THE ENVIRONMENTAL DETERMINANTS OF THE FYNBOS / SUCCULENT KAROO BOUNDARY IN MATJIESRIVIER NATURE RESERVE, WESTERN CAPE

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ABSTRACT

The central aim of this thesis was to explore the environmental determinants of the fynbos / succulent karoo boundary in the eastern Cederberg Mountains, Western Cape. This work was carried out at Matjiesrivier Nature Reserve (MNR), which straddles the boundary between fynbos and succulent karoo. MNR was an ideal place to study the environmental determinants of this boundary because it has a relatively unique combination of steep climatic and edaphic gradients, and is free of the confounding influence of fire. This thesis followed a logical procession from an inductive vegetation survey with multivariate analyses, through to a deductive experiment that tested the hypotheses generated in this earlier work. A further chapter investigated the application of predictive mapping using the survey results.

Seven major communities, derived from the survey using TWINSPAN analyses, described the vegetation of MNR using both floristic and growth form characters. These communities were incorporated into later chapters. The advantages and disadvantages of floristic versus growth form characters for vegetation surveys was reviewed. The proportions of shared and independent variance attributable to floristic and growth form composition were quantified using variance partioning techniques. Most of the floristic variance was independent of growth form composition, while most of the growth form variance was shared with floristic composition.

The environmental variables that best accounted for the distribution of the major communities and the fynbos / succulent karoo boundary were investigated using canonical correspondence analysis (CCA). Both species and growth forms were distributed along two families of gradients: topo-climatic and edaphic. There was a slow transition from fynbos into succulent karoo that corresponded to a gradient of increasing aridity from west to east across MNR. Within this climatic gradient, at a finer scale, gradients of soil moisture availability (controlled by texture), pH and conductivity caused separation of fynbos and succulent karoo species and growth forms. These inductive analyses, combined with a literature review, gave rise to the hypothesis that the fynbos / succulent karoo boundary was controlled by gradients of moisture availability (mediated by precipitation and soil texture) and nutrient status.

This hypothesis was tested in a glasshouse experiment where the performance (i.e. biomass accumulation and survival) of fynbos and succulent karoo seedlings was compared under treatments of precipitation, soil texture and nutrient status. Nutrients did not seem to play an important role compared to moisture availability. The physical environment directly limited fynbos seedling survival. Fynbos seedlings were unable to survive low levels of soil moisture, a consequence of either low precipitation or of fine-textured soils. In comparison, the succulent karoo seedlings survived under any moisture or soil conditions, indicating that they were not limited directly by the environment. The fynbos seedlings did, however, grow significantly faster than the succulent karoo seedlings under most treatments. This suggested, but did not prove, that succulent karoo seedlings were at a competitive disadvantage to fynbos seedlings. There may be a biotic interaction between fynbos and succulent karoo that prevents succulent karoo from expanding into fynbos. This hypothesis requires further testing.

The application of predictive mapping and extrapolation of vegetation units was also investigated during this thesis. I attempted to predict the occurrence of communities, growth forms and the fynbos / succulent karoo boundary using three easily-measured environmental variables (altitude, geology and landtype). The results from the vegetation survey were incorporated into generalised linear models (GLMs), within a geographic information system (GIS), to generate models that could predict the occurrence of a vegetation type with a certain probability. None of the environmental variables were significant in any of the growth form models. Although the models could only predict the occurrence of most communities with a probability of < 0.5, maps generated in the GIS, based on the GLMs, were very similar to the actual vegetation map generated during the survey. The biggest problem with the models was that they could not account for the transitional nature of the fynbos / succulent karoo ecotone. The models supported the hypothesis that moisture and geology were the primary determinants of the fynbos / succulent karoo boundary.

The results from the classification, multivariate analyses, generalised linear modelling and seedling experiment all complemented each other. The primary determinant of the fynbos / succulent karoo boundary at MNR is topo-climatic (altitude and precipitation). Edaphic gradients of texture, pH and conductivity impose further separation of fynbos and succulent karoo within this topo-climatic gradient.

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7. To sum up the research presented in chapters 2-5 and provide a summary discussion, relating the research back to the central themes of the thesis.

(Chapter Seven: **General Discussion and Summary**)

1.3 THE PHYSICAL ENVIRONMENT AND GENERAL BIOTA OF MATJIESRIVIER NATURE RESERVE

1.3.1 Background Information

Geography

Matjiesrivier Nature Reserve is located east of the Cederberg Wilderness Area in the Cederberg Mountains, Western Cape, South Africa (Figure 1.1). The rectangle that includes the outer boundary of MNR is described by the co-ordinates:

32° 25’ 00” S, 19° 17’ 30” E and 32° 33’ 10”S, 19° 30’ 30” E.

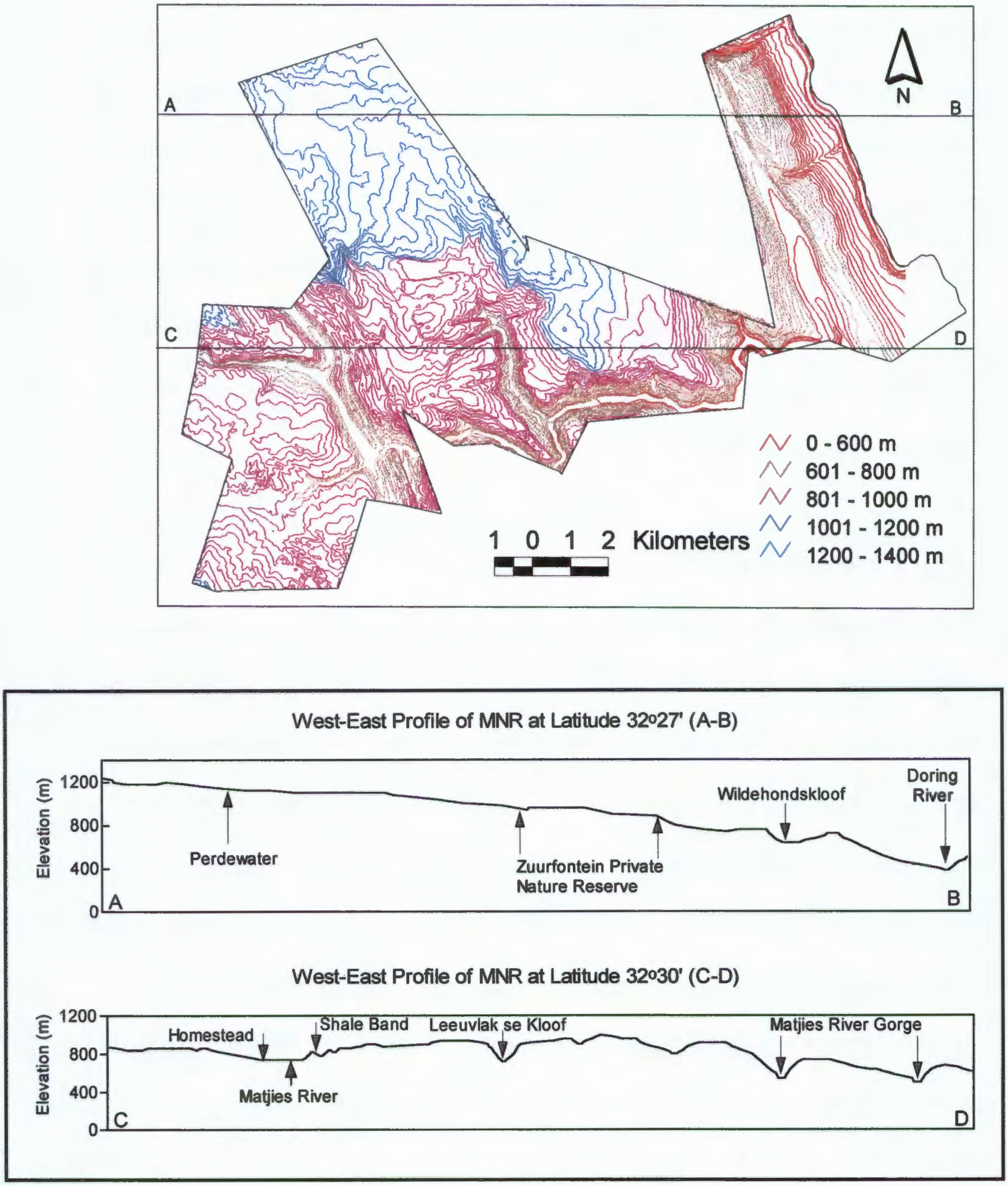
Matjiesrivier Nature Reserve covers an area of approximately 12 700 hectares (127km^2) and comprises several farms (Figure 1.1). MNR is bounded on three sides by stock farms, which support herds of goats, sheep and cattle. Cederberg Private Nature Reserve and Zuurfontein, both private nature reserves, lie between the two northward extensions of MNR (Figure 1.1).

Above and east of the Bokkeveld Group lies the Witteberg Group (Figure 1.2), which also comprises sedimentary layers of sandstone, quartzite and occasional sandy shale lenses. Most of the area of MNR lies over the Witteberg Group. There has been little tilting and some folding in the Witteberg Sandstone, particularly in the east, which has caused some unusual landscape features such as the Wildehondskloof Valley (Figure 1.1). In comparison to the Table Mountain Group, the rocks from the Witteberg Group are less coarse-grained and more fertile.

1.3.3 Topography

There is a great variety of topographical features at MNR (Figure 1.3) which may contribute to the high vegetation diversity. In the west, water weathering of the Table Mountain Group sandstones has given rise to many dramatically shaped sandstone blocks, including the famous Stadsaal Caves. Tracts of deep aeolian sands separate these blocks. Much of the topography in MNR is orientated north-south, including the series of parallel Bokkeveld shale-sandstone valleys and ridges in the middle of MNR and a large anticlinal valley in the east (Wildehondskloof). The importance of aspect as a factor influencing the distribution of vegetation communities is examined in later chapters.

There are also extensive areas of relatively flat topography in MNR. These are in the north-west region, near Perdewater, and in the middle, near Vaalvlei (Figures 1.1 & 1.3). The horizontal sandstone bedding planes, which lie just beneath the soil surface, are often exposed in large sheets. These bedrock sheets have a profound influence on the vegetation.



West-East Profile of MNR at Latitude 32o27' (A-B)

West-East Profile of MNR at Latitude 32o30' (C-D)

Figure 1.3 The topography of MNR in surface view and with two profiles (A - B & C - D).

A profile of MNR from west to east at 32°27' S (Figure 1.3) shows the gentle altitudinal gradient from approximately 1200m to 450m. A similar profile at 32°30' S (Figure 1.3) shows several steep-walled river valleys in the southern part of MNR. The Matjies River has incised a deep gorge, which runs along the southern boundary of MNR with an east-west orientation. Several tributaries, such as the Leeuvlak River, join the Matjies Rivier along its course, giving rise to deep north-south orientated valleys. The steep topography has resulted in skeletal soil and marked vegetation differences between opposing slopes.

1.3.4 Drainage

There are several perennial rivers and many annual or ephemeral streams that flow in MNR (Figure 1.4). The eastern boundary of MNR is the Doring River; a large perennial river flowing northwards. The perennial Matjies River and its tributary, Krom River, flow east from the Cederberg catchment and join near to the homestead in MNR. The Matjies River meanders through a deeply incised valley, which corresponds approximately to the southern boundary of MNR, until it drains into the Doring River outside MNR. The relatively large annual Leeuvlak River flows southwards, during the winter rainy season, from the middle of MNR into the Matjies River.

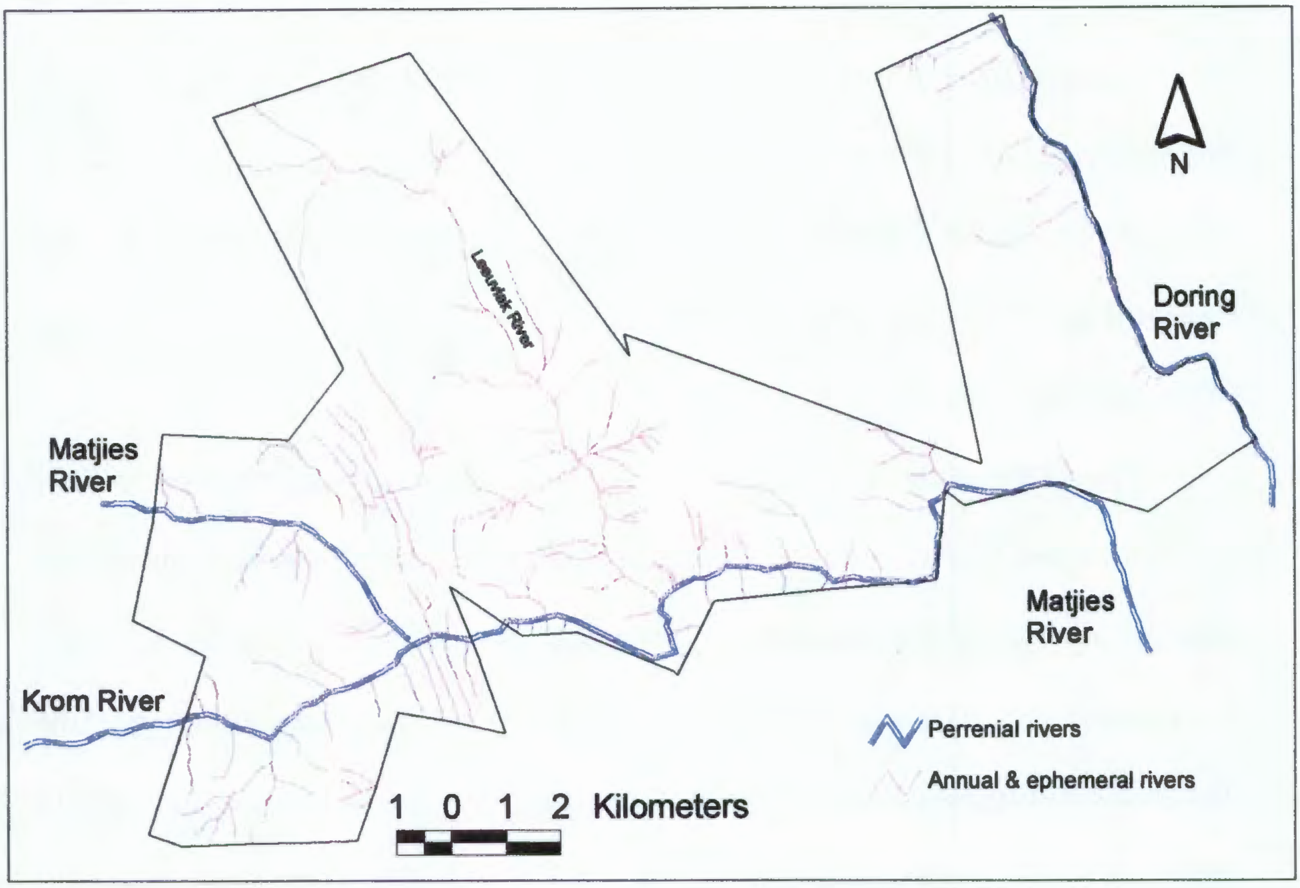


Figure 1.4 The drainage of MNR, showing the perennial, annual and ephemeral rivers. The Matjies and Krom Rivers drains to the east. The Doring River drains to the north.

1.3.5 Climate

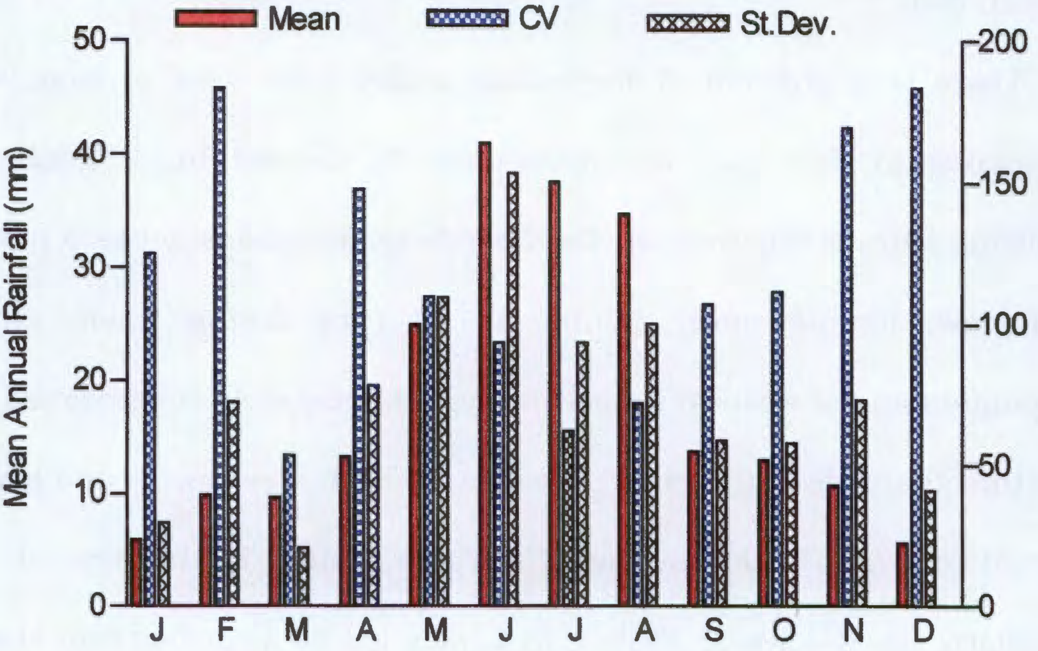
Matjiesrivier Nature Reserve has a "mediterranean-type" climate typical of the western part of the fynbos biome (Deacon, *et al.* 1992). There are no rainfall data available for MNR itself. The two nearest weather stations are Dwarsrivier and Keurbosfontein, both of which are situated to the west of MNR (Figure 1.1) in the mesic region of the moisture gradient. There are no data for the xeric region near the eastern boundary of MNR. Data from Keurbosfontein and interpolated rainfall data from the Computing Centre for Water Research (CCWR, 1996) were used for the following description.

The MNR area is semi-arid to arid, experiencing approximately 50 - 350mm of precipitation a year. Most of the rainfall occurs during the winter months of July to August while the summer months of October to April are dry (Figure 1.5). The absence of rain during the hot summer causes extreme drought conditions compared to summer rainfall regions, and is thought to be one of the selective forces resulting in the structure of fynbos and succulent karoo plants (Cowling & Holmes, 1992; Stock *et al.* 1997). The coefficient of variability for rainfall (Figure 1.5) shows that the winter rainfall is very reliable, while summer rainfall is largely unpredictable.

Precipitation is mostly in the form of rainfall and sometimes snow, both of which occur during or after frontal conditions. The higher land in the west of MNR receives considerable precipitation in the form of mists and low clouds during the frontal conditions (personal observations). Convection thunderstorms, sometimes accompanied by hail, occur during autumn, but are uncommon (van der Merwe & Barnard, 1996). Heavy frost appears to be common during the winter months, mostly on high-lying areas (personal observations).

There is a gradient of increasing aridity from west to east, which corresponds to, but may not necessarily be caused by, a gradient of decreasing altitude (Figure 1.6). The Cederberg Mountains act as a powerful rainshadow, forcing moist frontal air to cool during uplift, causing precipitation on the western slopes and highest peaks. As the dryer air flows down the other side of the range, towards the east, it re-warms and loses its potential to form clouds and rain. The high ground in the west of MNR, particularly the Bokkeveld shale ridges, may act as a further rain shadow, exacerbating the eastwards increase in aridity. Rain squalls appear to move westwards down from the Cederberg Mountains until they are deflected south by the Bokkeveld ridges and thus do not penetrate into the easterly regions of MNR (personal observations). Topographic control of moisture availability is reflected in the distribution of vegetation units, and is discussed later.

Temperatures range between very cold in winter, often falling below zero, and very hot in summer, often above 40°C (Personal observations and communications with local managers). The prevailing winds are south-easterly in summer and north-westerly in winter. Hot Berg winds may occur during the winter months (van der Merwe & Barnard, 1996).



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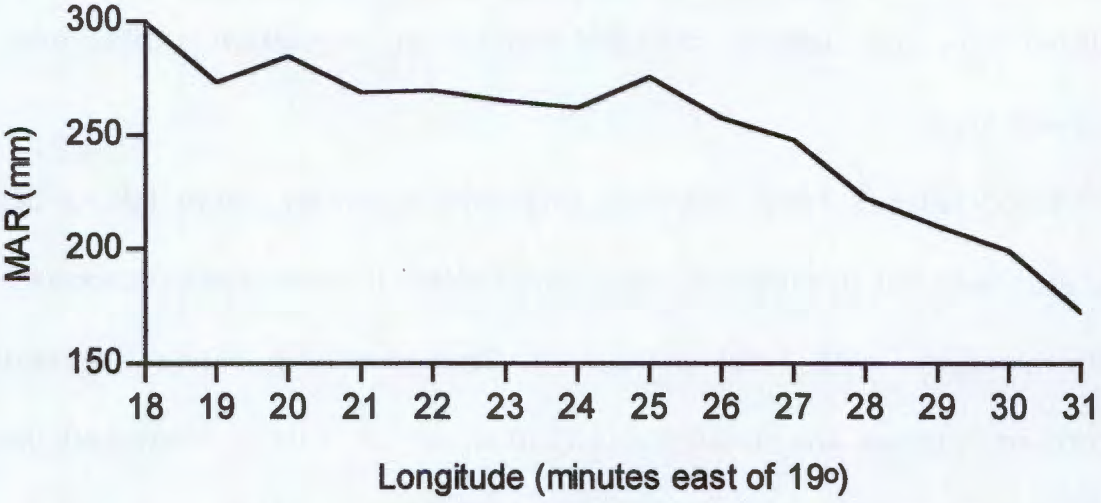

Figure 1.6 The mean annual rainfall (MAR) trend from east to west across Matjiesrivier Nature Reserve. Rainfall data from the CCWR (1996).

Soils

Soil forms and depth

There are a variety of soil forms at MNR, although the rocky and skeletal Mispah and Glenrosa forms (MacVicar *et al.* 1991) are most common. Over much of the area of MNR, soils have formed *in situ* from weathering of the parent sandstone rocks. These soils are well developed, and appear to be leached (particularly on the plateau areas). These sandy soils are pale, coarse-grained and are of the Fernwood Form (van der Merwe & Barnard, 1996). Scattered through MNR are deposits of fine-grained aeolian sands, which make up extensive flat plains. These relatively fine-textured aeolian sands are mostly yellow-brown to brown, suggesting that, although having good drainage, they are not leached. Deposits of coarse-grained alluvial sands, which are typically washed and white, are found along the larger rivers. Both of these sand deposits show only minor soil structure and rudimentary division into horizons, indicating their youth. The soils on the Bokkeveld Group are fundamentally different to those on the Table mountain and Witteberg Groups. Differences in soil chemical and physical conditions are discussed below and Chapter Six.

The soils are fairly shallow throughout MNR, mostly because of the high degree of rockiness and presence of surface bedrock. The soils on the rocky slopes are skeletal and have lost most of their weathered substrate as they are associated with erosional surfaces (van der Merwe & Barnard, 1996). The deepest soils (> 1.2m deep) were always found on the aeolian sand plains. In the high rainfall areas, near Perdewater, there was evidence of waterlogging and gleying at about one meter deep. This was because the soils lie above a hardpan of ferricrete, which reduces drainage.

Soil chemistry and cations

Soils from five widely spread areas in MNR, were analysed for pH, resistance, sodium, phosphorus, potassium, acidity (H+Al), Calcium, Magnesium, Copper, Zinc, Manganese and Boron (Elsenburg Soil Science Division, Dept. Agriculture: Western Cape, P.bag X1, Elsenburg, 7607). Overall, the pH of the soils was slightly acidic (all < 5) except for the aeolian sand near Wildehondskloof (in the arid part of MNR) which was slightly alkaline (pH = 7.4).

There was a wide range of electrical resistance values from 26800 ohms in the sandstone-derived soils to 20 ohms in the shale-derived soil. Sodium content varied between 10 and 20 (mg/kg) in the sandy soils but was exceptionally high in the shale-derived soils (1450 mg/kg). All the soil samples showed less than 10 mg/kg of phosphorus, which is low compared to other karoo soils (Cowling *et al.* 1986). The shale-derived soil showed considerably higher acidity, copper, potassium, boron, manganese, zinc, magnesium and calcium than the sandy soils (see Chapter Six). Similarly, the Wildehondskloof soil showed much higher values for these elements that the other sandy soils, which may be a reflection of the low rainfall of this eastern region. A particle size analysis of these soil samples showed that the shale-derived soils had a much higher clay content than the sandstone-derived soils and aeolian soils.

1.3.7 Flora

This section briefly outlines the background information available about the vegetation at MNR. Obviously, I will go into much greater detail about the vegetation and its ecology in later chapters. The flora at MNR comprises elements of three major vegetation types:

1) An asteraceous form of Mountain Fynbos (Rebelo, 1996b) in the west.
2) Central Mountain Renosterveld (Rebelo, 1996a) near and on parts of the Bokkeveld shale band. This is equivalent to Acocks (1988) Mountain Renosterveld (veldtype 43).
3) Lowland succulent karoo (Hoffman, 1996), or Acocks (1988) Succulent Karoo (veldtype 31) in the east.

Fynbos-clad areas at MNR appeared to be relatively species poor compared to similarly sized areas in the Cape Peninsula. This may be due to MNR lying in the eastern extreme of the fynbos biome, away from the centre of fynbos diversity. However, all the typical fynbos growth forms: proteoids, restioids, ericoids and graminoids, are present. The renosterveld is characterised by a dominance of members of the Asteraceae (Typically *Elytropappus* species) and Fabaceae (*Aspalathus* species). There should be a high cover of grasses in renosterveld, but many years of stock grazing have probably negatively affected the grass populations. The succulent karoo in the eastern part of MNR is characterised by a high proportion of stem- and leaf-succulent dwarf shrubs, mostly from the Mesembryanthemaceae and Crassulaceae: families which have their centres of diversity in the succulent karoo (Hofffman, 1996). There is also a good representation of woody and succulent Asteraceae and deciduous shrubs.

1.3.8 Fauna

There are a few small mammals present at MNR, including bat-eared foxes, aardvarks, caracal, jackal, baboons, klipspringer and grysbok. There are currently no large grazing or browsing mammals although future introductions of these are probable. Little is known about the bird, reptile or insect life at MNR.

CHAPTER TWO

Classification of the Vegetation at Matjiesrivier Nature Reserve

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2.1 INTRODUCTION

The flora at Matjiesrivier Nature Reserve (MNR) is structurally and floristically complex, as it comprises elements from three distinct and typically diverse vegetation types: mountain fynbos (Rebelo, 1996a), central mountain renosterveld (Rebelo, 1996b) and lowland succulent karoo (Hoffman, 1996). These vegetation types are structurally very different (Table 2.1) The high degree of environmental heterogeneity in terms of topography, geology and micro-climate at MNR provides ample niche space for the co-existence of many plant species and communities. The combination of the convergence of fynbos, renosterveld and succulent karoo and the heterogenous environment with steep environmental gradients causes the high beta (or between community) diversity that is apparent at MNR.

The main aim of vegetation classification is to simplify the vegetation into robust units that are recognisable and repeatable through the landscape. There is major benefit for nature conservation that arises from mapping the natural resources: the subdivision of the landscape into homogenous units and the use of these units as a basis for management planning (Pressy & Bedward, 1991). The vegetation at MNR is difficult to classify phytosociologically because it comprises a complex mosaic of communities at a fine scale. Such communities would be impossible to map or treat as management units. Nonetheless, these fine-scale communities may be ecologically important (Campbell, 1985). Therefore, for management purposes, it was necessary to design a classification system that overlooked the fine-scale complexity and defined more pragmatic communities that were both mappable and meaningful for management (Pressy & Bedward, 1991). It is, however, still important to recognise the fine-scale mosaic of communities particularly in terms of conserving species diversity.

The juxtaposition of three major vegetation types (Table 2.1) in a single reserve raises problems for the management and conservation of the flora at MNR. Each vegetation type, particularly succulent karoo and fynbos, needs to be managed separately, as they respond differently to certain management actions such as fire and have different grazing capacities (compare Van Wilgen *et al.* 1992 and Milton & Dean, 1996).

Table 2.1 The major structural differences between the three vegetation types converging at Matjiesrivier Nature Reserve (adapted from Low & Rebelo, 1996)

Vegetation Type	Major Structural Characteristics
Asteraceous Fynbos	A mid-high to tall shrubland characterised by the presence of three elements: 1) ericoid shrubs with evergreen, rolled, sclerophyllous and leptophyllous leaves; 2) restioid reeds with aphyllous and photosynthetic stems and 3) proteoid shrubs with broad, isobilateral leaves.
Central mountain renosterveld	A low to mid-high shrubland dominated by evergreen plants with cupressoid and leptophyllous leaves. High proportion of grasses and geophytes when not over-grazed. Often transitional between fynbos and succulent karoo.
Lowland succulent karoo	A Dwarf shrubland dominated by leaf- and stem-succulent plants. Grasses are relatively rare.

2.1.1 A Review of Vegetation Classification in the Fynbos / Succulent Karoo Transition

There is currently no classification of the vegetation at MNR. Indeed, very little work has been done on classifying the vegetation in the fynbos - succulent karoo transition, or even in the succulent karoo itself. Although the fynbos biome has received considerable attention in terms of vegetation classification, little work has been done in the arid fynbos and renosterveld of the north-west region of the fynbos biome (Cowling *et al* 1997). Some of the vegetation types in the vicinity of MNR have been classified in some way and are discussed below.

Mountain fynbos

Mountain fynbos has been classified according to both floristic composition and structure. Campbell (1985) classified the mountain vegetation of the fynbos biome, including the Cederberg Mountains that lie just to the west of MNR. He used a combination of structural characteristics and higher taxa (families) to derive four major vegetation categories: three non-fynbos and one fynbos. Within each category, Campbell described a number of communities; and I will only discuss those communities that are relevant to the vegetation at MNR. Two of Campbell's (1985) non-fynbos categories, Forest & Thicket and Karroid & Renoster Shrubland occur, at least in part, at MNR. Forest & Thicket was characterised by a high cover of large shrubs or trees with leaves other than leptophylls. In MNR, this community was usually found within the fynbos matrix at sites which receive run-off from rocky outcrops and appear to be protected from fire.

Karroid & Renoster Shrubland occurred over a large part of MNR where the annual rainfall was too low to support fynbos, or where soil conditions resulted in a pronounced summer aridity (see the review of fynbos / karoo boundary in Cowling & Holmes, 1992 and Cowling *et al.* 1997). Two of Campbell's (1985) fynbos communities occurred in MNR: Dry asteraceous fynbos on the rocky slopes and dry restioid fynbos on the sand plains. Dry asteraceous fynbos is a xeric version of asteraceous fynbos (Table 2.1) characterised by evergreen ericoid shrubs, mainly members of the family Asteraceae, and by a low occurrence of restioids. Dry restioid fynbos is characterised by the dominance of restioids and other graminoids, and the relatively low occurrence of ericoid shrubs.

Using floristic characters, Taylor (1996) classified the vegetation of the northern Cederberg Mountains into 26 communities. The only non-fynbos community identified was thicket, and no succulent karoo or renoster shrubland was encountered. Considering that this classification covers a centre of diversity for mountain fynbos, it is not surprising that Taylor (1996) derived so many communities. However, many of his communities cannot be treated as management units as they form part of a complex mosaic that would not be practical to resolve and map for management purposes.

The classification of vegetation in other regions of the fynbos biome has received attention from a number of authors. However, because these surveys were carried out a different scales and due to the high turnover in species between regions (gamma diversity) (Bond, 1981) I have not referred to these studies in any detail. Cowling & Holmes (1992) and Cowling *et al* (1997) provide good reviews of these phytosociological studies.

Succulent Karoo

Little work has been done on classifying succulent karoo vegetation, partly because of taxonomic problems in the dominant family, the Mesembryanthemaceae (Hilton-Taylor, 1987). Milton (1978) classified the vegetation at Andriesgrond near Clanwilliam, which is on the western side of the Cederberg (approximately 60km northwest of MNR). Ten communities, including succulent and broken karoo, were classified based on floristic and environmental characteristics. However, none of these communities were found at MNR, although there were definitely karroid elements common to both areas. Lane (1978) briefly surveyed the Tanqua / Doorn Karoo using structural characters and derived four communities separated along a moisture gradient. Snijman & Perry (1987) described the flora of the Niewoudville Wild Flower Reserve that lies on the ecotone between mountain fynbos and karroid shrublands. Their survey, however, did not produce any communities that were apparent at MNR, probably because the Niewoudville reserve lies on dolorite, which gives rise to soil very different from shale- or sandstone-derived soils.

2.1.2 Comparing Floristic and Growth Form Approaches to Vegetation Classification

There has been some debate over the relative merits of using growth form rather than floristic characteristics in classifying floristically complex vegetation (Werger & Sprangers, 1982) such as fynbos. Bond (1981) suggested that the high species turnover along environmental gradients in fynbos makes floristic classification of limited practical use. He stated that it is very difficult to extrapolate floristic communities in fynbos from one area to another because of the high gamma diversity (species turnover between geographic areas) characteristic of fynbos. Campbell (1983, 1985, 1986) supported Bond (1981) by arguing that a structural classification is more appropriate in fynbos for practical and theoretical reasons. The very high diversity typical of fynbos means that users of a floristic classification need to know a large number of species names, which may not be feasible. The high level of geographic turnover apparent in fynbos suggests that structural-functional classification may be more effective in revealing ecological gradients than floristic classification (Cowling & Holmes, 1992).

Fynbos and Succulent Karoo are also taxonomically complicated. Not only is the largest succulent karoo family, the Mesembryanthemaceae, in taxonomic disarray (Chesselet *et al.* 1995), but species of mesembs are notoriously difficult to identify in the field. Similarly, the bewildering number of species in fynbos makes field identification extremely difficult, even for people with botanical experience. Thus the taxonomic complexity of fynbos and succulent karoo makes classification of these vegetation types, and use of the classification, difficult based on floristic composition alone.

This is especially relevant if the classification is to be of use to managers who have little botanical training.

Taylor (1996) suggested that some environmental factors, such as fire, radically alter structural characteristics of vegetation. This is true to some extent in fynbos, which does undergo massive structural changes during a fire (especially in the height of the vegetation), but the same argument can apply to the floristic composition. Fire is thought to be one of the more important factors in maintaining floristic diversity in fynbos by causing a high species turnover in time (Bond *et al.* 1992). Cowling (1987) suggested that stochastic population processes caused by differential post-fire recruitment of fynbos species could explain the random 'noise' apparent in many phytosociological studies.

Werger *et al.* (1972) concluded that the typical Braun-Blanquet approach to a phytosociological survey was appropriate for fynbos, despite its floristic richness. However, their study area was relatively small and their conclusion may not be correct for much larger areas with a high gamma diversity (Campbell, 1986). Also, extrapolation of their classification to other areas may not be appropriate due to the gamma diversity.

Taylor (1996) maintains that without the floristic data, it is difficult to identify communities with rare and endangered species, and these are important conservation considerations. There are a number of biogeographical and ecological questions that can only be answered with data from floristically-based phytosociological surveys (Cowling & Holmes, 1992). However, there are taxonomic difficulties in the identification of many fynbos species and up to 20% of the species collected by Campbell (1986) could not be identified to the species level. Similarly, Bond (1981) left 15% of the species that were differential for his communities unidentified. These identification problems arise because of the massive diversity of plants in fynbos (>7300 species) and succulent karoo (>5000 species) (Cowling & Hilton-Taylor, 1997). Also, many floral characters that are necessary for floristic identification are not present on the plant during the time of collection (Campbell, 1986).

Cowling & Holmes (1992) and Taylor (1996) provide good summaries of the comparative benefits of a floristic and structural approach to vegetation surveys. Floristic-based methods, which require relatively detailed knowledge of the flora, are more appropriate for long term management including the conservation of rare and endemic species. They are also more applicable to smaller areas. Structure-based methods are more useful for experimental and autecological studies, which require a detailed record of short-term changes in the vegetation (e.g. establishing how structural traits vary along resource and nutrient gradients). Structure-based methods, being quicker to use than floristic-based methods, are also more appropriate for surveying extensive areas of floristically complex vegetation such as fynbos and succulent karoo, especially considering time and financial constraints.

Management strategies may not be applicable to all the vegetation types together; e.g. fire, which is an important management tool in fynbos, is very destructive in Succulent Karoo (Milton, *et al.* 1997). There was thus a need for the vegetation in the fynbos / succulent karoo transition to be classified into meaningful management units, which would allow the application of different management strategies to different vegetation communities. To be meaningful for managers, who may not necessarily have botanical training, the classification needed to be relatively simple and based on easily identifiable structural characters, higher taxa and dominant genera or species.

2.1.3 Objectives

The first aim of this chapter was to classify the vegetation of MNR into ecologically meaningful units (communities) that were easily identifiable using simple growth form and floristic characters. The communities must be ecologically meaningful so that management prescriptions can be applied on the basis of community boundaries. The communities also served as units in the later ordination and modelling analyses. To incorporate the communities into a management plan, a map of the vegetation of MNR was required. The second aim of this chapter was to provide such a map of the vegetation communities in MNR that could be used for management.

2.2 METHODS

2.2.1 Gradsect Sampling and Geographic Information Systems

The sites for the vegetation survey were positioned through MNR using an approach similar to that employed by gradsect sampling (Gillison & Brewer, 1985; Austin & Heyligers, 1991). Gradsect sampling is the deliberate positioning of transects along the potentially most important environmental gradient in the area. Assuming that plant species or communities are separated along an environmental gradient, positioning sites within a gradsect ensures that the greatest range of vegetation is included in the sampling (Austin & Heyligers, 1991). Gradsect sampling may be seen as a trade-off between statistical rigour and logistic considerations.

Gillison and Brewer (1985) give a detailed account of the statistical theory behind gradsect sampling. Most statistical approaches to vegetation inventory have been derived from agricultural research and are thus constrained by random or systematic sampling procedures. Such approaches ignore the underlying non-random biological pattern that exists in vegetation and may be of limited use in vegetation surveys. The main problem of statistically rigorous methods, which employ random or systematic sampling, is that they require a lot of time and money. Gillison & Brewer (1985) compared three methods of survey: random transects, simple stratification of transects and purposely placed gradsects. Their results showed that the gradsects recovered significantly more information than the other methods and that the gradsect technique offers a substantial improvement over non-gradient directed methods and need not be criticised on statistical grounds.

Euston-Brown (1995) used gradsect sampling to survey the Baviaanskloof, Eastern Cape; a complex area of fynbos, renosterveld, karoo and subtropical thicket. He sampled along a climatic gradient (represented by altitude) stratified by geology, and located all the plots in close proximity to the road network. This approach gave good results that were easily interpretable with respect to the measured environmental variables. Other South African examples of gradient-directed vegetation analyses include Bond (1981), Campbell (1985) and Cowling & Campbell (1985).

The most intuitively obvious environmental gradient at MNR was an eastward increase in aridity that corresponded to an altitudinal gradient from approximately 1200m in the west to 500m in the east. Interpolated rainfall data from the Computing Centre for Water Research (CCWR, 1996) minute-by-minute rainfall database supported this observation (Figure 1.6). The gradsects used to survey the vegetation at MNR were aligned from west to east. The final positioning of the gradsects was subjective and biased by road accessibility. Fortunately, the moisture gradient coincided with the main access road that traverses MNR from west to east (Figure 2.1). The sampling effort was mostly confined to areas within about one kilometre from the road. Two other environmental variables were regarded as important in determining vegetation distribution at MNR: geology and landtype. Gradsects were stratified using combinations of these two environmental variables.

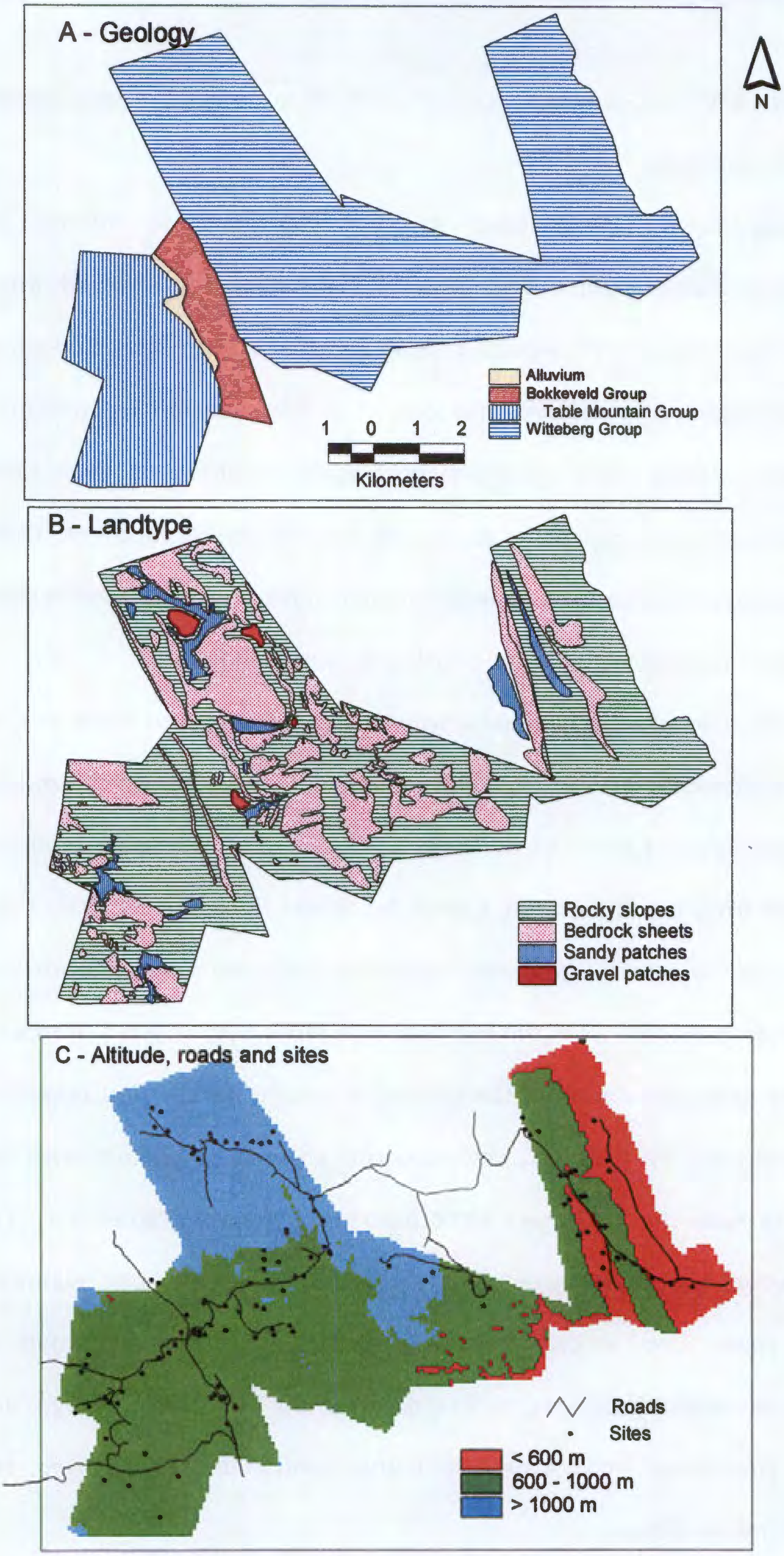


Figure 2.1 The main environmental variables used to direct the sampling effort at MNR. a) Geology; b) Landtype; c) Altitude (showing the distribution of sites and roads)

The environmental variables (rainfall, geology and landtype) which were used to align and stratify the gradsects were mapped in a GIS (ARC/INFO and ARCVIEW 3 software) (Figure 2.1). Geology (Table Mountain Sandstone, Bokkeveld Shale or Witteberg Sandstone) and landtype (sand plains, rock sheets, gravel pans or rocky slopes) were digitised from 1:10 000 enlarged aerial photographs (Appendix A). Altitude was classified into three categories: high (>1000m), middle (600-1000m) and low (<600m). The coverages of geology, landtype and altitude were overlaid within the GIS to give a composite cover indicating the area of each possible combination of the environmental variables (each combination was termed an environmental class). The area of the environmental classes in the GIS was used as a rough guide to divide the sampling effort between the classes.

2.2.2 Sampling Methods

Fieldwork was conducted during the winter season (June to September 1996) as this was when most of the deciduous plants had leaves and many species were flowering, which aided their identification. The sampling unit or site was a 10m x 10m quadrat. This quadrat size is adequate for phytosociological studies in fynbos (Bond, 1981: p 55; Taylor, 1996: p11) and succulent karoo vegetation (Milton, 1978; Smitheman & Perry, 1990: p529). The 125 sites were located near the access roads that run through MNR (Figure 2.1). The sites were located subjectively in areas of homogenous environment that appeared to be typical of the environmental class being sampled. The abundance and cover of every floristic species present in each site were estimated. Annual plants were ignored, as they tended to have specific emergence times that were not consistent over the sampling period.

2.2.3 The Data Sets

Two data sets were created from the sampling, one based on floristic composition at the generic and specific level and the other on 20 growth forms (Cowling *et al.* 1994).

Floristic Data

In the floristic data set, almost all species were identified to at least the genus level, but were not combined within the genus, *i.e.* species were treated as different although not identified. The cover and abundance data for each species were combined using the Domin scale into nine categories (Appendix B). This was done to account for species that had a very low abundance but represented a large proportion of the vegetation cover (*e.g.* *Leucadendron bruiniodes* which has individual plants that can cover up to 25% of a 10x10m plot) and *vice versa.*

I eliminated from the data set all rare species that had a Domin value of three or less (*i.e.* had less than 1-% cover) or that occurred in fewer than two sites. The removal of rare species from the data set can be problematic as it represents a loss of data that may be important in explaining community distributions (Causton, 1988: p 42). However, there was a logistic constraint of having too many species for the classification program

TWINSPAN. Considering that the community descriptions were going to be based largely on the most obvious species, I felt that elimination of the rare species from the classification would be an acceptable simplification. After removal of rare and annual species, the 84 remaining species in the data set were thought to be the most important differential species for potential communities, and this data set was used in all subsequent analyses. Species that were differential in the classification, or were notably dominant in a community were identified.

Growth form Data

Every species (not just the 84 used in the final floristic data) recorded during the survey was classified into one of 23 growth forms using very broad growth form features and life history characteristics (Table 2.2).

Table 2.2 The growth forms used to classify the vegetation of MNR, with their abbreviations. The growth forms are based on those used by Cowling *et al* (1994)

Growth Form	**Abbreviation**	**Growth Form**	**Abbreviation**
Forb	FORB	Parasitic plant	PARA
Sedge	SEDGE	Geophyte	GEO
Grass	GRASS	Restioids (dwarf, low, medium & tall)	D-RES, L-RES, M-RES, T-RES
Dwarf shrubs (<0.25m)		**Medium shrubs** (1-2m)	
Leaf-succulent	DS-LS	Leaf-succulent	MS-LS
Stem-succulent	DS-SS	Stem-succulent	MS-SS
Evergreen	DS-EG	Evergreen	MS-EG
Deciduous	DS-DC	Deciduous	MS-DC
Low shrubs (0.25-1m)		**Tall shrubs** (>2m)	
Leaf-succulent	LS-LS	Leaf-succulent	TS-LS
Stem-succulent	LS-SS	Stem-succulent	TS-SS
Evergreen	LS-EG	Evergreen	TS-EG
Deciduous	LS-DC	Deciduous	TS-DC

The growth forms used represented functional types that have known differences in eco-physiological behaviour (Cowling *et al.* 1994). The cover data for all species that fell into the same growth form taxon were summed within each site. Abundance data were not used, as they did not contribute to the classification of the growth forms.

Environmental data

A number of environmental variables were measured or estimated in each site. These data are discussed in detail in Chapter Four. However, in order to outline the environmental conditions prevalent in each community, I calculated the mean and standard deviation of several environmental variables for all the sites comprising a community (based on the floristic classification).

2.2.4 Classification Analysis

The data were analysed using the polythetic classification computer program TWINSPAN (Hill, 1979). The default settings were used in the floristic-based classification except for the five pseudospecies cut-off levels which were set at 0, 3, 5, 7, 9 to account for the Domin scale. In the structure-based classification, all the default settings were used. Sites 7 and 19 were removed as they were atypical and disrupted the classification.

2.2.5 Exploratory Classification

I initially classified the vegetation using both the floristic and growth form data sets separately and compared the two classifications. Ultimately, the vegetation was classified into communities or management units based on a combination of the growth form and floristic classifications and field notes made during the survey. In the final classification, I used a combination of obvious growth form characteristics combined with the specific names of the dominant species. Although not strictly objective, this method provided a workable and robust set of communities, which were a satisfactory compromise between ecological meaning and manageability.

2.2.6 Comparison of the Floristic and Growth form Classifications

I compared the two classifications using Sorenson's Coefficient of similarity (SI). This simple index gave an indication of how many of the same sites are assigned to same community in both classifications.

$$SI = 100 \times 2C / (A+B)$$

where C = the number of sites in common to both floristic and growth form communities and A and B are the number of sites in each community.

2.2.7. The Vegetation Map

A map of the vegetation at MNR, based on the communities derived from the classification was prepared using a combination of GIS coverage's, aerial photographs and field notes. The boundaries of the communities were checked in the field. The map was produced in a GIS framework so that it can be revised and updated if necessary.

2.3 RESULTS

Below I briefly present the results of the floristic and growth form classifications separately before describing the final combined classification and individual communities in some detail.

2.3.1 Floristic Classification

The floristic classification gave rise to seven major communities (Figure 2.2). The TWINSPAN differential species were given for the division at each level. These differential species were not always used as the diagnostic species in the final classification. The first division of sites was into fynbos & thicket and succulent karoo. At the second division the succulent karoo sites were divided into two communities based on underlying geology: one located exclusively on shale-derived soils (**shale succulent karoo**) and the other on sandstone-derived soils. The fynbos sites did not split into meaningful communities at the second division.

At the third level, the succulent karoo sites on shale were divided into two forms (1 and 2), with no obviously apparent ecological significance. The other succulent karoo sites on sandstone were divided into two communities based on landtype. **Sandy succulent karoo** was found on deep sand plains while **succulent karoo matrix** was found on the rocky slopes. The fynbos sites were divided into four communities based on landtype. **Dwarf bedrock shrubland** was found on bedrock sheets, **restioid sandy fynbos** on extensive and deep sand plains, **kloof thicket** around large outcrops of rock and **asteraceous fynbos matrix** on the rocky slopes and cliff tops.

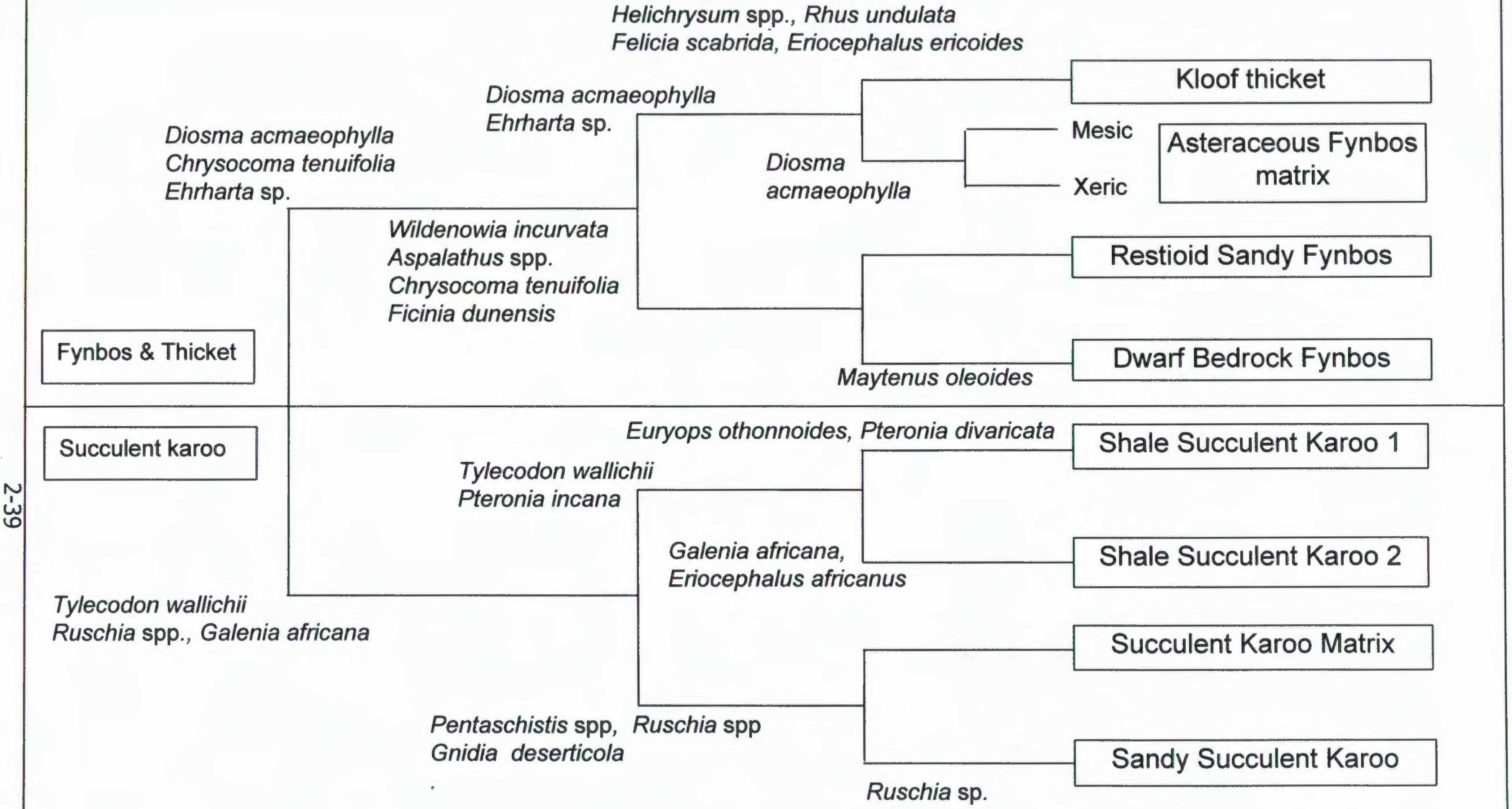
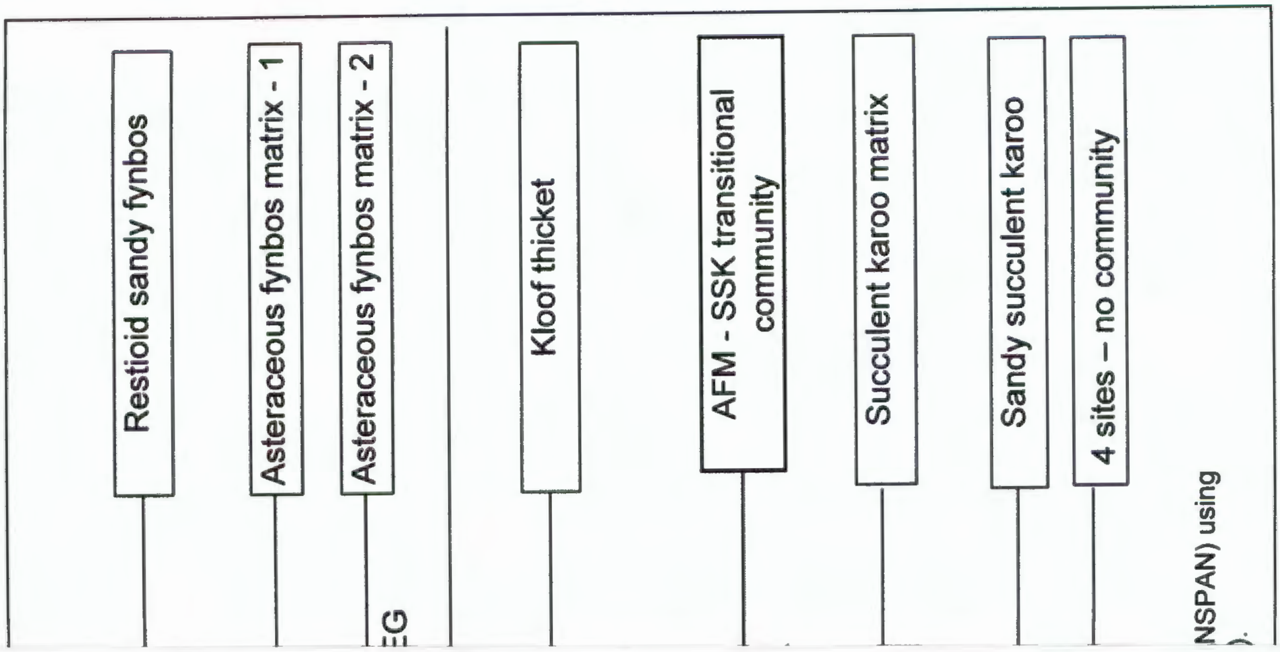


Figure 2.2. A classification of the 125 sites surveyed in MNR based on the floristic data, using Two-Way Indiator SPecies ANalysis (TWINSPAN). The species and genera are the TWINSPAN differential species for each division. See text for details and community escriptions.

The communities and their ecological significance are discussed in the community descriptions. One community in the floristic classification, which was not derived in the growth form classification, was dwarf bedrock shrubland. This community was under-represented in terms of the number of sites (2), but was included as an important component of the vegetation based on field observations. A list of all the species names used in the classification, with their authors is given in Appendix D.

2.3.2 Growth Form Classification

The growth form classification (Figure 2.3) was fundamentally similar to the floristic classification and all the communities except dwarf bedrock shrubland were resolved. The differential growth forms at each division of the classification gave some indication of the dominant growth forms characteristic of each community. The initial division of sites was into fynbos and non-fynbos based on the presence of low restioids and sedges in the fynbos, and dwarf to medium leaf-succulent or deciduous shrubs in the non-fynbos. At the second division, a small group of sites were split off from the fynbos sites based on the presence (<5% cover) of medium restioids. These sites were congruent with the **restioid sandy fynbos** in the floristic classification. The remaining fynbos sites made up the **asteraceous fynbos matrix** from the floristic classification. The non-fynbos sites were split into succulent karoo, with low leaf- and stem-succulent shrubs (<5% cover), and a fynbos-succulent karoo transitional group with dwarf to medium evergreen shrubs (5-20% cover) and sedges (< 2% cover).



CHAPTER ONE

General Introduction and Description of Matjiesrivier Nature Reserve

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1.1 INTRODUCTION

The vegetation transition from fynbos into succulent karoo in the western Cape takes place over a short distance, ranging from a few kilometres to a few metres. There is almost a complete turnover of species between these two biomes. The question of whether this boundary between fynbos and succulent karoo is maintained predominantly by climatic, edaphic or other factors is still unresolved (Cowling & Holmes, 1992; Cowling *et al.* 1997). Understanding the determinants of the boundary between these biomes is important, not only at the landscape scale for management, but also at the regional scale. Effective conservation and management of nature reserves, such as Matjiesrivier Nature Reserve (MNR), that span the fynbos - succulent karoo transition requires an understanding of the ecology of both these biomes.

At the third division, the asteraceous fynbos matrix sites were divided into two forms not similar to the two forms in the floristic classification. These forms were not resolvable as mapping units. One form (AFM-1) was characterised by a canopy of low to medium evergreen shrubs (5-10% cover) and an understorey of dwarf to low leaf-succulent or deciduous shrubs (<5% cover). The other form (AFM-2) was characterised by low restioids (10-20% cover). The group of succulent karoo sites remained largely intact except for four sites with dwarf deciduous shrubs (10-20% cover) that split off. There was no apparent ecological reason for this split. The transitional (AFM - SSK) group split into two; one having a canopy of tall evergreen shrubs (2-5% cover) and an understorey of dwarf deciduous shrubs (5-10% cover); and the other with dwarf leaf-succulent shrubs (<2% cover) and geophytes (5-10% cover). The sites in the first group were congruent with those in the **kloof thicket** community of the floristic classification.

The sites in the latter group were a combination of **shale succulent karoo** and **asteraceous fynbos matrix** from the floristic classification and probably represented a transitional zone between these two communities.

At the fourth level of division, further resolution was only obtained by splitting the succulent karoo sites into two groups. The one group had sites congruent with **sandy succulent karoo** while the other had sites congruent with **succulent karoo matrix** in the floristic classification.

2.3.3 Comparing the Floristic and Growth Form Classifications

Although apparently similar, communities from the floristic and growth form classifications (Figure 2.2 and 2.3) did not share many of the same sites. Sorenson's Coefficient of Similarity (SI) between the floristic and growth form communities (Table 2.3) showed that the communities derived in each classification had few sites in common. Only SKM showed a good similarity between the two classifications. There were also communities in both the growth form and floristic classifications that were not represented in the other classification. Dwarf bedrock shrubland was only apparent in the floristic classification, but I included this community in the final classification, based on my observations in the field. In the growth form classification, a transitional community between fynbos and succulent karoo with sites from both asteraceous fynbos matrix and shale succulent karoo was apparent.

Table 2.3. The similarity of the floristic and growth form classifications based on the number of sites in common and unique to the communities in both classifications, using Sorenson's coefficient (SI = 100*2C/(A+B)).

Community / Formation	**Floristic sites (A)**	**Growth Form sites (B)**	**Sites in common (C)**	**SI**
Asteraceous Fynbos Matrix	36	20	13	**46**
Restioid Sandy Fynbos	13	9	7	**64**
Dwarf Bedrock Shrubland	2	-	0	**0**
Kloof Thicket	10	8	5	**55**
Shale Succulent Karoo	33	24	15	**53**
Succulent Karoo Matrix	26	33	24	**81**
Sandy Succulent Karoo	5	8	4	**57**

2.3.4 Environmental Data

There were considerable differences between the means and standard deviations of several environmental variables for all the sites in each community (based on the floristic classification) (Table 2.4). The differences between the means of each variable in each community are discussed where relevant in the community descriptions, under the Distribution and Habitat section. Chapter Four examines these vegetation-environment relationships more closely.

2.4 COMMUNITY DESCRIPTIONS

The final classification of the vegetation was made from an intuitive combination of the growth form and floristic classifications. The communities in the final classification were thought to be ecologically significant and were used to map the vegetation (Figure 2.4) and in later ordination and modelling analyses (Chapters Four and Five). Seven major communities were identified and are described below according to their growth form and floristic composition. Community descriptions include a list of the sites assigned to the community by each of the classifications separately and the sites which occurred in both classifications. Where relevant, reference is made to related communities described in other authors' classifications.

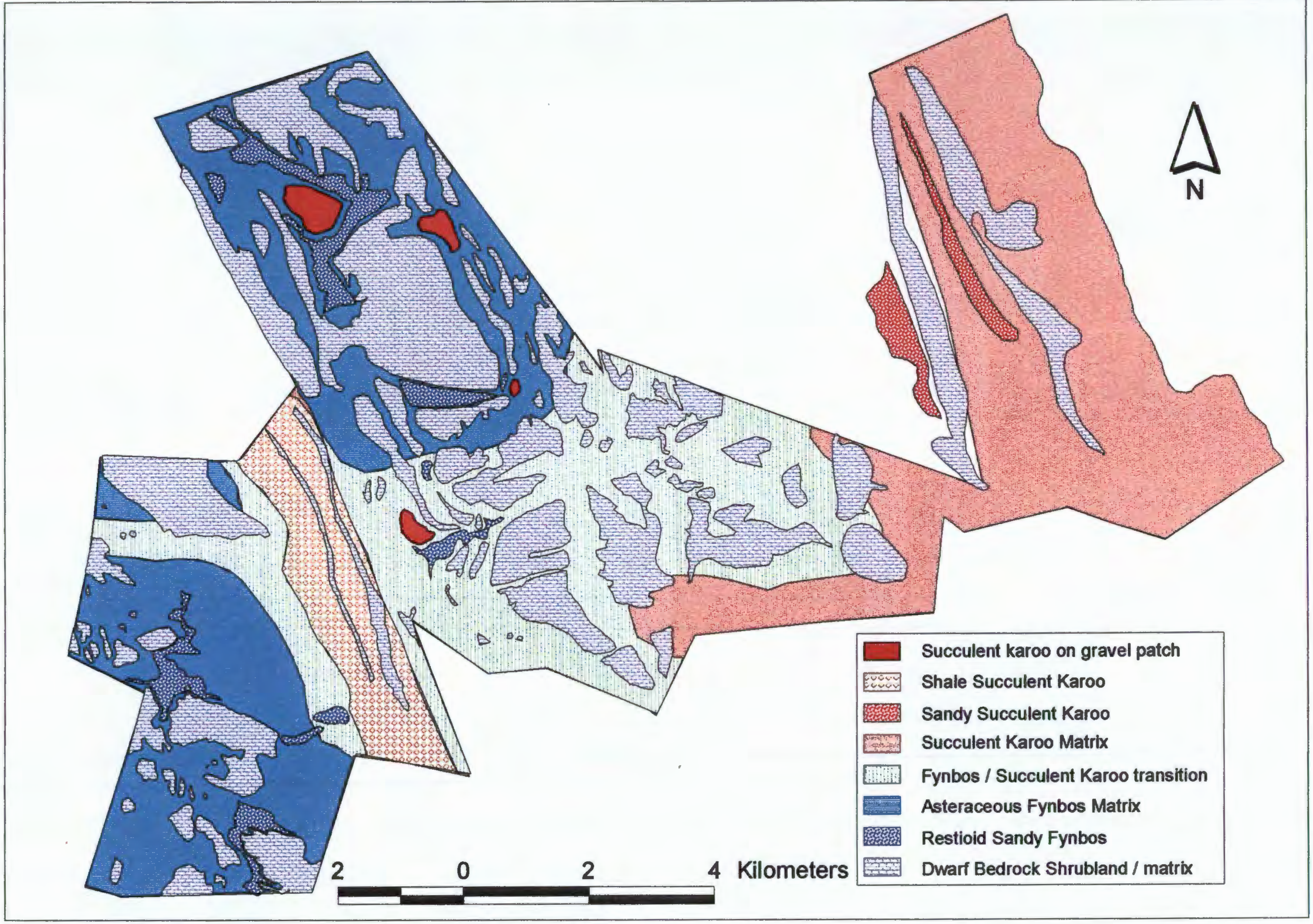

Figure 2.4 The distribution of the major fynbos and succulent karoo communities at Matjiesrivier Nature Reserve.

Table 2.4 The mean and standard deviation (Std) of environmental variables measured in all the sites making up the major communities (n = number of sites). **AMF** - asteraceous fynbos matrix; **DBS** - dwarf bedrock shrubland; **KT** - kloof thicket; **RSF** - restioid sandy fynbos; **SaSK** - sandy succulent karoo; **SKM** - succulent karoo matrix; **SSK** - shale succulent karoo. The environmental variables are **Altitude**; **EAR** - estimated annual rainfall; **Rock** - % rock cover; **Depth** - soil depth; **pH**; **Conduct**. - soil conductivity; **% coarse, medim, fine** - % sand fractions; **% sand, silt, clay** - % texture fractions.

Environmental	AMF n = 36		DBS n= 2		RSF n = 13		KT n = 10		SaSK n =5		SKM n = 26		SSK n = 33	
Variable	Mean	Std	Mean	Std	Mean	Std	Mean	Std	Mean	Std	Mean	Std	Mean	Std
Altitude (m)	978	151	890	14	999	112	962	67	582	18	673	147	834	93
EAR (mm)	283	32	247	1	287	32	270	19	221	26	238	32	246	27
Rock cover (%)	48	34	-	-	7	25	69	30	20	27	72	33	61	26
Depth (m)	0.5	1.7	0.8	1.1	0.8	0.6	0.1	0.0	0.8	0.6	0.2	0.3	0.1	0.0
pH	5.4	0.4	5.9	0.1	5.4	0.3	5.8	0.7	7.2	1.0	5.8	0.7	5.9	0.7
Conductivity ()	58.3	75	187	96	45	37	72	50	132	76	124	62	165	117
% Coarse sand	10	11	33	5	13	11	17	11	5	3	8	3	18	9
% Medium sand	43	11	42	10	51	9	41	7	44	11	39	9	30	12
% Fine sand	47	18	25	5	36	16	42	15	51	10	53	9	52	11
% Sand	94	3	92	2	97	3	93	4	93	7	92	4	90	5
% Silt	3	1	5	3	2	1	1	2	3	3	4	2	6	2
% Clay	3	1	3	0	1	1	4	2	4	2	4	2	4	2

2.4.1 Fynbos Communities

Fynbos at MNR was characterised by a few distinct growth forms, families and species. The dominant growth forms were low to medium woody shrubs with leptophyllous and sclerophyllous ericoid leaves; dwarf to tall restioids and dwarf to low sedges. One species that repeatably came up as an indicator species was *Diosma acmaeophylla* (Rutaceae), which is a medium to tall evergreen, ericoid shrub. Fynbos communities were restricted to the western half of MNR where rainfall and altitude are high and the soils derived from sandstone. Fynbos communities made up a mosaic in this half of MNR, depending on the landtype.

2.4.1.1. Asteraceous Fynbos Matrix (AFM)

Classification	Site numbers
Floristic (22)	15,22,23,24,38,55,62,72,73,75,85,90,90,94,102-106, 113,121,122.
Growth form (6)	14,65,66,71,79,84
Both (14)	29,61,67,68,77,86,87,107,115,116,118,119,120,125

Related communities: Campbell's (1985) Dry Asteraceous Fynbos

Plate: 2.1

General description:

AFM was the most heterogeneous community in MNR, and was more a 'dumping' category than a distinct community. Plant cover in the sites was approximately 40%. Two formations were defined in the floristic classification (Figure 2.2): a mesic and a xeric form. The mesic form was the 'true' fynbos in the western extreme of MNR (Plate 2.1a). The xeric form represented the transition from fynbos into succulent karoo towards the middle of MNR (Plate 2.1b).

AFM comprised a complex matrix of species associations at a fine scale that would be impossible to map or manage as separate units. The boundaries of these associations are probably maintained by a combination of biotic effects such as competition or facilitation, stochastic effects such as fire and climate; and edaphic, landtype and topographic heterogeneity (Bond *et al.* 1992; Cowling *et al.* 1997). Very few species or genera appeared as dominants in the community, a feature characteristic of fynbos (Taylor, 1978).

Floristic composition

All the typical elements of arid mountain fynbos (*i.e.* members of the Asteraceae, Proteaceae, Restionaceae, Poaceae, and several typically ericoid families) were present in AFM. Shrubs from the Asteraceae were proportionally the most abundant of all the shrub families in the fynbos, probably because MNR lies in the xeric extreme of the fynbos biome (Cowling & Holmes, 1992).

Diosma acmaeophylla was the only indicator species for AFM. However, a number of genera and species were relatively common throughout AFM and were locally abundant in the fine-scale species associations. The two forms of AFM, mesic and xeric, were separated on the basis of dominant genera. The mesic form had a greater proportion of more 'typical' fynbos taxa including: *Diosma acmaeophylla, Phylica odorata, Leucadendron pubescens, Aspalathus* spp., *Agathosma* spp., *Stoebe fusca,* *Felicia scabrida,* and many members of the Restionaceae. Geophytes and members of the Restionaceae (particularly of the genus *Cannomois*) and Cyperaceae (particularly *Ficinia dunensis*) dominated the understorey of the mesic form.

The xeric form of AFM was characterised by a greater proportion of woody shrubs from the Asteraceae including: *Eriocephalus africanus, Eriocephalus ericoides, Pteronia incana, Euryops wageneri, Euryops othonnoides, Dolichothrix ericoides* and *Elytropappus rhinocerotis* and several species of *Othonna.* Members of the Mesembryanthemaceae and Crassulaceae dominated the field layer. The xeric form of AFM could be considered the equivalent of central mountain renosterveld (Rebelo, 1996b).

Structure

Many of the sites classified as AFM in the floristic classification were classed as a transitional community with shale succulent karoo in the growth form classification (Figure 2.3). Low to medium evergreen shrubs, restioids and low leaf-succulent shrubs were the most abundant growth forms in AFM. The vegetation canopy was 0.5m to 1.5m tall with a few taller (>2m) evergreen shrubs in particularly mesic or fire protected sites. In terms of leaf size and form, the leaves of the characteristic shrubs were typically sclerophyllous, leptophyllous and either ericoid or elytropappoid. Low (0.25 - 1.0 m) sedges and low to medium (0.25 - 2 m) restioids occurred in dense clumps which were often locally dominant throughout AFM on small sandy patches. Low (< 0.1 m) leaf-succulent shrubs made up a significant proportion of the field layer of AFM, especially where the soil was shallow.

Distribution & habitat

Asteraceous Fynbos Matrix was widely distributed through the western half of MNR (Figure 2.4). There were two centres of mesic AFM, one south and west of the Matjies River and the other west of Perdewater in the northern arm of MNR (Figures 1.1 and 2.4). The eastern extreme of xeric AFM (and fynbos in general) was approximately in the middle of MNR (longitude: 19° 25" E; altitude: 800m; estimated annual rainfall: 270mm). The boundary between xeric AFM and succulent karoo matrix was characterised by a gradual loss of fynbos elements and a corresponding increase in succulent karoo elements (mostly non-succulent asteraceous shrubs). An increase in longitude and aridity, and decrease in altitude accompanied this transition. The environmental explanations for the transition from fynbos to succulent karoo are examined in chapters Four and Five.

The habitat characteristic of AFM can best be described as high altitude, mesic and rocky. AFM occurred in all topographic positions from flat plateaus and plains to steep slopes, wherever the soil was derived from sandstone or quartzite and where there was a high occurrence of surface rocks - either as talus or as partially exposed bedrock. Soil conditions were invariably sandy, with a very low clay content and electrical conductivity (Table 2.4). Isolated patches of AFM were scattered away from the centres of AFM throughout the western half of MNR, in the fynbos / succulent karoo transitional zone (Figure 2.4). These AFM patches occurred at locally mesic sites within the transitional zone. Such sites included many of the high elevation ridges that were more mesic, and sites where there was precipitation run-off into the soil due to the presence of large rock sheets.

2.4.1.2. Restioid Sandy Fynbos (RSF)

Classification	Site numbers
Floristic (6)	14, 65, 71, 79, 80, 117
Growth form (2)	105, 106
Both (7)	9, 10, 13, 69, 70, 81, 124

Related communities: Campbell's (1985) Dry Restioid Fynbos; Taylor's (1996) Community 18 *Wildenowia arescens - Thamnochortus platypteris*
Plate: 2.2

General description

Restioid sandy fynbos was generally low to medium in height (<2 m). A restioid layer, or occasionally a taller proteoid layer dominated the canopy. The understorey was either bare or dominated by dwarf (< 0.25 m) graminoids (restioids, grasses and sedges) and leaf-succulent woody shrubs from the Mesembryanthemaceae and Crassulaceae. The percentage cover and average height of plants in RSF appeared to depend on moisture availability. In mesic areas there was greater cover (up to 70%) of tall restioids and proteoids while the more xeric areas had lower cover (<40%) of shorter restioids.

Floristic composition

Members of the family Restionaceae (restioids) had the greatest cover in RSF. The most conspicuous and locally dominant genera in the Restionaceae were typically *Willdenowia, Restio, Thamnochortus, Hypodiscus,* *Ischyrolepis* and *Elegia*. Large isolated individuals (up to 2m high and 2m in diameter) from the genus *Willdenowia* were typically scattered through RSF. The most conspicuous and widespread species was *Willdenowia incurvata*. Some of the patches of RSF (such as near Perdewater or in many sandy river channels) were also characterised by the abundance (>10%) of *Leucadendron bruinioides* var. *bruinioides* (Proteaceae).

Depending on the apparent moisture availability, there was considerable variation in the understorey of RSF. Grass taxa, particularly the genera *Pentaschistis* and *Ehrharta,* were more apparent in the understorey of the xeric areas. There was also an increase in the proportion of mesembs and crassulas in the understorey with increasing aridity. In mesic areas, sedges, notably of the genera *Ficinia* and *Tetraria* replaced the grasses and shrubs in the understorey. The most widespread and abundant sedge was *Ficinia dunensis*. Geophytes and annual forbs were also quite common.

There was a distinct form of RSF near Perdewater that had a considerably shorter canopy than the other patches of RSF, and was dominated by *Ischyrolepis unispicatus* (>40% cover) and *Elytropappus rhinocerotis* (Asteraceae) (Plate 2.2b). This form of RSF only occurred where there was a high cover of small (< 0.05 m) pebbles scattered on or near the surface of the sand (Plate 2.5d). These pebbles were possibly derived from the erosion of an ancient Tertiary surface (Taljaard, 1949; Peter Holmes, personal communications).

Structure

In terms of structure, RSF was quite uniform, with the biggest variation being attributable to differences in height of the canopy. The dominant growth forms in RSF were medium to tall restioids and medium to short sedges and grasses. In a few patches there were very tall proteoid shrubs; otherwise there were few woody shrubs typical of AFM. Two arid sites (43 & 55), that occurred deep in the succulent karoo matrix, were classified as RSF based on growth forms. Both of these sites were on deep sands and had only a few restioid elements present on them. These sites represent extreme outliers of RSF.

Distribution and habitat

Restioid sandy fynbos was found exclusively on patches of deep sand throughout the western half of MNR (except for the outlier sites 43 & 55). The sand was probably of aeolian origin and was typically orange to white in colour. Evidence of water-logging at approximately one meter was present in some areas, notably around Perdewater. There were several large areas of deep sands in the western half of MNR (Figure 2.1) and all of these were covered by RSF. The patches of RSF formed islands within the fynbos matrix and had many elements in common with AFM (Figure 2.4). The sand patches were often interspersed with large sandstone outcrops and bedrock sheets, which harboured kloof thicket and dwarf bedrock shrubland communities.

2.4.2 Transitional Communities

2.4.2.1. Dwarf Bedrock Shrubland (DBS)

Classification	Site numbers
Floristic (2)	11, 12
Growth form (0)	None
Both (0)	None

Related communities: Taylor's (1996) Communities 5, 6 & 7
Plate: 2.3

General Description

Dwarf bedrock fynbos was only represented by only two sites in the floristic classification and was not defined as a community in the growth form classification. I have, however, included DBS as a distinct community because it was differentiated at the third level of division in the floristic classification. Also, based on field observations, DBS was an important component of the vegetation and may harbour a large number of rare or endemic species.

Typically, there was a very low cover of vegetation on the rocksheets, as there are only a limited number of cracks and erosion hollows where enough soil could collect to support woody shrubs. The limited soil volume available to most of the shrubs has resulted in stunted or 'bonsai' growth. Individuals of species which were typically medium to tall in more amenable habitats, remained at <0.5m, with only their thick and twisted stems testifying to their age.

Floristic composition

The characteristic species listed below were based largely on my field observations, as the differential species derived from the floristic classification were unreliably based only on two sites. In mesic areas, DBS was characterised by stunted ericoid, sclerophyllous shrubs typical of fynbos. The families Ericaceae, Proteaceae and Rhamnaceae were most common. Three species: *Phylica buxifolia, Erica maximiliani* and *Protea glabra,* were particularly conspicuous on bedrock sheets throughout the western half of MNR. The *P. glabra* attained large sizes (up to 5m high) (Plate 2.3a), with roots penetrating deep into cracks in the bedrock. These large specimens of *P. glabra* occurred up to the extreme eastern boundary of the fynbos / succulent karoo transition. The dominant species in DBS (based on abundance as there was never a high cover of vegetation) depended on the surrounding vegetation, which acts as a source for the propagules that get lodged in the rock cracks.

Towards the arid east of MNR, taxa common in succulent karoo increased relative to the fynbos taxa. Even within the fynbos matrix there were small populations of members of the Mesembryanthemaceae (*Ruschia, Lampranthus, Conophytum*) and Crassulaceae (*Crassula, Tylecodon*) that were able to survive the harsh, xeric conditions of the shallow soil (Plate 2.3b).

Structure

DBS was structurally diverse and combined typical fynbos and succulent karoo growth forms. Ericoid and sclerophyllous shrubs and dwarf leaf-succulent shrubs were found together, which was why DBS was considered a transitional community. This was also the reason why DBS did not arise as a distinct community in the growth form classification.

Distribution and habitat

As the name suggests, DBS was confined to the surfaces of the large rock sheets and outcrops that occurred throughout MNR (Figures 2.1 and 2.4). The rock sheets are exposed sandstone or quartzite bedding planes that are typically flat. There were few occurrences of exposed sheets of horizontal shale strata at MNR for comparison between geological groups. The surfaces of the bedrock sheets are typically eroded into channels, crevices and depressions where enough soil and organic matter collects to provide micro-sites for the growth of woody plants. The depth of the crack (and thus soil) appeared to dictate the type and structure of plant that could grow there.

The rocky habitat presented two extremes of water availability to plants that survived on them. During the dry summer season, the exposed rock sheets were exceptionally xeric as they had little soil to act as a reservoir for moisture. During the wet season, the depressions in a rocksheet have an over-abundance of water due to the very high run-off from the rock sheet, and may become water-logged. Plants would be unable, in most cases, to penetrate sub-surface water unless the rock crack in which they were growing was deep enough (as was the case for *P. glabra*). Thus the plants living in rock cracks must be able to survive extended periods of extreme drought during summer, very wet conditions during winter, and rapid changes between a state of moist soil and dry soil.

2.4.3 Non-Fynbos Communities

2.4.3.1. Kloof Thicket (KT)

Classification	Site numbers
Floristic (5)	74, 76, 83, 84, 89
Growth form (3)	11, 90, 117
Both (5)	78, 92, 93, 98, 99

Related communities: Campbell's (1985) Forest & Thicket; Taylor's (1996) Community 4, *Olea europaea* subsp. *africana* - *Myrsine africana* on sand flats and mesic screes.
Plate: 2.4

General description

Kloof thicket was confined to locally mesic habitats between large rock outcrops. The vegetation canopy was tall to very tall (>2m) and cover was high compared to the surrounding fynbos matrix. The floristic composition of KT was derived from a combination of typical sub-tropical thicket shrubs and a number of typical fynbos shrubs. The restioid and proteoid growth forms were generally absent from KT.

Floristic composition

Kloof thicket appeared in the floristic classification as a sub-set of AFM, with *Rhus undulata* as a differential species. Other thicket species, which I observed as common in KT (but were not apparent in the floristic classification), included *Maytenus oleioides* and *Dodonaea angustifolia*.

Depending on the location of the rock outcrop, there were several other woody shrub species more typical of fynbos or the transition from fynbos into succulent karoo such as *Diosma acmaeophylla, Phylica buxifolia, Pteronia* spp., *Eriocephalus ericoides* and *Helichrysum* spp.

Structure

Kloof thicket was structurally easy to identify. It was characterised by tall (>2m) woody shrubs with large (mesophyllous) evergreen leaves, and by a lack of the restioid and proteoid growth forms. Forbs, ferns and deciduous dwarf shrubs were characteristic of the understorey.

Distribution and Habitat

Kloof thicket was typically found between the large sandstone outcrops that were dotted through the western half of MNR (Plate 2.4b). They were restricted to mesic areas and became less frequent with increasing aridity. KT occurred on patches of shallow aeolian sand trapped between the large outcrops. There is probably considerable run-off from the outcrops during precipitation and thus the soil around the edge of the outcrops receives more effective precipitation surrounding vegetation.

The protected nature of the KT sites, which are hemmed in by large outcrops of sandstone, suggested that they are fire-refuges. However, fire does not seem to be a regular occurrence in the fynbos communities of MNR. Fire is believed to be a factor that maintains the boundary between fynbos and thicket (Cowling & Holmes, 1992) and it is possible that fires occur infrequently, forcing KT into fire refugia.

2.4.4 Succulent Karoo Communities

Succulent karoo sites were separated from fynbos sites on the basis of a number of floristic and growth form characteristics. The main succulent karoo families at MNR included the Mesembryanthemaceae, Asteraceae and Crassulaceae. The abundance of leaf- and stem-succulent and deciduous shrubs, and the absence of evergreen leptophyllous shrubs with ericoid leaves were probably the most important growth form features separating succulent karoo from fynbos at MNR.

2.4.4.1. Shale Succulent Karoo (SSK)

Classification	Site numbers
Floristic (16)	1,3,7,18,19,26,27,28,66,82,96,100,101,112,111,113.
Growth form (6)	23,24,72,85,88,91
Both (20)	2,4,5,6,8,16,17,20,21,25,30,95,97,108,109,110, 114,123

Related communities: Campbell's (1985) Succulent Shrubland
Plate: 2.5

General description

SSK was exclusively confined to a band of exposed shale strata from the Bokkeveld Group (Figure 2.1). Deciduous shrubs from the Asteraceae, stem-succulent species from *Euphorbia*, and leaf- and stem-succulent members of the Mesembryanthemaceae and Crassulaceae dominated SSK. The vegetation in SSK was relatively sparse, with less than 30% cover and with a canopy height of about one meter. The understorey also was typically sparse, comprising dwarf leaf- and stem-succulent shrubs and many annual ferns, forbs and geophytes.

Floristic classification

Two differential species, *Tylocodon wallichii* (Crassulaceae) and *Pteronia incana* (Asteraceae) characterised SSK in the floristic classification. Other genera from the Asteraceae that were particularly abundant in SSK included: *Euryops, Pteronia* and *Eriocephalus. Pteronia divaricata, Galenia africana, Eriocephalus africanus* and *Eriocephalus ericoides* were most abundant. Large individuals of *Euphorbia mauritanica* and *Tylecodon paniculatus* were dotted through the community. Although these individuals did not account for a large proportion of the cover, they were a conspicuous and diagnostic feature of SSK. Species diversity in SSK was relatively low compared to the other succulent karoo communities.

Two formations, SSK-1 and SSK-2, were derived in the floristic classification based on the presence of *Euryops othonnoides* and *Pteronia divaricata* in SSK-1 and *Galenia africana* and *Eriocephalus africanus* in SSK-2. The separation of SSK sites into these formations did not make ecological sense. In this respect, SSK was mapped as single management unit.

Heuweltjies or mima-like earth mounds (Knight *et al.* 1989; Moore & Picker, 1991) were quite common throughout SSK (Plate 2.5b). These mounds were about 0.1 - 0.5m high and about 2 - 10 m in diameter. *Heuweltjies* differ from the surroundings in terms of soil nutrient, organic matter and moisture status (Milton *et al.* 1997) and those at MNR supported 'islands' of vegetation that were noticeably different from the surrounding matrix vegetation. I only sampled three sites on these *heuweltjies*. In both the floristic and growth form classifications these sites were assigned to

SSK-2. Two species were characteristic of *heuweltjies* in SSK-2: *Pteronia divaricata* and *Tylecodon paniculatus.*

Structure

There was no distinct group of sites in the growth form classification that corresponded to the SSK sites in the floristic classification. There was considerable overlap between AFM and SSK and thus, in the growth form classification, SSK appeared to be part of a transitional community from fynbos into succulent karoo. This was not surprising considering that most of the growth forms found along the shale band were also found in the fynbos / succulent karoo transition. It was only the charismatic and conspicuous growth forms such as the large stem- and leaf-succulents (*Tylecodon paniculata* & *Euphorbia mauritanica*) which caused the vegetation on the shale band to look different to the surrounding matrix.

Distribution and habitat

SSK was found exclusively on the bands of shale and sandstone from the Bokkeveld Group that are exposed along their bedding planes near the homestead at MNR (Figures 2.1 and 2.4). These alternating layers of shale and sandstone gives rise to a series of parallel north-south orientated ridges of sandstone and valleys of shale (Plate 1.1a). The shale bedrock was exposed in many places and there was often an overburden of sandstone debris on the slopes from the sandstone ridges. The soil on these slopes is dark brown and has a relatively high proportion of silt and clay, giving rise to a fine-textured loam compared to the surrounding sandstone-derived sands (Table 2.4). It is these fine-textured soils which are thought to increase the effect of summer drought on the vegetation, resulting in the occurrence of more succulent karoo taxa compared to the surrounding matrix vegetation (see Chapter Six).

The succulent karoo vegetation growing on the gravel patches (Figure 2.1 and Plates 2.5c & 2.5d) was classified as SSK. There was another localised occurrence of shale in MNR, on a south-facing slope in the middle of the Matjiesrivier gorge. There is extensive folding of the rock strata at this point, and the river has exposed an anticline of Bokkeveld Group shale beneath the Witteberg Group sandstone. The vegetation on this shale was dominated by dwarf shrubs (mostly *Pteronia* spp.), leaf-succulent mesembs and the stem-succulent *Euphorbia hamata*. There was a very low total cover; probably because the surface was unstable with almost no soil (steep slope and gravelly shale soil which must have had a very high rate of erosion).

The proximity of the Bokkeveld Group ridges and valleys to the homestead and perennial water (the Matjies River) suggested that the SSK community would have been under considerable grazing pressure during the approximately 200 years MNR was a stock farm. Thus the current vegetation and community description is unlikely to reflect what the vegetation would be like under ungrazed conditions.

2.4.4.2. Succulent Karoo Matrix (SKM)

Classification	Site numbers
Floristic (2)	41,88
Growth form (9)	1,12,26,27,42,55,62,80,111
Both (24)	31,32,33,34,36,37,39,40,43,44,45,48,49,51,52,53,54,56,57,58,59,60,63,64

Related communities: a xeric version of Campbell's (1985) Succulent Shrubland that occurs on quartzitic soils.
Plate: 2.6

General description

The most distinguishing feature of SKM was the dominance of leaf-succulent members of the Mesembryanthemaceae and Crassulaceae, both in terms of relative cover in the vegetation and species diversity. The vegetation in SKM was generally less than one metre high and total vegetation cover relatively low (< 30%). As in AMF, there were two forms within SKM, which reflected the transition from fynbos into succulent karoo. One form occurred in the arid part of the transitional zone and had a combination of typical succulent karoo and fynbos taxa and growth forms. The other form, which occurred in the extreme arid part of MNR was 'proper' succulent karoo with very few fynbos elements. These forms comprised an intricate matrix, depending on local environmental conditions that influence water availability, and were not mappable as separate units.

Floristic composition

Numerous members of the Mesembryanthemaceae and Crassulaceae dominated SKM. There was high species richness in these two families in SKM, which was expected considering that the succulent karoo is the centre of diversity for these families (Milton *et al.* 1997). In the floristic classification, two *Ruschia* species, the grass genus *Pentaschistis* and the shrub *Gnidia deserticola* (Thymeleaceae) were differential taxa for SKM (Figure 2.2).

In the transitional form of SKM, shrub genera from the Asteraceae, particularly *Pteronia, Eriocephalus* and *Elytropappus,* were most common. There were also a number of fynbos taxa present wherever there was enough moisture, such as on south-facing slopes. A number of other conspicuous species such as *Euphorbia hamata, Euphorbia mauritanica, Tylecodon paniculatus* and *Hoplophyllum spinosa* were distributed sparsely through the arid part of the transitional formation.

The 'true' SKM form (Plate 2.6b) was almost totally dominated by members of the Mesembryanthemaceae and Crassulaceae and there were few shrubs from other families (*Gnidia deserticola* was a notable exception as a locally dominant species). Two very common genera from the Mesembryanthemaceae found in SKM were *Ruschia* and *Lampranthus.*

Structure

Dwarf to low leaf-succulent woody shrubs dominated the vegetation in SKM, increasing relative to the non-succulent shrubs along the aridity gradient. In the 'true' SKM form there were few typical fynbos growth forms such as evergreen ericoid shrubs. Medium-height leaf-succulent shrubs, geophytes, grasses and deciduous dwarf shrubs were differential growth forms for this formation (Figure 2.3). In the 'transitional' form, low to medium evergreen shrubs, growth forms more typical of the fynbos communities, were differential. The transitional forms reflected a change from evergreeness to deciduosity and an increase in leaf-succulence.

Distribution & Habitat

SKM occurred in the eastern half of MNR (Figure 2.4). There was a gradual transition from fynbos into succulent karoo marked by an increase in the appearance of typical karroid elements with increasing longitude and a corresponding loss of fynbos elements. SKM occurred into the fynbos part of the transitional zone wherever there was localised aridity. Examples of this included the steep slopes of the Matjies River gorge and its tributaries in the western half of MNR (described below). The 'true' SKM form was found in the eastern extreme of MNR, near the Doring River. The western boundary of this formation appeared to be along the ridges of the Wildehondskloof and above Klipbokkloof (Figures 2.1 and 2.4), although this boundary was indistinct.

The Matjies River Gorge

The following description of SKM in the Matjies River gorge is based only on notes made during an exploratory fieldtrip. No sites were located in the gorge due its inaccessibility. The Matjies River gorge represented a corridor that extends the distribution of SKM west, deep into the fynbos-succulent karoo transition. This was because the steep slopes (estimated at > 45°), and particularly the north-facing slopes, represented very arid habitats. The steep angle results in rapid run-off and erosion and thus the soil was relatively shallow on these slopes, and there was probably not much of a soil-water reservoir. The north-facing slopes were considerably more arid than the opposing south-facing slopes, due to differences in radiation. The soil on the slopes was always sandy, derived from Witteberg sandstone, and there was generally a very high cover of medium sized sandstone boulders (<0.5m across). The sandy soil (low water retention) and high light reflectance from the quartzitic rocks made the gorge slopes a very arid habitat indeed.

The cooler south-facing slopes tended to have fewer leaf-succulents than the north-facing ones and more shrub species from the Asteraceae (*Pteronia* spp., *Eriocephalus africanus, Hoplophyllem spinosa, Elytropappus rhinocerotis*). Occasional, but very conspicuous, large specimens of *Rhus undulata, Euphorbia mauritanica* and *Tylecodon paniculatus* occurred on the south facing slopes.

The more arid north-facing slopes had a higher degree of succulence and fewer asteraceous woody shrubs. The leaf-succulent Mesembryanthemaceae and Crassulaceae were the most common taxa seen. There were no individuals of *R. undulata, E. mauritanica* or *T. paniculatus* present on the north-facing slopes.

2.4.4.3. Sandy Succulent Karoo (SaSK)

Classification	Site numbers
Floristic (1)	42
Growth form (4)	3,38,41,82
Both (4)	35,46,47,50

Related communities: none

Plate: 2.7

General description

Sandy succulent karoo was the karroid equivalent of restioid sandy fynbos on arid sites. SaSK generally had a sparse cover of vegetation with large spaces between the individual plants. The canopy height was generally less than 0.5 metres and there were few understorey species. The vegetation was quite patchy with relatively dense mono-specific populations of several species occurring repeatably through the landscape. In total, SaSK comprised a relatively small area of MNR, and was confined largely to a single valley floor in the eastern part (Wildehondskloof, Figure 2.4).

Floristic composition

SaSK was characterised by locally dense populations of *Ruchia* spp., *Euphorbia deccusata* and *Zygophyllum retrofractum.* Perennial grasses such as *Stipagrostis namaquensis* were also common except near the old kraal sites, which are dotted through the landscape. Very infrequent patches of *Willdenowia incurvata* occurred in locally mesic areas of deep sand.

Structure

Structurally, SaSk was characterised by localised patches of dwarf leaf-succulent or fleshy-leaved shrubs and stem-succulent, aphyllous plants. Grasses were common, and formed relatively dense stands except around the old kraal sites. In the more mesic sites of SaSK, localised patches of low to medium restioids occurred.

Distribution and Habitat

Sandy succulent karoo was found exclusively on deep sands within the karoo matrix in the eastern part of MNR. The only example in MNR was the valley floor of Wildehondskloof (Figure 2.4) where the yellow soil was generally deeper than 1.2m and there was a very low surface cover of rocks. The sandy soil appeared to be well drained and was probably of aeolian origin, similar to the patches in the fynbos matrix.

2.5 DISCUSSION

The aim of this discussion is to provide a brief overview of all the vegetation communities described above, how they were distributed through the landscape at MNR and how they relate to each other. I also evaluate the methods used to classify the vegetation and the practicality of the derived communities for mapping and management.

2.5.1 Community-Environment Generalisations

Fynbos Communities

The fynbos communities are confined to the west of MNR, which is generally higher altitude, and thus cooler, and receives a more precipitation. Asteraceous fynbos matrix, which occurs on all the rocky talus slopes and areas of partially exposed bedrock, covered most of this mesic area. Within the fynbos matrix, the other fynbos communities are separated according to landtype. The deep sandy soils on the flat plains support RSF. Fire-protected and mesic outcrops of sandstone support Kloof Thicket with its tall shrubs and trees that typically have mesophyllous evergreen leaves. The rocky outcrops and exposed rocksheets support a combination of stunted fynbos shrubs and leaf-succulent succulent karoo shrubs that are confined to growing wherever enough soil has collected.

Succulent Karoo Communities

Moving eastward along the aridity gradient, there is a gradual transition from fynbos into succulent karoo. This transition is characterised by a slow turnover of growth forms and species from leptophyllous and sclerophyllous fynbos shrubs to leaf-succulent dwarf shrubs, and by the loss of the restioid growth form. The transitional zone between fynbos and succulent karoo is indistinct. There are many areas where fynbos and succulent karoo elements extend deep into the other, in response to localised moisture gradients caused by geological or topographic features such as the Matjies River Gorge. The steep north-facing slopes of the Matjies

River Gorge, which represent a relatively arid environment, give rise to a corridor of succulent karoo deep into the fynbos side of the transitional zone.

2.5.2 Evaluation of Methods and Practicality of Communities

The use of TWINSPAN as a method for classifying vegetation communities has received much criticism, although it is still frequently used by phytosociologists. Van Groenewoud (1992) tested the robustness of TWINSPAN on simulated data and found it erratic and a poor descriptor of pattern. He found that each successive division of the classification becomes less accurate and ecologically meaningful. The classifications I used were not taken below the third level of division and thus the communities make ecological sense and are relatively accurate representations of the vegetation on the sites.

By combining the differential species from both the growth form and floristic classifications with personal notes made during the fieldtrips, I believe that the communities derived during this survey are ecologically meaningful and will have use in management planning. The communities were easily identifiable by a few key species, simple growth form groups and knowledge of the different landtypes. Thus the communities fulfil the desired characteristics of being easily identifiable, ecologically meaningful and useful for mapping and management.

CHAPTER THREE

Quantifying the Independent and Shared Variance Attributable to Growth Form and Floristic Composition

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3.1 INTRODUCTION AND OBJECTIVES

3.1.1 Introduction

Vegetation communities are often described either by their floristic composition or their growth form mix. The floristic and growth form attributes of plant communities are most often investigated separately and there are few techniques available to compare or combine these properties (Fullerton, 1997). As reviewed in Chapter Two, there have been several surveys of fynbos and succulent karoo vegetation based on either the floristic or growth form attributes of the vegetation (e.g. Campbell, 1986 and Taylor, 1996). Those surveys that have made an effort to investigate both vegetation properties independently have not quantified the contributions made by each property to community structure, nor have they assessed the interactions between the two properties. Fullerton (1997) is, to my knowledge, the first to make use of variance partitioning techniques to separate out the variance attributable to floristic and growth form composition. Complete analysis of vegetation communities involves a quantification of the contributions of floristic and growth form properties to community structure and an assessment of the interactions between these properties (Fullerton, 1997).

Where floristic and growth form composition relate differently to the environment, floristic-growth form gradients might arise where each property varies independently of the other. It then becomes important to identify the common and independent variance attributable to each property to improve the resolution of community structure and to provide functional insights into community structure (Fullerton, 1997). Community patterns may potentially be produced and maintained by both the individual properties of floristic composition and structure (Drake, 1990, 1991). In order to understand fully the patterns in community structure, the individual properties must be examined. In this way, patterns that are uniquely attributable to either floristic composition, growth form composition, or both can be assessed (Fullerton, 1997).

Variance in community patterns of vegetation may reflect combinations of variance due to the individual properties uniquely, or to their common variance. Investigation of a single property may not be tenable as an approach to understanding community structure, even though such an investigation may provide meaningful insights into the community structure. However, in order to examine the interactions between floristic composition and structure, the individual properties need to be interpreted independently (Fullerton, 1997).

3.1.2 Research Objectives, Rationale and Hypotheses

The objective of this chapter was to assess whether vegetation community structure at MNR could be explained adequately by either floristic composition or growth form composition alone. This was tested by quantifying the proportions of independent and shared variance attributable to floristic and growth form composition. This question was decomposed into two testable hypotheses.

1) *There was no difference in the amount of variance attributable to floristic composition and growth form composition independently.*

2) *There was no difference in the amount of variance shared between the floristic and growth form composition.*

3.2 METHODS

The method described below was adapted from that used by Fullerton (1997) and is a means of variance partitioning available in the program CANOCO (vers. 3.12, ter Braak, 1991). The floristic data, comprising the 83 most abundant species, and the growth form data, comprising 22 growth forms (Chapter Two), were used in the following analyses.

A combination of correspondence analysis (CA) (Hill, 1973) and canonical correspondence analysis (CCA) (ter Braak, 1986; 1987) was used to determine the variance components attributable to each property. CANOCO has the function of variance partitioning whereby the variance of specified covariables can be removed from the ordination and the remaining variance can be quantified. The variance partitioning sequence was broken into six steps for clarity. No effort was made to remove the variance due to spatial auto-correlation (Chapter Four) as this was impossible to do simultaneously with variance partitioning.

Step 1

Correspondence analyses (CA) were performed on the floristic and growth form data separately. These analyses calculated the relative distribution of sites and species in ordination space, unconstrained by environmental variables. The trace (sum of the unconstrained axis eigenvalues) from CA gave a measure of the total dispersion of the species data.

Step 2

Partial CA was performed on the floristic data with the growth form data as covariables. Thus the variance attributable to growth form composition was removed from the analysis, leaving a revised trace. The revised trace was a measure of the variance of the floristic data that was independent of growth form composition. The difference between the trace of the unpartialled CA (step 1) and the revised trace was a measure of the variance held in common by both floristic and growth form composition.

Step 3

Step 2 was repeated except the partial CA was performed on the growth form data with the floristic data as covariables. Thus the variance in the growth form data shared with and independent of floristic composition was quantified in a similar way.

3.3 RESULTS

The total variance in the floristic data (trace = 22.6) was considerably greater than that for the growth form data (trace = 5.8) (step 1). Partial CA of the floristic data, with the variance due to the growth form data partialled out (step 2), showed that 66% (revised trace = 13.8) of the variance in the floristic data was independent of the growth form data, while 34% was shared (Figure 3.1).

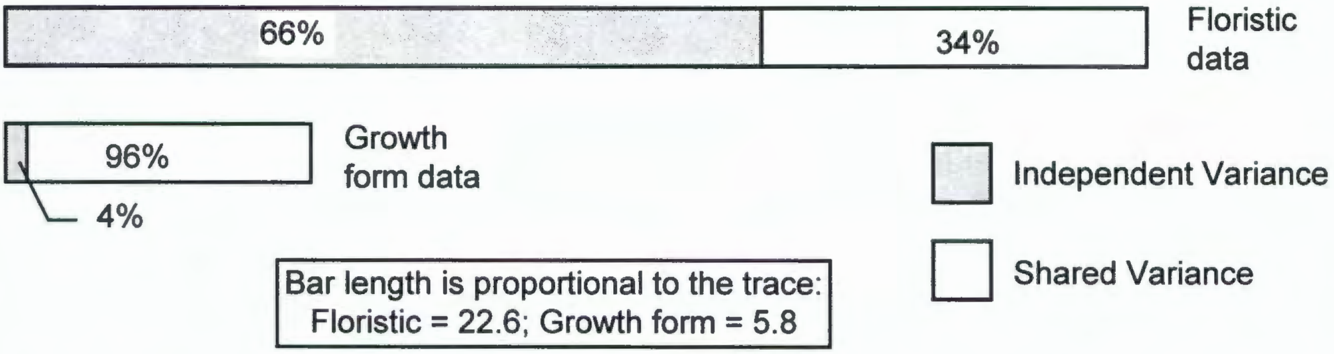

Figure 3.1 Quantifying the total, shared and independent variance components in the floristic and growth form data using partial CA.

Partial CA of the growth form data (step 3) showed that a mere 4% (revised trace = 0.2) of the variance in the growth form data was independent of the floristic data while 96% was shared (Figure 3.1). Quite obviously, the proportions of shared and independent variance in the growth form and floristic data were not symmetrical. A considerably greater proportion of the variance in the floristic data was independent compared to that of the growth form data.

3.4 DISCUSSION

Most of the variance in the floristic data was independent of growth form composition, while very little of the variance in the growth form data was independent of floristic composition. This result suggested that floristic composition alone may well be a more ecologically appropriate means of assessing vegetation community structure. This obviously depends also on the questions being asked in the research. Neither fynbos nor succulent karoo are structurally diverse, and there is very little turnover of growth forms along climatic and edaphic gradients (Cowling *et al.* 1997; Milton *et al.* 1997). It may be that growth form composition of the vegetation does not contribute much to our understanding of community structure in fynbos and succulent karoo.

A number of growth forms are shared between fynbos and succulent karoo, especially the woody shrubs (Chapter Two). However, the small amount of variance in the growth form data which is independent of floristic composition may be ecologically significant (ter Braak, 1987), and should not be dismissed.

Bear in mind the floristic data comprised 83 species, while the growth form data had only 22 broad growth forms. Thus, small amounts of variance in the growth form data may be of greater ecological significance than similar amounts of floristic variance (Fullerton, 1997). However, there are no methods available for assessing the relative ecological significance of portions of variance in each property.

Further, because floristic composition is defined by more attributes than growth form composition, it is likely that variance in the floristic data is influenced more by random 'noise' and may be of less ecological significance. The dynamics of both fynbos and succulent karoo are driven by stochastic environmental and biotic events. Fire driven succession and 'lottery model' recruitment are examples of stochastic factors determining community patterns in fynbos (Cowling *et al.* 1997). Stochastic climatic events like above-average rainfall and droughts are thought to be responsible for driving karoo vegetation community dynamics and structure (Wiegand *et al.* 1993; Wiegand & Milton, 1996; Milton *et al.* 1997). Thus, even though floristic composition has much greater independent variance than growth form composition, this variance may be a result of stochastic events, and may not be ecologically interpretable.

3.5 CONCLUSIONS

The variance of the floristic data was considerably greater than the variance of the growth form data. Most of the variance in the floristic data was independent of growth form composition. In contrast, most of the variance in the growth form data was shared with floristic composition. The conclusion from these analyses was that it is untenable to use growth form data alone for vegetation surveying, as a huge amount of potentially meaningful variance may be missed.

CHAPTER FOUR

Vegetation - Environment Relationships at Matjiesrivier Nature Reserve: Climatic and Edaphic Determinants of the Fynbos - Succulent Karoo Boundary

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4.1 INTRODUCTION

Matjiesrivier Nature Reserve (MNR) and the surrounding landscape support three major vegetation types from the fynbos and succulent karoo biomes: asteraceous mountain fynbos, central mountain renosterveld and succulent karoo shrubland (Rebelo & Low, 1996; Table 2.1). These three vegetation types were described briefly in Chapter One. The fact that MNR straddles the boundary between fynbos and succulent karoo, makes it an ideal place to study this boundary. There has been an interest in the environmental determinants of the boundary between these biomes elsewhere in the western Cape (e.g. Bond, 1981; Campbell, 1986; see review in Cowling *et al.* 1997). Most of these studies have employed descriptive techniques such as vegetation surveys and multivariate analyses, and few experiments have been performed to test the results of such analyses. Although several hypotheses have been suggested and are supported by descriptive evidence, no concrete conclusion can yet be made about what environmental factors control the boundary between fynbos and succulent karoo.

Considering the current interest in the effect that predicted global climate changes are likely to have on the distribution of major vegetation types, it has become increasing important that the environmental determinants of biome boundaries be resolved. Almost no such work has been done in the north-west of the fynbos biome (Cowling *et al.* 1997).

4.1.1 The Environmental Determinants of Fynbos and Succulent Karoo

The environmental factors that have been suggested to control the transition from fynbos into non-fynbos can be divided into three groups: fire, climatic and edaphic (Cowling *et al.* 1997). Fire is the most dynamic of these factors and most difficult to account for in predictive models because of its stochastic nature. In terms of the fynbos / non-fynbos boundary, fire is thought to be important in controlling the transition from fynbos into thicket and forest (Acocks, 1988; Manders, 1990, Cowling *et al.* 1997). Fire does not appear to be a factor in maintaining the fynbos - succulent karoo boundary. The boundary between fynbos and succulent karoo is generally in the semi-arid climatic extreme of the fynbos biome and the vegetation often does not have sufficient biomass to support regular fires. Indeed, succulent karoo elements are commonly found within fynbos near the boundary. For this reason, fire cannot be invoked as a mechanism for preventing the expansion of succulent karoo into fynbos at MNR.

Moisture availability, mediated by the interaction between climatic and edaphic factors, has repeatably been invoked as a determinant of the fynbos / succulent karoo boundary at a landscape scale (Campbell, 1986; Miller, 1985; Cowling & Holmes, 1992; Cowling et al. 1997). Levyns (1950) investigated the relationship between fynbos and succulent karoo in the Ladismith district of the Little Karoo. She concluded that moisture availability was the most important environmental factor determining the relative distribution of fynbos and succulent karoo. She also suggested that 250 mm was the minimum annual rainfall that could support fynbos, and that more arid areas would support succulent karoo. The mean annual rainfall, in the most mesic areas of MNR, is about 300 mm, which suggests MNR is at the arid extreme of fynbos distribution.

Campbell (1985, 1986) classified the montane vegetation of the entire fynbos biome and attempted to establish which environmental variables were responsible for the separation of the communities. He concluded that the interaction between climate and soil texture, and its effect on moisture availability, exerted the primary influence on the fynbos / succulent karoo boundary. Campbell (1988) later identified the environmental determinants of growth form distributions in the Cape Mountains using correlative and multivariate techniques. He concluded again that moisture availability, mediated by climate, topography and soil texture, was important for explaining growth form distribution. However, he also concluded that soil fertility, specifically carbon and nitrogen contents, often had an over-riding influence on vegetation patterns, and were a good variable for explaining the distribution of growth forms.

Euston-Brown (1995) suggested that the interaction between geology (and its effects on soil conditions) and climate was the determining factor of the fynbos / non-fynbos (renosterveld and succulent thicket) transition. He found that the amount of rainfall during the wet season was the most important variable in explaining the distribution of fynbos and non-fynbos units. Geology, which is a broad substitute for various soil factors, was also found to be an adequate variable in predicting the differentiation of fynbos and non-fynbos. He suggested that detailed soil analyses may not be important in determining the transition from fynbos to non-fynbos as suggested by several authors (Specht & Moll; 1983; Cowling & Campbell, 1983; Campbell, 1986; Campbell & Werger, 1988).

Milton *et al.* (1997) invoke climatic factors as the primary explanation for the transition from fynbos into succulent karoo. They state that succulent karoo is characterised by a low but reliable rainfall, which falls predominantly in winter, resulting in high summer aridity. They suggest that fynbos is restricted to the south-western Cape where there is higher rainfall and a cooler summer period, *i.e.* a less intense summer drought. Even within the succulent karoo, mountain ridges, which are cooler and receive more precipitation, have fynbos elements on them. Likewise, locally xeric sites within fynbos are known to support karroid vegetation (Campbell, 1986; Euston-Brown, 1995).

Milton *et al.* (1997) also invoke nutrient status and particle size distribution as factors influencing the relative distributions of fynbos and succulent karoo in areas with similar climates. Succulent karoo often grows on shale-derived soils, which are typically fine-textured, less-acidic and nutrient-rich, under the same climatic conditions as fynbos on sandstone based soils. In the Cape Floristic Region, fynbos typically occurs on infertile sandy soils generally derived from Table Mountain Group sandstone and quartzite (Cowling & Holmes, 1992). Succulent karoo is found mostly on base-rich loam derived predominantly from shale (Hoffman, 1996). It is however, difficult to elucidate the different effects of soil nutrient status and soil moisture as they are mediated by climate and soil texture, the latter of which is influenced in turn primarily by geology, then climate (Brady, 1974).

Climate has been invoked as a factor responsible for the characteristic growth forms and growth form traits in fynbos and succulent karoo. Traits found repeatably through fynbos, such as sclerophylly, leptophylly and low stature, have been interpreted as responses to optimising water usage during the summer drought that is characteristic of mediterranean-type climates (Campbell, 1988; Stock *et al.* 1992). Similarly, the ubiquity of evergreeness in fynbos, even in the face of summer drought, is thought to be an adaptation to the base-poor soils (Stock *et al.* 1992).

The abundance of leaf- and stem-succulent and deciduous plants in succulent karoo is thought to be a response to extreme summer drought and relatively nutrient-rich soils (Milton *et al.* 1997). Such growth forms adaptations show the extent to which fynbos and succulent karoo are influenced by climate and soil conditions. It is likely then that the relative distribution of fynbos and succulent karoo may also be controlled by the interaction of climatic and edaphic factors.

Even within biomes, edaphic factors are believed to have an important influence on the distributions of communities. Richards *et al.* (1995) investigated community – environment relationships at a fine scale within fynbos. They concluded that edaphic gradients, primarily of soil depth, pH and texture fractions, adequately explained the variance in the community distributions. However, Richards *et al.* (1995) emphasised from the outset that they were concentrating on edaphic factors without considering climatic factors. Their study does indicate that, within fynbos, community patterns can be elucidated at a relatively fine scale using various edaphic variables.

Within both fynbos and succulent karoo, abrupt distinctions between plant communities may occur along edaphic boundaries (Milton *et al.* in press). Examples of such edaphic control of the vegetation are Mima-like mounds or heuweltjies. Heuweltjies, which tend to have a higher base status and a finer texture, support unique vegetation communities in both fynbos and succulent karoo (Knight *et al.* 1989; Milton *et al.* 1997).

Considering the above, it is likely that a combination of climatic and edaphic factors maintains the fynbos / succulent karoo transition in parts of the Cape Floristic Region. Matjiesrivier Nature Reserve, which has an interesting combination of edaphic and climatic gradients, lends itself to further examination of these hypotheses. There is a relatively steep gradient of decreasing rainfall across MNR from west to east. The geology of MNR comprises three groups in the Cape Supergroup. The shale and silty sandstone of the Bokkeveld Group lie between the sandy sandstone and quartzite of the Table Mountain and Witteberg Groups (Figure 1.3). The conformity between the rocks of these different geologic groups is often narrow, giving rise to steep edaphic gradients. It is this relatively unique combination of edaphic and climatic gradients that may allow us to resolve the environmental control of the fynbos / succulent karoo transition. The apparent absence of fire at MNR makes it an even more ideal location for separating the effects of soil and climate of the boundary.

The transition from fynbos into succulent karoo vegetation can be described in terms of both floristic composition and vegetation structure. Analysis of the environmental determinants of this transition would be incomplete if it did not include both floristic composition and vegetation structure (see Chapter Three). Thus, in order to derive a clear understanding of the vegetation - environment relationship, the analyses were applied to both the floristic and growth form data.

The aim of this chapter was to use descriptive multivariate methods to determine the environmental correlates of the fynbos / succulent karoo transition. Part of the analyses involved investigating the variance components of the species data to derive a better understanding of what determines community distributions at MNR. Also, in order to understand the ecological significance of the vegetation communities described in Chapter Two, the environmental determinants of the major communities need to be investigated.

4.1.2 Research Questions

During this research I attempted to answer the following questions.

1) Does the spatial distribution of sites account for a significant proportion of the variance in the vegetation at MNR?
2) Do the environmental variables used in the analysis account for a significant proportion of the variance in the vegetation?

3) Which environmental variables best account for the transition between fynbos and succulent karoo at MNR?
4) Are the major communities at MNR (Chapter Two) distributed along meaningful environmental gradients?

4.2 METHODS

4.2.1 Data sets

4.2.1.1 Vegetation data

The same floristic and growth form data sets that were used to derive the communities in Chapter Two were used in the ordination analyses. The floristic data comprised the 84 most abundant species that occurred through the 125 sites measured at MNR. The growth form data comprised 22 growth forms based on the criteria described in Chapter Two. The growth forms were assumed to represent unique functional types for resource use (Cowling *et al.* 1994).

4.2.1.2 Environmental Data

Eighteen environmental variables (Table 4.1) were measured or estimated for each site. These environmental data were used in the multivariate analyses to establish which environmental variables were most influential in explaining the distribution of species and sites in the ordination space.

4.2.1.3 Soil Variables

Soil depth for each site was measured by hammering a steel rod into the soil at least five randomly placed points. The depth was read off from gradations on the rod and an average depth established for the site. A soil sample was taken from each site by removing, at random, several soil cores from the top 10 cm and mixing them together. These soil samples were air-dried and sieved through a 2-mm mesh. Dry soil colour was measured using a Munsell Colour Chart. Electrical conductivity was measured using a conductivity meter (Jenway 4070) in a solution of 10 g of soil shaken for 20 min in 20 ml distilled water (Rowell, 1994). The pH of the same solution was measured using a pH meter (WTW pH320). The proportions of clay, silt and sand and the proportions of coarse, medium and fine sand in each soil sample were determined using the a settling method (Appendix C).

Table 4.1 The environmental variables measured or estimated for each site, the abbreviations used in the ordination analyses, their units or categories, and the method used to determine them.

Variable	Abbrev.	Units or Classes	Method
Geology	GEOL	Shale and sandstone	1:250 000 geol. Map, & field observations
Locality	n/a	Decimal degrees	GPS & 1:50 000 maps
Altitude	ALT	Metres	1:50 000 maps
Aspect	n/a	N, E, S, W or flat	Compass bearing
Slope Angle	n/a	Flat, medium, steep	Estimate
Winter, equinox and summer radiation	WRAD ERAD SRAD	$10^6 J.m^{-2}.Day^{-1}$	Model combining aspect and slope angle at 32°S (Schulze 1975)
Slope Position	SPOS	Ridge, slope, valley	Estimate
Rainfall	RAIN	Mean annual rain (mm)	CCWR database
Soil Depth	DEPTH	Metres	Metal rod
Soil Colour	SCOL	5YR, 7.5YR or 10YR	Soil Colour chart
Soil pH	pH	pH scale	pH Meter
Soil Conductivity	COND	mS	Conductivity meter
Soil Particle size	SAND, SILT, CLAY	% Sand, % Silt, % Clay	Appendix C
Sand texture	FS, MS, CS	% Fine, Medium, Course	Appendix C
Landtype	LTYPE	Bedrock, Sand Plain, Rocky slope, Gravel Pan	Field Observations
Tertiary gravel	TG	Presence / absence	Field Observations
Mean rock size	RSIZE	5 classes	Estimate
Rock cover	RCOV	Percentage	Estimate

4.2.1.4 Tertiary Gravels

The presence of a surface and sub-surface layer of medium-sized dark-brown pebbles (1-5 cm diameter) was noted at several locations at MNR. These gravel plains were often associated with very distinct vegetation communities with abrupt boundaries (Plates 2.2b & 2.5c & d). The pebbles, which were sub-angular, may have been the result of *in situ* weathering of a Tertiary erosion surface (Taljaard, 1949; Peter Holmes, personal communications). The presence, if any, of these pebbles in a site was noted.

4.2.1.5 Rainfall Data

There are no measured rainfall data for MNR and the nearest recording stations were at Keurbosfontein and Dwarsrivier (Figure 1.1), both within 5km from the western boundary of MNR. I used interpolated data from the Computing Centre for Water Research (1996). These rainfall data were generated from a minute-by-minute interpolation model of rainfall for the whole of South Africa. The model, which is based on all the weather stations with over 20 years rainfall data, accounts for topography (aspect and altitude) and prevailing weather systems. The accuracy of the model is questionable in an area like MNR, where there are few weather stations to provide points for the interpolation. Also, the rugged topography results in steep rainfall gradients, which may not be reflected in the model. There were, however, no other climatic data available. Mean annual rainfall for each site was taken as the value of the nearest data point of the minute-by-minute estimated rainfall grid (CCWR, 1996).

4.2.1.6 Radiation

Winter, summer and equinox radiation at each site were estimated using a landscape-based model (Schulze, 1975). This model combines aspect and slope angle at certain latitudes to give an estimate of radiation regime.

4.2.2 Analyses

4.2.2.1 Spatial Auto-correlation

Spatial correlation may be defined as the property of random variables taking values that are more (positive correlation) or less (negative correlation) similar than expected for random associations, because they are situated a certain distance apart from each other (Legendre, 1993). Spatial correlation is a feature of all ecological systems where there are biotic processes such as predation, dispersal, migration and many others, that impose a pattern in the distribution of organisms. The spatial pattern (or spatial correlation) due to biotic processes is often separate from pattern caused by the environmental control of species distributions and must be accounted for before the species-environment relationship can be investigated fully (Bocard *et al.* 1992).

Spatial correlation becomes a problem in statistical analysis of vegetation data because every site where vegetation response is measured is not an independent observation. The vegetation of each site can be predicted to some extent, based on observations of the surrounding sites, and thus each site represents less than one degree of freedom (Legendre, 1993). Thus, before statistical analyses can be performed on site-by-attribute vegetation data, the variation due to space should be removed. However, in an ecological context, it is often better to incorporate the spatial variation into the statistical analysis in an attempt to quantify and explain it. The biotic factors that cause species to display a non-random pattern in space may be of importance in understanding what is driving the dynamics of the vegetation. In other words, if more of the variation in the species data can be explained by spatial variables compared to environmental variables, then unmeasured biotic factors are having a greater effect on vegetation distribution than the measured environmental variables. Spatial correlation analyses can be extended to include a full partitioning of the variance in vegetation data. Thus the variance due to locality, the environment and to random noise can be separated, generating a number of interesting questions about the distribution of the vegetation.

4.2.2.2 Quantifying the Variance Attributable to Locality

As explained above, it is important to quantify and account for the variance component in the species data that is attributable to spatial factors or locality. To do this, I used a process of variance partitioning within canonical correspondence analysis (CCA) which is an option in the ordination program CANOCO 3.12 (ter Braak, 1991). A sites by 'two-dimensional spatial variables' matrix was created using a third order polynomial (Bocard *et al* 1992):

$$z = b_1x + b_2y + b_3x^2 + b_4y^2 + b_5xy + b_6x^2y + b_7xy^2 + b_8x^3 + b_9y^3 \quad \text{(eq. 1)}$$

where z is a function of the spatial variance and x and y are longitude and latitude respectively. The use of a third order polynomial (as opposed to only the 'x' and 'y' co-ordinates) extracts not only the linear gradient patterns in the species data, but also complex patch and gap patterns (Legendre, 1990). This requires the quadratic and cubic terms of the co-ordinates and their interactions to be described in the manner of trend-surface analysis (Legendre, 1990). To prevent artificial increase of the explained variance by chance, the spatial matrix of terms was submitted to the process of forward selection of explanatory variables in CANOCO to determine which of the terms in the equation were significant (Bocard *et al.* 1992). This process was repeated for both the floristic and growth form data sets. The significance of each term's contribution to the variance explained was tested using a Monte Carlo permutation test in CANOCO. Only the significant terms were retained in the matrix and the rest removed. This modified 'spatial matrix' was then used to partition out the variance due to two-dimensional spatial variables. This was done in the following way (Bocard *et al.* 1992):

1) CCA of the species data constrained by the environmental matrix.
2) CCA of the species data constrained by the spatial matrix.
3) CCA of species data, constrained by the environmental matrix, with the spatial matrix as co-variables.
4) CCA of species data, constrained by the spatial matrix, with the environmental matrix as co-variables.

The variance in the species data accounted for by each step was calculated by taking the sum of the canonical eigenvalues as a percentage of the sum of eigenvalues in a CA of the species data (trace or total inertia). The total variance explained (by both spatial and environmental explanatory variables) is calculated by summing the variance of steps (1+4) or (2+3). The whole variance of the species data can then be partitioned into four components (Figure 4.1) (Bocard, *et al.* 1992; Legendre, 1993). This process was repeated for both the growth form and floristic species data sets and the results compared.

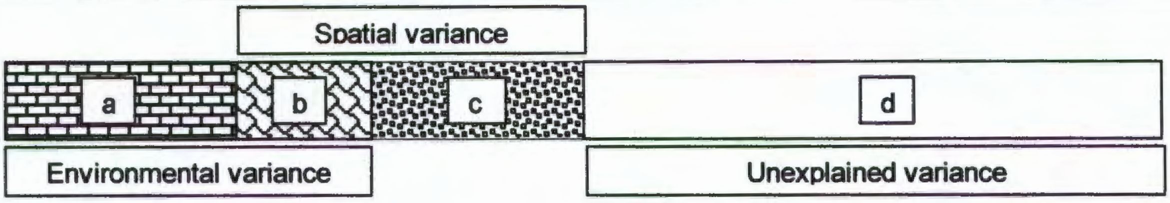


Figure 4.1. Variance partitioning of hypothetical species data. **a)** environmental variation not shared with spatial variation (step 3); **b)** spatially-structured environmental variance (step 1-step 3 or step 2-step 4); **c)** spatial variance not shared with environmental variance (step 4); **d)** unexplained variance (100 - total variance explained)

4.2.2.3 Multivariate Analyses

Canonical correspondence analyses (ter Braak, 1986,1987; Palmer, 1993) were used to ordinate the floristic and growth form data sets and environmental data after the spatial variance component had been partitioned out, using the program CANOCO 3.12. CCA is a direct gradient method that selects ordination axes that are the linear combination of standardised environmental variables (i.e. standardised to mean 0 and variance 1). CCA maximises the dispersion of species scores. Site scores are calculated as the weighted average of the constrained species scores (ter Braak, 1987).

The floristic and growth form data sets were analysed separately. Initially, a CCA of each data set, with the variance due to significant spatial covariables partialled out and constrained by all the environmental variables was performed. All environmental variables with a variance inflation factor (VIF) greater than 20 were removed. A variable with VIF > 20 means that variable is collinear with another and that its canonical coefficient uninterpretable (ter Braak, 1986). Similarly, all variables with non-significant canonical coefficients (tested using a t-test in CANOCO) were also removed. Canonical coefficients were calculated in CANOCO by regressing the sample scores against the standardised environmental variables.

Considering that the sample scores were calculated in part from the environmental variables (the nature of direct gradient analysis), the canonical coefficients did not have the same statistical properties as 'true' regression coefficients. Canonical coefficients typically have a greater variance than regression coefficients (ter Braak, 1986). Thus, the Student's t-test used in CANOCO to assess the significance of the regression coefficients was not really appropriate for canonical coefficients. Nonetheless, ter Braak (1986) suggested that the t-values for canonical coefficients still have exploratory use, especially for selecting a subset of explanatory environmental variables.

The remaining environmental variables were put through the process of forward selection in CANOCO and their significance in explaining the variance in the species data tested using a Monte Carlo permutation test. Various interactions (chosen intuitively) of significant environmental variables were tested in a similar manner. In all CANOCO analyses, the standard settings of the program were used.

Pearson Product Moment correlation coefficients, calculated in CANOCO, were used to assess the importance of the significant environmental variables in accounting for the variance in the species data. The correlation was made between the unconstrained sample scores and the environmental variable values. The sample scores for each axis in this case were derived directly from the species scores by weighted averaging, before being constrained by the environmental variables.

4.3 RESULTS

4.3.1 Selection of Spatial Co-variables and Environmental Explanatory Variables

4.3.1.1 Selection of Two-dimensional Spatial Terms

Forward selection of spatial terms from Equation 1 for the floristic and growth form data sets showed that many of the terms were not significant in explaining the variance in the respective data sets (Table 4.2). The significant terms were similar for both floristic and growth form data sets. Only the significant terms were retained in the polynomials used to partition out spatial variance from the floristic and growth form data sets:

(x = longitude, y = latitude)

Floristic: $z = b_1x + b_5xy + b_7xy^2 + b_8x^3 + b_9y^3$ (eq. 2)

Growth Form: $z = b_1x + b_5xy + b_7xy^2 + b_8x^3$ (eq. 3)

Table 4.2. The F-ratio and percentage variance explained by the significant spatial terms of the third order polynomial (eq.1); based on the results from forward selection of variables and a Monte Carlo permutation test in CANOCO. ** $p < 0.01$; * $p < 0.05$; ns – non-significant. '% var.' is the variance attributable to each term, calculated as a percentage of the total explained variance.

Spatial Term	Floristic data		Growth Form data	
	F-ratio	% var.	F-ratio	% var.
Longitude (x)	1.92 *	18	2.5 **	16
Longitude * Latitude (xy)	1.89 **	16	2.67 **	18
Longitude * Latitude² (xy²)	1.54**	13	1.62 *	10
Longitude³ (x³)	3.33**	29	6.78 **	44
Latitude³ (y³)	1.39*	12	ns	-
Total	-	**88**	-	**83**

The significant terms accounted for 88% and 83% of the variance explained by all the spatial terms in the floristic and growth form data sets respectively. In both data sets, most of the explained variance was accounted for by longitudinal terms, particularly longitude cubed (x^3). Such a pattern was expected because of the strong altitudinal and rainfall gradients from east to west across MNR.

4.3.1.2 Selection of Explanatory Environmental Variables

The initial selection of environmental variables with VIF's < 20 and significant canonical coefficients, indicated that many of the variables were not significantly correlated with the species axes of either the floristic and growth form data sets (Table 4.3). In CCA of the growth form data set, the non-significant variables together represented a loss of only 1% of the explained variance (Table 4.3). However, the non-significant environmental variables in the CCA of the floristic data set together represented a loss of 31% of the explained variance (Table 4.3).

Table 4.3. The environmental variables significant in explaining the variance in the growth form and floristic data sets; derived from forward selection in CANOCO. The F-ratio is from the Monte Carlo permutation Test. '% variance' is the variance attributable to each variable, calculated as a percentage of variance explained by all the environmental variables: ** $p < 0.01$; * $p < 0.05$; ns = non-significant

Category		Floristic data		Growth Form data	
	Variable	F-ratio	% var.	F-ratio	% var.
Climatic and topographic Variables	Altitude	2.50 **	9	-	-
	Summer Radiation	1.41 *	5	-	-
	Annual Rainfall	1.84 **	7	5.28 **	25
	Landtype	1.78 **	6	-	-
	Subtotal	-	*27*	-	*25*
Edaphic Variables	Soil Depth	-	-	4.30 **	20
	pH	2.76 **	10	3.56 **	16
	Conductivity	1.79 **	7	2.08 *	9
	% sand	2.38 **	9	3.49 **	16
	% Coarse sand	1.68 **	6	2.13 *	9
	% Medium sand	1.35 ^{ns}	5	-	-
	% Silt	-	-	0.91 ^{ns}	4
	% Clay	1.42 *	5	-	-
	Subtotal	-	*42*	-	*74*
	TOTAL	-	**69%**	-	**99%**

There were two main categories of significant explanatory variables: climatic (including topographic variables that influence micro-climate) and edaphic. In CCA of both the floristic and growth form data sets, edaphic variables together accounted for a greater proportion of the explained variance than did climatic variables (Table 4.3). Annual rainfall accounted for the largest single amount (one quarter) of explained variance in the growth form data set. Soil depth, which was the second most significant variable in the growth form CCA, was non-significant in the floristic CCA (Table 4.3). There was no single dominant explanatory variable in the floristic data set. This suggested that subtle interactions of the variables might have been important in explaining the variance in the floristic data set. However, none of the interactions tested were found to be significant.

4.3.2 Spatial Correlation and Variance Partitioning

The growth form data had a considerably smaller trace (total variance in correspondence analysis) than the floristic data (bar lengths of centre graph in Figure 4.2), indicating that there was much less variance in the growth form data. Both the growth form and floristic data sets showed similar partitioning of the total variance (Figure 4.2). In both data sets, the majority of the variance (75% and 78% for the growth form and floristic data sets respectively) remained unexplained. This suggested that the vegetation at MNR, in terms of growth forms and floristic composition, was not strongly influenced by the environmental variables used in the analyses.

The significant environmental variables used in the analyses accounted for a relatively high proportion (approximately 60%) of the explained variance in each data set (Figure 4.2). However, this translates into 25% and 22% of the total variance in the growth form and floristic data sets respectively. Spatially-structured environmental variance (i.e. that variance shared by spatial position and environmental variables) accounted for 10% of the explained variance in both the floristic data and growth form sets (Figure 4.2). These values were relatively unimportant in terms of the total variance. Variance due to locality alone (spatial variance) accounted for approximately 30% of the explained variance in both data sets.

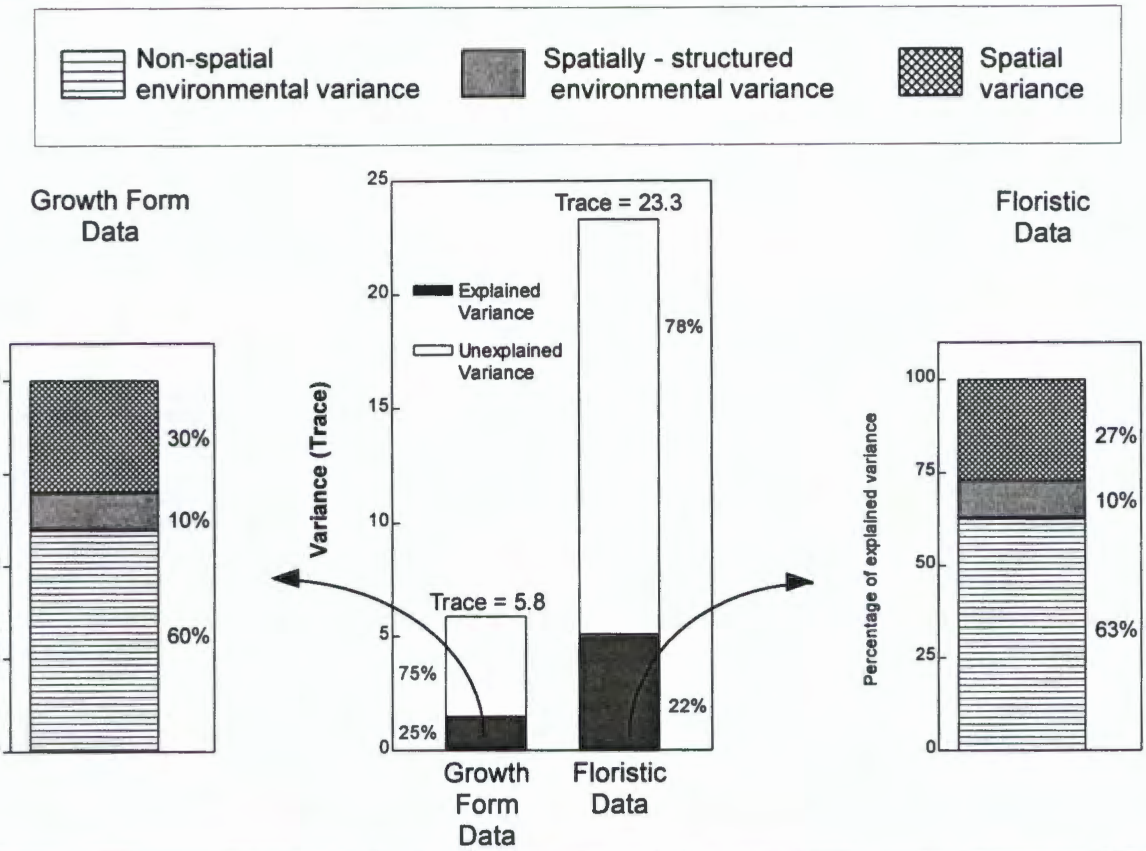


Figure 4.2 The explained and unexplained variance of the growth form and floristic data sets taken as a percentage of the total variance or trace (centre bar). The explained variance of each data set is divided into three components: non-spatial environmental variance; spatially-structured environmental variance and spatial variance independent of environment. The proportion of each component is shown in the two outer bars.

Thus locality was an important consideration in explaining the floristic and growth form composition of vegetation at MNR.

4.3.3 The Environmental Determinants of Community Distribution and the Fynbos-Succulent Karoo Boundary

4.3.3.1 The Summary Ordination Statistics

Floristic data

The four axes from CCA of the floristic data only accounted for 8.3% of the total variance in the data (Table 4.4). However, the eigenvalues for the four axes indicated that there was relatively good correlation between the site and species scores suggesting that the environmental gradients were long and strong (ter Braak, 1986). The species axes were well correlated with the environmental variables, all with coefficients between 0.75 and 0.9 (Table 4.4). The four axes together accounted for 56% of the variance in the species-environment relationship.

Table 4.4. The summary statistics from a CCA of (a) the floristic and (b) the growth form data, with the variance due to significant spatial covariables partialled out, and constrained by the significant environmental variables only.

Data	Statistic	Axis 1	Axis 2	Axis 3	Axis 4
a) Floristic data	Eigenvalues	0.51	0.45	0.44	0.33
	Species – environment Correlation	0.90	0.81	0.86	0.76
	Cumulative % variance of species data	2.5	4.7	6.8	8.3
	Cumulative % variance of species-environment relationship	16.7	31.4	45.7	56.4
b) Growth form data	Eigenvalues	0.24	0.18	0.15	0.08
	Species – environment Correlation	0.77	0.61	0.64	0.50
	Cumulative % variance of species data	4.7	8.2	11.2	12.6
	Cumulative % variance of species-environment relationship	31.9	56.1	76.1	86.0

Growth Form Data

The lower eigenvalues from CCA of the growth form data indicated that the environmental gradients were weaker and shorter in comparison to those of the floristic data (Table 4.4). The four CCA axes accounted for marginally more of the variance in the growth form data (12.6%) than in the floristic data. The species – environment correlations were slightly lower in the growth form CCA than in the floristic CCA, possibly as a result of the lower eigenvalues (shorter gradients). This suggested that the environmental variables had more influence on the distribution of species than on the distribution of growth forms.

4.3.3.2 Vegetation–Environment Correlations and Coefficients

Floristic data

The first species axis in CCA of the floristic data corresponded to strong decreasing gradients of altitude, rainfall and medium sand content, and to an increasing gradient of conductivity (Table 4.5). The second axis was negatively correlated with the size of the sand fraction and landtype values (1 = rocky slope, 2 = bedrock sheet, 3 = sand plain, 4 = gravel pan). Bearing in mind that the first two axes are generally the most important in CCA (i.e. have the highest eigenvalues), it appears that rainfall and altitude, the soil texture fractions and conductivity accounted for most of the explained variance in the data. These results were supported by the canonical coefficients of the standardised environmental variables (Table 4.6), except for landtype. Landtype was measured on a nominal scale that is difficult to interpret with ordinary correlation and regression techniques, as employed by CANOCO (Siegel & Castellan, 1988).

Table 4.5. The largest Pearson Product Moment correlation coefficients of the four species axes and environmental variables, derived from canonical correspondence analysis of the floristic and growth form data.

Species Axes	*Floristic Data*		*Growth Form Data*	
Axis 1	Altitude	-0.75	Rainfall	-0.67
	Rainfall	-0.71	% Silt	0.45
	Conductivity	0.61	Conductivity	0.45
	% Medium sand	-0.61		
Axis 2	Landtype	0.57	Soil depth	0.42
	% Sand	-0.67	% Sand	-0.43
Axis 3	pH	0.57	pH	0.45
	% Clay	0.45		
	% Course sand	0.41		
Axis 4	pH	0.35	Conductivity	0.32

The third axis was correlated to several edaphic gradients: pH, coarse sand content and clay content. Although landtype had the highest canonical coefficient for the third axis (Table 4.6), it was not well correlated with the unconstrained site scores. Summer radiation, landtype and rainfall also had significant canonical coefficients for the third axis (Table 4.6). The largest correlation coefficient for the fourth axis was for pH, but this correlation was relatively low (Table 4.5). The canonical coefficient for altitude on axis four were equal to one (Table 4.6) and were probably an artefact of the CANOCO program. Such high canonical coefficients do not indicate a realistic trend in the data worth interpreting (ter Braak, 1986).

Rainfall, soil conductivity, pH and the particle size fractions quite obviously had the best relationship with all four axes. Summer radiation and landtype were only important for the second and third axes. The remaining environmental variables generally did not have large correlation or canonical coefficients, and were thus relatively unimportant in explaining the variance in the floristic data set.

Table 4.6. Canonical coefficients of the standardised environmental variables for the four species axes of CCAs of the floristic data set. The variables are ranked according to the size of their coefficients for each axis. The most important variables lie near the top (positive relationship) and bottom (negative relationship) of each axis column. Significant variables (t-test in CANOCO: see text) are in bold: * $p < 0.05$; ** $p < 0.01$.

Axis 1	**Axis 2**	**Axis 3**	**Axis 4**
Conductivity **0.36****	**pH** **0.47****	**Landtype** **0.56****	**Altitude** **1.00****
Sum. Radiation 0.11	Landtype 0.37	**PH** **0.55****	**pH** **0.64****
% Coarse sand 0.06	Conductivity 0.11	**Rainfall** **0.53****	**Sum. radiation** **0.30***
PH -0.04	Sum. Radiation 0.08	**% Sand** **0.46****	% Clay 0.15
% Sand -0.05	Altitude 0.03	**% Coarse sand** **0.36****	% Medium sand -0.03
% Clay -0.09	% Medium sand -0.01	**% Clay** **0.26****	% Sand -0.03
Landtype -0.25	% Clay -0.07	**Conductivity** **0.18***	**Conductivity** **-0.29****
Rainfall **-0.30****	% Coarse sand -0.22	Altitude 0.04	**% Coarse sand** **-0.44****
% Medium sand **-0.33****	**Rainfall** **-0.37***	% Medium sand 0.01	**Landtype** **-0.63****
Altitude **-0.74****	**% Sand** **-0.57****	**Sum. Radiation** **-0.42****	**Rainfall** **-1.00****

The decreasing altitude gradient was closely correlated with a similar gradient of rainfall. It was unclear whether altitude and rainfall were just co-incidental or whether the decrease in rainfall is a direct result of a decrease in altitude. The matter is further confused in that altitude itself is a surrogate variable for a number of other environmental factors including soil moisture availability and temperature. In an attempt to resolve the effects of rainfall and altitude, partial CCA's were used in a method similar to that used to separate the effects of space and environment. In each CCA, either rainfall or altitude alone (i.e. no other environmental variables were used in the CCA) was used as the constraining variable or co-variable. These partial CCA's indicated that less than half of the explained variance was attributable to the interaction between rain and altitude, suggesting that rainfall and altitude are largely co-incidental and not causal. However, without further experimentation, no conclusions could be drawn about the interaction between rainfall and altitude.

Growth form data

Correlation coefficients for the environmental variables and axes were lower for the growth form data than the floristic data (Table 4.5), suggesting that there was less environmental control on the distribution of growth forms than for species. The first axis of the growth form CCA was correlated primarily with rainfall and less so with soil conductivity and percentage silt (Table 4.5). The canonical coefficient for rainfall (Table 4.7) was considerably greater than for any other significant environmental variables. The second axis was correlated with soil depth and sand content (Table 4.5). Although the unconstrained sample scores were not highly correlated with soil depth values (coefficient = 0.42), the canonical coefficient suggested soil depth was significant (Table 4.7). The canonical coefficients also suggested that rainfall was again the most significant variable in explaining the variance of axis two (although its correlation coefficient was only -0.25). The third axis was correlated most strongly with pH (Table 4.3). This was supported by the canonical coefficient for pH which was considerable larger than for any other significant variable for axis three. Coarse sand content and conductivity also had significant canonical coefficients (Table 4.7).

Table 4.7. Canonical coefficients of the standardised environmental variables for the four species axes of CCAs of the growth form data set. The variables are ranked according to the size of their coefficients for each axis. The most important variables lie near the top (positive relationship) and bottom (negative relationship) of each axis column. Significant variables (t-test in CANOCO: see text) are in bold: * p < 0.05; ** p < 0.01.

Axis 1	Axis 2	Axis 3	Axis 4
Conductivity **0.28****	**Soil depth** **0.47***	**pH** **0.83****	**% Coarse sand** **0.64****
pH **0.26****	% Coarse sand -0.02	Soil depth 0.23	pH 0.16
% Coarse sand **0.23***	Conductivity -0.03	% Silt 0.17	Rainfall -0.44
% Sand 0.07	% Silt 0.05	% Sand -0.05	% Silt -0.52*
% Silt -0.06	**% Sand** **0.42***	Rainfall -0.10	**% Sand** **-0.56***
Soil depth 10.19	**pH** **0.51****	**Conductivity** **-0.37****	**Conductivity** **-0.57****
Rainfall **-0.93****	**Rainfall** **-0.78****	**% Coarse sand** **-0.68****	**Soil depth** **-0.78****

Axis four was not well correlated with any variable, the highest correlation being with conductivity (0.32). The canonical coefficients for axis four suggested however, that soil depth, conductivity and the sand fractions were important (Table 4.5). Thus, although the same environmental variables are responsible for the total variance in the growth form data and floristic data, the axes are explained in part by different environmental variables.

Rainfall, conductivity, pH and soil texture fractions were the most important environmental variables in accounting for the distribution of both floristic species and growth forms. Soil depth was a further variable that accounts for a significant portion of variance in the growth form data.

4.3.3.3. Interpretation of Ordination Diagrams

Floristic data

There were two main trends in the distribution of species and environmental variables in site space (Figure 4.3a). The greatest dispersion of species was along the first axis, which reflected a gradient of decreasing rainfall and altitude, and increasing soil conductivity and clay content. Typical succulent karoo species, including *Tylecodon paniculatus, Zygophyllum morgsana, Galenia africana, Euphorbia mauritanica, Pteronia divaricata* and various members of the Mesembryanthemaceae (mesembs) were associated with low altitude, low rainfall regions of the ordination. The same species were also associated with regions of high clay content and high conductivity. Another group of succulent karoo species, represented by *Euphorbia decussata* and several other mesembs, was associated with the region of high pH in the ordination that was also partially correlated with landtype. These species were found on sand plains (landtype = 3) in the arid part of MNR. The soil of these plains had an unusually high pH (>7.5).

Typical fynbos species, including *Diosma acmaeophylla, Erica* spp., various members of the Restionaceae (restioids) and Cyperaceae (sedges), were concentrated at the high altitude, high rainfall region of the ordination. This region was also associated with a high medium sand content and low conductivity. Kloof thicket species, such as *Rhus undulata* and *Maytenus oleioides*, were also associated with these regions.

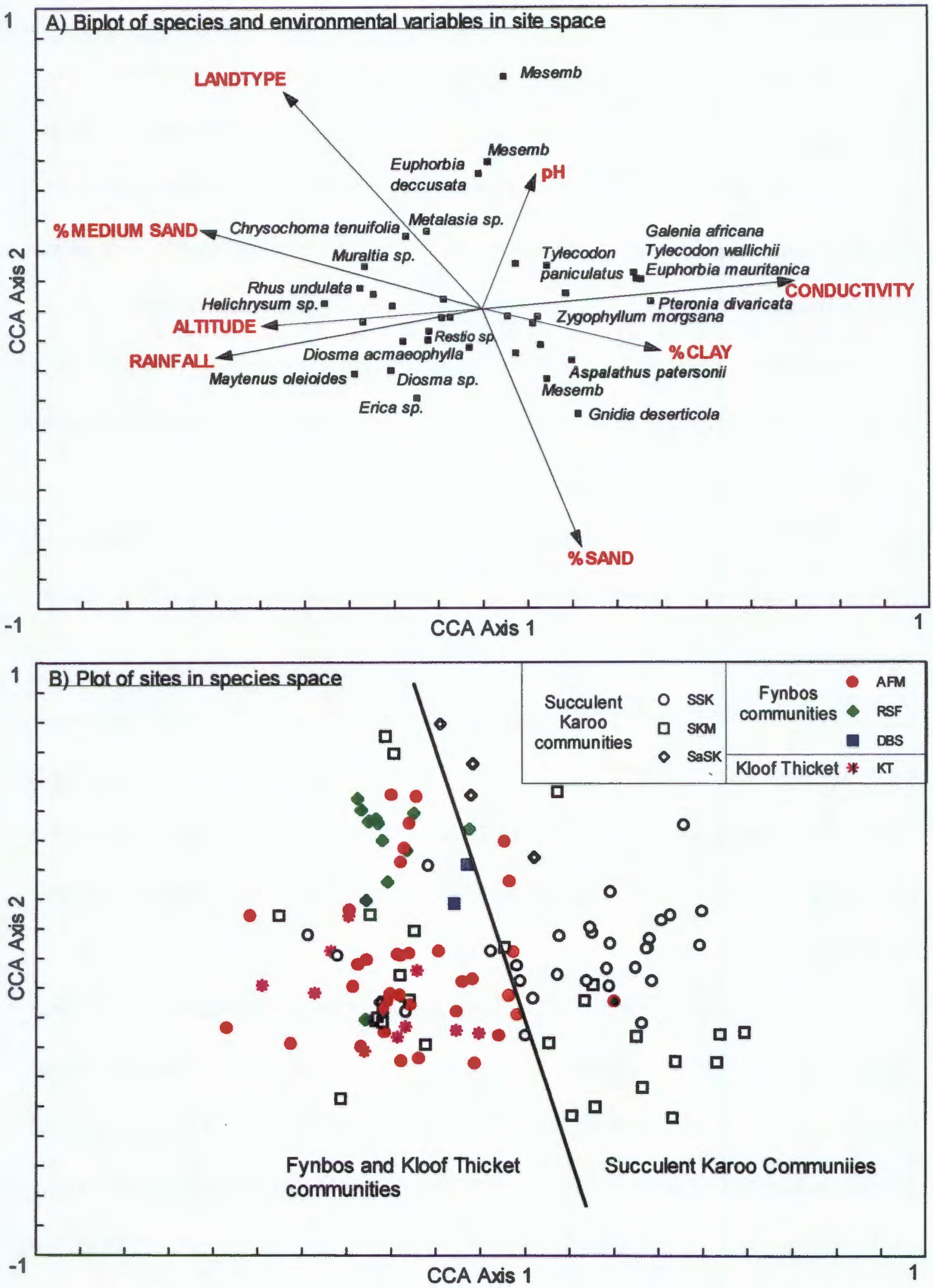


Figure 4.3. The first two axes from CCA of the floristic data, with spatial covariables partialled out, constrained by the significant environmental variables. The environmental arrows in diagram A also apply to diagram B. The sites are classified according to the communities derived from Chapter Two (see text for details).

The distribution of sites in species space showed that the seven communities (Chapter Two) were relatively well separated out along the first two CCA axes (Figure 4.3b). There was a clear distinction between fynbos and succulent karoo sites, with only a few sites overlapping.The fynbos sites tended towards the high altitude, high rainfall region of the ordination, where there was also a high medium sand content. The succulent karoo sites were concentrated in the low altitude, low rainfall areas, and were also associated with high electrical conductivity and high clay content.

The sites of the three succulent karoo communities were separated out along edaphic gradients of texture, pH and conductivity. The sandy succulent karoo (SaSK) sites were concentrated near the high pH region of the ordination. Not surprisingly, shale succulent karoo (SSK) sites, based on shale-derived soils, were located in the region of high clay content and high electrical conductivity. The succulent karoo matrix (SKM) sites, on sandstone-or quartzite-based soils, were concentrated in the region of high sand content.

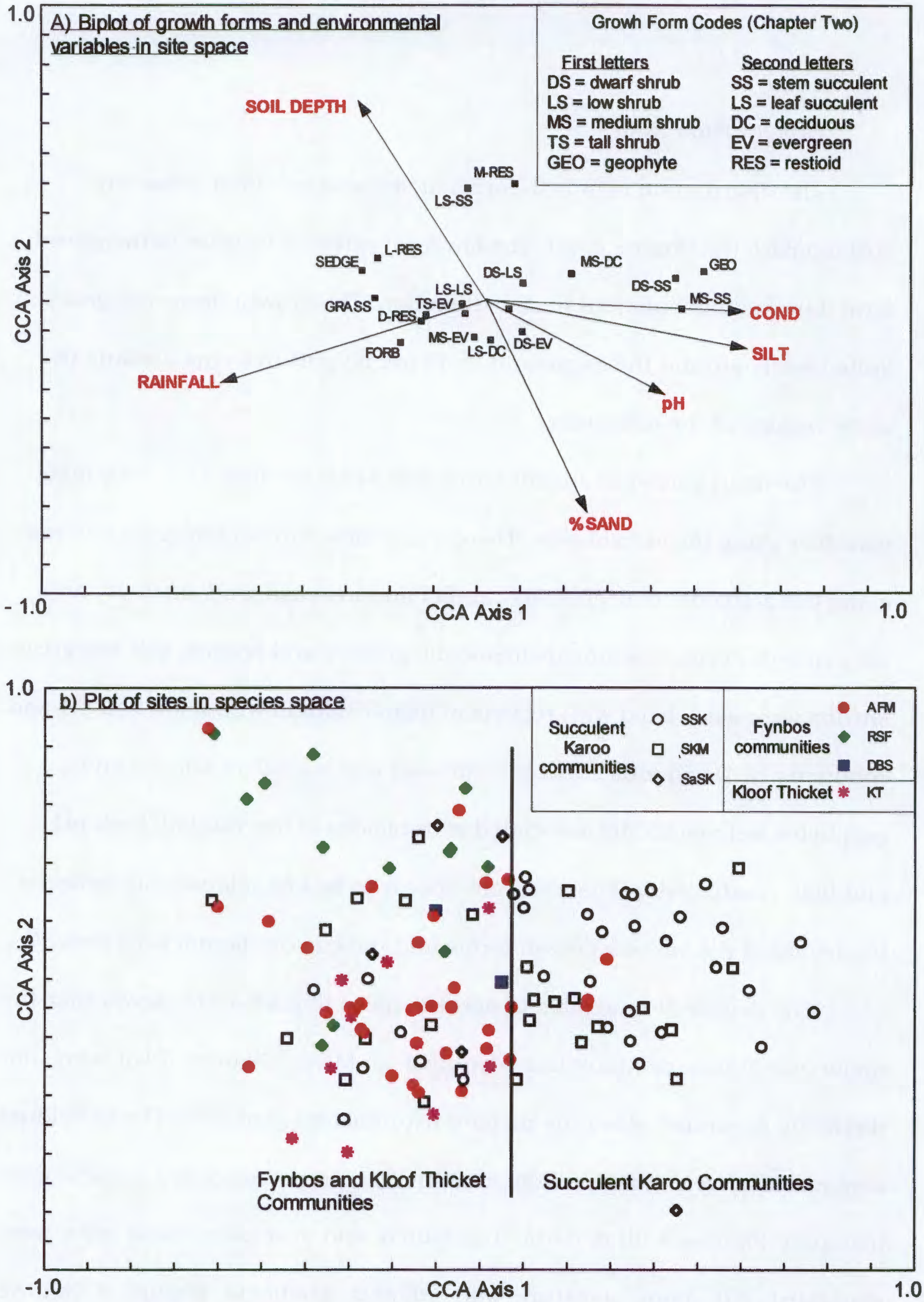
The kloof thicket (KT) sites did not form a distinct group separate from the fynbos sites (Figure 4.3b), suggesting that none of the environmental variables used in the CCA could account the occurrence of KT. The restioid sandy fynbos (RSF) sites were well separated, based on landtype, from most of the asteraceous fynbos matrix (AFM) sites. RSF generally only occurs on a single landtype – sandy plains.

Growth Form Data

The distribution of growth forms in site space did not show any striking patterns (Figure 4.4a). The low total variance or trace of the growth form data is quite apparent in the ordination. The growth forms are grouped quite closely around the origin and there are no growth forms towards the outer regions of the ordination.

The main spread of growth forms was along the first axis, with little variation along the second axis. There was a slow turnover of growth forms along the gradients of decreasing rainfall and increasing conductivity and silt content. Forbs, graminoids (restioids, grasses and sedges) and evergreen shrubs were associated with regions of higher rainfall with a low soil pH and conductivity. Deciduous shrubs, stem- and leaf-succulent shrubs and geophytes were generally associated with regions of low rainfall, high pH and high conductivity. There did not appear to be any relationship between the height of the various growth forms and the environmental variables.

The distribution of sites in species space (Figure 4.4b) shows that the major vegetation communities identified at MNR (Chapter Two) were not distinctly separated along the major environmental gradients. The individual communities were less apparent than in the ordination of the floristic data (compare Figures 4.3b & 4.4b). The fynbos and succulent karoo sites were separated out along moisture and edaphic gradients (Figure 4.4b). As expected, the succulent karoo sites were associated with low rainfall region while the fynbos sites were concentrated in the high rainfall region.


A) Biplot of growth forms and environmental variables in site space

b) Plot of sites in species space

Figure 4.4 The first two axes from CCA of the growth form data, with spatial covariables partialled out, constrained by the significant environmental variables. The environmental arrows in diagram A also apply to diagram B. The sites are classified according to the communities derived from Chapter Two.

As with the floristic data, the succulent karoo sites were grouped on clayey soils with high pH and electrical conductivity while fynbos sites were grouped on sandy soils with low pH and conductivity.

At a finer scale, restioid sandy fynbos (RSF), a major fynbos community, was clearly associated with deep sands. The kloof thicket (KT) sites were not separated from the fynbos sites, once again indicating poor environmental control of KT growth forms. The two major succulent karoo communities were separated primarily along an edaphic gradient of pH, conductivity and percentage silt. The sandstone-based succulent karoo matrix (SKM) was associated with regions of low pH and conductivity and low percentage silt. Not surprisingly, the shale-based shale succulent karoo (SSK) was associated with regions of higher conductivity and percentage silt.

The overlap between sites from the fynbos and succulent karoo communities (Figure 4.4b) was an indication that many of the growth forms are shared between these biomes. However, graminoids and evergreeness were mostly confined to the fynbos sites, while succulence and deciduosity were associated with the succulent karoo sites.

4.4 DISCUSSION

4.4.1 Spatial Auto-Correlation

Spatial variables alone contributed approximately 30% to the explained variance in both data sets. Longitude-related variables accounted for most of this variance. This result suggested that site location by itself was a reasonable predictor of floristic and growth form composition in a site. The underlying explanation of such a result is difficult to resolve without further research. Two families of explanations for spatial correlation exist (Legendre, 1993). First, there may be underlying biotic processes, such as reproduction, dispersal, competition and others, which have imposed a spatial pattern on the vegetation. Such a spatial pattern would be unrelated, at least in part, to the pattern caused by the measured environmental variables. Second, there may be environmental patterns that were not measured, but which have an underlying influence on both the vegetation and a number of the measured environmental variables.

There can be little doubt that biotic processes have influenced pattern in the vegetation at MNR. One important example would be herbivory, particularly livestock grazing and browsing. The vegetation at MNR has been influenced to some degree by both natural and commercial herbivores. This was most clearly seen in the vicinity of the old stock enclosures and routes to water sources, where all but the most unpalatable shrubs had been excluded by overgrazing. Even before commercial farmers made use of the vegetation, there would have been herds of grazing and browsing animals.

However, there was no way to account for this pattern, as no farm records were available. Competition (Folwer, 1986] and facilitation (Fonteyn & Mahall, 1981) may also be important biotic determinants of spatial autocorrelation in semi-arid environments. Both environmental and biotic explanations may explain the spatial autocorrelation at MNR, but were not investigated in any detail during this thesis. A further biotic factor that may be responsible for spatial patterns at MNR may be the limited dispersal distances characteristic of fynbos and succulent karoo. Ant dispersal in many fynbos taxa (Le Maitre & Midgley, 1992) and water dispersal in the Mesembryanthemaceae (Ihlenfeldt, 1994) do not allow dispersal over large distances.

One major edaphic factor, which has been suggested as important in controlling the distribution of fynbos and succulent karoo, is soil nutrient status (Campbell, 1988; Richards *et al.* 1995; and others). Unfortunately, I did not take nutrient status into account during this research for logistic reasons. Patterns in soil nutrient status are likely to be linked to geological, topographic and climatic influences, and may be partially responsible for the spatial auto-correlation recognised in the data. Once again, without further analysis, the influence of nutrient status on the distribution of communities could not be resolved. Thus, although spatial correlation did exist in the floristic and growth form data, no conclusive explanation for it could be suggested. However, in order to examine the influence of the measured environmental variables on the species data, without the confounding effect of spatial correlation, the variance due to locality was removed.

4.4.2 Quantifying the Variance Due to the Measured Environmental Variables

Approximately half of the 18 environmental variables were not significant and were removed from the final analyses. Annual rainfall, pH, conductivity, sand content and coarse sand content were significant in both the floristic and growth form analyses, suggesting that these were similar environmental determinants acting on species and growth form composition. The environmental variables retained in the analyses only accounted for approximately 15% of the total variance in the floristic and growth form data sets, leaving 75% unexplained (the 10% difference being explained by spatial variance). Such a huge fraction of unexplained variance suggests that the vegetation at MNR was not controlled by the environmental variables used in the analyses. However, other multivariate analyses in fynbos also encountered large amounts of unexplained variance (Richards, 1995; Simmons, 1996; McDonald, 1996; Privett, 1998). Such variance may be a natural feature of speciose systems such as fynbos and succulent karoo. Despite this, the first axis eigenvalues and overall CCAs for both the floristic and growth form CCAs were significant at the 1% level.

4.4.3 Vegetation-Environment Relationships and the Fynbos-Succulent Karoo Boundary

Environmental control of both floristic and growth form composition was dominated by two major gradients: climatic and edaphic. Annual rainfall and altitude were closely correlated and underlay the topo-climatic gradient of moisture availability. Species and growth forms turned over along this moisture gradient in a relatively predictable pattern. Fynbos species and growth forms, particularly the evergreen woody shrubs, graminoids and forbs were concentrated in the relatively moist regions. Considering that MNR lies at the climatic extreme of fynbos distribution, it was expected that fynbos would be found only in areas of highest moisture availability in MNR. Areas with annual rainfall lower than about 200 mm did not support fynbos species or growth forms.

Decreasing moisture availability from west to east across MNR was reflected in a switch from typical fynbos to succulent karoo species and growth forms. Members of the Mesembryanthemaceae, Crassulaceae, and other leaf- and stem-succulent shrubs became increasingly common with increasing aridity. The high degree of succulence characteristic of the succulent karoo has been suggested as a strategy to survive the intense and prolonged summer drought typical of Mediterranean climates (Milton *et al.* 1997). Evergreen fynbos shrubs and graminoids are unable to survive in the more arid regions because the low rainfall increases the duration of the intense summer drought (Milton *et al.* 1997).

Nutrient-poor soils and the Mediterranean climate are thought to be responsible for the evergreen nature of fynbos (Stock *et al.* 1997). Campbell & Cowling (1985) suggested that evergreeness in fynbos plants is a direct result of the nutrient-poor soils typical of the biome. Campbell (1988) also found that deciduous non-fynbos shrubs were associated primarily with nutrient-rich sites. A point is reached in the moisture gradient where the carbon cost of maintaining evergreen leaves cannot be supported (Miller, 1982), irrespective of nutrient status. At this point in MNR, there was a gradual switch from evergreen to deciduous shrubs as the dominant non-succulent plants. However, considering that nutrient status is also likely to change with rainfall and leaching regimes, it may be difficult to separate nutrient status and rainfall. Leached sites in high rainfall areas are typically nutrient-poor, while arid sites are typically nutrient-rich (Brady, 1974).

Other soil factors (pH, electrical conductivity and the texture fractions) also came out as strong explanatory variables in the CCA of the floristic and growth form data. Succulent karoo species and growth forms were associated with regions of high pH and conductivity and of high clay or silt content. Fynbos species and growth forms were more closely linked with regions of high medium sand content, low pH and low conductivity. Edaphic control of the fynbos / succulent karoo transition, within a climatic range suitable for fynbos, has been reported. Campbell (1983; 1988) suggested that fynbos is restricted to coarse-textured sandy soils with a low pH, while succulent karoo occurs on finer-textured loamy soils with a higher pH. Campbell & Cowling (1985) found that Karroid and Renoster shrubland was associated with high pH soils compared to other (mainly fynbos) communities that were found on low pH soils.

The soils derived from sandstone and quartzite of the Table Mountain and Witteberg Groups are typically light-coloured, acidic and coarse textured (Taylor, 1996). In comparison, loam from the Bokkeveld group was dark-coloured and fine-textured with a higher pH and conductivity. The association of various succulent karoo taxa and growth forms with these shale-derived soils is probably a reflection of soil moisture availability and possibly nutrient status. The fine-textured loam from the Bokkeveld Group increases drought stress in plants by having a relatively high osmotic potential (see Chapter Six). Thus, even though the Bokkeveld Group is exposed in an area climatically suited to fynbos, the droughty soils support karroid vegetation. However, soil chemical variables, pH, conductivity and salt content may also determine the distribution of fynbos and succulent karoo species and growth forms. The shale-derived soil had very high concentrations of various salts and elements (Chapter Six).

The fact that the shale-derived soils were fine-textured may have an indirect effect on the other soil variables measured. Movement of moisture through the soil profile is a function of texture. Coarse-textured soils are better drained than fine-textured soils (Brady, 1974). Leaching of cations from the upper zones of the soil profile should be less in fine-textured than coarse-textured soils. Low rates of leaching and the chemical composition of the parent shale causes the conductivity of shale-derived soils to be greater than that of sandstone-derived soils in MNR.

4.4.4 The Environmental Determinants of the Seven Communities

The seven communities derived from TWINSPAN in Chapter Two show some environmental control in the CCA of both the floristic and growth form data. In both cases, the succulent karoo communities were separated from the fynbos communities along gradients of decreasing rainfall and altitude and increasing clay content, conductivity and pH, as described above.

The succulent karoo communities were separated out along edaphic gradients of conductivity and soil texture. Shale succulent karoo (SSK) was quite distinctly associated with the high conductivity and fine texture fractions of shale-derived soils. Succulent karoo matrix (SKM) was separated from SSK on the basis of high sand content. The sandy soils derived from the Witteberg sandstone and quartzite support SKM where the rainfall is too low for fynbos. In the floristic CCA, sandy succulent karoo (SaSK) was separated from the other succulent karoo communities on the basis of pH and landtype. SaSK was confined to a unique habitat type (sandy plains in the arid regions) which had a relatively high pH. The high pH of these dry sand plains, compared to similar plains in more mesic regions, may have been a reflection of lower leaching rates or of the concentration of salts near the surface by the capillary action typical in arid soils (Brady, 1974).

Within the three fynbos communities, the greatest separation was between restioid sandy fynbos (RSF) and asteraceous fynbos matrix (AFM). RSF was separated from AFM on the basis of landtype in the floristic CCA and soil depth in the growth form CCA. RSF was largely confined to flat sandy plains (a unique landtype) that have deep sandy soils. Cowling *et al.* (1997) suggested that such restioid fynbos occurs on mesic sites where conditions are limiting for shrub growth, either by excessive waterlogging or drainage. At MNR, the sand plains would have had very good drainage, being coarse-textured. However, I also noted evidence of waterlogging (gleying and nodule formation) at approximately one metre deep in some of the sand plain sites, particularly near Perdewater. Thus it seems that RSF occurs on sandy plains wherever woody shrubs are unable to grow.

The transitional community, dwarf bedrock shrubland (DBS) was hardly separated from AFM in either CCA, suggesting that it is more closely affiliated with fynbos than succulent karoo. DBS was separated from the fynbos communities on the basis of landtype in the floristic CCA. By definition, DBS occurs on the large bedrock sheets (landtype = 2) that make up much of the area in MNR.

The last community, non-fynbos kloof thicket (KT), was also not well separated from AFM in either the floristic or growth form CCA. Once again, many of the species and growth forms in KT were derived from AFM. Cowling *et al.* (1992, 1997) suggested that thicket is separated from fynbos largely on the basis of protection from fire and that thicket is confined to fire-free habitats within the fynbos biome. Fire was not a factor investigated in this study, and this may explain why thicket is not well separated from fynbos. However, considering that the vegetation at MNR is rarely dense enough to support frequent or intense fires, this may not be the case.

Kloof thicket only occurs at the western extreme of fynbos at MNR, suggesting that moisture availability may also be important in determining its distribution. Even within the fynbos matrix, KT was restricted to locally mesic sites. Runoff from the large rock outcrops must greatly increase moisture availability in the soil at the base of these rocks, where KT was commonly found. Thus it seems that KT is restricted to fire-protected and locally mesic sites within the fynbos matrix.

4.5 CONCLUSIONS

The spatial position of sites accounted for a large proportion of the variance in both floristic and growth form data sets. Spatial auto-correlation at MNR probably reflects some underlying biotic or unmeasured abiotic variable that has a spatial pattern and which is a determinant of vegetation distribution. Without further research this cannot be resolved.

There was a lot of noise in the data sets and the CCAs explained little of the variance in both the floristic and growth form data. Edaphic gradients of soil texture, pH and conductivity accounted for the largest proportion of variance in the data sets. This was probably a result of the very speciose nature of the vegetation. The topo-climatic gradients of altitude and rainfall accounted for the next largest proportion of variance. Soil texture variables had greater explanatory power than soil chemical variables (pH and conductivity).

Fynbos and succulent karoo sites were separated primarily along to topo-climatic gradient and secondarily along gradients of soil texture, pH and conductivity. However, no causal relationships between fynbos and succulent karoo distribution and the physical environment can be concluded on the basis of inductive multivariate analyses.

CHAPTER FIVE

Predicting the Fynbos / Succulent Karoo Boundary and the Occurrence of Vegetation Communities and Growth Forms Using Generalised Linear Modelling and GIS

5.1 INTRODUCTION AND OBJECTIVES

5.1.1 Background to Predictive Mapping in Fynbos and Succulent Karoo

Plant community structure is dynamic. Floristic composition and vegetation physiognomy change over time and space in response to environmental gradients and biotic interactions (Barbour *et al.* 1987). Such dynamism has been noted particularly in fynbos (Bond, 1981; Cowling & Holmes, 1992; Cowling *et al.* 1997) and succulent karoo (Milton *et al.* 1997). There may be limited use in mapping the vegetation of an area as it only provides a snapshot of the current state of the vegetation (Franklin, 1995). Over time and at different spatial scales, a static vegetation map may lose relevance; particularly if the vegetation is renowned for its dynamism, as are fynbos and succulent karoo. There is a need to provide a more dynamic representation of the vegetation that will allow for, or even predict, changes in the vegetation distribution in response to changes in the environment and scale (van de Rijt *et al.* 1996).

There is considerable interest in the dynamics of the boundaries between biomes, and the fynbos / non-fynbos boundary in the Cape is no exception. Of particular interest, is the potential influence of climate change on the fynbos / succulent karoo boundary, a theme central to this thesis.

Climate changes are most likely to show their first effects in ecotonal zones between two climatically influenced biomes (Nielson, 1993). The use of predictive mapping may be particularly applicable for monitoring vegetation change in response to climate change, especially if satellite (or other remotely sensed) imagery can be used (Jury, 1993). There is a need to predict changes in the relative positions of fynbos and succulent karoo with changes in the environment, such as increased aridity. Such predictions could be tested by 'ground-truthing' should environmental changes occur.

Another problem with traditional vegetation maps is that they introduce artificial boundaries between communities. In reality, geographic variation in vegetation is often continuous and fluctuating (Austin, 1991). It is not uncommon for management decisions, such as those concerning fire regimes, to be based on artificial boundaries, and this can lead to inappropriate management of transitional zones between vegetation communities. In this respect there is a need to have more dynamic maps of the vegetation communities, which can be adapted with perceived changes in the environment. Such adaptations would be based on a significant relationship between the environment and vegetation communities.

Time and cost are key logistic factors that influence the design of vegetation surveys. There is always a need to streamline surveys so that they fall within the limited budgets of most land managers. In this respect, predictive mapping of vegetation, using several easily measurable environmental variables, allows much greater areas of land to be surveyed and incorporated into management planning than would otherwise be practical. Also, in landscapes such as that at MNR, with a large area and limited access, there is a need to be able to extrapolate the vegetation communities derived from a compact and efficient survey to the larger area. This rationale is particularly applicable to the MNR area. The reserve itself is a focal point surrounded by a much larger conservancy comprising many of the neighbouring private farms. These private farms are unlikely to have vegetation maps that can be incorporated into a single management map or plan. Thus it would be extremely useful for conservancy management to be able to extrapolate the major communities at MNR to the greater conservancy area, at little extra cost.

Such methodology would allow rapid surveys of inaccessible areas to be performed within the logistic constraints of cost and time. Even if the predicted survey of the vegetation does not provide as much information as a ground survey in terms of identifying rare or endemic species, it would assist in the identification of areas with potentially high conservation status. This can be done by identifying the area of vegetation type under-represented in the reserve system. Nicholls (1991) reviewed the use of generalised linear modelling (GLM) for predicting the environmental control of species distribution and species richness. Nicholls (1991) maintained that without some method of interpolation or extrapolation, all survey data remain as a snapshot of biological diversity or abundance and are thus location and time specific. This logic is particularly relevant if large areas of vegetation need to be mapped, based on survey data from a small area, or if the vegetation is expected to change in response to environmental fluctuations.

There are many studies that have shown that species distribution is determined to a large degree by the environment (Barbour *et al.* 1987). Indeed, there is an entire body of ecological theory, including niche theory, based on the perceived relationship between species and the environment. There has also been considerable work on modelling the distribution of individual species based on measurements of their distribution along some environmental gradient (Margules *et al.* 1987; Austin *et al.* 1990 and others: see review in Franklin, 1995). The same concepts have been applied to vegetation associations and communities (Austin *et al.* 1983, 1984; Valverde & Montana, 1996), but never in fynbos or succulent karoo, although McDonald *et al.* (1995) used a logistic regression approach to model the biological aspects of endemism in fynbos. Euston-Brown (1995) used GLM to predict the distribution of diagnostic families and growth forms in fynbos and succulent thicket, based on crude topographic, climatic and geologic variables. Euston-Brown (1995) noted that different families and growth forms within a biome responded differently to the environmental gradients. He concluded that topo-climate and geology were the primary determinants of the fynbos / non-fynbos dichotomy.

This chapter attempted to relate the distribution of the major communities and growth forms (Chapter Two) and the fynbos / succulent karoo boundary with several easily measurable environmental variables. The relationship between the vegetation and environment was then used as the basis for predicting and extrapolating the distribution of these vegetation units.

5.1.2. Objectives

The aim of this chapter was to answer three questions. First, could the distribution of the major communities or growth forms be predicted accurately across MNR, using easily measurable environmental variables? Second, could the geographical position of the boundary between fynbos and succulent karoo in MNR be predicted accurately and thus monitored using the same environmental variables? The third question addressed the application of the GLM's in a GIS environment. Could the regressions derived from the first two questions be used in a GIS to produce realistic maps of the vegetation of MNR based on the major vegetation types or growth forms? This question was answered by comparing the predicted vegetation map with the actual vegetation map (Chapter Two).

5.2 METHODS

5.2.1 Background to Generalised Linear Models (GLMs)

The data used in the following analyses were not distributed normally and included both categorical and continuous variables. Generalised linear models extend the regression framework to three situations where ordinary regression would not be appropriate. First, where the data do not follow a normal distribution. Second, where the data need to be transformed (using a link function) before a linear model can be fitted. Third, when a combination of categorical and continuous explanatory variables needs to be used

(Genstat 5 Committee, 1987; Crawley, 1993; Trexler & Travis, 1993). There are three main issues that need to be considered when using GLMs to predict the distribution of communities (Nicholls, 1991).

1) The selection of an appropriate statistical model (Section 5.2.2);
2) the selection of suitable variables to be used as predictors (Section 5.2.3 - 5.2.5); and
3) the critical evaluation of the fitted regression model for outliers and influential observations (Section 5.2.6).

5.2.2 The Response Variables and Assumptions

In each of the models below, the distribution of the response variable was assumed to be binomial and thus a logit link function was used (MaCullagh & Nelder, 1989).

5.2.2.1. The major communities

Each of the major communities (Table 5.1), except for dwarf bedrock shrubland (DBS), was modelled separately against the explanatory environmental variables. The response variable indicated the presence (1) or absence (0) of the relevant community in a site. The 125 sites used in these, and the following, analyses were assumed to be independent observations of the vegetation.

Table 5.1 The biomes, major communities and characteristic growth forms used in the generalised linear models

Biome	Communities	Growth Forms
Fynbos	Asteraceous fynbos matrix	Restioids and Evergreen shrubs
	Restioid sandy fynbos	
Succulent karoo	Shale succulent karoo	Succulent and Deciduous shrubs
	Sandy succulent karoo	
	Succulent karoo matrix	

5.2.2.2. The fynbos / succulent karoo boundary

Each site was coded as fynbos (1) or succulent karoo (0) based on the TWINSPAN classification (Chapter Two). The response variable indicated the presence or absence of fynbos in each site.

5.2.2.3. The diagnostic growth forms

Considering that individual growth forms respond differently to environmental gradients (e.g. Euston-Brown, 1995 for fynbos), it is unlikely that a community of growth forms will show a high correlation to any one environmental gradient. Both fynbos and succulent karoo have characteristic growth forms (Table 5.1). Restioids and evergreen shrubs characterise fynbos, while succulents and deciduous shrubs characterise succulent karoo. The distributions of these growth forms were modelled separately. The percentage cover of each growth form in each site was modelled against the environmental data. The cover data were assumed to have a binomial distribution (Nicholls, 1991: p55).

5.2.3 Choosing Environmental Variables for the Models

The basic requirement for predictive mapping is a simple, robust model of environmental variables that explains a significant proportion of the variance in the vegetation data. The reason for employing an environment-vegetation model is to extrapolate survey data to large areas without further survey effort. Thus, the model must use environmental variables that are easier to measure than vegetation variables. Most preferable is a model that can be derived from remotely sensed or computer-generated environmental data. Thus I chose to use only those environmental data that could be obtained easily from sources other than in the field.

Another criterion for choosing explanatory variables was based on the literature. Several environmental variables have been invoked as determinants of community distribution within and between the fynbos and succulent karoo biomes. I have reviewed the environmental determinants of the fynbos / succulent karoo boundary in Chapters Four and Six. To summarise this review, a combination of moisture availability and soil nutrient status control the fynbos / succulent karoo boundary. Rainfall, evaporation and soil texture (amongst other factors) control moisture availability. Soil nutrient status depends largely on parent material and soil water dynamics (leaching). Considering that most soil factors cannot be measured by remote sensing or without intensive sampling, a surrogate 'blanket' variable was needed. Geology has a strong influence on a number of soil variables and has been found to be an adequate explanatory variable in vegetation-environment models in place of detailed soil analyses (Euston-Brown, 1995).

Five explanatory variables were chosen that would reflect or influence, either directly or indirectly, the factors thought to be responsible for determining the fynbos / succulent karoo boundary (i.e. moisture availability and nutrients). Mean annual rainfall, altitude, radiation, geology and landtype were used as explanatory environmental variables in the model. All these variables could be obtained with little effort in the field. Although rainfall and altitude were closely correlated (Chapter Four), both were included in the initial model to see which had better explanatory power. Rainfall was later dropped as it always accounted for less variance in the vegetation data than altitude.

5.2.4 Generation and Evaluation of Environmental Variables Using GIS

It was important to ensure that the environmental variables were a reasonable reflection of the environment. Below I assess the integrity of the environmental variables used. **Annual rainfall data** were derived from a surface interpolation model (CCWR, 1996) that is based on averaged rainfall measurements (from climate stations with over 20 years of data) and topographic variables such as altitude, aspect, shading and slope angle. Unfortunately, there are only two rainfall stations with more than 20 years data within a radius of 5km of MNR. Thus it is possible that the interpolated values may not be accurate and there was no way of checking the data against real values. Also, the rugged topography of the area, with high mountains and deep valleys will tend to stretch the capabilities of the surface interpolation model. However, these rainfall data were all that were available, and it may explain why rainfall was not as good a predictor variable as altitude in the models. The interpolated rainfall data were incorporated into a GIS on a minute-by-minute grid. The nearest data point to each site was used as the mean annual rainfall value for that site. Preliminary analyses indicated that rainfall could be divided into two categories, above or below 200mm (Table 5.2), without a significant decrease in explanatory power.

Table 5.2 The various categories of geology, annual rainfall, altitude and landtype used in the GLMs to predict the occurrence of fynbos or one of the major communities in a site.

GLM Category	Geology, rain, altitude or landtype
Geology1	Table Mountain and Witteberg Group sandstones
Geology2	Bokkeveld Group shales
Rain1	< 200mm
Rain2	>200mm
Altitude1	< 800m
Altitude2	> 800m
Landtype1	Rocky talus slopes and flat gravel plains
Landtype2	Bedrock sheets
Landtype3	Flat sandy plains

Topographic data (altitude, aspect and slope angle) were derived from a surface elevation model (SEM) calculated in a GIS. These data were thus only as accurate as the data entered into the GIS and the mathematics behind the method used to build the SEM. The SEM was created from digital 1:50 000 map sheets 3219CB, 3219AD (Surveyor General, Mowbray, Cape Town). I checked these digital map sheets against the printed map sheets (which I had used extensively in the field and found to be accurate) and found no discrepancies. The method used to build the SEM from the digital contour data was the default method in the GIS program ARC/INFO-GRID. These interpolation methods are generally well accepted for building SEMs although a review of the intricacies of the methods was beyond the scope of this chapter. Preliminary analyses indicated that altitude could be simplified into two categories, above or below 800m (Table 5.2), with almost no loss in explanatory power.

Solar radiation data for summer, winter and the equinox were calculated for each site from aspect and slope angle regression equations (Schulze, 1975) for the latitude 32°S. Both aspect and slope angle were derived from the SEM. Radiation for all seasons was found to be insignificant in preliminary models that included geology, altitude or landtype, and was dropped from the analyses.

Three **geological** categories were digitised from a 1:250 000 geological sheet (3219 Clanwilliam) and 1:10 000 aerial photographs (Appendix A). These data were checked in the field during the survey and found to be accurate. Each site was coded as one of these sedimentary groups. After preliminary analyses, Table Mountain Group and Witteberg Group sandstones were grouped together and compared against the Bokkeveld Group shale (Table 5.2).

The same aerial photographs were used to digitise four **landtype** categories (Table 5.2) that were also checked in the field. The only inaccuracies that may have arisen would have been slight misplacing of boundaries from the digitising process and no large areas were put into the wrong landtype category. After preliminary modelling, gravel plains were grouped with rocky slopes to reduce model instability.

5.2.5 Selection of Suitable Predictor Variables

Once an initial set of explanatory variables was chosen (Sections 5.2.3 and 5.2.4), significant variables were selected for the models using a forward step-wise process (GENSTAT 5 Committee, 1987, Crawley, 1993). The process of model building was iterative. All the explanatory variables were added to the model singly on the first pass. The variable that accounted for the highest significant change in deviance was added to the model. All the remaining variables were then added to the new model singly and the one with the highest significant change in deviance retained. The null hypothesis, that there was no change in the likelihood ratio (deviance) for each addition, was tested by comparing the change in deviance with the χ^2 statistic (Crawley, 1993). This was repeated until no more significant variables remained. In each case, the interactions between the main explanatory variables were tested first. The main variables were only tested if there were no significant interactions. The continuous variable, radiation, was fitted both as a linear and quadratic function to test for possible curvature in the response between the transformed probability and the variable (Nicholls, 1991). The final minimum adequate model contained only the significant environmental variables.

Preliminary analyses showed that some of the categories in the environmental variables had a response that was always zero or one. For example, fynbos never occurred on shale (geology 2), and SSK was the only community ever to occur on shale. Variables with such structural zeros or ones were removed from the model as they caused instability (Lindsey, 1989), yet they were still biologically meaningful. These unstable variables were incorporated into the final models as a statement of fact, but did not have influence in the regression equation (Lindsey, 1989).

5.2.6 Critical Evaluation of the Model

Regression models fitted to data for predictive purposes must be evaluated in terms of some simple diagnostic measures (Nicholls, 1991). In all models, the fitted values were calculated as a function of the observed values and the residuals examined. Also, the error variance was plotted against the response variable.

Considering the crude manner in which the vegetation data were collected and classified, there was little value to generating precise models. The aim of the modelling was to predict the occurrence of coarse-scale vegetation units within a landscape using a few easily measured environmental variables. Bearing this in mind, little effort was made to adjust the models once a suitable set of predictor variables had been chosen, even when the standard errors, residuals or fitted values suggested that the model was not entirely stable.

5.2.7 Predicting the Distribution of the Major Communities, the Fynbos / Succulent Karoo Boundary and the Growth Forms

Three principal steps were employed to generate predictive vegetation models. The first was the generation of the GLMs described above. The second was incorporating the GLMs into a GIS of the explanatory variables that were significant in the model, and then predicting the distribution of the communities and fynbos based on these variables. The third step involved comparing the predicted map of vegetation types against the actual map (Chapter Two).

5.2.7.1. The Geographical Information System (GIS)

Polygon covers of the three categorical environmental variables used in the model, altitude, geology and landtype, were generated in a GIS (method described in section 5.2.4). A composite cover of all the environmental variables significant in a GLM was built by overlaying the individual covers within the GIS. The composite cover for each model thus comprised a number of polygons that had unique combinations of the significant environmental variables.

5.2.7.2. Incorporating the GLM into the GIS

The output from a GLM was a regression equation:

$$l = a + b_i.x_i + b_j.x_j + \ldots b_k.x_k \qquad \text{(eq.1)}$$

where l is the linear predictor; a is the regression constant; and b_i is the regression coefficient for the explanatory variable x_i. The probability (p) of a vegetation unit occurring in a polygon was calculated by:

$$p = \exp^{l} \div (\exp^{l}+1) \qquad \text{(eq.2).}$$

The standard error of p was calculated by:

$$se = \pm 1.96 \sqrt{(p * (1 - p) \div n)} \qquad \text{(eq. 3)}$$

The values of the environmental variables from each polygon in the composite GIS cover were substituted into the regression equation from the GLM. Thus the probability of a vegetation type or growth form occurring in every polygon in the composite GIS cover was calculated from the GLM. The polygons were colour coded according to their probability values to give a map showing the areas where that particular vegetation type or growth form was most likely to occur. In the case of the coverage with all the major communities, where there was an overlap of polygons with different probabilities, the polygon with the highest probability of occurrence superseded the other.

5.2.7.3. Comparing the predicted and actual vegetation maps

The predicted distributions of communities and the fynbos / succulent karoo ecotone were mapped in the GIS compared visually against the actual map derived from Chapter Two.

5.3 RESULTS

5.3.1 Predicting the Distribution of the Six Major Communities

Overall, the distributions of the six communities were not well explained by the three most significant environmental variables: altitude, geology and landtype. Although not a reliable measure of goodness-of-fit for models with categorical response variables, the low deviance of the minimum adequate models (Table 5.3) indicated poor explanatory power. In all models, altitude proved to be a better explanatory variable than estimated rainfall and was thus used as a surrogate variable for moisture climate (rainfall and temperature). Radiation was never significant as an explanatory variable and was dropped from the analyses.

Table 5.3 The deviance of the maximal (max dev.), full (full dev.) and minimum adequate (min dev.) models for the six major communities and the fynbos / succulent karoo dichotomy. Significant explanatory variables were chosen by a process of forward selection (see text). The estimate (est), standard error (se) and t-value (t) for each significant variable in the minimum model are given. Values of t greater than 2 are approximately significant at the 0.05 level.

Community	Max Dev.	Full Dev.	Min. adequate model		est	Se	t
			Dev.	Variables			
AFM	150	39	21	*Constant* + Altitude2	*-2.686* 2.375	*0.596* 0.639	*4.5* 3.7
RSF	83	41	24	*Constant* + Landtype3	*-3.481* 3.481	*0.717* 3.481	4.8 4.1
KT	70	14	-	-	-	-	-
SSK	144	76	70	*Constant*	*-2.037*	*0.307*	*6.6*
SKM	128	55	31	*Constant* + Altitude2	*-0.128* -2.790	*0.292* 0.589	*0.4* 4.7
SaSK	42	19	8	*Constant* + Landtype3	*-3.181* 1.872	*0.718* 0.957	*4.9* 2.0
Fynbos / succulent karoo	170	94	66	*Constant* + Altitude2	*-3.83* 4.64	*1.01* 1.04	*3.8* 4.5

The probability of a community occurring in a site was calculated by substituting *l* (the linear predictor) from each of the following equations (4-8) into equation 2. A comparison of the fitted values and the response variable was used an indication of the goodness-of-fit for all models.

5.3.1.1 Asteraceous Fynbos Matrix (AFM)

Only altitude and geology caused a significant change in deviance when added to the model. However, geology 2 (shale) had a very high standard error that caused model instability. This was because AFM was never found on shale and its occurrence was a structural zero that distorted the model. Thus geology was removed from the model and treated as a statement of fact. The final model (eq. 4) did not predict the occurrence of AFM well. Of the 36 sites with fynbos, the model correctly predicted 33 sites. However, the model incorrectly predicted the occurrence of AFM in 39 sites (Table 5.4).

Table 5.4 The number of sites correctly and incorrectly predicted by the models. Incorrect sites were either incorrectly classified as absent, or incorrectly classified as present.

Community / fynbos	Actual number of sites	Predicted numbers of sites		
		Correct	Incorrectly absent	Incorrectly present
Asteraceous fynbos matrix	36	33	3	36
Restioid sandy fynbos	15	9	6	9
Shale succulent karoo	33	21	12	0
Succulent karoo matrix	27	22	5	13
Sandy succulent karoo	5	3	0	5
Fynbos	54	53	1	15

On sandstone $l = -2.686 + (2.375 * \text{Altitude2})$; on shale $l = -\infty$ (eq. 4)

Table 5.5 The probability (p) of AFM occurring in a site, based on altitude and geology (eq. 4).

Altitude	Geology	$l =$	p ± se
< 800 m (1)	Sandstone (1)	-2.686	0.06 ± 0.04
	Shale (2)	-∞	0 ± 0
> 800 m (2)	**Sandstone (1)**	**-2.367 + 2.375**	**0.4 ± 0.08**
	Shale (2)	-∞	0 ± 0

The model predicted that AFM would only be found on sandstone geology above 800m (Table 5.5), irrespective of landtype. Below 800m there is not enough moisture to support fynbos communities. Similarly, shale-derived soils are too arid or have chemical properties that prevent fynbos from establishing on them (see Chapter Six). However, high-altitude sandstone also supports succulent karoo matrix (SKM) wherever conditions are locally xeric, such as on north-facing slopes or valley floors. This explained why the occurrence of fynbos could only be predicted with a probability of 0.4, and why so many sites were incorrectly classified. Considering radiation is a variable partially responsible for locally xeric sites on north-facing slopes (Shulze, 1975), it was surprising that radiation was not significant in the model.

5.3.1.2. Restioid Sandy Fynbos (RSF)

Landtype and altitude were the only significant variables in the model (Table 5.3). However, altitude1 (<800m) caused instability in the model because RSF was never found below 800m. Thus, altitude was treated as a statement of fact and removed from the model. Similarly, RSF was never found on bedrock sheets (landtype 2) and this was also treated as a statement of fact. The final model (eq. 5) did not predict the occurrence of RSF accurately. Only 9 of 15 sites were correctly classified (Table 5.4). The model also incorrectly predicted the occurrence of RSF in nine sites.

Below 800m or on bedrock $l = -\infty$; (eq. 5)
above 800m and on rocky slopes or sandy plains $l = -3.481 + (3.481 * \text{ltype3})$

The occurrence of RSF could thus be predicted with a probability of 0.5 on the basis of landtype and altitude (Table 5.6). RSF was restricted to high altitude sandy plains. Geology was not significant in the model, but his does not suggest that RSF occurred on shale. The reason is that landtype was the most significant predictor variable, and flat sandy plains never occur on shale.

Table 5.6 The probability (p) of predicting the occurrence of RSF in a site based on altitude and landtype (eq. 5).

Altitude	Landtype	$l =$	p ± se
< 800 m (1)	Rocky slopes (1)	$-\infty$	0 ± 0
	Bedrock sheet (2)	$-\infty$	0 ± 0
	Sandy plain (3)	$-\infty$	0 ± 0
> 800 m (2)	Rocky slopes (1)	-3.481	0.03 ± 0.03
	Bedrock sheet (2)	$-\infty$	0 ± 0
	Sandy plain (3)	**-3.481+3.481**	**0.5 ± 0.08**

The reason why the probability of predicting RSF was low, was because RSF also occurs on sand patches which were too small to be seen on the aerial photographs. These patches were classified as rocky slopes. There were also areas where AFM encroached onto the sandy plains.

5.3.1.3. Kloof Thicket (KT)

None of the environmental variables accounted for a significant change in deviance when added to the model. This suggested that neither altitude, nor geology, nor landtype controlled the distribution of KT. KT typically forms 'islands' in AFM, between the large rocky outcrops, and thus cannot be separated from AFM based on the environmental variables used in the analyses. What maintains these 'islands' of KT within AFM is uncertain, seeing that fire does not appear to be a factor at MNR. Possible explanations may be that fire occurs over a long time frame, or that increased run-off from the outcrops supports taller shrubs characteristic of KT.

5.3.1.4. Shale Succulent Karoo (SSK)

Geology was the only predictor variable to cause a significant change in deviance when added to the SSK model (Table 5.3). Geology2 (shale) caused the model to become unstable because SSK was the only community ever found on shale. Thus shale was treated as a statement of fact and removed from the model. Based on geology alone, the final model had relatively good predictive power. Only 12 of 33 sites were incorrectly classified. All the mis-classifications were due to sites that were incorrectly classified as non-SSK. These sites were all on sandstone geology, but all had some other feature, such as gravel patches, which gave rise to similar environmental conditions to the shale geology. The model was unable to account for these sites.

On sandstone $l = -2.037$; on shale $p = 1$ (eq. 6)

Table 5.7 The probability (p) of predicting the occurrence of SSK based on geology alone (eq. 6)

Geology	*l*	p ± se
Sandstone (1)	-2.037	0.1 ± 0.05
Shale (2)	-	**1 ± 0**

The model suggested that, although SSK was the only vegetation type to occur on shale-derived soil, it could also occur occasionally on sandstone-derived soil (Table 5.7). At MNR, the shale-derived soil is mostly restricted to the Bokkeveld Group shales. The very different soil physical and chemical conditions between shale-derived and sandstone-derived soils (Chapter Six) are probably responsible for the absence of SKM on shale. The distinction between sandstone and shale thus has an over-riding influence on succulent karoo composition, irrespective of altitude and landtype.

5.3.1.5. Succulent Karoo Matrix (SKM)

As with asteraceous fynbos matrix, the model for SKM was best described by altitude and geology (Table 5.3). Once again geology was incorporated into the final model (eq. 7) as a statement of fact to reduce model instability. In comparison to the AFM model, the SKM model was a better predictor of community distribution (Table 5.4). The model overestimated the occurrence of SKM, incorrectly predicting it in 13 sites, and under-estimated it in five sites. However, 22 out 27 sites were correctly classified (Table 5.4).

On sandstone $l = -0.128 + (-2.790 * \text{altitude2})$; on shale $l = -\infty$ (eq. 7)

Table 5.8 The probability (p) of predicting SKM in a site based on altitude and geology (eq. 7).

Altitude	Geology	l	p ± se
< 800 m (1)	**Sandstone (1)**	**-0.128**	**0.5 ± 0.08**
	Shale (2)	-∞	0 ± 0
> 800 m (2)	Sandstone (1)	-0.128-2.790	0.1 ± 0.05
	Shale (2)	-∞	0 ± 0

SKM is associated with low altitude sandstone sites (Table 5.8). Thus the distinction between SKM and AFM was one of altitude. Fynbos is found at high altitude, while succulent karoo is found at low altitude. As with AFM, the transitional nature of the fynbos / succulent karoo ecotone was responsible for the relatively low probability for predicting the occurrence of SKM (Table 5.8).

5.3.1.6 Sandy Succulent Karoo (SaSK)

Landtype and altitude caused the most significant changes in deviance when added to the model (Table 5.3). Because SaSK is never found above 800m, altitude was incorporated into the final model (eq. 8) as a statement of fact. As with its fynbos equivalent (RSF), SaSK was never found on bedrock sheets and this landtype was also treated as fact in the model. The model was a poor predictor of SaSK, with only three out of five sites being correctly classified. Five sites were incorrectly classified as SaSK (Table 5.4).

Below 800m and on rocky slopes or sandy plains l = -3.481 + (1.872 * ltype3);
above 800m or on bedrock sheets $l = -\infty$ (eq. 8)

Table 5.9 The probability (p) of predicting the occurrence of SaSK based on altitude and landtype (eq. 8).

Altitude	Landtype	l	p ± se
< 800 m (1)	Rocky slopes (1)	-3.481	0.1 ± 0.05
	Bedrock sheet (2)	$-\infty$	0 ± 0
	Sandy plain (3)	**-3.481 + 1.871**	**0.2 ± 0.07**
> 800 m (2)	Rocky slopes (1)	$-\infty$	0 ± 0
	Bedrock sheet (2)	$-\infty$	0 ± 0
	Sandy plain (3)	$-\infty$	0 ± 0

The low altitude sandy plains most often support SaSK. The same sandy plains support RSF at high altitude. The low probability of predicting the occurrence of SaSK (Table 5.9) is because the low altitude sandy plains also support SKM in places. Indeed, it was difficult to separate SaSk and SKM at a coarse scale. At best, the model predicts where SaSK will definitely not be located.

5.3.2 Predicting the Presence of Fynbos

Altitude and geology were the only significant variables in the model accounting for the distribution of fynbos. As with the other models, geology was treated as a statement of fact in the model, because fynbos was never found on shale. The model (eq. 9) had relatively good predictive power. Only one of 54 sites was incorrectly classified as non-fynbos (Table 5.4). The model did, however, incorrectly predict the occurrence of fynbos in 15 sites (Table 5.4).

On sandstone $l = -3.83 + (4.64 * \text{altitude2})$; on shale $l = -\infty$ (eq. 9)

Table 5.10 The probability (p) of predicting the occurrence of fynbos in a site based on altitude and geology (eq.9).

Altitude	Geology	*l*	p ± se
< 800 m (1)	Sandstone (1)	-3.83	0 ± 0
	Shale (2)	$-\infty$	0 ± 0
> 800 m (2)	**Sandstone (1)**	**-3.83 + 4.64**	**0.7** ± 0.08
	Shale (2)	$-\infty$	0 ± 0

The occurrence of fynbos could thus be predicted with a high probability (Table 5.10) on the basis of two easily measurable environmental variables – altitude and geology. In comparison to the individual communities, the model for fynbos was considerable more accurate.

5.3.3 Modelling the Distribution of Diagnostic Growth Forms

None of the four environmental variables accounted for a significant portion of the variance for any of the four growth forms. The maximal models for all growth forms accounted for between 5 and 14% of the deviance in the full model (Table 5.11). Thus it appeared that the growth forms used in the analyses are shared between fynbos and succulent karoo and do not respond to the measured environmental gradients.

Table 5.11 The deviance of the maximum and full model for the four growth forms used in the analyses

Growth form	Max. dev.	Full dev.
Restioids	232.1	14.8
Evergreen shrubs	103.6	14.1
Deciduous shrubs	149.7	8.1
Succulent shrubs	154.2	22.9

5.3.4 Critical Evaluation of the Models

The residuals from all the models were not random and the error variance was not constant. The models for fynbos and all communities, except SSK, overestimated the occurrence of the vegetation type. Although these features were problematic for making accurate predictions and extrapolations, I felt that the models were adequate for the purpose they were designed to fulfil, especially considering the crude manner of data collection. In all cases, the models were biologically meaningful and gave an estimate of the probability with which the occurrence of a community or the fynbos / succulent karoo boundary could be predicted. The models could be improved by including further explanatory variables, but this was not desirable in terms of the initial model requirements of a few easily-measured variables.

5.3.5 A Comparison of the Actual and Predicted Vegetation Maps

There were few differences between the actual and predicted distributions of the major communities (Figure 5.1). DBS was not included in the comparison as there were too few sites for accurate modelling. The occurrence of SSK and RSF were well predicted. The model was unable to account for the transitional nature of the AFM – SKM ecotone, and predicted that AFM would occur throughout the ecotone. Similarly, the model predicting the position of the fynbos / succulent karoo boundary could not account for the gradual transition (Figure 5.2) and fynbos was predicted to occur throughout the ecotone. There was no way to account for the ecotone with the variables used in the models. In this respect, it was surprising that radiation was not statistically significant in the models.

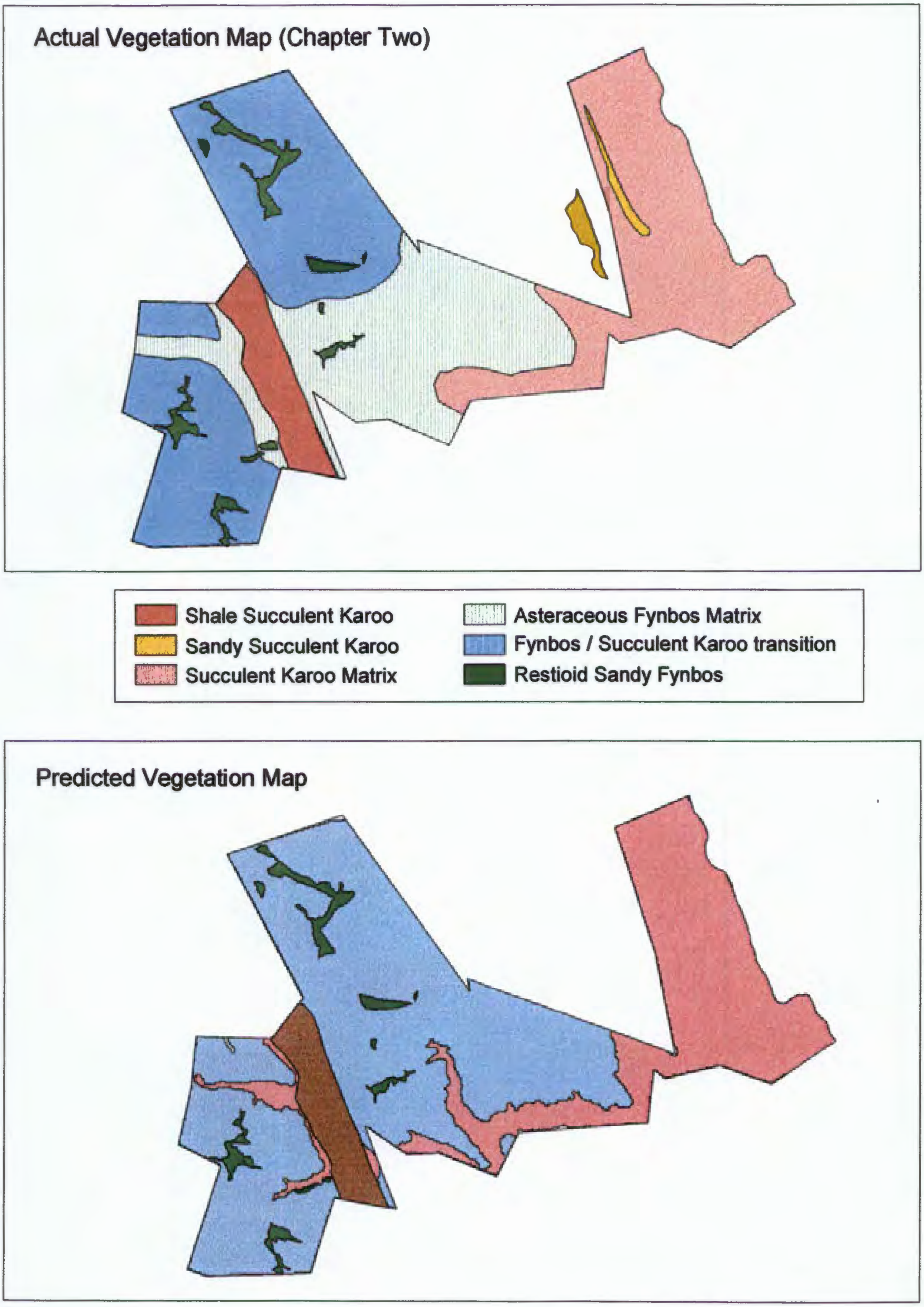


Figure 5.1 A comparison of the actual and predicted vegetation maps of MNR. The Dwarf Bedrock Shrubland community was not included in either map because no model was generated for this community. The community models did not account for the fynbos / succulent karoo transition.

Figure 5.2 A comparison of the actual and predicted position of the fynbos / succulent karoo boundary at MNR. The model was unable to account for the ecotone between fynbos and succulent karoo.

5.4 DISCUSSION

5.4.1 Predicting the Occurrence of Communities, Growth Forms and Fynbos

The main aim of this chapter was to establish whether the distribution of the communities, characteristic growth forms, and the fynbos / succulent karoo boundary could be mapped accurately using a few easily measured environmental variables.

5.4.1.1. Communities

The results from the GLMs showed that the occurrence of communities could be predicted with probabilities between 1 and 0.2. For those communities with a low probability, the question arose as to what vegetation would persist in a site if the predicted community did not occur there. Assuming that, had the models incorporated more explanatory variables, the probability of occurrence would be higher than was currently calculated, then it is likely that even models with relatively low probabilities would make accurate predictions about the occurrence of communities. Brown (1994) suggested that, although environmental variables may not explain the majority of variation in vegetation data, even weakly significant models warrant interpretation. It is likely that missing variables and use of surrogate topoclimatic variables limit the levels of model explanation (Brown, 1994).

The low probability of predicting the occurrence of the two largest communities, AFM and SKM, was attributable to the transitional nature of the ecotone between the fynbos and succulent karoo biomes. As described in Chapter Two, the ecotone is characterised by a gradual shift in proportion of fynbos elements to succulent karoo elements. Within this gradient, wherever there are locally mesic or xeric sites, the balance shifts to fynbos or succulent karoo, respectively. None of the explanatory variables retained in the models accounted for such heterogeneity in the environment. Radiation, which reflects aspect and slope angle, was expected to account for this variation, but was not significant in any of the models. The reason for this is unknown, especially since Holland & Steyn (1975) found marked vegetation differences on north and south aspects in the fynbos biome, which they attributed to radiation loads. Similarly, Bond (1981) stressed the importance of aspect in a PCA of fynbos vegetation.

RSF and SaSK were poorly predicted, probably because these communities were modelled on the basis of landtype. They were, however, not the only communities associated with this landtype. AFM and SKM were found occasionally on sandy plains. This problem arises because of the difficulty and inaccuracy in classifying landtypes into mutually exclusive categories. Some of the sites may have been transitional between landtypes and the models did not account for this.

Considering the original requirements of the GLMs, I felt the current models were sufficient for making biologically accurate predictions of community distributions, based on three very crude environmental variables.

5.4.1.2. Growth Forms

The spatial variability of the four growth forms was not significantly related to spatial variation of the measured environmental variables. These results suggested that these growth forms were shared between the two biomes and were not grouped along the environmental gradients. This was particularly unexpected for the restioid growth form, as restioids are usually strictly associated with the more mesic conditions suitable for fynbos (Cowling & Holmes, 1992). However, Campbell (1988) suggested that there is no relationship between restioid cover and the mesic-xeric gradient. Euston-Brown (1995) found that certain growth forms could be modelled successfully against crude environmental variables. In particular, Euston-Brown (1995) found that restioids were strongly influenced by geology.

The importance of moisture conditions in determining deciduousness and evergreenness in nutrient-rich Mediterranean areas was demonstrated by Mooney *et al.* (1975) and thus it was surprising that the models did not show environmental control of evergreen and deciduous shrubs. However, most of MNR lies over nutrient-poor soils and nutrient status may override the moisture effect. It is also possible that the growth form categories used in the models were too broad and had no underlying environmental control. Without further research, this issue cannot be resolved.

Similarly, the classical association of succulents with arid environments (Von Willert *et al.* 1992) should have been apparent from the modelling. The results suggested that the growth forms used in the analysis were not controlled by spatial variation of climatic and edaphic variables. Mackay (1993) found that climatic and substrate-related variables were very poor predictors of growth form distribution in Australian forests. The results from the vegetation survey (Chapter Two) indicated that all four growth forms, even restioids, were found throughout MNR, and only the proportions changed spatially. Restioids were found deep into the succulent karoo matrix, but only on locally mesic sites. Similarly, succulents were found throughout the fynbos, and were even abundant in areas supporting fynbos. Campbell (1988) also found that succulents made a large contribution to his Dry Asteraceous Fynbos community. The reason why the growth form models were not significant is probably because the fynbos / succulent karoo boundary is relatively diffuse when the substratum is sandstone or quartzite.

5.4.1.3. Fynbos

The fynbos / succulent karoo boundary could be predicted with a relatively high probability, using a model based on only two environmental variables: altitude and geology. That geology was a good predictor variable in these analyses supported the suggestion that geology can be used as a crude surrogate variable in place of detailed soil analyses for landscape-scale vegetation mapping (Euston-Brown, 1995). If this is so, then ignoring soil chemical and physical analyses could save time and money for large-scale surveys. There is an increasing literature on predictive mapping of soil properties based on their relationship with topographic variables (Franklin, 1995).

Although the model could not predict the occurrence of the fynbos / succulent karoo transition, it did predict climatic and edaphic boundaries across which fynbos was never found. Of particular interest for climate change monitoring is the topoclimatic boundary of 800m altitude. Should there be an increase in aridity or temperature that corresponds to a shift in altitude, then the lower limit of fynbos should shift to a higher altitude. Euston-Brown (1995) predicted that fynbos families would be forced to higher altitudes and onto south-facing slopes should the climate become more arid and warmer. A similar pattern of change between Mediterranean and arid ecosystems was measured in the Judean Mountains, where, although a gradual change in vegetation was measured along a rainfall gradient, a drastic change occurred at approximately 300mm annual rainfall (Kutiel, *et al.* 1995). The ecotone between the Mediterranean and arid ecosystems shifted in a direction determined by annual rainfall. An increase in rainfall caused an ecotone shift to the Mediterranean ecosystem (Kutiel, *et al.* 1995). At MNR, predicted shifts of the fynbos boundary could be monitored with permanent plots where fynbos seedling establishment is measured regularly and correlated with climate changes.

5.4.2 Applications of Predictive Mapping

Goodchild (1994) and Franklin (1995) have reviewed the application of GLM and GIS. There are many management applications for vegetation mapping using predictive models (e.g. Nicholls, 1991; Franklin, 1995; Valverde & Montana, 1996). The fact that the fynbos / succulent karoo boundary and occurrence of the major communities in MNR can be predicted within a GIS environment has implications for management and monitoring projects. In the case of MNR, the neighbouring farms that have joined the Cederberg conservancy can be crudely mapped with relative ease and low cost, based on a few crude environmental variables. Such maps can then be used for management and conservation, and may form the basis for more intensive mapping. Simple statistics, such as calculating the areas represented by fynbos and succulent karoo respectively, can be performed and incorporated into management decisions. Any information that improves the databases of resource managers is useful (Nicholls, 1989) and use of GLMs to expand on existing surveys is a good start to such a database. In many cases, the costs of vegetation surveys, in terms of money and manpower, will prevent inventories of regions ever being completed, or even undertaken, before management decisions need to be made (Nicholls, 1989). Using GLMs in a GIS is an important first step to aiding decision making. Further flexibility of predictive models within a GIS is that they can be adjusted easily should the environment change or the vegetation–environment algorithm be improved.

In the case of potential climate change, the fluctuations of the fynbos / succulent karoo boundary can be predicted and monitored using the current model, based on the altitude below which fynbos plants do not establish and survive. However, it is very difficult to make accurate predictions about climate-directed vegetation change, based purely on correlation modelling approaches alone, because no mechanism of change is inferred (Nielson, 1993). Also, biotic interactions between plants, such as competition or facilitation, are not considered in correlative modelling.

Similarly, extrapolation of correlation models beyond the current data is unreliable (Nielson, 1993).

5.4.3 The Determinants of the Fynbos / Succulent Karoo Boundary

This topic is explored in greater detail in the next chapter, although there are model results worth interpreting. The occurrence of fynbos in a site could be predicted with a probability of 0.7 on the basis of two very crude environmental variables. Altitude, divided into above and below 800m and geology divided into shale and sandstone. Both of these variables indirectly control moisture availability to plants. Precipitation decreases with altitude, which means that less moisture enters the soil at low altitude than at high altitude. Furthermore, temperature increases with decreasing altitude, resulting in higher potential evaporation at low altitude. These gradients explain why fynbos is never found at low altitude (<800m) – it is too dry for fynbos plants to establish. These results are supported by other authors who suggest moisture availability is the primary factor separating fynbos and succulent karoo (see reviews in Cowling *et al.* 1997; and Milton *et al.* 1997).

Apart from this moisture-altitude gradient, soil texture also controls moisture availability to plants. Shale-derived soils, which are fine-textured, are effectively more arid than coarse-textured, sandstone-derived soil (see Chapter Six). This is why fynbos was never predicted on shale-derived soils at MNR, irrespective of altitude. These result supported the results from the experiment with fynbos and succulent karoo seedlings (Chapter Six), in which moisture and soil texture were shown to be the factors controlling the establishment of fynbos seedlings in the fynbos / succulent karoo ecotone. Ellis & Lambrechts (1986) found that succulent karoo is typically found on fine-grained soils with a high pH and cation exchange capacity. The crude nature of the geology variable used in the modelling did not allow the influence of soil chemical and physical factors on the fynbos / succulent karoo boundary to be separated. This topic is investigated in the next chapter.

Considering the model was unable to account for the transitional ecotone between the biomes, there must be other factors which also determine the fynbos / succulent karoo boundary. Ellery *et al.* (1991) suggested that fynbos was separated from succulent karoo on the basis of a longer growing season, i.e. fynbos requiring water for a longer period. Within a landscape, locally mesic sites essentially have a longer growing season and thus support fynbos. It is likely that factors, such as radiation, aspect, slope angle or slope position, which partly control moisture patchiness in the landscape, are responsible for the intermingled patches of fynbos and succulent karoo.

5.5 CONCLUSIONS

Generalised linear models were able to predict the occurrence of the major communities and the eastern extreme of fynbos accurately. The models used only three very crude environmental variables: altitude (above and below 800m), geology (shale or sandstone) and landtype (sandy plain, rocksheet or rocky slope). The main failing of the models was that they were unable to account for the transitional nature of the fynbos / succulent karoo ecotone, reflected in a gradual shift in the proportion of fynbos and succulent karoo elements. The occurrence of growth forms characteristic of fynbos and succulent karoo could not be modelled, as none of the explanatory variables were significant in the GLM.

The GLMs were incorporated into a GIS environment with relative ease, and were used to generate maps of the predicted distributions of the communities and the fynbos limit. The probability of a community or fynbos occurring in a site could be also be calculated and incorporated into the GIS.

CHAPTER SIX

The Roles of Moisture, Soil Texture and Nutrients in Seedling Establishment in the Fynbos / Succulent Karoo Ecotone

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6.1 INTRODUCTION

The preceding chapters have described the vegetation communities at MNR (Chapter Two) and have indicated the main environmental factors that determine the boundary between fynbos and succulent karoo (Chapters Four & Five). However, neither the descriptive nor analytical techniques employed during this earlier work present conclusive evidence to support or reject hypotheses made about the determinants of the fynbos / succulent karoo boundary. Such evidence can only be derived from experiments designed to test predictions deduced from the hypotheses developed during descriptive studies. Both the literature, outlined below, and the results of the earlier chapters suggest that moisture availability, mediated by precipitation and particle size distribution of the soil, and nutrient status are important environmental determinants of the fynbos / succulent karoo boundary.

6.1.1 Determinants of the Fynbos / Succulent Karoo Boundary

Research into the factors that determine the boundary between fynbos and succulent karoo has been descriptive. Levyns (1950) gave a narrative account of the boundary between the Cape and Karoo floras near Ladismith (Little Karoo). She suggested that moisture availability, mediated primarily by rainfall and secondarily by aspect-controlled evaporation, determined the transition from fynbos, through renosterveld, into succulent karoo. Levyns (1950) developed this hypothesis on the basis of qualitative observations of vegetation patterns along rainfall and energy (aspect) gradients.

Miller (1982) suggested that a combination of soil moisture availability and carbon economy controlled the fynbos / succulent karoo boundary. In low-rainfall karroid sites, drought-deciduous and succulent leaves are favoured because the carbon cost of non-succulent evergreen leaves cannot be recovered. In this respect, considering that fynbos is an evergreen sclerophyllous shrubland, fynbos shrubs should perform poorly on karroid sites (Miller, 1982). In low-nutrient fynbos sites the nutrient cost of deciduous leaves cannot be recovered and evergreen plants are common (Campbell & Werger, 1988). Succulent plants are at a competitive disadvantage compared to more vigorous fynbos shrubs (Euston-brown, 1995), and cannot survive the fire regimes typical of fynbos. Thus deciduous and succulent karroid shrubs would be outcompeted in sites that can potentially support fynbos, but are free of fire.

Campbell (1986) used discriminant analyses to identify the environmental factors separating fynbos and succulent karoo sites in a study of the montane plant communities across the entire fynbos biome. Annual rainfall was the most important discriminant function, although a number of soil variables, particularly pH and texture, were important in separating fynbos and succulent karoo sites. The karroid sites were associated with low-rainfall, high-pH and fine-textured soils. Campbell (1986) suggested that although soil chemical variables appeared to be more important, soil texture should be included as a factor determining the fynbos / succulent karoo boundary. He concluded that it was difficult to determine whether climatic factors were more important than edaphic factors as determinants of this boundary. The discriminant scores of the soil factors were closely correlated with those of the rainfall. In other words, low-rainfall sites also tended to have fine-textured, high-pH soils. All of Campbell's (1986) suggestions were based on descriptive analyses.

Euston-Brown (1995) investigated the determinants of the fynbos / non-fynbos (mainly succulent thicket and renosterveld) boundary in the Eastern Cape, using both descriptive and experimental methods. Rainfall was the most important variable in explaining the distribution of vegetation units. Geology, although secondary to rainfall, was also important in explaining vegetation patterns. Euston-Brown (1995) suggested that broad edaphic variables, such as geology, were adequate predictors of pattern. If correct, then detailed soil analyses investigating particle size distribution, chemistry and nutrient status are not necessary for determining the fynbos / non-fynbos boundary. This was supported by the results of Chapter Five. However, at high rainfall levels, fynbos grows on fine-textured soils derived from shales and other softer sediments (Campbell 1986; Cowling & Holmes, 1992; Euston-Brown, 1995).

An experiment where seedlings were transplanted across biome boundaries showed that edaphic factors controlled the distribution of fynbos in arid environments, and that fynbos distribution was directly limited by mortality of seedlings (Euston-Brown, 1995). In comparison to fynbos plants, which are directly limited by the environment, succulent karoo plants are primarily limited by the outcome of competitive interactions (Yeaton & Esler, 1990). The potential growth rates of the succulent karoo plants, and thus the outcome of competitive interactions, is determined by the interaction between their biology and the environment. Fynbos seedlings were not limited to nutrient-poor sites, so long as there was enough moisture available for them to survive (Euston-Brown, 1995).

Fire is also a factor that may be responsible for maintaining the fynbos / succulent karoo boundary (Cowling *et al.* 1997). Thus, in order to separate the effects of climatic and edaphic factors, sites should be chosen where fire is not a factor. The low rainfall and very rocky landscapes of MNR do not support sufficient biomass for regular fires. Indeed, I never encountered evidence of past fires during my work at MNR. This is one of the reasons why MNR is such a good area in which to investigate the determinants of the fynbos / succulent karoo boundary.

Thus it appears from the literature (see reviews in Cowling & Holmes, 1992; Cowling *et al.* 1997; Milton *et al.* 1997 and Chapter Four) that precipitation, soil texture, nutrient status, pH and conductivity are implicated, either separately or interacting together, as determinants of the fynbos / succulent karoo boundary. The central aim of this chapter was to separate the effects of moisture, soil texture and nutrient status on the growth and survivorship of fynbos and succulent karoo seedlings.

6.1.2. Rationale for Use of Seedlings in the Experiment

Seed and seedling biology are crucial in determining the composition and dynamics of species in communities. The migration of plants can only effectively occur during seed dispersal (Leishman *et al.* 1992; Pitelka *et al.* 1997). Any stage in the life history of a plant that has very high mortality will strongly influence the population structure of the plant (Harper, 1977). It follows then, that the environmental or biotic variables that influence the survival of individuals in that important stage will have the greatest effect on the distribution of that plant. Davis (1991) suggested that both biotic and abiotic stresses would be most severe at the recruitment stage in all mediterraneum-climate regions. Seedling regeneration is important in both fynbos and succulent karoo as these plants are typically short-lived because of frequent disturbances by fire or drought, and most do not sprout after disturbance (Cowling & Holmes, 1992; Cowling *et al.* in press; Cowling & Hilton-Taylor, in press). For example, Von Willert, *et al.* (1985) noted that a 12-month drought in the Richtersveld killed 80% of Mesembryanthema plants in the field. Seedling mortality is relatively high in arid and semi-arid regions, including the succulent karoo (Esler & Philips, 1994). The early seedling stage is an important bottleneck in the population dynamics of certain karroid species (Esler, 1993). Similarly, the environmental determinants of seedling survival have been shown to dictate adult plant distribution patterns in fynbos (Mustart & Cowling, 1993a; 1993b). Thus the determinants of seedling survival of fynbos and succulent karoo plants may, in turn, determine the relative distributions of these vegetation types.

6.1.3 Aims and Hypotheses

The aim of this chapter was to investigate experimentally the interactions of moisture and soil conditions on performance of seedlings of fynbos and succulent karoo species. Performance was measured in terms of biomass accumulation and survival of seedlings. The results from this study supported the descriptive analyses used in earlier chapters. The fundamental question that I attempted to answer was: what are the roles of soil texture, nutrient conditions and moisture in determining seedling establishment across the fynbos / succulent karoo boundary in MNR? This question was broken down into the following testable hypotheses:

1. *Moisture effect*

There would be no differences in the performance of seedlings (fynbos or succulent karoo) grown under *mesic* versus *xeric* moisture regimes in the *same soil type.*

2. *Texture effect*

There would be no differences in the performance of seedlings (fynbos or succulent karoo) grown in *fine-textured* versus *coarse-textured* soils under a *xeric moisture regime* (assuming water is the most limiting factor).

3. Nutrient effect

There would be no differences in the performance of seedlings (fynbos or succulent karoo) grown in *nutrient-rich* versus *nutrient-poor* soils under a *mesic moisture regime* (assuming that water is not limiting).

4. Species effect

There would be no differences in the performance of *fynbos* versus *succulent karoo* seedlings grown under the *same moisture regime* (xeric or mesic) and in the *same soil type* (fine-texture, nutrient-rich or coarse-textured, nutrient-poor).

6.2 METHODS

6.2.1 Soil Collection and Preparation

Two soils were collected from MNR: a shale-derived, fine-textured soil and a sandstone-derived, coarse-textured soil. The soil from both sites was air-dried for two weeks and sieved through a 2mm mesh to remove any pebbles or large pieces of organic matter. Particle-size distribution, acidity, pH, electrical conductivity and elemental composition (K, Na, Mg, B, P) of each soil were measured by Elsenburg Soil Science Division (Dept. Agriculture: Western Cape, P.Bag X1, Elsenberg, 7607). The total nitrogen content of each soil was measured using the Kjedahl method by Matrolab

Laboratory Services (Box 1106, Brackenfell). The matric potential of each soil was measured at five negative pressures (-10, -33, -100, -1000, -1500 kPa) using the pressure plate method by South African Sugar Association Soil Laboratories (Private Bag X02, Mount Edgecomb, Kwazulu-Natal, 4300). Only a single replicate from each soil was analysed.

6.2.2 Seed Collecting and Germination

Seeds from several fynbos and succulent karoo species were collected from plants in MNR during December 1996. The species were chosen on the basis of their being a typical dominant species of fynbos or succulent karoo vegetation as well as seed availability. I tried to represent each of the typical fynbos elements, *i.e.* the restioid, proteoid, and ericoid components. Seed from five fynbos species was harvested: *Leucadendron pubescens* (Proteaceae)*; Diosma acmaeophylla* (Rutaceae)*; Passerina vulgaris* (thymelaeaceae)*; Phylica buxifolia* (Rhamnaceae) and *Wildenowia incurvata* (Restionaceae). Hereafter I refer to these species by their generic names only. For each species, seeds from several individuals in different areas were harvested. Whole cones were harvested from *Leucadendron,* dried in an oven at 40°C for seven days and the seeds extracted from the opened cones with forceps. Whole capsules of *Diosma* and *Phylica* were harvested, placed in a box covered by stocking-mesh material and left in the sun. The capsules opened explosively when dry, releasing the seeds. *Passerina* and *Wildenowia* seeds were collected from the soil surface beneath plants. This was done to ensure the seed was ripe (assuming that ripe seed would fall from the plant) and because it was easier to pick the seeds up from depressions where they were concentrated by wind. Insects had predated upon many of *Wildenowia* seeds. The seeds were sorted by placing them in water and discarding the non-viable seeds that floated.

Capsules from six succulent karoo *Ruschia* species, (Mesembryanthemaceae) were harvested. Seeds were removed from the *Ruschia* capsules by dissection. As there was uncertainty as to the names of the *Ruschia* species, voucher specimens of the two species used in the experiment were lodged in the Bolus Herbarium, Department of Botany, University of Cape Town.

All the fynbos seeds were soaked for 24 hours in a commercial smoke-water extract made from burnt fynbos vegetation by the National Botanical Institute, Kirstenbosch. Smoke treatment is a requirement for the germination of many fire-adapted fynbos species (Brown, 1993). The seeds of *Leucadendron* and *Wildenowia,* which have hard seed coats, were also soaked for 24 hours in a 1% hydrogen peroxide solution to improve oxygen uptake and stimulate germination (Brown, 1993). Seeds from the *Ruschia* species were not expected to have any germination cues other than a low temperature requirement (Esler *et al.* 1992) and were not treated with smoke-water or hydrogen peroxide solution.

The seeds from all species were placed in separate petri dishes (approximately 25 seeds per dish) on four layers of filter paper and treated with fungicide (0.125% Sodium Benlate). The petri dishes were placed in a controlled environment growth chamber with day (10h, 20°C) and night (14h, 10°C) light and temperatures set to simulate the autumn-winter period when most germination of fynbos (le Maitre & Midgley, 1992) and succulent karoo (Esler *et al.* 1992 and Esler, 1993) seeds occurs. The filter paper in the petri dishes was kept moist during germination and periodically sprayed with the same fungicide solution.

6.2.3 Seedling Establishment

Once seeds had germinated, the seedlings were planted in 250ml polystyrene cups that had holes punched in their bases. Three seedlings of a species were planted into each cup. The aim was to thin these down to one seedling per cup prior to the start the experiment. The cups were kept in the growth chambers for two days after transplanting the seedlings to reduce transplanting stress. Once the seedlings had established in the soil, the cups were moved to a glasshouse at the Department of Botany, UCT. To prevent desiccation of the still fragile seedlings, the cups were covered for two days with petri dish lids. Thereafter, the seedlings were exposed to the air directly.

The seedlings were left to establish for three months in the glasshouse. The cups were shuffled randomly every week to prevent spatial effects. The soil in all pots was kept relatively mesic until the start of the experiment. This establishment watering regime would have corresponded to a high winter rainfall in MNR. The seedlings were sprayed periodically with a fungicide (0.125% sodium benlate) and an insecticide (Malathion).

Conditions in the glasshouse did not simulate those at MNR. Winter at MNR is characterised by very cold conditions with heavy frosts and the possibility of snow. The glasshouse temperatures were not controlled and thus reflected ambient temperatures which would have been considerably milder than at MNR. Humidity in the glasshouse would have been higher than in the field due to the circulation of air through water-cooled air conditioners.

Unfortunately, seeds from some species did not germinate, or did not produce enough seedlings for the experiment and were discarded. At the start of the experiment only *Passerina vulgaris*, *Leucadendron pubescens*, *Ruschia* A and *Ruschia* B had sufficient individuals for the experiment. In pots where more than one seedling survived to the start of the experiment, the extra seedlings were killed by cutting at ground level.

6.2.4 Experimental Design

The experiment was designed to separate the effects of soil texture and moisture on the performance of fynbos and succulent karoo seedlings using a 2*2*2 factorial treatment structure (Figure 6.1). There were two soil types: shale-derived and sandstone-derived; two moisture treatments: xeric (no water) and mesic (10ml for coarse soil, 20ml for fine soil); and 2 groups of species (fynbos and succulent karoo). The rationale behind the mesic treatment was to ensure that moisture was not limiting to seedling growth and that the soil remained relatively moist. Moisture was assumed not to be limiting to the seedlings in the mesic treatment. No effort was made to imitate field moisture conditions. The seedlings were watered every two days unless the soil was still mesic from the previous watering.

After two months, once all the fynbos seedlings in the xeric treatment had died, the watering frequency was reduced to every four days to further stress the succulent karoo seedlings that were not responding to the previous watering frequency. Each treatment had between four and ten replicates, depending on how many individual seedlings died before the start of the experiment. The pots were randomised weekly during the experiment to prevent spatial effects.

Unfortunately, the seeds of the same and different species did not germinate simultaneously and there were seedlings of different ages and sizes at the start of the experiment. This was countered by ranking the seedlings within a species and soil type according to height, and assigning the first to the mesic moisture regime, the second to the xeric moisture regime and so on. In this way, each moisture regime should have had a range of seedling sizes similar to the other regime.

The number of days until death was recorded for each replicate of a treatment. A seedling was considered dead when it no longer had any green leaves or shoots (Esler & Philips, 1994). The above-ground portions of dead plants were dried in an oven at 50°C for three days and weighed on an electronic balance. The experiment was started 1st July 1997 and terminated 16th September 1997 (77 days). At the end of the experiment, all surviving seedlings were harvested, dried in an oven at 50°C for one week, and weighed on an electronic balance.

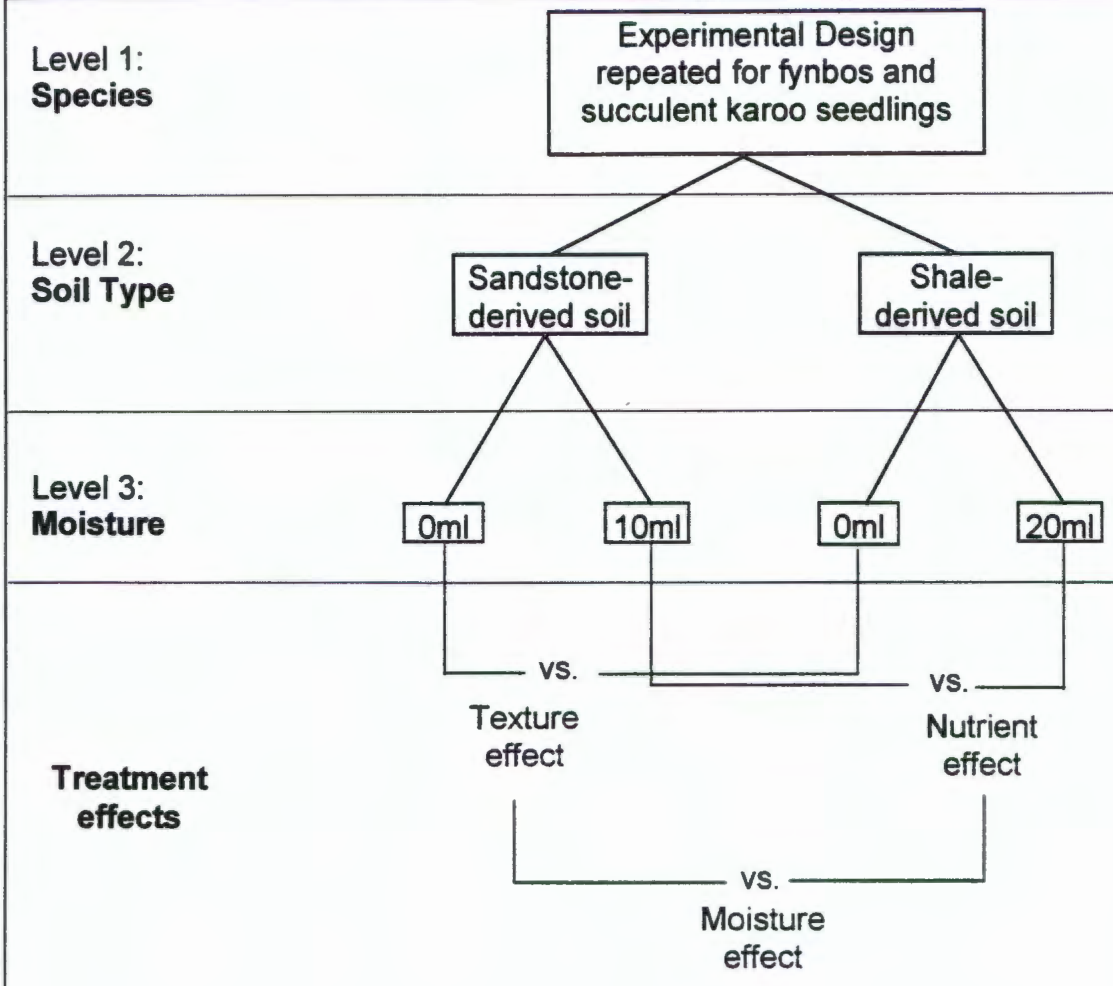

Figure 6.1. The 2x2x2 factorial experiment designed to separate the effects of soil texture, soil nutrients and moisture on the biomass and survival of fynbos and succulent karoo seedlings.

6.2.5 Statistical Analyses

The four hypotheses were tested by comparing the mean performance (biomass and time-until-death) of seedlings between pairs of treatments (Table 6.1). The distribution of the biomass data was tested for normality using marginal tests (GENSTAT vers. 5). The biomass data were significantly different from a normal distribution even when log transformed. Thus seedling biomass and days-until-death were compared between treatments using Mann-Whitney U tests with a normal approximation in GENSTAT. The percentage of seedlings that survived to the end of the experiment was also calculated for each treatment, although these were not compared statistically.

Table 6.1 Pair-wise treatment comparisons used to test the four null hypotheses.

Null hypotheses	Treatments compared	Treatments held constant
Moisture availability has no effect on seedling performance	Xeric vs. Mesic regime	Sandstone-derived soil
		Shale-derived soil
Soil texture has no effect on seedling performance	Fine- vs. coarse-textured soil	Xeric, fynbos
		Xeric, Succulent karoo
Soil nutrient status has no effect on seedling performance	Nutrient-rich vs. nutrient-poor soil	Mesic moisture regime
There is no difference in performance between fynbos and succulent karoo seedlings	Fynbos vs. succulent karoo seedlings	Xeric, sandstone soil
		Mesic, sandstone soil
		Xeric, shale soil
		Mesic, shale soil

Preliminary analyses of the soil texture comparison showed that all the fynbos seedlings died rapidly because of the xeric moisture regime, under which this comparison was carried out. Any differences in biomass between the fynbos seedlings grown in the two soil types would be a reflection of the pre-experiment growth (and thus probably more related to soil nutrient status). Thus the soil texture analyses were performed only on the succulent karoo seedling data. Likewise, comparisons of biomass accumulation between the fynbos and succulent karoo seedlings were made only for those seedlings under the mesic moisture regime.

6.3 RESULTS

6.3.1 Soil Particle Size Distribution, Water Retention and Nutrient Status

The shale-derived soil was finer-textured than the sandstone-derived soil, as expected, and had a much higher clay content (Table 6.2). Both soils had similar amounts of fine sand and coarse sand. However, the sandstone-derived soil had a considerably higher proportion of medium sand than did the shale-derived soil. As a consequence of the different particle size distributions of the two soils, there were considerable differences between the water content of soils at a range of matric potentials (Figure 6.2). The shale-derived soil was able to retain more water at all matric potentials than the sandstone-derived soil. These results indicated the osmotic potential plant roots would have to achieve in order to extract water from the different soils at the onset of drought. In other words, plant would find it more difficult to extract water from the shale-derived soil than the sandstone-derived soil.

Table 6.2 The particle size distribution and sample density of the shale-derived and sandstone-derived soils used in the experiment

Texture Fraction	Shale soil	Sandstone soil
Clay (%)	21.6	1.0
Silt (%)	10.9	2.0
Fine sand (%)	52.7	50.8
Medium sand (%)	8.0	42.3
Coarse sand (%)	6.8	3.9
Sample density (g/cc)	1.585	1.756

The shale-derived soil had greater concentrations of nitrogen (7x), sodium (150x), calcium (9x), magnesium (128x), potassium (20x), copper (2.5x), zinc (227x), manganese (7x) and boron (25x) than the sandstone-derived soils (Table 6.3). The considerably lower resistance of the shale-derived soil suggested that it had a higher cation exchange capacity and S-value than the sandstone-derived soil (Marshal & Holmes, 1979). The higher conductivity and pH of the shale-derived soils is probably a result of the greater concentrations of the various elements. These results support the hypothesis that shale-derived soils are finer-textured and nutrient-rich compared to sandstone-derived soils (Campbell, 1986).

Table 6.3 The pH, resistance, acidity and concentrations of various elements in the shale-derived and sandstone-derived soils used in the experiment.

Element or property	Shale soil	Sandstone soil
PH	4.5	4.2
Resistance (ohms)	20	26800
Acidity (me%)	0.86	0.37
Calcium (me%)	2.72	0.29
Magnesium (me%)	7.68	0.06
Nitrogen (mg/kg)	1053	157
Phosphorus (mg/kg)	5	5
Sodium (mg/kg)	1485	10
Potassium (mg/kg)	156	8
Copper (mg/kg)	0.64	0.26
Zinc (mg/kg)	2.27	0.01
Manganese (mg/kg)	86.7	12.8
Boron (mg/kg)	0.75	0.03

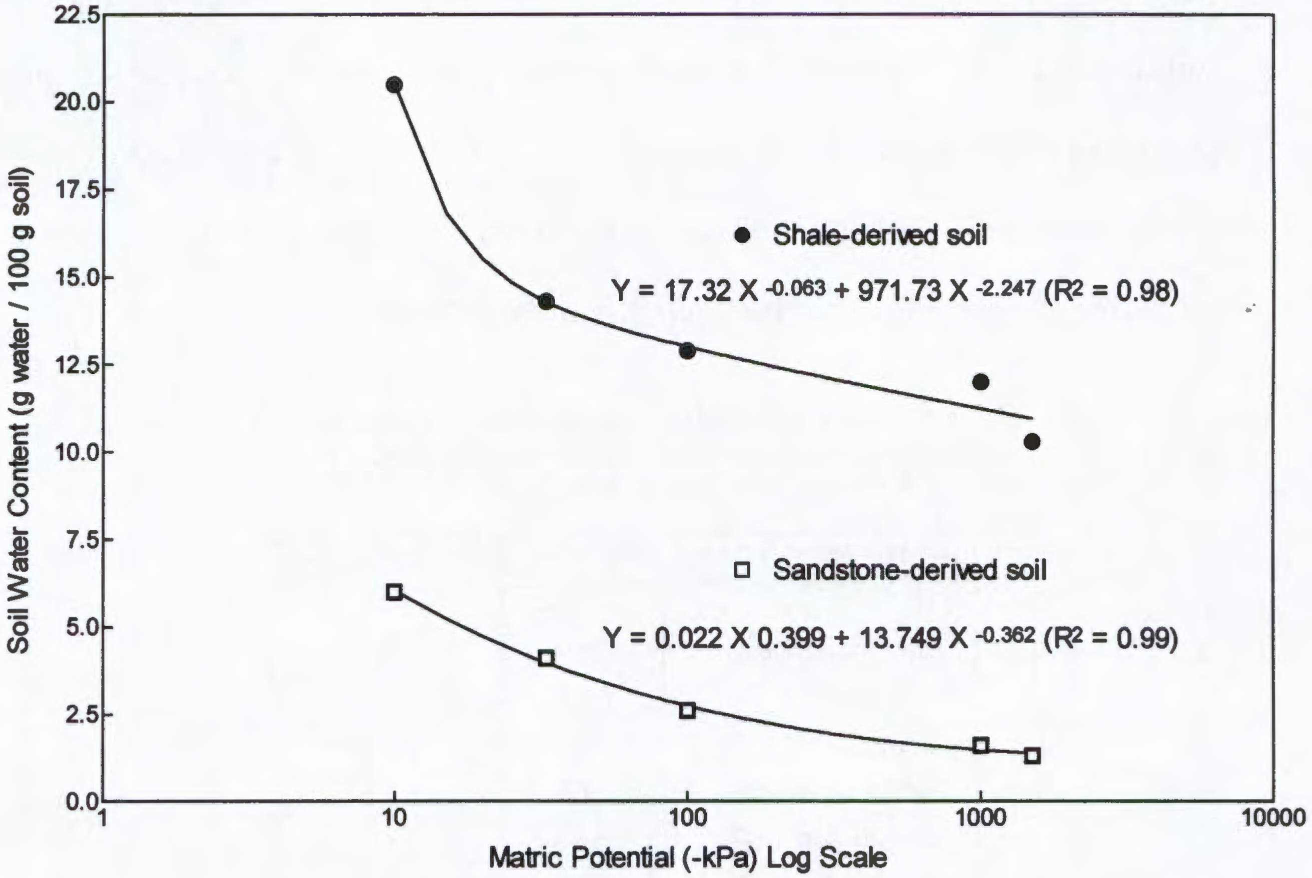

Figure 6.2 Power curves of soil moisture content of the shale-derived and sandstone-derived soils as a function of matric potential (-10, -33, -100, -1000, -1500 kPa). See text for details.

6.3.2 The Influence of Moisture Alone on Seedling Performance

6.3.2.1. Biomass Accumulation

Seedlings grown under the xeric moisture regime in both soils accumulated approximately one third of the biomass of seedlings grown under the mesic regime in the same soil (Table 6.4). Thus the null hypothesis that moisture regime has no effect on seedling biomass accumulation was rejected for both soil types ($p<0.001$).

6.3.2.2. Survival

The seedlings in the mesic regime survived for significantly longer than seedlings in the xeric regime, irrespective of soil type (Table 6.5). Also, many more seedlings survived in the mesic treatment compared to the xeric treatment (Table 6.5). Thus, the null hypothesis that moisture has no effect on seedling survival was rejected for both soil types ($p<0.001$).

Table 6.4 Mann-Whitney statistics (U) and their normal approximation (NA) of the pair-wise treatment comparisons used to test the null hypotheses (Table 6.1). The mean biomass (± standard deviation) and number of replicates (n) for each treatment are given. Significance levels: p<0.001*** ; p<0.01** ; p<0.05* ; not significant – ns.

Hypothesis	Conditions held constant	Biomass ± st. dev. (mg)	n	U	NA
Moisture effect	Sandstone-derived soil	Xeric = 54.3 ± 69.7 Mesic = 152.0 ± 158.0	39 39	327	4.33 ***
	Shale-derived soil	Xeric = 28.1 ± 51.3 Mesic = 87.4 ± 95.9	23 25	121	3.43 ***
Texture effect	Succulent karoo	Fine = 2.9 ± 2.0 Coarse = 19.2 ± 14.2	14 19	6	4.6 ***
Nutrient effect	Fynbos	Rich = 167.7 ± 167.7 Poor = 228.3 ± 189.1	9 20	73	0.8 ns
	Succulent karoo	Rich = 42.3 ± 32.1 Poor = 71.6 ± 53.6	19 16	94	1.92 *
Species effect	Mesic, sandstone-derived soil	Fynbos = 228.3 ± 189.1 Karoo = 71.6 ± 53.6	20 19	108	2.3 *
	Mesic, shale-derived soil	Fynbos = 167.7 ± 167.7 Karoo = 42.3 ± 32.1	9 16	25	2.66 **

Table 6.5 The percentage of seedlings in each treatment which survived to the end of the experiment (%) with the number of replicates (n). The mean days-until-death ± standard deviation (days ± st. Dev.) was compared with Mann-Whitney tests (U) with a normal approximation (NA). Significance levels: *** $p < 0.001$; ns = not significant. The duration of the experiment was 77 days.

Hypothesis	Conditions held constant		n	%	Days ± st. Dev.	U	NA
Moisture effect	Sandstone-derived soil		39	100	Mesic = 77.0 ± 0.0	370	3.90 ***
			39	50	Xeric = 50.7 ± 26.0		
	Shale-derived soil		23	80	Mesic = 68.8 ± 19.5	0	3.97 ***
			25	50	Xeric = 52.2 ± 26.8		
Texture effect	Succulent karoo		14	80	Fine = 71.4 ± 13.1	104	1.04 ns
			19	100	Coarse = 77.0 ± 0.0		
Nutrient effect	Fynbos		9	67	Rich = 59.0 ± 27.7	60	1.41 ns
			20	100	Poor = 77.0 ± 0.0		
	Succulent karoo		16	87	Rich = 74.4 ± 10.5	142	0.37 ns
			19	100	Poor = 77.0 ± 0.0		
Species effect	Sandstone-derived soil	Xeric regime	20	0	Fynbos = 25.8 ± 2.9	0	5.34 ***
			19	100	Karoo = 77.0 ± 0.0		
		Mesic regime	20	100	Fynbos = 77.0 ± 0.0	180	0 ns
			18	100	Karoo = 77.0 ± 0.0		
	Shale-derived soil	Xeric regime	9	0	Fynbos = 22.4 ± 7.2	0	3.97 ***
			14	80	karoo = 71.4 ± 13.1		
		Mesic regime	9	67	Fynbos = 59.0 ± 27.7	52	1.13 ns
			16	87	Karoo = 74.4 ± 10.5		

6.3.3 The Influence of Soil Texture on Seedling Performance

Due to the mortality of all the fynbos seedlings in this treatment as a response to the xeric moisture regime and not soil texture, the following texture treatment results are only for the succulent karoo seedlings.

6.3.3.1. Biomass accumulation

The succulent karoo seedlings grown in coarse-textured soil under xeric conditions accumulated approximately six times the biomass of seedlings grown in fine-textured soil (Table 6.4). Thus the hypothesis that soil texture does not affect seedling biomass accumulation was rejected for the succulent karoo seedlings ($p<0.001$). These results support the theory that water availability, mediated by soil texture, does affect the growth rates of succulent karoo seedlings.

6.3.3.2. Survival

There was no significant difference in the time-until-death between succulent karoo seedlings grown in the fine-textured or coarse-textured soils (Table 6.5). Similarly, there was little difference in the percentage of seedlings surviving between the fine-textured and coarse-textured treatments (Table 6.5). Thus the hypothesis that soil texture has no effect on seedling survival was accepted for succulent karoo seedlings.

6.3.4 The Influence of Soil Nutrients on Seedling Performance

6.3.4.1. Biomass Accumulation

Under the mesic regime, moisture was assumed not to limit seedling growth. The shale-derived and sandstone-derived soils were thus assumed to represent nutrient-rich and nutrient-poor conditions respectively (Section 6.3.1). There was no significant difference between the biomass accumulation of fynbos seedlings grown in nutrient-rich and nutrient-poor soils (Table 6.4). However, the succulent karoo seedlings grown in nutrient-poor soils accumulated significantly more biomass than those grown in nutrient-rich soils (Table 6.4). Thus the hypothesis that soil nutrient status has no effect on biomass accumulation was rejected only for succulent karoo seedlings ($p<0.05$).

6.3.4.2. Survival

Soil nutrient status had no significant effect on the time-until-death of either fynbos or succulent karoo seedlings (Table 6.5). There was however, slightly higher mortality of both fynbos and succulent karoo seedlings in the nutrient-rich soils (Table 6.5). The hypothesis that soil nutrient status has no effect on seedling survival was accepted.

6.3.5 The difference in performance between fynbos and succulent karoo seedlings

6.3.5.1. Biomass Accumulation

Due to the mortality of all the fynbos seedlings in the xeric moisture regime, biomass comparisons were only made between fynbos and succulent karoo seedlings under the mesic regime. The fynbos seedlings accumulated significantly more biomass than the succulent karoo seedlings in both soil types (Table 6.4). Thus the hypothesis that there was no difference between the biomass accumulation of fynbos and succulent karoo seedlings was rejected for both the shale-derived ($p<0.01$) and sandstone-derived ($p<0.05$) soils (Table 6.4).

6.3.5.2. Survival

a) Xeric moisture regime

In both soil types, the succulent karoo seedlings lived for significantly longer than the fynbos seedlings ($P<0.001$) (Table 6.5). The clearest result from the experiment was that almost no succulent karoo seedlings died, even under the xeric regime in the fine-textured soil. However, by the end of the experiment, the leaves of the succulent karoo seedlings growing in the xeric regime appeared shrivelled, and they must have been close to the end of their water reserves. In contrast, all the fynbos seedlings in the xeric regime died within 25 days of the start of the experiment, irrespective of soil type (Table 6.5).

b) Mesic moisture regime

There was no significant difference in the time-until-death of fynbos and succulent karoo seedlings grown in the mesic regime, irrespective of soil type (Table 6.5). Similarly, there was no significant difference in percentage survival between fynbos and succulent karoo seedlings grown under mesic conditions in the sandstone-derived soil. Neither group of seedlings suffered any mortality (Table 6.5). However, in the shale-derived soil more fynbos seedlings died than succulent karoo seedlings. Indeed, under mesic conditions, fynbos seedlings in the shale-derived soil performed poorly compared to those in sandstone-derived soil (personal observations). The succulent karoo seedlings remained unaffected by soil type.

6.4 DISCUSSION

6.4.1 The Influence of 'Precipitation' on Seedling Performance

Needless to say, water availability affects plant growth. The difference in seedling biomass accumulation between the two moisture regimes resulted from differences in seedling growth periods during the experiment. The growth of seedlings, especially fynbos seedlings, exposed to the xeric regime probably slowed rapidly soon after water was withheld, and many died prior to the end of the experiment. In comparison, seedlings under the mesic regime continued growing, and lived longer than those in the xeric regime and thus accumulated biomass over a longer period. Unfortunately, days-until-death could not be used as a co-variable in the analyses because it was also influenced by the treatments.

Seedlings, even of drought tolerant species, require water to survive as they have not yet developed the root systems or storage organs that aid adult survival. It is this vulnerability of seedlings that makes the seedling stage so important when considering plant migration (Davis, 1991). Under the xeric regime, both fynbos and succulent karoo seedlings received no water for 77 days. Almost all seedling mortality in the xeric moisture regime was attributable to the fynbos seedlings, which died due to drought stress. Euston-Brown (1995) also found that transplanted fynbos seedlings died rapidly under arid conditions, suggesting that fynbos is directly limited by the physical environmental factors.

6.4.2 The Influence of Soil Texture on Succulent Karoo Seedling Performance

Soil water availability is controlled primarily by two variables: precipitation and soil texture. Coarse-textured, sandy soils are easily drained and retain most of their water in capillaries between the sand grains (Brady, 1974). They have a small internal surface area and are typically made up of quartz grains which have few surface charges (Marshal & Holmes, 1979). These characteristics make it easy for plants to extract water from sandy soil. In contrast, fine-textured soils have a considerably greater internal surface area and typically have particles with many surface charges. Clay particles in particular have adhesion properties that are greater than for sand particles. Fine-textured soils thus have the potential to retain more water than coarse-textured soils (Marshal & Holmes, 1979).

The differences in moisture contents of the shale- and sandstone-derived soils under a range of matric potentials supported this theory. It is more difficult for plants to extract water from fine-textured soils (i.e. the plants must be able to generate a very low osmotic potential in their roots). Thus, for a given precipitation event, there is less water available to plants in fine-textured soils compared to coarse-textured soils. Also, the fine-textured soils become droughty before the coarse-textured soils at the onset of the summer dry season, even though they may contain more water. The intensity and duration of summer drought on plants is therefore exacerbated by fine-textured soils. To generalise, under low moisture conditions, such as those at MNR, sandy soils are a better environment for plant growth; under high moisture conditions, clayey soils provide a better environment (Scholes, 1997).

Under the xeric regime, differences in performance of succulent karoo seedlings grown in the two soils were assumed to represent differences in soil texture. Considering that moisture was limiting in this treatment, the significant differences in seedling biomass between the two soil types arose because of the greater water retention in fine-textured soils. Seedlings growing in the fine-textured soil were less able to extract water from the soil than those growing in coarse-textured soil. These seedlings experienced drought stress sooner than those growing in the coarse-textured soil, and thus accumulated less biomass.

The fact that there was no difference between the survival of succulent karoo seedlings grown under different soil textures or moisture regimes may be because the experiment was terminated too soon. Had the experiment continued for a few months more, significant differences in succulent karoo seedling survival may have arisen between the fine-textured and coarse-textured soils. Esler & Philips (1994) noted *Ruschia spinosa* seedlings survived more than 400 days without any water, indicating the seedling hardiness of this widespread karoo species.

6.4.3 The Influence of Nutrient Status on Seedling Performance

The results suggested that the fynbos species used in the experiment were unable to make use of nutrient-rich conditions, supporting the theory that fynbos should not be able to respond to nutrient-rich conditions because it evolved in a nutrient-poor environment (Witkowski & Mitchell, 1989). Some authors even suggested that nutrient-rich conditions may be detrimental to fynbos plants (Chapin, 1980; Chapin *et al.* 1986). The overall condition of fynbos seedlings grown in the nutrient-rich soil was poor, and there was greater mortality of fynbos seedlings in the nutrient-rich soils. A possible explanation for this may be the high conductivity and concentrations of some cations of the shale-derived soil (Table 6.3). Campbell (1986) showed that fynbos elements are negatively associated with a high pH and S-value. However, Euston-Brown (1995) found that seedlings of several fynbos species grew well on nutrient-rich, fine-textured soils, so long as there was sufficient moisture. It is difficult to compare results like this as the species in the experiments were different, as were the soil conditions. No generalisations can thus be made from the results about the ability of fynbos seedlings to cope with nutrient-rich conditions.

A surprising result was that the succulent karoo seedlings accumulated significantly more biomass in nutrient-poor soils than in nutrient-rich soils. As with the fynbos seedlings, there may be so other over-riding soil chemical factors, such as conductivity, that masked the effect of nutrients on seedling growth. This is supported by the fact that some succulent karoo seedlings died in the nutrient-rich soil, even with sufficient moisture. The fact that there was such a great difference in conductivity between the two soils made it difficult to conclude that there was a real nutrient or texture effect on seedling performance.

6.4.4 The Determinants of Seedling Establishment in the Fynbos / Succulent Karoo Boundary

The results from this experiment indicated that fynbos and succulent karoo seedlings responded differently to moisture, texture and nutrient treatments. The fundamental question of what effect moisture, soil texture and nutrient status have on fynbos and succulent karoo seedling performance is central to our understanding of the determinants of the fynbos / succulent karoo boundary. To this end, there are two crucial questions that need answering. 1) What limits the expansion of fynbos seedlings into succulent karoo? 2) What limits the expansion of succulent karoo seedlings into fynbos?

Although I discuss the results in terms of fynbos and succulent karoo, it is untenable to extrapolate results from only two species to an entire biome. These results can thus only provide indications as to biome responses to changes in environmental conditions.

6.4.4.1 What Limits the Expansion of Fynbos into Succulent Karoo?

The most important result from the experiment was that fynbos seedlings could not tolerate xeric conditions, and not one seedling survived the duration of the experiment under the xeric moisture regime. The results suggested that low moisture availability is the factor that prevents fynbos from expanding eastwards down the aridity gradient at MNR (i.e. more arid). Two factors that control moisture availability to plants are toop-climate (altitude and precipitation) and soil texture. Thus fynbos seedlings are unable to establish at low altitude or on the fine-textured soils of the Bokkeveld Group. The results from the previous chapter suggest that critical altitude is 800m, below which fynbos is rarely found. Euston-Brown (1995) found similar patterns in survival of fynbos seedlings transplanted to xeric sites, particularly on fine-textured soils.

Should the climate become more arid with greater uncertainty of rainfall (Tyson, 1993), then I would predict that fynbos seedlings would only be able to establish at higher altitude. In the absence of disturbance, many plant communities are resistant to invasion (Pitelka *et al.* 1997), and fynbos seems to be able resist invasion by succulent karoo when undisturbed. However, drought disturbance may stress and kill adult fynbos plants at lower altitudes and these would become less able to compete with succulent karoo shrubs. Thus, I predict that succulent karoo plants would move into areas where fynbos is no longer able to survive.

6.4.4.2 What Limits the Expansion of Succulent Karoo?

Succulent karoo seedlings were able to grow successfully irrespective of moisture regime or soil type. Fire, which is very destructive in succulent karoo (Huntley, 1984; Forrester, 1988) and prevents succulent karoo species from invading fynbos sites, does not appear to be an important factor at MNR. Several leaf-succulent shrubs were observed throughout the fynbos at MNR (Chapter Two). It is quite clear that succulent karoo is not limited by the environment to the same extent as fynbos is, an observation supported by an experiment where succulent and fynbos seedlings were transplanted into each other's habitat (Euston-Brown, 1995). In the southern Karoo, plants growing in relatively mesic habitats indicated a long history of biotic interactions with animals (Milton, 1990). Thus there must be some other factor that prevents succulent karoo plants from growing in sites that support fynbos.

The second important biome determinant suggested by the results was that fynbos seedlings grew faster (i.e. accumulated more biomass), under almost all soil texture and nutrient conditions, than succulent karoo seedlings, but only when water is not limiting. Obviously, this result is negated when water is limiting, because the fynbos seedlings die. Three problems arose in the interpretation of these results. First, the fynbos species employ a fundamentally different photosynthetic pathway, C_3, to the succulent karoo species, which are presumably CAM (Von Willert *et al.* 1992). This inherently differently photosynthetic physiology may have been reflected in different growth rates that masked the possible effects of the treatments. Second, the high carbon and energy investment needed to build up suitable water storage tissues prohibits succulents from growing quickly (Von Willert *et al.* 1992). Third, both the fynbos species used in the experiment had large seeds compared to the succulent karoo species. The difference in seed reserves may have confounded the results, although there was no way to overcome this. The seedlings, however, would have grown past the stage of using seed reserves by the time the experiment was started.

The faster growth rate of fynbos seedlings was thus construed as a competitive advantage over the slow-growing succulent karoo seedlings. Euston-Brown (1995) found similar patterns in the growth of fynbos and succulent thicket seedlings. Succulent karoo plants may have a conservative growth rate that reflects the harsh environmental in which they typically grow. Few data are available comparing growth rates in fynbos and succulent karoo. Fynbos can accumulate 1000 – 4000 kg ha^{-1} yr^{-1} dry mass (Richardson & Cowling, 1992) while succulent karoo only accumulates 200 – 1000 kg ha^{-1} yr^{-1} dry mass (Rutherford & Westfall, 1986). In comparison to fynbos plants, which are able to grow faster, succulent karoo plants are likely to be inferior competitors under more mesic conditions. This observation may explain why succulent karoo species do not grow in fynbos in areas where fire is not a factor. The succulent karoo plants are not able to compete with the more vigorous fynbos plants. Isolated mesembs were observed throughout the fynbos matrix through MNR. These results suggest that competition, rather than physical factors, limit the expansion of succulent karoo species into fynbos. In this respect, I would predict that wherever conditions are less than optimal for fynbos, succulent karoo species would invade.

6.5 CONCLUSIONS

The fundamental question I attempted answer from this experiment was: what are the roles of moisture, soil texture and nutrients in controlling the establishment of seedlings in the fynbos / succulent karoo ecotone? Four hypotheses generated from this question were tested and the following conclusions drawn.

1) Moisture

Moisture availability directly influenced the growth of both fynbos and succulent karoo seedlings. Water limiting conditions reduced seedling growth. Fynbos seedlings were intolerant of water limiting conditions and died after only a few days. In contrast, succulent karoo seedlings survived through water-limiting conditions for 77 days.

2) Texture

Only the results for the succulent karoo seedlings were used. Seedlings in the coarse-textured soil grew much faster than those in the fine-textured soil. Soil texture influenced succulent karoo seedling growth indirectly, most likely by controlling moisture availability. No conclusion could be drawn about the influence of texture on seedling survival because the experiment was terminated too soon.

3) Nutrients

The results from this section were contradictory and no conclusions were drawn. It appeared that some other soil factor, such as conductivity, masked the effects of nutrients.

4) Seedlings

Under almost all treatments, the fynbos seedling grew faster than the succulent karoo seedlings. Although not conclusive, these results suggested that fynbos is competitively superior to succulent karoo.

In terms of the determinants of fynbos and succulent karoo biomes, no definite conclusions can be drawn on the basis of only four species. However, the results and literature suggest that fynbos is directly limited by the environment, particularly moisture availability (mediated by precipitation and soil texture). In contrast, succulent karoo plants are not directly limited by the environment, but are limited more by interactions (e.g. competition) with other plants.

CHAPTER SEVEN

General Discussion and Summary

The central aim of this thesis was to establish the environmental determinants of the fynbos / succulent karoo boundary. The results from the component studies were interpreted within a theoretical framework of predicted climate change, and its likely effect on biome distribution. The study area, Matjiesrivier Nature Reserve in the Cederberg Mountains, was ideal as it contained strong topo-climatic and edaphic gradients and was apparently free of fire. The study followed a logical progression of observation, induction and deduction. The results from the classification, multivariate direct gradient analyses, modelling and experiment, complemented each other and gave rise to several central conclusions.

The survey of the vegetation in MNR gave rise to seven robust and easily-identifiable communities that had an ecological basis. This part of the study aimed at producing a classification and map of the vegetation of MNR that could be used by the reserve managers. A combination of floristic and growth form characters was used to generate and describe the communities. The apparent ecological significance of the communities implied that there was strong environmental control of the vegetation.

The relationship between the vegetation and environment was explored in two ways. First, canonical correspondence analysis (CCA) was used to extract the main gradients within the vegetation and environmental data. The analyses were performed on both the fynbos and growth form data separately to see if the species and growth forms responded to the same environmental gradients. Second, generalised linear modelling (GLM) was used to predict the occurrence of the communities and the fynbos / succulent karoo boundary. The three explanatory variables used in the modelling were crude, but represented the main environmental gradients apparent at MNR: topo-climatic and edaphic.

CCA of both the floristic and growth form data showed three important trends. First, the locality of sites was an important determinant of species or growth form composition. This suggested that some unmeasured environmental or biotic factor was influencing the vegetation. Second, the majority of the variance in both the floristic and growth form data remained unexplained by the environmental variables used in the CCA. Whether this was a reflection of the 'noise' that seems to be characteristic of fynbos and succulent karoo data, or because some important environmental variable had been missed was unclear. Third, topo-climatic and edaphic variables accounted for most of the explained variance. Topo-climatic variables (altitude and annual rainfall) were more important than the edaphic variables. Within the edaphic variables, soil texture was more important than pH and conductivity. Fynbos species, growth forms and sites were associated with high altitude, high rainfall regions on coarse-textured, sandstone-derived soils that had a low pH and conductivity. Succulent karoo species, growth forms and sites were associated with low altitude, low rainfall regions on sandstone, or with fine-textured, shale-derived soils that had a high pH and conductivity.

Although not the primary objective for using GLM, the major vegetation – environment relationships were confirmed by the models. Three environmental variables were used: altitude as a surrogate for rainfall, geology as a blanket for all soil variables, and landtype. The occurrence of most communities and the fynbos / succulent karoo boundary could be predicted quite accurately on the basis of these variables. Altitude was the primary explanatory variable for separating fynbos and succulent karoo. The cut-off altitude below which fynbos was not found was 800m. Geology was also important, as fynbos was never found on shale. The success of geology as a predictor variable suggested that, for predicting coarsely-defined vegetation units, there is no need for detailed soil analyses. Landtype and geology separated the communities within the fynbos and succulent karoo biomes.

Two main gradients now appeared to be responsible for most of the vegetation pattern at MNR: a topo-climatic gradient and a soil texture gradient, both of which influence soil moisture availability. However, a further biome determinant, soil nutrient status, has been suggested in the literature (see reviews in Chapters Four, Five and Six). Fynbos is associated with nutrient-poor soils and succulent karoo associated with nutrient-rich soils. I designed an experiment where the roles of moisture, texture and nutrients in determining fynbos and succulent karoo seedling establishment could be separated. Although the results cannot be extrapolated to the biome scale, they suggested that the environment, particularly soil moisture availability (mediated primarily by precipitation and secondarily by texture), directly limits fynbos seedlings survival. In contrast, the succulent karoo seedlings were able to grow under all environment conditions, but were unable to grow as fast as the fynbos seedlings. This suggested that succulent karoo would be unable to compete successfully in sites occupied by fynbos.

The classification, ordination, modelling and seedling experiment results confirm the determinants of the fynbos and succulent karoo biomes. Fynbos is prevented from expanding into the succulent karoo by the physical environment. Below 800m the climate becomes too dry (a combination of low rainfall and high temperature) for fynbos seedlings to establish. Similarly the arid nature of shale-derived soils means that fynbos never establishes on shale unless the climate is very mesic. Other soil variables, pH and conductivity, may also prevent fynbos from establishing on shale.

Succulent karoo plants are not limited by the environment to the same extent as fynbos plants. Leaf-succulent and other succulent karoo plants were found throughout fynbos at MNR, suggesting they are able to survive under most environmental conditions at MNR. However, succulent karoo plants only dominate where fynbos plants are unable to grow; at low altitude and on shale. This implies that there is a biotic interaction between fynbos and succulent karoo plants that prevents succulent karoo from establishing where fynbos is able to grow.

Based on these results, the influence of climate change on the fynbos and succulent karoo biomes can be predicted. In the expected scenario for South Africa, of increasing temperatures, decreasing rainfall and greater unpredictability of rainfall events, I would predict that the succulent karoo expands into the fynbos. Fynbos in or near the biome ecotone would be restricted to locally mesic refugia on the top of ridges and on upper south facing slopes. Assuming that climate change will have the greatest effect on fynbos seedlings, the rate of invasion would depend on the turnover of plants in fynbos and the dispersal ability of succulent karoo.

There were problems with some of the research undertaken durings this project. The community, dwarf bedrock shrubland, was underrepresented in the survey and thus also in later chapters. This can be rectified in future if need be. The direct gradient multivariate analyses should have incorporated nutrient status as a variable to further clarify the nutrient-moisture-texture debate. It may also have accounted for the spatial auto-correlation in the analyses. More species were needed for the seedling experiment. It was incorrect to generalise about biome-scale ecology on the basis of two species. It was unfortunate that not enough of the seeds from the other species collected did not germinate.

This initial research raises a number of interesting questions. Future research should be undertaken on competition experiments, to establish the result of interaction between typical fynbos and succulent karoo plants. To clarify the nutrient-moisture debate, nutrient addition and watering experiments could be established under field conditions. It is also important to establish the role, if any, of fire in the fynbos / succulent karoo ecotone. In light of climate change, long-term monitoring plots should be established across the fynbos / succulent karoo boundary. If fenced, such plots could also be used to assist managers to monitor vegetation change in response to grazing and browsing.

REFERENCES & APPENDICES

CAMPBELL, B.M. & COWLING, R.M. 1985. Relationships between vegetation structure and the environment in the Cape, Southern Africa: a review. Annali Di Botanica 43: 245-255.

CAMPBELL, B.M & WERGER, M.J.A 1988. Plant form in the mountains of the Cape, South Africa. *Journal of Ecology* 76: 637-653.

CAUSTON, D.R. 1988. Introduction to Vegetation Analysis. Principles, Practice and Interpretation. Unwin Hyman, London.

CCWR 1996. Computing Centre for Water Research. University of Natal, Pietermaritzburg, KwaZulu-Natal.

CHAPIN, F.S. 1980. The mineral nutrition of plants. *Annual Review of Ecology and Systematics* 11: 233-260.

CHAPIN, F.S., SCHULZE, E-D. & MOONEY, H.A. 1992. Biodiversity and ecosystem processes. *Trends in Evolution and Ecology* 7: 107-108.

CHESSELET, P., MASSMER, M. & SMITH, G.F. 1995. Research priorities in the succulent plant family, Mesembryanthemaceae Fenzl. *South African Journal of Science* 91: 197-209.

COWLING, R.M. 1987. Fire and its role in coexistence and speciation in Gondwana Shrublands. *South African Journal of Science* 83: 106-111.

COWLING, R.M. & CAMPBELL, B.M. 1983. The definition of leaf consistence categories in the fynbos biome and their distribution along an altitudinal gradient in the south eastern Cape. *Journal of South African Botany* 49: 87-101.

COWLING, R.M. & CAMPBELL, B.M. 1985. Relationships between vegetation structure and the environment in the Cape S.A. *Vegetatio* 67.

COWLING, R.M. & HOLMES, P.M. 1992. Flora and Vegetation. In: The Ecology of Fynbos. Nutrients, Fire and Diversity. R.M. Cowling (ed). Oxford University Press, Cape Town.

COWLING, R.M., ESLER, K.J., MIDGLEY, G.F. & HONIG, M.A. 1994. Plant functional diversity, species diversity and climate in arid and semi-arid southern Africa. *Journal of Arid Environments* 27: 141-158.

COWLING, R.M. & HILTON-TAYLOR, H.C. 1997. Phytogeography, Flora and Endemism. In: The Vegetation of Southern Africa. R.M. Cowling, D.M. Richardson & S.M. Pierce (eds). Cambridge University Press, Cambridge.

COWLING, R.M. & HILTON-TAYLOR, H.C. In Press. Plant Biogeography, endemism and diversity. In: The Karoo: Ecological Patterns and Processes. W.R.J. Dean and S.J. Milton (eds). Cambridge University Press, Cambridge.

COWLING, R.M., RICHARDSON, D.M. & MUSTART, P.J. 1997. Fynbos. In: The Vegetation of Southern Africa. R.M. Cowling, D.M. Richardson & S.M. Pierce (eds). Cambridge University Press, Cambridge.

COWLING, R.M., ROUX, P.W. & PIETERSE, A.J.H. 1986. The Karoo Biome: A preliminary Synthesis. Part 1 - Physical Environment. South African National Scientific Programmes Report 124.

COWLING, R.M., RUNDEL, P.W., DESMET, P.G. & ESLER, K.J. In Press. Extraordinarily high regional scale plant diversity in southern African arid lands: subcontinental and global comparisons. *Diversity and Distributions.*

CRAMER & LEMANS. 1993. Assessing impacts of climate change on vegetation using climate classification systems. In: Vegetation Dynamics and Global Change. A.M. Solomon & H.H Shugart (eds). Chapman & Hall, New York.

REFERENCES

ACOCKS, J.P.H. 1988. Veld Types of South Africa. *Memoirs of the Botanical Survey of South Africa* 57.

AUSTIN, M.P. 1991. Vegetation theory in relation to cost-efficient surveys. In: Nature Conservation: Cost Effective Biological Surveys and Data Analysis. C.R. Margules & M.P. Austin (eds). CSIRO.

AUSTIN, M.P., CUNNINGHAM, R.B. & GOOD, R. 1983. Altitudinal distribution of several *Eucalyptus* species in Southern New South Wales. *Australian Journal of Ecology* 8: 169-180.

AUSTIN, M.P., CUNNINGHAM, R.B. & FLEMING, P.M. 1984. New approaches to direct gradient analysis using environmental scalars and statistical curve-fitting procedures. *Vegetatio* 55: 11-27.

AUSTIN, M.P. & HEYLIGERS, P.C. 1991. New approach to vegetation survey design: gradsect sampling. In: Nature Conservation: Cost Effective Biological Surveys and Data Analysis. C.R. Margules & M.P. Austin (eds). CSIRO.

AUSTIN, M.P., NICHOLLS, A.O. & MARGULES, C.R. 1990. Measurement of the realised qualitative niche of plants species: examples of the environmental niches of five *Eucalyptus* species. *Ecological Monographs* 60: 161-177.

BARBOUR, M.G., BURK, J.H. & PITTS, W.D. 1987. Terrestrial Plant Ecology (2nd Edition). Benjamin / Cummings, California.

BOCARD, D., LEGENDRE, P. & DRAPEAU, P. 1992. Partialling out the spatial component of ecological variation. *Ecology* 73: 1045-1055.

BOND, W.J. 1981. Vegetation Gradients in the Southern Cape Mountains. Unpublished M.Sc. Thesis, University of Cape Town.

BOND, W.J., COWLING, R.M. & RICHARDS, M.B. 1992. Competition and Coexistence. In: The Ecology of Fynbos. Nutrients, Fire and Diversity. R.M. Cowling (ed). Oxford University Press, Cape Town.

BOND, P. & GOLDBLATT, P. 1984. Plants of the Cape Flora. A descriptive catalogue. *South African Journal of Botany*, Supplementary Vol. 13.

BRADY, N.C. 1974. The Nature and Properties of Soils. (8th Edition). Macmillan Publ. Co., New York.

BROWN, N.A.C. 1993. Promotion of germination of fynbos seeds by plant-derived smoke. *New Phytologist* 123: 575-583.

BROWN, D.G. 1994. Predicting vegetation types at treeline using topography and biophysical disturbance variables. *Journal of Vegetation Science* 5: 641-656.

CAMPBELL, B.M. 1983. Montane plant environments in the Fynbos Biome. *Bothalia* 14: 283-298.

CAMPBELL, B.M. 1985. A classification of the mountain vegetation of the Fynbos Biome. *Memoirs of the Botanical Survey of South Africa,* no. 50.

CAMPBELL, B.M. 1986. Montane plant communities of the Fynbos Biome. *Vegetatio* 66: 3-16.

CAMPBELL, B.M. 1988. Plant form in the mountains of the Cape, South Africa. *Journal of Ecology* 76: 637-653.

CRAWLEY, M.J. 1993. Methods in Ecology: GLIM for Ecologists. Blackwell Scientific Publ.

DAVIS, S.D. 1991. Lack of niche differentiation in adult shrubs implicates the importance of the regeneration niche. *Trends in Ecology and Evolution* 6: 272-274.

DEACON, H.J., JURY, M.R. & ELLIS, F. 1992. Selective Regime and Time. In: The Ecology of Fynbos. Nutrients, Fire and Diversity. R.M. Cowling (ed). Oxford University Press, Cape Town.

DRAKE, J.A. 1990. Communities as assembled structures: do rules govern pattern? *Trends in Ecology and Evolution* 5: 159-164.

DRAKE, J.A. 1991. Community-assembly mechanics and the structure of experimental species ensemble. *American Naturalist* 137: 1-26

ELLERY, W.N., SCHOLES, R.J. & MENTIS, M.T. 1991. An initial approach to predicting the sensitivity of the South African grassland biome to climate change. *South African Journal of Science* 89: 449-503.

ELLIS, F. & LAMBRECHTS, J.J.N. 1986. Soils. In: R.M. Cowling, P.W. Roux & A.J.H. Pieterse (eds) The Karoo Biome: a preliminary synthesis. Part 1 – the physical environment. South African national Scientific Programmes Report no. 124. CSIR, Pretoria.

ESLER, K.J. 1993. Vegetation patterns and plant reproductive processes in the Succulent Karoo. Unpublished Ph.D. thesis, Department of Botany, University of Cape Town.

ESLER, K.J., COWLING, R.M. & IVEY, P. 1992. Seed biology of three species of Mesembryanthema in the southern succulent Karoo. *South African Journal of Botany* 58: 343-348.

ESLER, K.J. & COWLING, R.M. 1993. Edaphic factors and competition as determinants of pattern in South African karoo vegetation. *South African Journal of Botany* 59: 287-295.

ESLER, K.J. & PHILIPS, N. 1994. Experimental effects of water stress on semi-arid Karoo seedlings: implications for field seedling survivorship. *Journal of Arid Environments* 26: 325-337.

EUSTON-BROWN, D. 1995. Environmental and dynamic determinants of vegetation distribution in the Kouga and Baviaanskloof Mountains, Eastern Cape. Unpublished M.Sc. Thesis, University of Cape Town.

FONTEYN, P.J. & MAHALL, B.E. 1981. An experimental analysis of structure in a desert plant community. *Journal of Ecology* 69: 883-898.

FORRESTER, J. 1988. Fire in the K.N.G floral reserve. *Veld & Flora* 74: 5.

FOWLER, N. 1986. The role of competition in plant communities in arid and semiarid regions. *Annual Review of Ecology and Systematics* 17: 89-110.

FRANKLIN, J. Predictive vegetation mapping: geographic modelling of biospatial patterns in relation to environmental gradients. *Progress in Physical Geography* 19: 474-499.

FULLERTON, R. 1997. Community Ecology of Cliff-top Coastal Heathlands in Botany Bay National Park, Sydney. Unpublished Ph.D. Thesis. Department of Environmental Biology and Horticulture, University of Technology, Sydney.

GASTON, K.J. 1995. Rarity. Chapman & Hall, London.

GENSTAT 5 COMMITTEE. 1987. GENSTAT 5 Reference Manual. Clarendon Press, Oxford.

GILLISON, A.N. & BREWER, K.R.W. 1985. The use of gradient directed transects or gradsects in natural resource surveys. *Journal of Environmental Management* 20: 103-127.

GOODCHILD, M.F. 1994. Integrating GIS and remote sensing for vegetation and modelling: methodological issues. *Journal of Vegetation Science* 5: 615-626.

HARPER, J.L. 1977. The Population Biology of Plants. Academic Press, New York.

HILL, M.O. 1973. Reciprocal averaging: an eigenvector method of ordination. *Journal of Ecology* 61: 237-249.

HILL, M.O. 1979. TWINSPAN - A FORTRAN Program for Arranging Multivariate Data in an Ordered Two-way Yable by Classification of the Individuals and Attributes. Microcomputer Power, Ithaca, New York.

HILTON-TAYLOR, C. 1987.Phytogeography and origins of the Karoo flora. In: The Karoo Biome: a Preliminary Synthesis. Part 2 - Vegetation and History. R.M. Cowling & P.W. Roux (eds). South African National Scientific Programmes Report 142. CSIR, Pretoria.

HOFFMAN, T. 1996. Lowland Succulent Karoo. In: Vegetation of South Africa, Lesotho and Swaziland. A.B. Low & A.G. Rebelo (eds). Department of Environmental Affairs and Tourism, Pretoria.

HOLLAND, P.G. & STEYN, D.G. 1975. Vegetation responses to latitudinal variations in slope angle and aspect. *Journal of Biogeography* 2: 179-183.

HOLMES, PETER. Personal communications. Department of Environmental and Geographical Science, University of Cape Town.

HUNTLEY, B.J. 1984. Characteristics of South African Biomes. In: P. Booysen & N.M Tainton (eds) Ecological Effects of Fire in South African Ecosystems. Springer-Verlag, Berlin.

IHLENFELDT, H.D. 1994. Diversification in an arid world: The Mesembryanthemaceae. *Annual Review of Ecology and Systematics* 25: 521-546.

JURY, M.R. 1993. A preliminary note on the rainfall and vegetation trends in the south-western Cape: 1985-1988. *South African Journal of Botany* 59: 265-269.

KUTIEL, P., LAVEE, H. & SHOSHANY, M. 1995. Influence of a climatic gradient upon vegetation dynamics along a Mediterranean-arid transect. *Journal of Biogeography* 22: 1065-1071.

KNIGHT, R.S., REBELO, A.G. & SIEGFRIED, W.R. 1989. Plant assemblages on Mima-like earth mounds in the Clanwilliam District, South Africa. *South African Journal of Botany* 55: 465-472.

LANE, S. 1978. An ecological study of the Tanqua / Doorn Karoo based on a structural – physiognomic survey. *South African Archaeological Bulletin* 33: 128-133.

LEGENDRE, P. 1990. Quantitative methods and biogeographic analysis. In: Evolutionary Biogeography of the Marine Algae of the North Atlantic. D.J. Garbary & G.R. South (eds). NATO ASI Series. Springer-Verlag, Berlin.

LEGENDRE, P. 1993. Spatial autocorrelation: trouble or new paradigm? *Ecology* 74: 1659-1673

LEISHMAN, M.R., HUGHES, L., FRENCH, K., ARMSTRONG, D. & WESTOBY, M. 1992. Seed and seedling biology in relation to modelling vegetation dynamics under global climate change. *Australian Journal of Botany* 40: 599-613.

LE MAITRE, D.C. & MIDGLEY, J.J. 1992. Plant Reproductive Ecology. In: Ecology of Fynbos: Nutrients, Fire & Diversity. R.M. Cowling (Ed.). Oxford University Press, Cape Town.

LEVYNS, M.R. 1950. The relations of the Cape and Karoo floras near Ladismith, Cape. *Transactions of the Royal Society of South Africa.* 37: 235-246.

LINDSEY, J.K. 1989. The Analysis of Categorical Data using GLIM. Springer-Verlag, New York.

LOW, A.B. & REBELO, A.G. 1996. Vegetation of South Africa, Lesotho & Swaziland. Dept. Environmental Affairs & Tourism, Pretoria.

MACKEY, B.G. 1993. Predicting the potential distribution of rain-forest structural characteristics. *Journal of Vegetation Science* 4: 43-54.

MACVICAR, C.N., DE VILLIERS, J.M. & Soil Classification Working Group. 1991. Soil Classification. A taxonomic System for South Africa. Memoirs of the Agricultural Natural Resources of South Africa No. 15. Dept. Agricultural Development, Pretoria.

MANDERS, P.T. 1990. Fire and other variables as determinants of forest/fynbos boundaries in the Cape Province. *Journal of Vegetation Science* 1: 483-490.

MARGULES, C.R & AUSTIN, M.P. (Editors). 1991. Nature Conservation: Cost Effective Biological Surveys and Data Analysis. CSIRO, Australia.

MARGULES, C.R., NICHOLLS, A.O. & AUSTIN, M.P.1987. Diversity of *Eucalyptus* species predicted by a multi-variable environmental gradient. *Oecologia* 71: 229-232.

MARSHAL, T.J. & HOLMES, J.W. 1979. Soil Physics. Cambridge University Press, Cambridge.

McCULLAGH, P. & NELDER, J.A. 1989. Generalized Linear Models (2nd Edition). Chapman and Hall, London.

McDONALD, D.J., JURITZ, J.M., COWLING, R.M. & KNOTTENBELT, W.J. 1995. Modelling the biological aspects of local endemism in South African fynbos. *Plant Systematics and Evolution* 195: 137-147.

MILLER, P.C. 1982. Some bioclimatic and pedalogic influences of the vegetation in the mediterranean - type region of South Africa. *Ecologia Mediterranea* 8: 141-156.

MILLER, J. 1985. Plant water relations along a rainfall gradient between the succulent karoo and mesic fynbos in the Cederberg Mountains near Clanwilliam, South Africa. Unpublished M.Sc. Thesis, University of Cape Town.

MILTON, S.J. 1978. Plant communities of the Andriesgrond, Clanwilliam District. Unpublished notes, Habitat Working Group, Bolus Herbarium, University of Cape Town.

MILTON, S.J. 1990. Life styles of plants in four habitats in an arid Karoo shrubland. *South African Journal of Ecology* 1: 63-72.

MILTON, S.J. & DEAN, W.R.J. 1996. Karoo Veld: Ecology and Management. Agricultural Research Council, Range and Forage Institute, Lynn East, South Africa.

MILTON, S.J., YEATON, R.I., DEAN, W.R.J. & VLOK, J.H.J. 1997. Succulent Karoo. In: Vegetation of Southern Africa. R.M. Cowling, D.M. Richardson & S.M. Pierce (eds). Cambridge University Press, Cambridge.

MOONEY, H.A., HARRISON, A.T. & MORRROW, P.A. (1975). Environmental limitations of photosynthesis on a California evergreen shrub. *Oecologia* 19: 293-301.

MOORE, & PICKER, 1991. Heuweltjies (earth mounds) in the Clanwilliam district Cape Province South Africa - 4000-year-old termite nests. *Oecologia* 86: 424-430.

MUSTART, P.J. & COWLING, R.M. 1993a. The role of regeneration stages in the distribution of edaphically restricted fynbos Proteaceae. *Ecology* 74: 1490-1499.

MUSTART, P.J. & COWLING, R.M. 1993b. Effects of soil and seed characteristics on seed germination and their possible roles in determining field emergence patterns on four Agulhas Plain (South Africa) Proteaceae. *Canadian Journal of Botany* 71: 1363-1368.

NAVARRETE, S.A. & MENGE, B.A. 1996. Title. *Ecological Monographs* 66: 409-429.

NICHOLLS, A.O. 1989. How to make biological surveys go further with generalised linear models. *Biological Conservation* 50: 51-75.

NICHOLLS, A.O. 1991. Examples of the use of Generalised Linear Models in Analysis of Survey Data for Conservation Evaluation. In: Nature Conservation: Cost Effective Biological Surveys and Data Analysis. C.R. Margules & M.P. Austin (Eds). CSIRO, Australia.

NIELSON, R.P. 1993. Transient ecotone response to climatic change: some conceptual and modelling approaches. *Ecological Applications* 3: 385-395.

ØKLAND, R.H. & EILERTSEN, O. 1994. Canonical correspondence analysis with variation partitioning: some comments and an application. *Journal of Vegetation Science* 5: 117-126.

OWEN-SMITH, N. & DANCKWERTS, J.E. 1997. Herbivory. In: Vegetation of Southern Africa. R.M. Cowling, D.M. Richardson & S.M. Pierce (eds). Cambridge University Press, Cambridge.

PALMER, M.W. 1993. Putting things in even better order: the advantages of canonical correspondence analysis. *Ecology* 74: 2215-2230.

PITELKA, L.F. and the Plant Migration Workshop Group. 1997. Plant migration and climate change. *American Scientist* 85: 464-473.

PRESSY, R.L. & BEDWARD, M. 1991. Mapping the environment at different scales: benefits and costs for nature conservation. In: Nature Conservation: cost effective biological surveys and data analysis. C.R. Margules & M.P. Austin (eds). CSIRO, Australia.

PRIVETT, S. 1998. Unpublished M.Sc. Thesis, Department of Botany, University of Cape Town.

REBELO, A.G. 1996a. Central Mountain Renosterveld. In: Vegetation of South Africa, Lesotho and Swaziland. A.B. Low & A.G. Rebelo (eds). Department of Environmental Affairs and Tourism, Pretoria.

REBELO, A.G. 1996b. Mountain Fynbos. In: Vegetation of South Africa, Lesotho and Swaziland. A.B. Low & A.G. Rebelo (eds). Department of Environmental Affairs and Tourism, Pretoria.

RICHARDS, M.B. 1993. Soil Factors and Competition as Determinants of Fynbos Plant Species Distributions in the South-Western Cape, South Africa. Unpublished Ph.D. Thesis, Department of Botany, University of Cape Town.

RICHARDS, M.B., STOCK, W.D. & COWLING, R.M. 1995. Water relations of seedlings and adults of two fynbos *Protea* species in relation to their distribution patterns. *Functional Ecology* 9: 575-583.

RICHARDSON, D.M. & COWLING, R.M. 1992. Why is mountain fynbos invasible and which species invade? In: Fire in South African Mountain Fynbos. B.W. Van Wilgen, D.M. Richardson, F.J. Kruger & H.J. Van Hensbergen (eds) Springer-Verlag, Berlin.

ROWELL, D.L. 1994. Soil Science: Methods and Applications. J.Wiley, Essex.

RUTHERFORD, M.C. & WESTFALL, R.H. (1986). Biomes of Southern Africa – an Objective Characterization. *Memoirs of the Botanical Survey of South Africa* 54: 1-98.

SALISBURY, F.B. & ROSS, C.W. 1992. Plant Physiology, 4th Edn. Wadsworth Publishing Company, California.

SCHOLES, R. 1997. In: Vegetation of Southern Africa. R.M. Cowling, D.M. Richardson & S.M. Pierce (eds). Cambridge University Press, Cambridge.

SHULZE, R.E. 1975. Incoming radiation fluxes on sloping terrain: a general model for use in South Africa. *Agrochemophysika* 7: 55-61.

SIEGEL, S. & CASTELLAN, N.J. 1988. Nonparametric Statistics for the Behavioural Sciences. McGraw-Hill, New York.

SIMMONS, M. 1996. Unpublished M.Sc. Thesis, Department of Botany, University of Cape Town.

SMITHEMAN, J. & PERRY, P. 1990. A Vegetation survey of the Karoo National Botanic Garden, Worcester. *South African Journal of Botany* 56: 525-541.

SNIJMAN, D. & PERRY, P. 1987. A floristic analysis of the Nieuwoudtville Wild Flower Reserve, north-western Cape. *South African Journal of Botany* 53: 445-454.

SPECHT, R.L. & MOLL, E.J. 1983. Heathlands and sclerophyllous shrublands – an overview. In: Mediterranean-Type Ecosystems. The role of Nutrients. F.J. Kruger, D.T. Mitchell & J.U.M. Jarvis (eds). Springer-Verlag, Berlin.

SOLBRIG, O.T. 1992. Biodiversity, global change and scientific integrity. *Journal of Biogeography* 19: 1-2.

STOCK, W.D., VAN DER HEYDEN, F. & LEWIS, O.A.M. 1992. Plant structure and function. In: The Ecology of Fynbos: Nutrients, Fire and Diversity. R.M. Cowling (ed.). Oxford University Press, Cape Town.

STOCK, W.D., ALLSOPP, N., VAN DER HEYDEN, & WITKOWSKI, E.T.F. 1997. Plant form and function. In: Vegetation of Southern Africa. R.M. Cowling, D.M. Richardson & S.M. Pierce (eds). Cambridge University Press, Cambridge.

TALJAARD, M.S. 1949. A Glimpse of South Africa. University of Stellenbosch Publ. P 48-49.

TAYLOR, H.C. 1978. Capensis. In: Biogeography and Ecology of Southern Africa. M.J.A. Werger (ed). Junk, The Hague.

TAYLOR, H.C. 1996. Cederberg Vegetation and Flora. *Strelitzia* 3. National Botanical Institute, Pretoria.

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

TER BRAAK, C.J.F. 1987. The analysis of vegetation-environment relationships by canonical correspondence analysis. *Vegetatio* 69: 69-77.

TER BRAAK, C.J.F. 1991. Update notes: CANOCO version 3.12. Agriculture Mathematics Group, Wageningen, The Netherlands.

TREXLER, J.C. & TRAVIS, J.1993. Nontraditional Regression Analyses. *Ecology* 74: 1629-1637.

TYSON, P.D. 1993. Recent developments in the modelling of the future climate of South Africa. *South African Journal of Science* 89: 494-505.

VALVERDE, P.L. & MONTANA, C. 1996. A rapid methodology for vegetation survey in Mexican arid lands. *Journal of Arid Environments* 34: 89-100.

VAN DER MERWE, J.H. & BARNARD, W.S. 1996. Die Matjiesrivierlandgoed, Distrik Clanwilliam. Internal Project, Department van Geografie en Omgewingstudie, Universiteit van Stellenbosch.

VAN DE RIJT, C.W.C.J., HAZELHOFF, L. & BLOM, C.W.P.M. 1996. Vegetation zonation in a former tidal area: a vegetation-type response model based on DCA and logistic regression using GIS. *Journal of Vegetation Science* 7: 505-518.

VAN GROUNEWOUD, H. 1992. The robustness of Correspondence, Detrended Correspondence and TWINSPAN analysis. *Journal of Vegetation Science* 5: 239-246.

VAN WILGEN, B.W., BOND, W.J. & RICHARDSON, D.M. 1992. Ecosystem management. In: Ecology of Fynbos: Nutrients, Fire & Diversity. R.M. Cowling (Ed.). Oxford University Press, Cape Town.

VISSER, J.N.J. 1986. Geology. In: The Karoo Biome: a Preliminary Synthesis. Cowling, R.M. & Roux, P.W. (eds). South African Scientific Programmes Report 124, Pretoria.

VON WILLERT, D.J., BRINCKMANN, E., SCHEITHER, B. & ELLER, B.M. 1985. Availability of water controls Crassulacean acid metabolism in succulents in the Richtersveld (Namib desert, South Africa). *Planta* 164: 44-55.

VON WILLERT, D.J., ELLER, B.M., WERGER, M.J.A., BRINCKMANN, E. & IHLENFELDT, H-D. 1992. Life Strategies of Succulents in Deserts. Cambridge University Press, Cambridge.

VON WILLERT, D.J., HERPPICH, M. & MILLER, J.M. 1989. Photosynthetic characteristics and leaf water relations of mountain fynbos vegetation in the Cedarberg area (South Africa). *South African Journal of Botany* 55: 288-298.

WERGER, M.J.A. 1972. Species area relationship and plot size: with some examples from South African vegetation. *Bothalia* 10: 583-594.

WERGER, M.J.A. & SPRANGERS, J.T.C. 1982. A comparison of floristic and structural classification of vegetation. *Vegetatio* 50: 175-183.

WERGER, M.J.A., KRUGER, F.J. & TAYLOR, H.C. 1972. A phytosociological study of the Cape fynbos and other vegetation at Jonkershoek, Stellenbosch. *Bothalia* 10: 599-614.

WIEGAND, T., MILTON, S.J. & WISSEL, C. 1994. A simulation model for a shrub-ecosystem in the semi-arid karoo, South Africa. *Ecology* 76: 2205-2221.

WIEGAND, T. & MILTON, S.J. 1996. Vegetation change in semiarid communities. *Vegetatio* 125: 169-183.

WITKOWSKI, E.T.F. & MITCHELL, D.T. 1989. The effects of nutrient additions on above-ground phytomass and its phosphorus and nitrogen contents of sand-plain lowland fynbos. *South African Journal of Botany* 55: 243-249.

YEATON, R.I. & ESLER, K.J. 1990. The dynamics of a succulent Karoo vegetation: a study of species associations and recruitment. *Vegetatio* 88: 103-113.

Appendix A. The aerial photographs that cover MNR (Surveyor General, Mowbray, Cape Town)

Internal Boundary	Job	Strip	Photo	Date
Perdewater	976	2	792	1994
Riffels	976	3	340	1994
Wildehondskloof	976	2	792	1994
Vyfhoek	892	18	6452	1986
Truitjieskraal	892	17	6420	1986
Moordhoek	892	17	6422	1986
Matjiesrivier	892	18	6453B	1986
Vaalvlei	892	19	6486	1986

Appendix B. The Domin Scale used to combine cover and abundance data

Domin	Cover (%)	Abundance
1	< 1	1
2	< 1	2
3	< 1	> 2
4	1 - 4	> 2
5	5 - 9	> 2
6	10 - 19	> 2
7	20 - 29	> 2
8	30 - 39	> 2
9	40 - 50	> 2
10	> 50	> 2

Appendix C: Measuring the Soil Texture Fractions

The proportions of clay, silt and sand were determined using a settling method. 50g of air-dried and sieved (2mm mesh) soil was shaken vigorously in a glass jar with 50ml CALGON solution (120g sodium hexametaphosphate and 27.3g sodium carbonate dissolved in 3000ml of distilled water) and approximately 150ml of tap water, then left to stand. After 20 minutes the partially dispersed sample was transferred to a 1000ml glass cylinder and the suspension was topped up to the 1000ml level and left to stand. After approximately 15 hours the dispersed soil was re-suspended by upending the cylinder vigorously for 30 seconds and then left to stand again. The time when the cylinder was steadied after upending was noted. The amount of silt and clay left suspended was measured using a hydrometer after exactly seven minutes (the time estimated for the sand fraction to settle out). Similarly, the amount of clay left in the suspension was measured after 7 hours (the time estimated for the silt fraction to settle out). A blank reading for the hydrometer in a separate cylinder with 50ml CALGON and 950ml water was subtracted from the clay and silt readings. The percentages of clay and silt in the soil sample were estimated by multiplying the result (reading - blank) by two. The time periods between shaking and measuring were rounded off to seven minutes and seven hours for logistic reasons as the fraction measurements were only to be used as a comparison between samples and not with external data.

Measuring the Sand Fractions

The silt and clay fractions were washed from the cylinder by shaking the soil in tap water and leaving to stand for 7 minutes before decanting the supernatent suspension. This was repeated until the supernatent was clear (*i.e.* all the silt and clay had been washed out). The remaining sand was transferred to a small jar and dried overnight in an oven at 110°C. The dried sand was weighed on an electronic scale and sieved through a tower of meshes (0.5mm and 0.25mm) on an electronic shaker for 5 minutes. The separated sand fractions graded into three categories (course = > 0.5mm, medium = 0.5mm - 0.25mm, fine < 0.25mm) and weighed using an electronic balance. The categories were expressed as a percentage of the total mass before sieving.

Appendix D: The Species Listed During the Thesis.

Nomenclature and authors from Bond & Goldblatt (1984)

Genus or species	Family
Agathosma spp.	Rutaceae
Aspalathus spp.	Rutaceae
Cannomois spp.	Restionaceae
Chrysocoma tenuifolia *(Bergius)*	Asterceae
Conophytum spp.	Mesembryanthemaceae
Crassula spp.	Crassulaceae
Diosma acmaeophylla *(Eckl. & Zeyh.)*	Rutaceae
Dodonaea angustifolia *(L.f.)*	Sapindaceae
Dolichothrix ericoides *(Lam. Hilliard & Burtt)*	Asteraceae
Ehrharta spp.	Poaceae
Elegia spp.	Restionaceae
Elytropappus spp.	Asteraceae
Elytropappus rhinocerotis *(L.f.)*	Asteraceae
Erica maximiliani *(Guthrie)*	Ericaceae
Eriocephalus spp.	Asteraceae
Eriocephalus africanus *(L.)*	Asteraceae
Eriocephalus ericoides *(L.f.)*	Asteraceae
Euphorbia decussata (E.May. Ex. Bois.)	Euphorbiaceae
Euphorbia hamata *(Haw)*	Euphorbiaceae
Euphorbia mauritanica *(L.)*	Euphorbiaceae
Euphorbia spp.	Euphorbiaceae
Euryops othonnoides *(DC.)*	Asteraceae
Euryops wageneri *(Compton)*	Asteraceae
Felicia scabrida *(DC.)*	Asteraceae
Ficinia dunensis *(Levyns)*	Cyperaceae
Galenia africana *(L.)*	Aizoaceae
Gnidia deserticola *(Gilg)*	Thymeliaceae
Helichrysum spp.	Asteraceae
Hoplophyllum spinosum (DC.)	Asteraceae
Hypodiscus spp.	Restionaceae
Ischyrolepis unispicata *(Linder)*	Restionaceae
Lampranthus spp.	Mesembryanthemaceae
Leucadendron bruiniodes *(R.Br.)*	Proteaceae
Leucadendron pubescens *(R.Br)*	Proteaceae
Maytenus oleoides *(Lam.)*	Celastraceae
Othonna spp.	Asteraceae
Pentaschistis spp.	Poaceae
Phylica buxifolia *(L.)*	Rhamnaceae
Phylica odorata *(Schltr.)*	Rhamnaceae
Protea glabra *(Thunb)*	Proteaceae
Pteronia spp.	Asteraceae
Pteronia divaricata *(P.J. Bergius)*	Asteraceae

Pteronia incana *(Burm.)*	Asteraceae
Restio spp.	Restionaceae
Rhus undulata *(Jacq.)*	Anacardiaceae
Ruschia spp.	Mesembryanthemaceae
Stipagrostis namaquensis (Nees)	Poaceae
Stoebe fusca *(L.)*	Asteraceae
Tetraria spp.	Cyperaceae
Thamnochortus spp.	Restionanceae
Tylecodon paniculatus *(L.)*	Crassulaceae
Tylecodon spp.	Crassulaceae
Tylecodon wallichii *(Harvey)*	Crassulaceae
Willdenowia incurvata *(Thunb.)*	Restionanceae
Wildenowia spp.	Restionanceae
Zygophyllum retrofractum *(Thunb.)*	Zygophyllaceae