromontane on the basis of relative contribution to basal area of the various phytochorological elements.

Clear similarities between forests of the Cape Peninsula and those at Stanford were indicated by species distribution patterns, family associations and divisive information analysis. Of the total number of species assessed in the study, 25% had a widely disjunct distribution, with half of this number found only on the Cape Peninsula and at Stanford. In addition, the families Celastraceae and Oleaceae were well represented in both areas. The high number of Tongaland-Pondoland elements recorded on the Cape Peninsula was not expected and provides further evidence for a link between the forests at Stanford and those on the Cape Peninsula. A possible explanation may be that in the past, when sea levels were lower, a continuous band of coastal forest may have stretched between the Cape Peninsula and Stanford. A subsequent rise in sea level resulted in the removal of the low-lying representatives, with the remaining traces confined to higher ground.

By relating species numbers to forest area, a clear distinction was identified between the larger, species-rich southern Cape forests and the smaller, depauperate forests of the southwestern Cape. A similar subdivision was evident within the southwestern Cape region with the comparatively species-rich forests of the Cape Peninsula and the low diversity woody vegetation of the Cederberg separated from the other areas included in the study.

CONCLUSION

The analysis of similarities between forests using phytochorological information proved to be successful. The predominance of Afromontane elements in southwestern Cape forests with a high representation of Tongaland-Pondoland species at Stanford is consistent with the findings of White (1978) and McKenzie and Moll (in press). However, the higher numbers of Tongaland-Pondoland species found on the Cape Peninsula was not expected and a link between the Stanford forests and the Cape Peninsula is proposed.

Although the influence of seed type and dispersal characteristics on species numbers was not investigated in this study, an analysis of this nature would assist greatly in understanding the complexities of forest composition and the potential for species increases.

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CONCLUSION

CONCLUSION

An investigation of forest boundary dynamics in the southwestern Cape has not only enhanced our understanding of the structure and composition of forests and their ecotonal communities, but also has provided valuable information on the relationship between forest vegetation and the environment. The level of investigation varied from a general assessment of forest types and their environmental constraints to a more detailed documentation of the distribution and abundance of individual species along the forest-fynbos gradient. Major findings of the study will now be outlined in relation to the key questions and objectives and avenues for future research will be identified.

Structural differences between riparian forest and scree forest were evident at both the recently burnt site of Swartboskloof and the fire-protected catchment area of Orange Kloof. The reverse J-shaped distribution pattern produced by riparian communities at Swartboskloof was not emulated by riparian communities at Orange Kloof and the reduced densities noted in the higher height classes was attributed to either a past disturbance event or phasic regeneration.

Floristic differences were also apparent between the two forest types, with riparian forests at Swartboskloof dominated by *Rapanea melanphloeos* and *Kiggelaria africana* in contrast to the main scree forest contributors of *Maytenus acuminata, Podocarpus latifolius, Olinia ventosa* and *Myrsine africana*. At Orange Kloof, differences in forest composition were not so obvious, although a predominance of *Apodytes dimidiata* and *Rapanea melanophloeos* was found in the riparian forests in contrast to the high representation of *Podocarpus latifolius* in scree forest. *Olea capensis* and *Cassine peragua* were well represented in all three forests sampled.

An assessment of environmental similarities between forest types and along the forest-fynbos gradient revealed significant differences between the scree forest environment and the riparian location. Although no difference in conditions were evident along the forest-fynbos gradient at Orange Kloof, significant differences were noted along scree transects at Swartboskloof. Subsequent analyses relating environmental variables to vegetation composition identified soil depth, soil moisture and slope as important factors influencing vegetation structure and composition at Swartboskloof and Orange Kloof. Soil nutrient status did not play an important role in determining the forest-fynbos ecotone at Swartboskloof although levels of K and Na generally declined from forest to fynbos.

The recognisable differences noted between the two forest types resulted in the separate analysis of riverine and scree forest edges of differing post-fire age. In addition to the immediate post-fire condition of Swartboskloof and the fire-protected environment of Orange Kloof, two intermediate stages were sampled in order to determine the effects of the length of protection from fire on edge dynamics and composition. However, in view of significant differences in environmental conditions at each of the four sites sampled, no predictive statements regarding forest development and succession could be determined from vegetation patterns obtained from older post-fire sites and related to more recently burnt sites. The analysis of vegetation change over time was further complicated by species compositional differences at each site but a general comparison of vegetation-environment relationships and boundary dynamics at each site was nevertheless informative.

The presence of forest seedlings beyond the scree forest boundary at Betty's Bay for example, was attributed to high levels of soil moisture, deep soils and low rock cover. Although environmental conditions were considered suitable for forest expansion at Orange Kloof, the absence of forest seedlings adjacent to scree forests was linked to episodic seed production. The lack of large individuals in the older fynbos areas adjacent to scree forests suggested that fire was not the sole factor influencing the dynamics of the scree forest boundary and that local environmental conditions and forest composition played an important part in determining the structure and composition of the forest-fynbos transition zone.

A comparison of riverine boundaries of differing post-fire age again identified soil moisture as an important prerequisite for seedling growth and establishment. In addition, the deep soils and low rock cover recorded some distance away from the forest edge at

Orange Kloof and Wynand Louwsbos were accompanied by the presence of hygrophilous saplings such as *Apodytes dimidiata, Cunonia capensis* and *Hartogiella schinoides* and provided a clear indication of environmental conditions necessary for forest expansion. In the light of these findings, it is unlikely that forest expansion will occur in the lower reaches of the Swartboskloof valley where fynbos soils were generally shallow, rocky and dry. Environmental conditions in the vicinity of Platbos appeared suitable for expansion although forest individuals were not recorded beyond the forest edge. This was attributed to the recently burnt condition of the margin and implies that the length of the post-disturbance period is an important determinant of the rate of forest expansion.

In keeping with most scientific research, clear answers to the initial objectives and key questions identified were not always apparent, and the complex interactions of vegetation, environment and fire-history made generalisations on the dynamics of the forest-fynbos boundary difficult. The findings of this study do, however, indicate that southwestern Cape forests are dynamic entities capable of expansion, given adequate fire protection and suitable environmental conditions. No evidence of regression was noted and the rate of expansion and potential for colonisation was dependant on forest type and the time elapsed since the last disturbance,

Soil moisture, soil depth and the amount of rock cover were key factors influencing the dynamics of the forest-fynbos ecotone with forest composition and consequent availability of seed also important.

The categorisation of individuals into different growth forms provided relevant information on the post-fire regeneration strategies adopted by southwestern Cape forests. Differences in vegetative regeneration, seedling production and sapling survival were noted between forests of differing post-fire age with seedling production and coppice growth best represented in the immediate post-fire condition. The higher numbers of saplings and adults recorded along the forest-fynbos transect in fire-protected areas was accompanied by reduced seedling representation and lower coppice production. This implies that coppice production is an immediate, reactionary mode of regeneration following disturbance and that seedling establishment and subsequent growth of saplings occurs soon after the disturbance event. The absence of seedlings in scree fynbos areas at Orange Kloof suggests an episodic recruitment strategy which is influenced by species composition and seed production.

The role of seed dispersal by birds and the intricacies of fruiting strategies were not investigated in this study and may contribute greatly to our understanding of ecotonal dynamics and the biogeography of forest patches. An investigation of phytochorological affinities of southwestern Cape forest patches provided an interesting assessment of the floristic similarities of sites in the study area which could then be related to differences in forest location. The proximity of forests to each other and the presence of a nearby 'mainland' source area was not fully investigated in this analysis and it is suggested that further studies of a biogeographical nature be carried out.

Despite the complexities of soil-vegetation relationships and differences in forest composition, the study of vegetation change along the forest-fynbos ecotone in the southwestern Cape has provided a valuable insight into understanding forest boundary dynamics in the face of recurrent disturbance. The identification of two distinct forest types and the subsequent differences in vegetation behaviour across their ecotones was not envisaged at the outset of the investigation and thus provided a new perspective to the study. It is hoped that future research on forest boundary dynamics will not be confined to the southwestern Cape and comparative studies will soon be undertaken.

APPENDIX

Species codings used in ordinations

APOD YTE = *Apodytes dimidiata* E.Mey. ex Arn.
BERZ LIA = *Berzelia spp.*
BRAB JUM = *Brabejum stellatifolium* L.
BRAC NER = *Brachylaena neriifolia* (L.) R. Br.
CANT INE = *Canthium inerme* (L. f.) Kuntze
CASS PER = *Cassine peragua* L.
CHIO NAN = *Chionanthus foveolata* (E. Mey.) Stearn
CLIF FOR = *Cliffortia spp.*
CLUT PUL = *Clutia pulchella* L.
CUNO CAP = *Cunonia capensis* L.
CURT DEN = *Curtisia dentata* (Burm. f.) C.A. Sm.
CUSS ONI = *Cussonia thyrsiflora* Thunb.
DIOS GLA = *Diospyros glabra* (L.) De Winter
DIOS WHY = *Diospyros whyteana* (Hiern) F. White
FYNB OS2 = Unknown fynbos seedling 2
FYNB OS1 = Unknown fynbos seedling 1
HALE RIA = *Halleria lucida* L.
HART SCH = *Hartogiella schinoides* (Spreng.) Codd
HEER ARG = *Heeria argentea* (Thunb.) Meisn.
ILEX MIT = *Ilex mitis* (L.) Radlk.
KIGG AFR = *Kiggelaria africana* L.
KNOW LTN = *Knowltonia vesicatoria* (L. f.) Sims
LAUR CAP = *Laurophyllus capensis* Thunb.
LEUC DEN = *Leucadendron spp.*
MAYT HET = *Maytenus heterophylla* (Eckl. & Zeyh.) N.K.B. Robson
MAYT ACU = *Maytenus acuminata* (L. f.) Loes.
MAYT OLE = *Maytenus oleoides* (Lam.) Loes.

MYRQ UER = *Myrica quercifolia* L.

MYRS AFR = *Myrsine africana* L.

OLEA EUR = *Olea europaea* L. *subsp. africana* (Mill.) P.S. Green

OLEA CAP = *Olea capensis* L. *subsp. capensis*

OLIN VEN = *Olinia ventosa* (L.) Cufod.

OSMI TOP = *Osmitopsis spp.*

PEUC GUM = *Peucedanum spp.*

PLAT TRI = *Platylophus trifoliatus* (L. f.) D. Don

PMUN DII = *Protea mundii* Klotzsch

PODO LAT = *Podocarpus latifolius* (Thunb.) R. Br. ex Mirb.

PODY CAL = *Podalyria calyptrata* Willd.

PROT NIT = *Protea nitida* Mill.

PSOR PIN = *Psoralea pinnata* L.

RAPA MEL = *Rapanea melanophloeos* (L.) Mez

RHUS TOM = *Rhus tomentosa* L.

RHUS ANG = *Rhus angustifolia* L.

RHUS LUC = *Rhus lucida* L.

SECA MON = *Secamone alpini* Schultes

SOLA NIG = *Solanum nigrum* L.

TEED LUC = *Teedia lucida* Rudolphi

WIDD NOD = *Widdringtonia nodiflora* (L.) Powrie

ZANT DEC = *Zantedeschia aethiopica* (L.) Spreng.