

ECOLOGICAL ASPECTS OF THE SUBSTRATE AND WATER RELATIONS
OF DECIDUOUS AND EVERGREEN PLANT FORMS
IN THE WESTERN KAROO

A thesis presented for the degree of
Master of Science
at the University of Cape Town

by
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DECLARATION

This dissertation has not been submitted for degree purposes at any other university.

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PREAMBLE

The work described in this thesis concerns two main aspects of the physiological ecology of perennial shrubs in a semi-arid mediterranean region. In accordance with the practice encouraged at the University of Cape Town, these aspects have been presented in the form of two papers (Parts three and four) which will be submitted for publication. This ensures that research results will ultimately be available to a wider readership. However, because of some interlinking between these aspects, there is a limited amount of unavoidable repetition within the thesis.

Part one serves as an introduction, providing a broad background to the research, and outlining the main aim and objectives of the project. Part two, the literature review, is not intended to be an exhaustive overview, but rather a selective discussion about the theoretical bases of the two main areas of research undertaken in the project. Parts three and four stand independently, and represent the main body of research reported on in the thesis. Part five draws together the conclusions reached in parts three and four, and provides a synthesis.

ABSTRACT

The principle aim of this work was to ascertain the relative importance of water and nutrient supply in determining the success of deciduous and evergreen plant forms on two main substrate types in the Worcester-Robertson valley, situated in the Succulent Karoo Biome. The substrate types selected for study represent soils of zoogenic soil mounds (locally termed "heuweltjies", and often referred to in the literature as "Mima-like" mounds), and soils immediately adjacent to and surrounding the soil mounds. The distribution of deciduous and evergreen plant forms in the Worcester-Robertson valley was analysed relative to the selected substrate types. Foliar elemental concentrations of four selected species growing on both substrates at five separate sites within the valley were determined. Also, the patterns of seasonal water stress exhibited by three deciduous and five evergreen non-succulent woody perennials growing in both substrates were investigated on high radiation (equator-facing) and low radiation (pole-facing) slopes at one intensive study site, the Worcester Veld Reserve.

Plant form distribution data were interpreted in relation to the water infiltration, pH and nutrient characteristics of each substrate, and in the light of substrate-related differences in the foliar elemental concentrations of the selected species.

Plant water relations patterns were related to seasonal changes in soil water content of the two substrate types on high and low

radiation slopes, and were interpreted in the light of the water retention characteristics of the soil types and inferred rooting characteristics of the selected species.

Deciduous plant growth forms were found to occur predominantly on-mound, and evergreen forms off-mound. On-mound soils were neutral to alkaline, typically Ca-rich, and had higher macro- and micro-elemental concentrations than acid off-mound soils. Only higher soil N concentrations on-mound were significantly reflected in the foliar analyses of all species investigated. On-mound soils had higher water contents in the 0-150mm depth zone in autumn, winter and spring seasons than off-mound soils, possibly because of greater water infiltration on-mound. However, it is likely that soil water potential in the two substrate types was similar during these periods, because of their different water retention characteristics. This was reflected in the similar base water potentials of species growing in each substrate type, irrespective of slope aspect, during periods of high soil water content.

Deciduous and evergreen plant forms could not be differentiated on the basis of their seasonal water potential characteristics. Rather, observed seasonal trends in water potential suggest that plant water acquisition, as determined by rooting characteristics, was primarily responsible for the extent of seasonal water stress experienced by the selected species, regardless of leaf habit.

It is suggested that the more favourable N and possibly P status and an inferred greater, pH-dependent, availability of nitrate on-mound is conducive to the success of deciduous growth forms, while the generally lower nutrient status off-mound favours the evergreen habit. While higher soil water content on-mound may facilitate soil microbial activity and promote nutrient turnover on-mound, it is unlikely that soil water per se determines the success and distribution of deciduous and evergreen forms on the two substrate types.

PART 1

INTRODUCTION

OVERVIEW

The central and western regions of southern Africa, locally known as the Karoo, are characterised by shrubland vegetation which is exposed to severe climatic and anthropogenic stresses. These regions (Figure 1.1) receive a mean annual precipitation of 400mm or less (Schulze & McGee 1978, Vorster & Roux 1983), and have been subjected to inappropriate management practices by the small stock farming industry (Roux & Theron 1987). Poor rangeland management practices are thought to have resulted in the continuing desertification of karoo shrublands (Roux & Vorster 1983; Roux & Theron 1987), and their spread into adjacent, potentially more productive rangeland (Acocks 1953; Moll & Gubb 1989). The rationale for current karoo management systems has been reviewed and criticised by Hoffman (1988).

The phytogeographical Karoo-Namib region has the most extensive continuous area of shrubland in southern Africa (Moll & Gubb 1989). At a coarse scale it appears that this region can be divided into distinct biomes (Rutherford & Westfall 1986) on the basis of plant life form dominance, and a correlated climatic index: the summer aridity index (SAI). Thus the central and northern parts have been termed the Nama-Karoo Biome, whose vegetation is dominated by both chamaephyte and hemicryptophyte life forms, and the western and southern parts have been termed the Succulent Karoo Biome, dominated mainly by chamaephyte life forms (Figure 1.2). The two biomes differ in terms of range of SAI (3,6 to 5,1 for Nama-Karoo; 4,8 to 7,5 for Succulent Karoo) and in terms of rainfall seasonality, with the Nama-Karoo

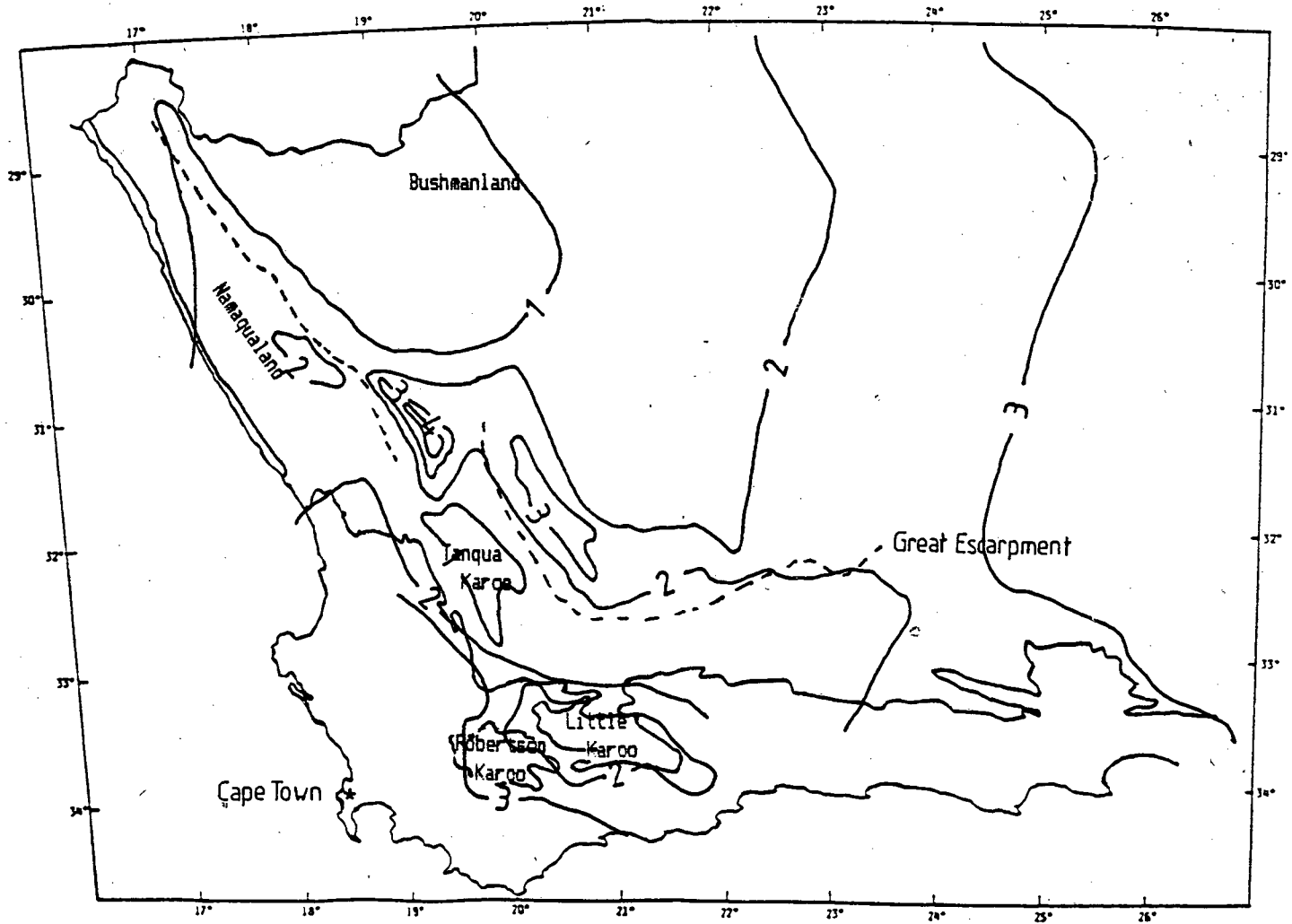


Figure 1.1 Karoo regions in the western and southwestern Cape (after Vorster & Roux 1983) - the overlay gives isohyets of mean annual rainfall (x100mm)

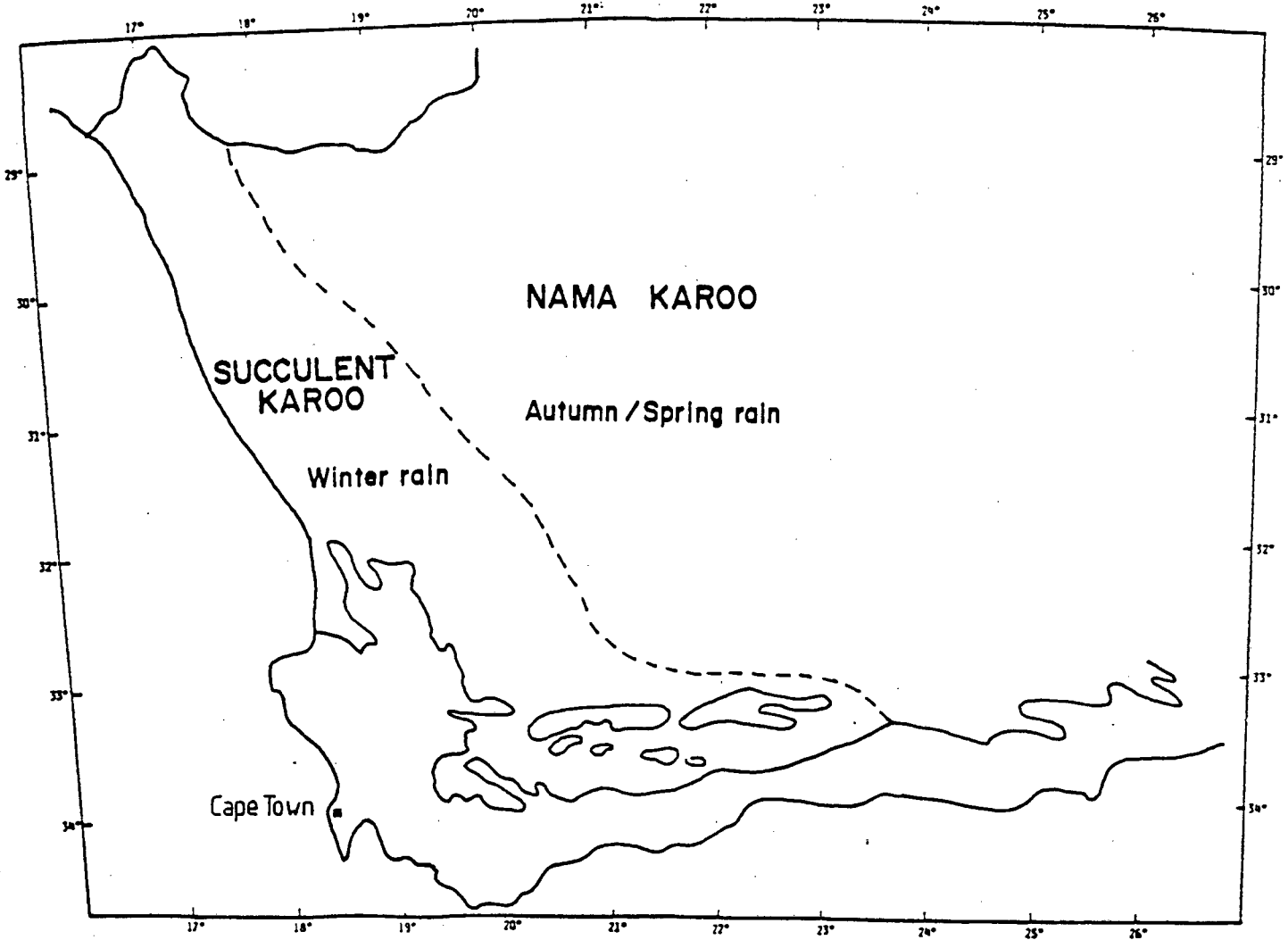


Figure 1.2 Karoo biomes in relation to broad climatic regions
(after Hoffman and Cowling 1987)

experiencing summer rainfall and most of the Succulent Karoo winter rainfall (Rutherford & Westfall 1986).

The Karoo-Namib has been recognised as a distinct chorological region within the African part of the Palearctic Kingdom since Monod's (1957) review of African chorology (Hilton-Taylor 1987). More recent treatments (Werger 1978, White 1983) have supported this view. However, there is some controversy concerning phytochorological subdivisions within the Karoo-Namib region, and its phytogeographic status in relation to the adjacent Cape Floristic Kingdom (Bayer 1984). At the biome level it appears that the Succulent Karoo and Fynbos Biomes are more closely related, in terms of Sorensen's coefficients of similarity, percentage of shared taxa and centres of diversity of large taxa, than the two karoo biomes (Gibbs Russell 1987), although the data set for this analysis is not complete. This preliminary finding supports Bayer's (1984) argument for the recognition of a Winter Rainfall Biome, which emphasises the importance of a mediterranean-type winter rainfall regime in determining vegetation structure and function in the south and southwestern Cape, and western Karoo. The decisive phytogeographic analysis needed to resolve this question is limited directly by poor floristic sampling in many karoo areas (Gibbs Russell et al. 1984) and the incomplete taxonomic treatment of several plant families which are characteristic of the Karoo-Namib region (Hilton-Taylor 1987), and indirectly by the high species diversity of the Succulent Karoo Biome, which, among succulent species, is unparalleled elsewhere in the world (Hilton-Taylor 1989).

The Succulent Karoo Biome has incorporated within it several of the western karroid veld types described by Acocks (1953, Figure 3). Boucher and Moll (1981) and Moll et al. (1984) have suggested that western karroid areas be regarded as mediterranean shrublands. However, although the western parts of the Karoo region receive predominantly winter rain, gradients of increasing aridity to the north and east and an increasing summer rainfall component towards the east may disqualify these areas as truly mediterranean (sensu Aschmann 1983).

Rutherford and Westfall (1986) remark that the Succulent Karoo Biome can be divided naturally into two major divisions, the border lying between 115mm and 125mm isohyets. The vegetation of more arid of the two regions has a high proportion of succulent elements, with low canopy height and vegetation cover, while the more mesic has a smaller proportion of succulent elements. This more mesic zone corresponds to the geographical term 'western Karoo' used in this thesis. The vegetation can be regarded as a mediterranean-type shrubland, with a prominent succulent component, but having a high proportion of non-succulent shrubs and a notable absence of hemicryptophytic graminoids.

RATIONALE

A major research direction in mediterranean-type regions has been the identification of relationships between plant structure and function. This has been a necessary part of interpreting convergence in plant form among species of different mediterranean regions worldwide, and has also improved the

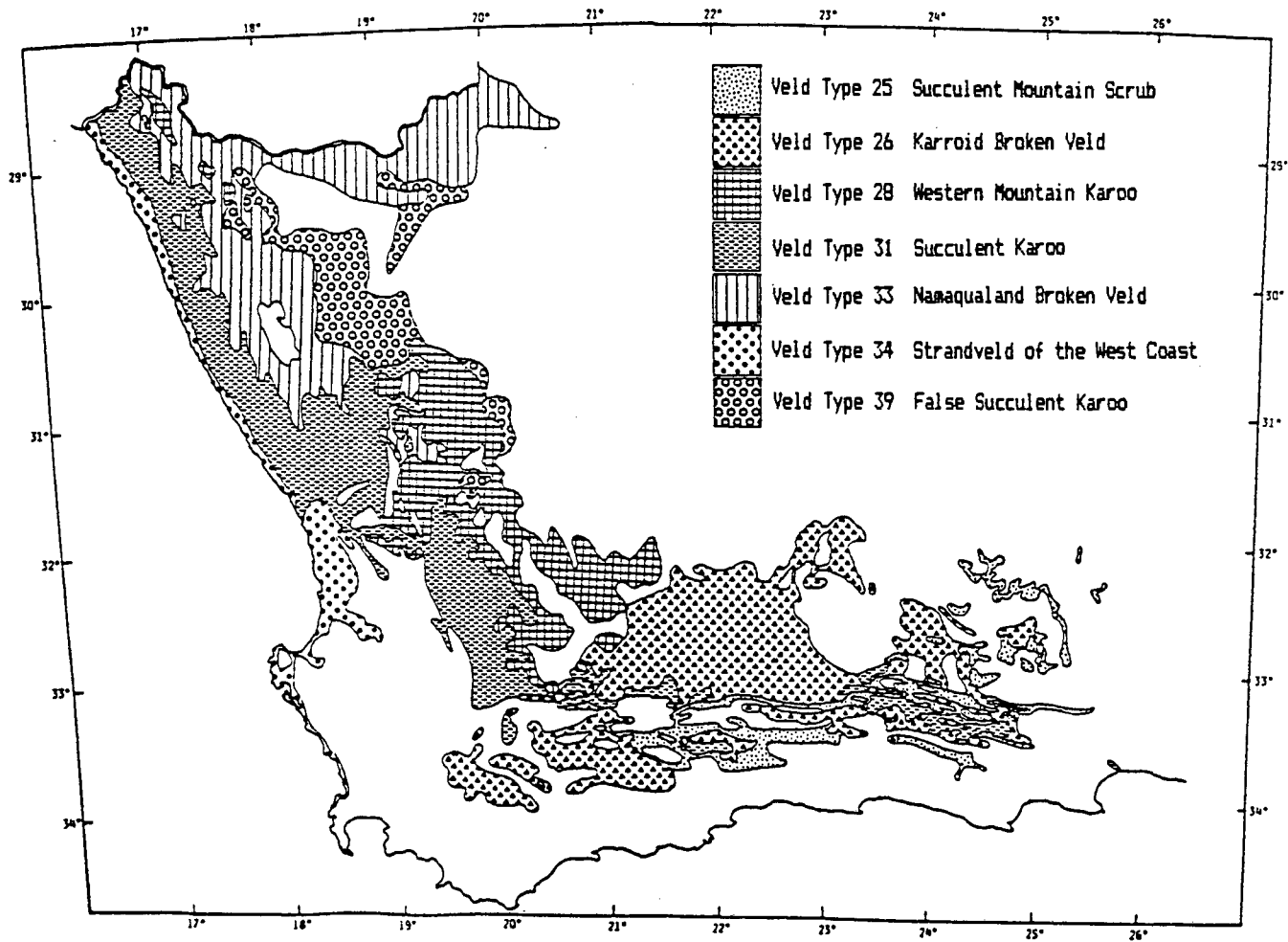


Figure 1.1 Karroid veld types in the western and southwestern Cape
(after Acocks 1953)

general understanding of the adaptive significance of plant morphological characters in mediterranean regions. In the important shrub component, a primary distinction has been made between deciduous and evergreen plant forms (Mooney 1983). These forms are thought to represent distinct functional groups, as their patterns of leaf habit are considered to be optimal solutions to different sets of environmental constraints (Solbrig 1979).

The deciduous and evergreen habit have been investigated in relation to both water (Mooney & Harrison 1972, Poole & Miller 1975, Orians & Solbrig 1977, Beard 1983, Fanjul & Barradas 1987) and nutrient (Merino et al. 1982, Gray 1983, Gray & Schlesinger 1983, Merino et al. 1984) limitations. It seems that a limited nutrient supply results in the the dominance of evergreen plant forms in a wide variety of habitats (Small 1973). However, the relative adaptive value of leaf habit in relation to limitations in water supply is not clear. Although the sclerophyllous leaves of many evergreen shrubs are by nature xeromorphic, it seems that deciduous species are better adapted to extreme aridity than are evergreens (Mooney & Dunn 1970, Szarek & Woodhouse 1977, Poole & Miller 1978).

The presence of both plant forms in the western Karoo is therefore of particular interest, as an understanding of their co-occurrence may shed light on differences between them in terms of their acquisition and use of water and nutrient resources. This kind of information may then allow predictions to be made

about the relative success of these growth forms under a range of nutrient and water stress conditions.

OBJECTIVES

The work described in this thesis had two main objectives:

1. To identify fundamental differences in the patterns of water acquisition and use of deciduous and evergreen perennial plant forms in the western Karoo.
2. To determine the distribution of deciduous and evergreen perennial plant forms of the western Karoo in relation to substrate nutrient characteristics.

The principle aim of this work was to ascertain the relative importance of water and nutrient supply as determinants of the success and distribution of deciduous and evergreen perennial plant forms on two main substrate types in the Worcester-Robertson valley, a part of the western Karoo.

RESEARCH LIMITATIONS

Certain limitations to the scope of this study had to be defined, in keeping with time and manpower constraints. The most obvious limitation was that of geographical area (see methods sections in Parts 3 and 4). The other main limitation was the number of species and growth forms which could be investigated in detail.

This in turn was determined by the type of research carried out. In accordance with the research objectives, two lines of enquiry were pursued:

1. An analysis of the distribution and relative abundance of deciduous and evergreen forms in relation to two main substrate types in the Worcester-Robertson valley, Cape Province, together with analyses of the nutrient and water characteristics of both substrate types, and of the foliar nutrient contents of selected species occurring on both substrate types.
2. An investigation of the patterns of seasonal water stress exhibited by selected deciduous and evergreen non-succulent woody perennial plant forms growing in these substrate types on low radiation (pole-facing) and high radiation (equator-facing) slopes at one intensive study site, the Worcester Veld Reserve, situated in the Worcester-Robertson valley.

The substrate types selected for study represent soils of large, circular, slightly raised earth mounds, and soils adjacent to and surrounding these formations. The soil mounds are thought to have been formed by the combined activities of termites and molerats (Cox and Lovegrove 1986, Lovegrove & Siegfried 1987). There are clearly visible differences in the structure and composition of vegetation growing on these two substrate types, and this pattern provided the basis for a 'natural experiment' approach (Diamond 1986) utilised in this study.

Special methodological constraints prevented the investigation of the water relations of succulent plant forms. This was unfortunate, as succulents form an important component of the vegetation in the study area. Therefore succulents, as a functional group, were considered only in the analysis of plant form-substrate nutrient relationships.

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PART 2

LITERATURE REVIEW

Introduction

Mediterranean shrublands occur in five separate regions of the world, namely the Mediterranean Basin, California, Chile, southwestern and southern Australia and South Africa. The origin of the mediterranean-type climate, which is characterised by cool, moist winters and hot, dry summers (Aschmann 1983), is thought to be fairly recent in geological time (Axelrod 1973, Raven 1973). Even so, each of these regions has a highly diverse floristic composition (di Castri 1981). Striking similarities between these regions in terms of vegetation structure and dominant plant forms (di Castri & Mooney 1973) have prompted the study of evolutionary convergence (Johnson 1973) among various mediterranean areas at different levels of spatial scale. Convergence has been shown in vegetation structure (Naveh 1967, Specht 1969a,b, Parsons & Moldenke 1975, Cowling & Campbell 1980), patterns of resource use and resource use-efficiency (Miller 1981), and the morphological (Mooney & Dunn 1970a), life history (Orshan et al. 1989), water relations (Poole et al. 1981) and physiological (Mooney & Dunn 1970b) characteristics of dominant plant forms.

Significant differences in soil nutrient status do exist between mediterranean regions (Specht & Moll 1983). These may be responsible for observed divergences (di Castri 1981) between some mediterranean regions in certain aspects of ecosystem function, such as seasonal nutrient cycling (Shaver 1981). Phylogenetic sources of divergence are also thought to be important, but cannot be accurately estimated (di Castri 1981).

The plant growth form most characteristic of mediterranean ecosystems, and which has been the focus of considerable research effort, is the evergreen sclerophyllous shrub or small tree (Specht & Moll 1983). Sclerophylly has been interpreted as an adaptive response to both water limitation (Mooney et al. 1983) and nutrient stress (Beadle 1966, Seddon 1974, Sobrado & Medina 1980), while evergreenness has been interpreted primarily as a nutrient stress adaptation (Monk 1966, Small 1972, Schlesinger & Chabot 1977, Mooney & Rundel 1979, Moore 1980).

Towards the dry limits of the climatic range of mediterranean regions, vegetation becomes dominated by drought-deciduous (Harrison et al. 1971) or semi-deciduous, seasonally dimorphic, semi-succulent or even succulent (Specht & Moll 1983) plant forms. This change has been interpreted mainly as a response to decreased water availability (Mooney et al. 1970, Miller 1979). Few investigations in mediterranean systems have assessed the relative importance of water and nutrient supply as determinants of plant success and distribution patterns. This is possibly because the interaction between soil moisture and nutrient availability is not well understood (Kruger 1987).

Leaf habit characteristics in relation to water limitation

Miller (1979) has proposed that the duration of summer drought conditions determines the boundary between areas dominated by evergreen and drought-deciduous species within mediterranean regions. The performance and carbon investment characteristics of leaves of evergreen and deciduous plant forms have been subjected to cost-benefit analysis by Orians and Solbrig (1977). They also

proposed a relationship between the photosynthetic capacity of different leaf types and soil water potential. These analyses suggest that patterns of soil water availability through the season may determine the relative success of evergreen and drought-deciduous species. The distribution of evergreen-dominated chaparral and deciduous-dominated coastal sage vegetation in mediterranean-climate California, and the performance of representative shrubs from these vegetation types (Harrison et al. 1971), concur with the analyses of Orians and Solbrig (1977), and support the proposition of Miller (1979).

In arid and semi-arid regions, surface soil layers are saturated more frequently than intermediate layers, but intermediate layers retain water for longer periods at lower matric potential. Solbrig (1979) has suggested that, because of this pattern, drought-deciduous plants with mesophytic leaves should have superficial rooting systems to enable the optimal function of their leaves, while evergreen plants with xeromorphic leaves should have more deeply deployed rooting systems. However, it has been found that phreatophytic plant species avoid seasonal water stress by accessing perennially available water stores, presumably at considerable soil depth (Nilsen et al. 1983). Therefore the modifying influence of rooting depth on constraints on the leaf characteristics of mediterranean shrubs should not be ignored.

Leaf habit characteristics in relation to nutrient limitation

Chapin (1980) has proposed that natural selection in fertile environments has resulted in plant forms with rapid resource

capture and growth characteristics, while infertile environments favour forms with slow resource capture and growth patterns. Generally, it has been found that evergreens occur on soils of lower nutrient status than those on which deciduous species occur (Mooney 1983). However, there is no unequivocal frame of reference for assessing soil fertility, and this complicates the interpretation and cross-comparison of field data, the design of manipulative experiments and even reduces the framing of hypotheses to broad generalizations.

It is difficult to isolate a particular soil mineral element as a potential determinant of plant performance and success, both because it is not realistic to equate measured levels of soil nutrients directly with levels which are available to plants (Specht & Moll 1983), and because species exposed to the same nutrient availability show markedly different nutrient uptake capacities (Kruger 1987).

It has been proposed that levels of soil P are responsible for the delimitation of sclerophyllous and mesomorphic communities in heath vegetation of eastern Australia (Beadle 1966). However, heathland soils are generally highly oligotrophic (Specht 1981), and characterised especially by limiting levels of soil P and N (Groves 1981), therefore this pattern may not be applicable to mediterranean shrubland vegetation.

Deciduous shrubs can be clearly differentiated from evergreens on the basis of their higher carbon-gaining capacity per unit leaf area (Mooney 1983), which seems to be directly related to their higher leaf N content (Field & Mooney 1986). Gray (1983) found

that deciduous species of Californian coastal sage had greater nutrient use efficiency than co-occurring evergreen species of chaparral vegetation. More detailed laboratory investigation (Gray & Schlesinger 1983) revealed that the growth of a deciduous species was more closely coupled with available N than was growth of an evergreen species. Even so, some evergreen sclerophyllous plants also have been found to show an adjustment of leaf N content in response to changes in N availability, with concomitant changes in photosynthetic capacity (Mooney et al. 1978).

It is generally held that soil N most frequently limits plant growth in terrestrial systems (Ellenberg 1977, Gray & Schlesinger 1981). It is possible, therefore, that soil N status and factors relating to N availability determine the relative success of deciduous and evergreen plant forms more than the availability of any other soil nutrient, except under extreme soil conditions such as soil salinity or soil elemental toxicity.

Relationships between water and nutrient limitations as determinants of vegetation structure in mediterranean ecosystems

Mediterranean regions intergrade with semi-arid and arid areas on their inland borders, allowing analyses of vegetation change in relation to changes in water availability. Gradients of soil nutrient status are more difficult to interpret, given the constraints of interpreting soil chemical analyses.

Along a gradient of decreasing moisture availability in Baja California (Mooney & Harrison 1972) and in southern California and central Chile (Parsons & Moldenke 1975), evergreen

sclerophyllous forms were replaced by deciduous mesophytic forms and, to a lesser extent, succulent forms when rainfall decreased below about 300mm to 500mm per year.

Beard (1983) provided evidence that water availability, rather than nutrient availability, determined changes in the physiognomy of vegetation in southwestern Australia. These changes did not, however, include a shift from evergreen to deciduous vegetation types.

Miller (1985) reported some evidence that water availability determined the change from evergreen fynbos vegetation to deciduous and succulent Karroid shrubland along a gradient of decreasing rainfall in South Africa, but also noted that nutrient availability may have determined vegetation structure and composition under conditions of high rainfall (above about 650mm per year).

Rabinovitch-Vin (1983) sampled soil nutrient status and vegetation structure and composition along a soil catena in northern Israel, at sites where rainfall ranged from 600mm to 1100mm. He concluded that soil nutrient availability determined vegetation structure and composition, primarily through the form in which soil N was available i.e. nitrate or ammonium.

Gray (1983) provided evidence that soil nutrient status determined the relative success of deciduous and evergreen shrubs of coastal sage and chaparral vegetation, at a site where rainfall was roughly 650mm per year (calculated from two years rainfall data cited in Gray 1983). Follow-up work (Gray & Schlesinger 1983) indicated that levels of soil N were important

in this relationship.

Cowling and Campbell (1983) investigated the distribution of several plant morphological features in coenoclines (Whittaker 1967) of Cape fynbos shrublands on shallow infertile soils, and thicket and forest vegetation on deeper, heavier, more fertile soils along a rainfall gradient (from about 900mm to 400mm per year) in the southeastern Cape, South Africa. In fynbos soils, it was found that low nutrient availability overrode the potential effects of decreasing soil moisture availability on vegetation structure. In the more fertile soils, decreasing water availability was reflected in a change of leaf consistency from orthophylly to sclerophylly, but not in an increased dominance of deciduous species. However, the study area was not characterised by a winter rainfall regime, and rainfall could be expected at any time of year. Therefore, under the climatic conditions prevailing in this area, evergreenness was seen as a solution to the problem of unpredictable rainfall, and increased sclerophylly as a necessary xeromorphic adaptation for long lived leaves to tolerate intermittent periods of low soil water potential.

It seems, therefore, that soil nutrient status is a primary determinant of vegetation structure and composition in mediterranean-climate areas either if water availability is relatively high (i.e. mean annual rainfall above about 600mm), or if soil nutrient status is excessively low. In either case, the mechanism by which soil nutrient status determines vegetation structure and composition may be through the availability of soil

N for plant uptake, and the form in which it is available, i.e. nitrate or ammonium.

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PART 3

SUBSTRATE EFFECTS OF ZOOGENIC SOIL MOUNDS
ON VEGETATION COMPOSITION IN THE WORCESTER-ROBERTSON VALLEY,
WESTERN KAROO.

ABSTRACT

Vegetation data obtained from raised, circular zoogenic soil mounds and adjacent off-mound habitats in the Worcester-Robertson valley were subjected to a Correspondence Analysis. Vegetation is described and classified according to habitat preference. Vegetation on- and off-mound differed in structure and composition. Deciduous plant growth forms, particularly succulents, occurred predominantly on-mound, and evergreen forms off-mound. On-mound soils were alkaline, typically Ca-rich and had higher water contents and macro- and micro-elemental concentrations than acid off-mound soils. Only higher soil N concentrations on-mound were reflected in the foliar analyses of all species. It is suggested that the more favourable soil N on-mound, in combination with an improved water status, provides conditions conducive to the success of deciduous growth forms. Phosphorus may be indirectly implicated.

INTRODUCTION

Large, evenly-spaced lenticular or conical soil mounds occur throughout a wide range of altitudinal and climatic zones over extensive areas of Africa (Darlington 1985). These may be bare or well vegetated, and, like ant-formed Formica mounds (Beattie & Culver 1981; King 1977; Culver & Beattie 1980), often have a different flora, soil chemistry and texture from their surroundings (Darlington 1985). Their formation has been attributed to termite action, either active or residual (Michelmore 1939; Vesey-Fitzgerald 1963; Mielke 1978; Darlington 1985), burrowing by mole-rats (Cox & Gakahu 1983), or a combination of these two factors (Lovegrove & Siegfried 1986, Cox & Lovegrove 1987). Although some controversy exists as to the precise agents responsible for their formation (Darlington 1985; Lovegrove & Siegfried 1986), they are clearly, like Formica mounds, of zoogenic origin.

In the south western Cape Province, numerous raised circular soil mounds, about 1m high and 30m in diameter, are found restricted to inland flats, mountain valleys and west coast lowlands (Lovegrove & Siegfried 1986). The formation of these mounds has been attributed to burrowing by termites and mole-rats as influenced by waterlogging of shallow soils during the long winter rainfall season (Lovegrove & Siegfried 1986; Cox & Lovegrove 1987). Soil mounds of the south-western Cape appear similar (Lovegrove & Siegfried 1986) to those which occur over large areas of western and south-western North America (Price 1949) and the Peruvian altiplano (Scheffer 1958). They have been described as Mima-like

(Lovegrove & Siegfried 1986; Cox & Lovegrove 1987), since the type locality of North American mounds is Mima Prairie in Washington State, U.S.A. (Cox 1984).

Most research on African zoogenic soil mounds has concentrated on identifying the mechanisms involved in their formation. Little is known about their effects on soil structure and chemical composition, and the structure and composition of associated vegetation, which can be of economic and ecological importance. For example, abandoned termite mounds in Kenya are used as foci for small-scale cultivation (Mielke 1978) and serve as nuclei for forest expansion (Burt 1942).

In vegetation surveys of the Worcester-Robertson valley, southern Cape, Olivier (1966), Joubert (1968) and Norton (1977) observed that vegetation composition on-mound differed from that in adjacent off-mound (inter-mound) habitats, though the principal vegetation groups associated with each habitat were not delimited. Olivier (1966) attributed differences in vegetation composition between on- and off-mound habitats to differences in soil pH. Norton (1977) noted similarities between on-mound vegetation and that occurring in shaded gullies and drainage lines of the area, and suggested that improved soil water status on-mound may account for vegetation differences between the two habitats. In this paper, these broad hypotheses are further investigated through the analysis of the relationship between vegetation structure and composition and soil water and chemical characteristics in on- and off-mound situations, in order to

identify the principle determinants of the vegetation differences between these habitats.

METHODS

Study area

The Worcester-Robertson valley ($33^{\circ}39'S$ $19^{\circ}27'E$ - $33^{\circ}50'S$ $19^{\circ}54'E$) lies approximately 100km north-east of Cape Town at an altitude of 150 to 220m in an area bounded by the Langeberg, Riviersonderend, Boschjesveld and Stettyn mountain ranges. Climate is typically mediterranean with a mean annual rainfall ranging from 225mm in the West to 345mm in the East (Fuggle 1981). Soils are shallow (less than 0,5m deep), weakly developed (Harmse 1978) and derived mainly from Bokkeveld and Witteberg parent formations (Theron 1983). The vegetation of this area, included within the Succulent Karoo Biome (Rutherford & Westfall 1986), is dominated by chamaephytes, many of which are succulent. Within this biome, species diversity is high, there are a considerable number of rare and endangered species (Hall *et al.* 1980) and many species are endemics or near endemics (Werger 1978).

Correspondence Analysis

Vegetation survey data from 23 pairs of adjacent on- and off-mound releves (stands) in the Worcester-Robertson valley were obtained from three unpublished sources, viz. Olivier (1966), Joubert (1968), and Norton (1977). Cover data from each source were converted to cover importance values according to a modified Domin-Krajina scale (Mueller-Dombois & Ellenberg 1974) to

establish uniformity in expression of vegetation cover. Because this study was concerned particularly with patterns exhibited by the more abundant species of the area, and to prevent distortion of the ordination, those species which occurred in less than 20% of the stands were excluded from the data set. Data were subjected to a stand and species ordination using Correspondence Analysis (Greenacre 1984; Underhill & Peisach 1985).

Soil and foliar analyses

Soils, for chemical analyses, were sampled both on- and off-mound at five sites whose distribution represented a similar range of parent materials as presented in Olivier (1966), Joubert (1968) and Norton (1977). At each site and in each habitat, three soil cores, each 100mm in diameter and 200mm deep, were taken 4m apart at distances of 150 to 300mm from the nearest plant canopy edge. Samples were air-dried and sieved through 2mm mesh. Total nitrogen was determined by the Kjeldahl method (Black et al. 1965a). Macro- and micro-elemental concentrations were determined using a Direct Current Plasma Spectrometer following extraction of soil minerals in 1% citric acid solutions at 80°C. Soil pH was determined according to the method of Schofield and Taylor (1955).

Soil water contents were determined from soil cores sampled monthly, with a Wehrmeyer-type auger at three different soil depths, viz: 0 - 50mm, 51 - 100mm, 101 - 150mm, on- and off-mound at one site. Cores were sealed in pre-weighed air-tight phials, weighed, dried at 105°C to a constant mass and reweighed. Soil water content was expressed as a percentage of oven dried

soil (Black et al. 1965b).

Four species were selected for foliar analysis on the basis of their habitat preference, derived from the Correspondence Analysis of vegetation data. These were Pteronia incana and P. paniculata, two closely related evergreen non-succulent species, the evergreen leaf succulent Ruschia caroli and the deciduous stem succulent Euphorbia burmannii. Foliar material was collected at the end of the growing period (November) from four randomly selected individuals in each habitat at the same localities where soils were sampled for nutrient analyses. In each species, foliar material was separated from the shoots and bulked, except in E. burmannii where stem segments of the current years growth constituted the photosynthetic tissue. Samples were oven-dried at 60°C to a constant mass, and milled. Total nitrogen was determined by the micro Kjeldahl method (Association of Official Agricultural Chemists 1975). Macro- and micro-elemental concentrations were determined using a Direct Current Plasma Spectrometer after dry-ashing of samples and extraction of residue in 5% HCl.

Differences in soil water, soil and foliar elemental concentrations between on- and off-mound habitats were tested by the Kruskal-Wallis H-test (Sachs 1982).

RESULTS

Correspondence Analysis

In the stand ordination, a clear separation was evident along the first ordination axis between on- and off-mound stands, with the exception of one stand (Figure 3.1a). This was the only off-mound stand extracted from the Norton (1977) data set which was located in a low-lying, run-on situation, and had a species composition similar to that on-mound. Soil pH data included for survey localities by Olivier (1966), Joubert (1968) and Norton (1977), indicated that on-mound stands occurred on weakly acid to alkaline soils (pH 6,0 - 8,0) and off-mound stands on strongly acid soils (pH 3,0 - 5,0). The separation of stands along the second ordination axis possibly reflected a decrease in rainfall from east (Norton sites) to west (Joubert sites).

Three groups were distinguished in the species ordination (Figure 3.1b), viz: An On-Mound Community, an Off-Mound Community and an Indiscriminate Group. The composition of each group is presented in Table 3.1. Species included within each are subdivided into a number of categories on the basis of cover importance and frequency in each habitat. With the exception of E. burmannii, which occurred as a co-dominant of both on- and off-mound habitats, and Ehrharta calycina, a member of the Poaceae, all deciduous species were clearly associated with the on-mound habitat (Figure 3.1b). In this habitat, the deciduous growth form occurred with a much higher frequency and cover importance than off-mound (Table 3.2). The opposite was true of the evergreen growth form. Irrespective of deciduousness or

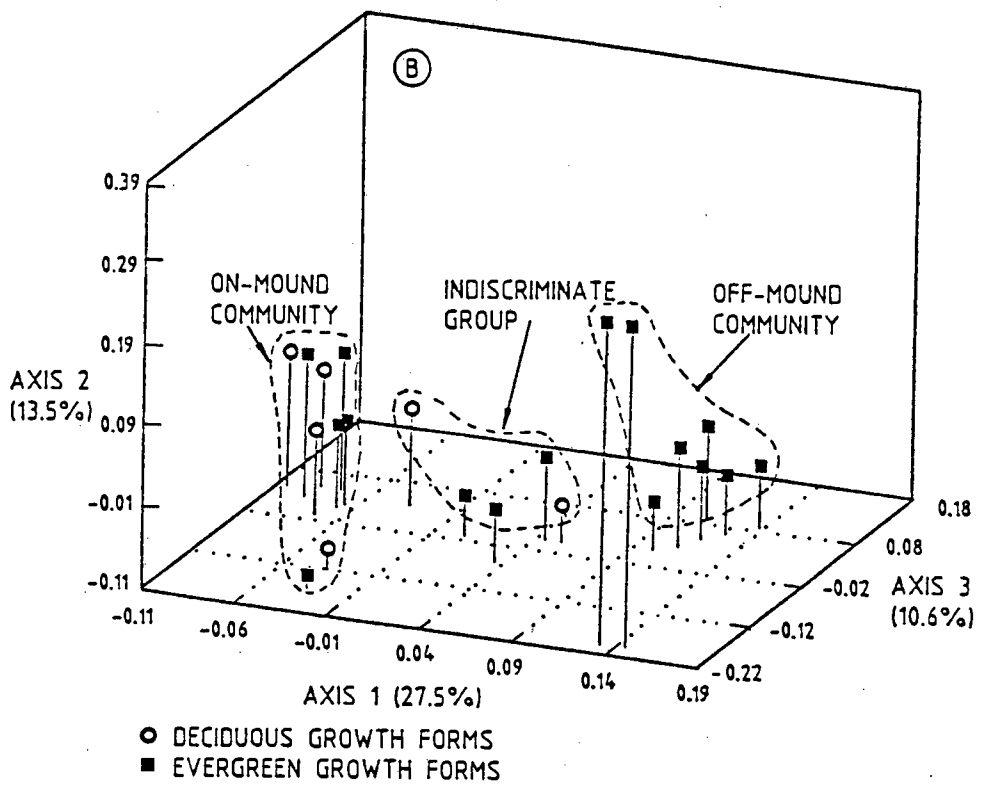
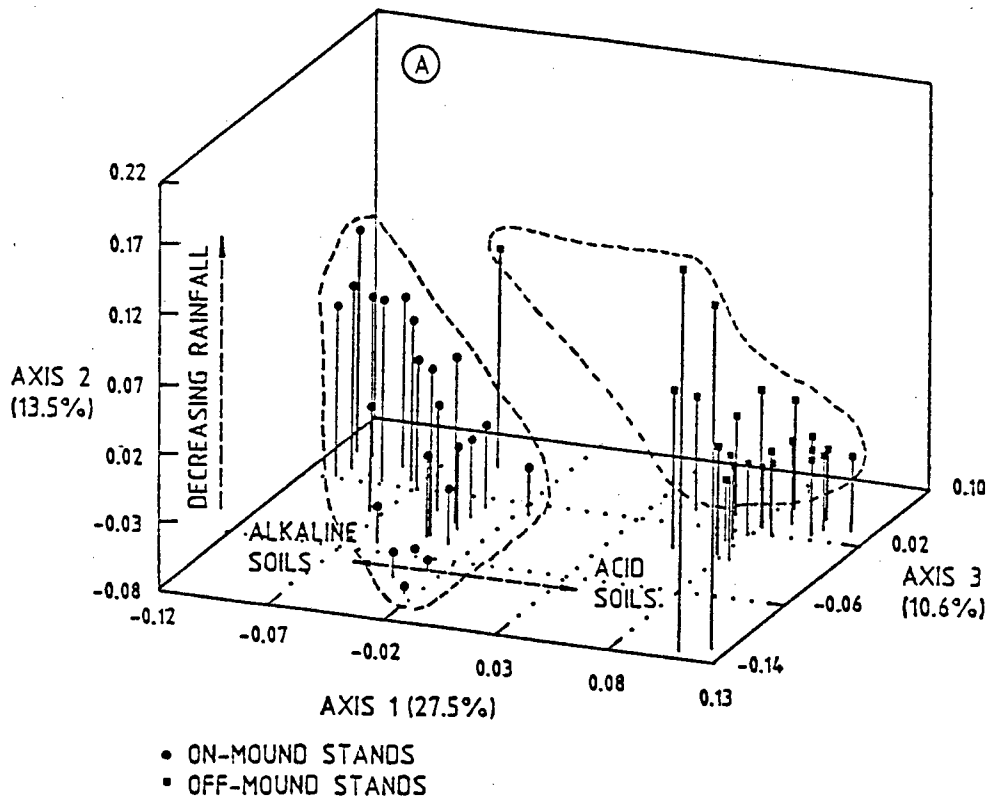


Figure 3.1 Correspondence Analysis of on- and off-mound vegetation data (A - stand ordination; B - species ordination)

Table 3.1 Vegetation classification according to habitat preference derived from the Correspondence Analysis

SPECIES	OFF-MOUND		ON-MOUND		GROWTH FORM*
	Frequency	Cover value	Frequency	Cover value	
ON-MOUND COMMUNITY					
<u>Exclusive species</u>					
<u>Lycium cinereum</u>	0,0	0,0	34,8	0,65	D/NS
<u>Dominant species</u>					
<u>Euphorbia mauritanica</u>	4,3	0,43	95,7	5,48	D/S
<u>Galenia africana</u>	21,7	0,22	87,0	3,96	E/NS
<u>Pteronia incana</u>	17,4	0,56	87,0	3,52	E/NS
<u>Common species</u>					
<u>Tylecodon paniculatus</u>	4,3	0,43	73,9	2,39	D/S
<u>Pentzia incana</u>	13,0	0,13	43,5	1,61	D/NS
<u>Aloe microstigma</u>	4,3	0,04	47,8	0,78	E/S
<u>Crassula subaphylla</u>	4,3	0,04	30,4	0,74	E/S
<u>Drosanthemum delicatulum</u>	4,3	0,04	26,1	0,87	E/S
INDISCRIMINATE GROUP					
<u>Co-dominant species</u>					
<u>Ruschia caroli</u>	95,7	6,17	78,3	4,74	E/S
<u>Euphorbia burmannii</u>	65,2	1,30	100,0	4,26	D/S
<u>Common species</u>					
<u>Ehrharta calycina</u>	43,5	0,83	21,7	0,70	D/NS
<u>Leipoldtia jacobseniana</u>	34,8	0,56	34,8	1,22	E/S
<u>Delosperma pageanum</u>	30,4	0,39	21,7	0,30	E/S
OFF-MOUND COMMUNITY					
<u>Common species</u>					
<u>Crassula anomala</u>	26,1	0,26	4,3	0,04	E/S
<u>Dominant species</u>					
<u>Pteronia paniculata</u>	100,0	7,39	43,5	0,48	E/NS
<u>Exclusive species</u>					
<u>Haworthia pumila</u>	26,1	0,52	0,0	0,0	E/S
<u>Drosanthemum speciosum</u>	17,4	0,43	0,0	0,0	E/S
<u>Adromischus mammillaris</u>	39,1	0,39	0,0	0,0	E/S
<u>Felicia filifolia</u>	17,4	0,35	0,0	0,0	E/NS
<u>Lampranthus haworthii</u>	30,4	0,35	0,0	0,0	E/S
<u>Crassula nudicaulis</u>	26,1	0,26	0,0	0,0	E/S

* E = evergreen
D = deciduous
S = succulent
NS = non-succulent

Table 3.2 Relative frequency and cover of different plant growth forms in on- and off-mound habitats

GROWTH FORM	OFF-MOUND		ON-MOUND	
	relative frequency	relative cover	relative frequency	relative cover
DECIDUOUS				
succulent	11,8	10,2	32,5	38,2
non-succulent	9,0	4,5	12,0	9,3
subtotal	20,8	14,7	44,5	47,5
EVERGREEN				
succulent	54,2	44,9	29,3	27,4
non-succulent	25,0	40,4	26,2	25,1
subtotal	79,2	85,3	55,5	52,5
TOTAL				
succulent	66,0	55,1	61,8	65,6
non-succulent	34,0	44,9	38,0	34,4

evergreenness, succulent and non-succulent forms were uniformly distributed, in terms of frequency and cover importance, between on- and off-mound habitats. However, deciduous succulents occurred with a higher frequency and cover importance than evergreen succulents on-mound, with this pattern reversed off-mound.

Soil and foliar analyses

On-mound soil water contents were significantly higher ($P < 0,05$) at all depths during autumn, winter and spring, the active growth period for most species in the study area (Joubert 1970), than those off-mound (Table 3.3). During summer, however, soil water contents on-mound were significantly higher ($P < 0,05$) than those off-mound only at soil depths greater than 100mm. Soil water contents on-mound rose more rapidly during autumn and winter, attained higher levels than those off-mound, and declined less rapidly during spring and summer (Figure 3.2). Water infiltration off-mound appeared to be poor during winter, since soil water contents were always higher in shallow (0 - 50mm) than deeper layers (51 - 150mm).

Soils on-mound were alkaline, typically Ca-rich and, with the exception of Na, had significantly higher ($P < 0,05$) macro- and micro-elemental concentrations than acid off-mound soils (Table 3.4). Differences in soil elemental concentrations between habitats, however, were not reflected in the foliar analyses, with the exception of N which was significantly higher ($P < 0,05$) in all species growing on-mound (Tables 3.5 and 3.6), and P, B and Mg which were significantly higher ($P < 0,05$) in P. incana and

Table 3.3 Statistical comparison between on- and off-mound habitats of seasonal soil water contents (means of 15 measurements) at three different depths

SEASON/ SOIL DEPTH (mm)	SOIL WATER CONTENT (% dry mass)		STATISTICAL ANALYSIS	
	off-mound	on-mound	H-statistic	significance level
SUMMER				
0 - 50	1,05	1,56	3,16	NS
51 - 100	1,04	1,52	3,15	NS
101 - 150	1,61	2,16	6,61	P < 0,05
AUTUMN				
0 - 50	1,77	3,44	6,61	P < 0,05
51 - 100	2,16	3,60	4,90	P < 0,05
101 - 150	2,11	3,78	10,15	P < 0,05
WINTER				
0 - 50	5,28	11,37	12,52	P < 0,001
51 - 100	3,49	9,67	18,80	P < 0,001
101 - 150	3,45	8,18	15,69	P < 0,001
SPRING				
0 - 50	1,57	4,66	15,94	P < 0,001
51 - 100	1,85	4,28	18,79	P < 0,001
101 - 150	2,02	5,40	20,64	P < 0,001

NS = not significant at P = 0,05

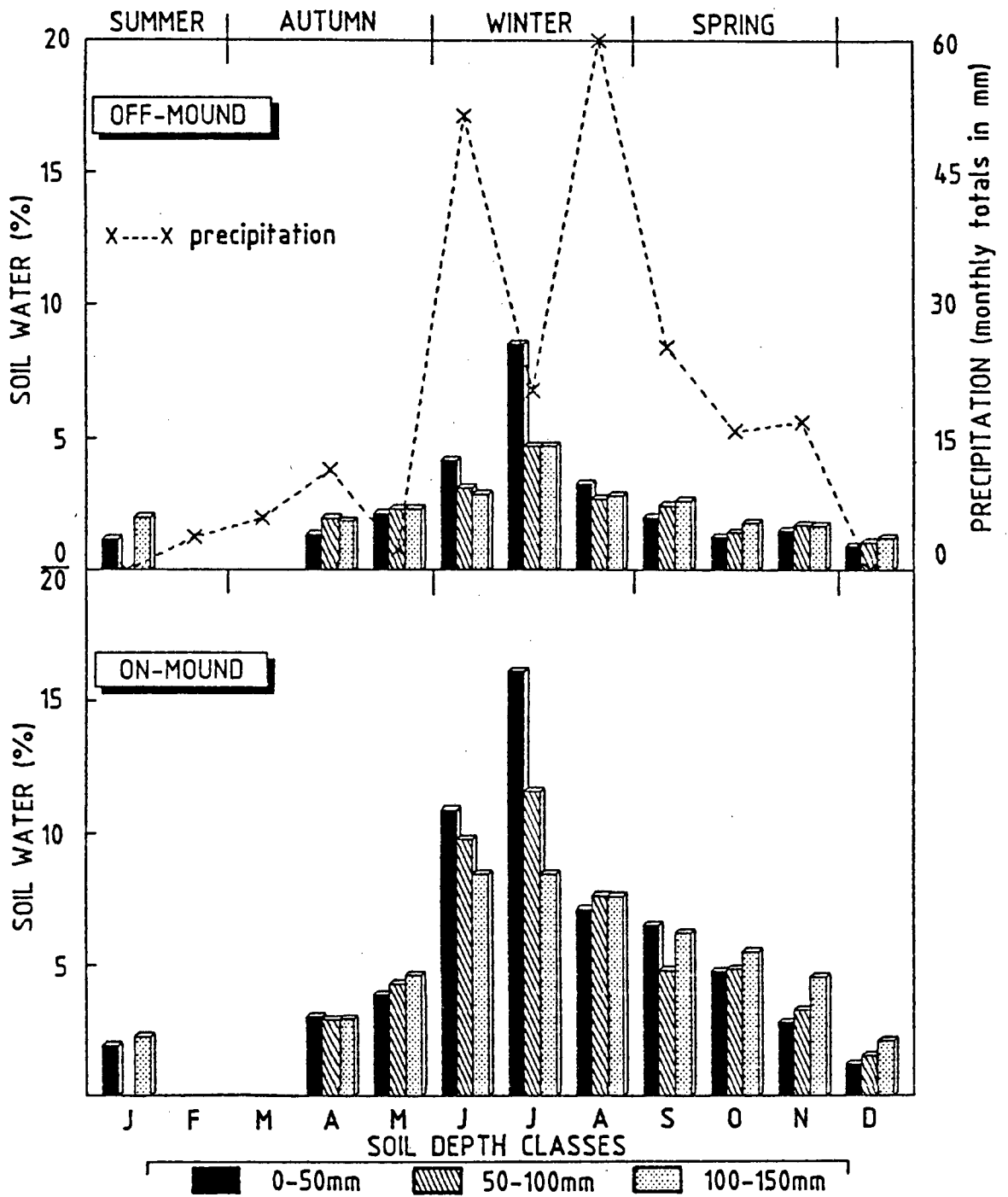


Figure 3.2 Total monthly precipitation and soil water content (means of five measurements) at different depths in on- and off-mound habitats (total rainfall during August was 63,1mm)

Table 3.4 Statistical comparison between on- and off-mound habitats of soil elemental concentrations (means of fifteen measurements)

ELEMENT	CONCENTRATION (milliequivalents/kg)		STATISTICAL ANALYSIS	
	off-mound	on-mound	H-statistic	significance level
pH	4,43	7,09	17,41	P < 0,001
N	0,0620	0,0846	6,44	P < 0,05
P	0,54	2,43	4,68	P < 0,05
K	2,21	7,97	11,17	P < 0,001
Ca	22,30	318,0	19,51	P < 0,001
Na	6,60	7,00	0,07	NS
Mg	17,90	91,40	14,72	P < 0,001
Cu	0,0102	0,0247	10,19	P < 0,05
Zn	0,0243	0,1109	14,63	P < 0,001
Mn	2,53	13,14	14,08	P < 0,001
B	0,1156	0,4283	8,40	P < 0,05
Fe	2,98	5,86	13,66	P < 0,001
Al	18,46	31,73	10,46	P < 0,05

NS = not significant at P = 0,05

Table 3.5 Statistical comparison of foliar elemental concentrations (means of five measurements) of two species growing in on- and off-mound habitats

ELEMENT	FOLIAR CONCENTRATION (milliequivalents/kg)		STATISTICAL ANALYSIS	
	off-mound	on-mound	H-statistic	significance level
<u>Ruschia caroli</u>				
N	406,85	513,92	4,93	P < 0,05
P	19,89	33,58	3,59	NS
K	703,29	788,19	0,01	NS
Ca	852,67	686,63	6,00	P < 0,05
Mg	748,60	886,80	6,00	P < 0,05
Na	594,83	776,00	1,55	NS
Cu	0,08	0,08	0,01	NS
Zn	0,39	0,38	0,53	NS
Mn	28,71	33,69	0,02	NS
B	1,91	1,61	1,84	NS
Fe	3,68	4,09	1,32	NS
Al	4,23	3,63	0,88	NS
<u>Euphorbia burmannii</u>				
N	451,10	619,60	4,81	P < 0,05
P	45,52	58,24	0,88	NS
K	432,7	583,09	1,58	NS
Ca	256,48	362,27	1,32	NS
Mg	259,87	255,68	0,54	NS
Na	122,40	152,15	0,53	NS
Cu	0,13	0,11	0,53	NS
Zn	0,57	0,35	5,77	P < 0,05
Mn	3,46	1,43	4,84	P < 0,05
B	2,32	1,90	1,10	NS
Fe	1,78	1,90	0,27	NS
Al	4,75	2,59	3,93	P < 0,05

NS = not significant at P = 0,05

Table 3.6 Statistical comparison of foliar elemental concentrations (means of five measurements) of two congeneric species, each dominant in different habitats

ELEMENT	FOLIAR CONCENTRATION (milliequivalents/kg)		STATISTICAL ANALYSIS	
	off-mound	on-mound	H-statistic	significance level
	<u>Pteronia paniculata</u>	<u>Pteronia incana</u>		
N	786,94	1154,89	4,90	P < 0,05
P	40,93	67,74	6,05	P < 0,05
K	427,73	535,52	1,50	NS
Ca	270,15	313,37	1,50	NS
Mg	169,46	134,91	1,51	NS
Na	241,63	233,15	0,06	NS
Cu	0,28	0,19	1,50	NS
Zn	0,49	0,45	0,54	NS
Mn	4,66	2,36	6,00	P < 0,05
B	6,65	13,80	6,00	P < 0,05
Fe	3,82	3,36	0,06	NS
Al	6,12	6,35	0,00	NS

NS = not significant at P = 0,05

R. caroli respectively growing on-mound. Significant differences in other foliar elemental concentrations, e.g. Zn, Mn, Al in E. burmannii and Ca in R. caroli, were species specific and inversely related to soil elemental concentrations.

DISCUSSION

On- and off-mound soils can be clearly distinguished on the basis of their chemical composition and water status. Soils on-mound are alkaline, typically Ca-rich and have higher water contents and elemental concentrations than acid off-mound soils. Judged by cation status only, according to the standards of Day (1983), on-mound soils can be classified as agriculturally rich, eutrophic soils and those off-mound as nutrient poor, oligotrophic soils. On- and off-mound soils are similar in chemical composition to limestone and acid peat soils of calcicole and calcifuge habitats respectively, described by Jefferies & Willis (1964), and limestone and sandstone soils of the Cango Valley, southern Cape, described by Raitt & Moffet (1987). However, Ca, Na and Mg concentrations off-mound are higher than those reported by these authors for acid soils. Higher soil P and K levels on-mound are in broad agreement with studies of Formica mounds (Czerwinski et al. 1971; Malozemova & Koruma 1973; Petal 1978) where higher levels are most pronounced in the centres, diminishing both with depth and distance from the perimeters (Malozemova & Koruma 1973), and persist even after mounds have been abandoned by ants for several months (Petal 1978). In the south-western Cape, residual effects

of zoogenic mounds on the performance of vine cultivars (Saayman 1973) and wheat (¹Thompson pers. comm.) have been observed, even after several years of intensive cultivation.

The marked pH differences between on- and off-mound soils suggests that plant growth and survival in acid off-mound soils could be limited through an increase in heavy metal solubility (Epstein 1972) and Al toxicity (Roy et al. 1988). Though heavy metals are potentially extremely toxic to plants (Turner 1969; Levitt 1972) and Al can interfere with the uptake and transport of several essential elements (Roy et al. 1988), no evidence of toxicity or nutrient deficiency was detected in plants of either habitat using guidelines presented by Marschner (1986 pp. 392-393). In fact, Al and heavy metal concentrations were much higher in the alkaline on- than acid off-mound soils, but were not reflected in the foliar analyses, with the exception of B in P. incana. Higher soil K levels on-mound could increase plant tolerance of some heavy metals (Simon 1977). Lower soil water levels off-mound could reduce heavy metal toxicity in the acid soils, since micro-elements are less available for root uptake under conditions of low soil water content (Gauch 1972; Bidwell 1974; Soltanpour et al. 1979).

Higher soil water levels on-mound are indicative of better water infiltration, which is probably either a direct or residual effect of burrowing by termites and mole-rats. This has been

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demonstrated by Cox (1987) in the formation of grass-dominated vegetation circles through gerbil burrowing in areas of the southern Namib desert. It appears unlikely, however, that the predominance of deciduous forms on-mound, and other differences in vegetation composition, are related entirely to differences in soil water status between on- and off-mound habitats. Under arid conditions, the deciduous habit is not necessarily indicative of a higher water availability than the evergreen habit (Schulze 1982). In vegetation of mediterranean climates (Mooney & Dunn 1970; Poole & Miller 1978) and the Sonoran (Szarek & Woodhouse 1977) and Saharan deserts (Stocker 1971), it has been found that deciduous forms are often better adapted to extremes of aridity than evergreen forms.

It has been reported that deciduous plant forms have a greater requirement for nutrients than evergreens due to their shorter leaf duration and more rapid leaf turnover rate (Chabot & Hicks 1982). Deciduous forms are found more frequently in habitats with higher soil nutrient levels and rates of turnover than those in which evergreens occur (Mooney 1983). This suggests that that the distribution of growth forms on- and off-mound may be related to differences in soil nutrient status between these two habitats.

As a first approximation of possible nutrient limitation, and in the absence of suitable local standards, soil elemental concentrations in both habitats were compared with standards established by Soltanpour et al. (1979) for indigenous and improved forage grasses. In both habitats, soil macro- and micro-elemental concentrations could be classified as adequate,

i.e. not deficient in any macro-nutrient and having micro-nutrient levels above those considered adequate for growth. Foliar micro- and macro-elemental concentrations in both habitats, were also above values considered adequate (Epstein 1972) and typical (Hewitt & Smith 1975) in foliage of normal plants, with the exception of N and P. Foliar N and P levels were below adequate in both habitats in all species investigated, with the exception of P in P. incana on-mound. Only higher soil N concentrations on-mound were significantly reflected in the foliar analyses of all species investigated, which suggests N limitation. This nutrient most frequently limits plant growth in terrestrial ecosystems (Ellenberg 1977; Gray & Schlesinger 1981). Since foliar N concentrations are closely correlated with photosynthetic rates (Field & Mooney 1986), and deciduous forms have higher photosynthetic rates and productivities than evergreen forms (Mooney 1983), it would appear that the more favourable soil N on-mound, in combination with improved soil water status, provides conditions conducive to the success of deciduous forms in this habitat. Phosphorus may also be indirectly implicated since P, like N, is essential for protein synthesis. Low foliar P levels (< 90 me/kg) are indicative of a low protein content, characteristic of sclerophyllous, P-limited vegetation (Loveless 1961,1962). Low levels can depress protein synthesis, as demonstrated in certain species (Loveless 1961, 1962).

CONCLUSIONS

Zoogenic soil mounds form localised areas of improved soil fertility. Mound formation is possibly initiated through the burrowing activities of termites and mole-rats which appear to improve soil water infiltration and possibly aeration. This, together with the importation of organic material by fossorial organisms, such as termites (Merryweather 1965), and its subsequent fragmentation (Edwards & Heath 1963), may result in an increased rate of humification, microbial degradation and mineralisation of organic matter (Marcuzzi 1970; Read & Mitchell 1983). These processes, which take place more rapidly under conditions of improved soil moisture (Billes et al. 1971; Marion 1981), are fundamental in rendering nutrients, such as N, available for plant growth in terrestrial ecosystems (Rosswell 1976; Ellenberg 1977; Lee & Stewart 1978). Better soil aeration on-mound could also enhance the nitrification process and N availability, since the N ion is more readily available for root uptake in its oxidised (nitrate) form due to its higher mobility in the soil (Delwiche 1983).

The improved soil N status on-mound provides conditions favourable for growth of deciduous forms, which have a high nutrient requirement due to their short leaf duration and more rapid leaf turnover rate (Chabot & Hicks 1982). Under these conditions, deciduous forms may have a competitive advantage over evergreens, due to their higher productivity and N utilisation efficiency (Mooney 1983), hence their predominance on-mound. Enhanced litter production on-mound, resulting from the presence

of these forms, should maintain the integrity of these formations, even in the absence of their zoological component. In the latter case, disturbance of mound formations, particularly the deciduous component, could result in their degradation.

Data on the photosynthetic capacities, rates of biomass production and water-use efficiencies of deciduous and evergreen forms of the area in relation to soil N and water availability are required to further substantiate these findings.

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PART 4

SEASONAL AND DIURNAL WATER POTENTIAL CHANGES
IN DECIDUOUS AND EVERGREEN WOODY PLANT FORMS OF THE WESTERN KAROO
IN RELATION TO WATER AVAILABILITY

ABSTRACT

Base and minimum shoot xylem pressure potential of selected evergreen and deciduous shrub species were determined at approximately monthly intervals during a fifteen month period on two different soil types on equator- and pole-facing slopes at a site in the western Karoo. Sites were chosen to represent soils of zoogenic soil mounds and adjacent off-mound soils. During the study period the site experienced climatic conditions characteristic of a semi-arid mediterranean-type region. Soil water contents in all situations were low in summer, but increased by different degrees in on- and off-mound soils after autumn and winter rains. Although higher soil water contents were measured in on- than off-mound soils during winter, it is likely that levels of plant available water and soil matric potential did not differ between these soil types during this period, due to the differences in their water retention characteristics. This was substantiated by the finding that species growing in the two soil types had similar base water potential during winter months. Species in both soil types on the pole-facing slope showed diverse seasonal water potential courses, possibly reflecting a range of rooting characteristics. However, on the equator-facing slope, species had more similar seasonal courses, and experienced severe water stress during summer, even though soil water content was similar to that on the pole-facing slope. This suggests that either 'perched' or ground water was available for deeper rooted species on pole- but not equator-facing slopes, or that rooting systems of some species were deployed differently on the two

slopes. The lack of consistent differences in seasonal water potential patterns between evergreen and deciduous plant forms suggests that water acquisition, as determined by rooting characteristics, rather than water loss, as determined by leaf habit, was primarily responsible for the extent of seasonal water stress experienced by the selected species.

INTRODUCTION

Plants of arid mediterranean climate zones are exposed to drought conditions which recur during summer months (Kappen et al. 1975, Bowman & Roberts 1985a, Lo Gullo & Salleo 1988). It appears that different combinations of morphological, physiological and phenological characteristics enable plants of diverse forms to survive arid conditions (Solbrig 1986). While hot deserts represent one of the most extreme habitats for plant life on earth (Bennert & Mooney 1979), arid mediterranean conditions place severe constraints on plant growth and reproduction, through a combined requirement for growth during unfavourable temperature conditions (van Rooyen et al. 1979) and for drought resistance during periods of high vapour pressure deficit and low soil water supply.

The ways in which perennial plants have evolved to flourish under these conditions have attracted considerable attention in mediterranean-type systems throughout the world. These have been found to include adaptive patterns of stomatal response to water stress (Tenhunen et al. 1982), seasonal changes of tissue elasticity (Bowman & Roberts 1985b) and leaf cell osmotic potential (Nunes et al. 1988), the capacity of plants to develop and endure low tissue water potential (Poole & Miller 1975, Burk 1978, Miller & Poole 1979, Roberts et al. 1981, Lo Gullo & Salleo 1988) and investment by plants in extensive rooting systems (Nilsen et al. 1983, Nilsen et al. 1984). Different patterns of leaf habit are also thought to be important in determining the relative performance of perennial plant forms under a range of

nutrient and water stress conditions (Miller & Hajek 1981, Sobrado 1986).

Studies of the patterns of seasonal and diurnal changes of plant water potential, in relation to rainfall and soil water, provide information regarding the characteristics of water acquisition and water use of perennial shrubs. These often comprise measurements of base (also termed pre-dawn) and minimum (midday or post midday) shoot xylem pressure potential. Plant base and minimum water potentials can be used, respectively, to infer the changing soil water conditions experienced by the plant, and the net loss of water by the plant through transpiration. These measures, therefore, allow investigation of the adaptive responses of plants to changing levels of soil water availability.

Different patterns of seasonal base water potential have been well correlated with plant rooting habit (Poole & Miller 1975, Giliberto & Estay 1978, Crombie et al. 1988). Studies of the water relations of perennial plant species of semi-arid mediterranean-type regions in California (Poole et al. 1981) and Chile (Giliberto & Estay 1978, Martinez & Armesto 1983) have afforded considerable insight into their patterns of water acquisition and their adaptive responses to seasonal drought conditions. However, little is known about the water relations of perennial plants of the western Karoo, an arid belt which borders on and interdigitates with the Cape Fynbos region, and which has a winter rainfall regime.

This study investigated seasonal and diurnal changes in shoot

water potential of evergreen and deciduous shrubs in response to seasonal changes in soil water availability. In order to provide a range of soil water conditions and atmospheric demand for water, the study was conducted on two soil types and on equator- and pole-facing slopes. The aims of this work were to determine:

1. The seasonal patterns of water stress exhibited by perennial non-succulent shrubs of different growth forms.
2. The effect of different conditions of soil water supply and evaporative demand on these seasonal patterns.
3. Whether species could be grouped functionally on the basis of their seasonal patterns of water stress.

METHODS

Study site

The work described in this study was conducted at the Worcester Veld Reserve (33°39'S 19°27'E), which is situated in the Worcester-Robertson valley, ca 100km NW of Cape Town. This area is included within the Succulent Karoo Biome (sensu Rutherford & Westfall 1986), which is characterized by the dominance of low shrub vegetation and an abundance of succulent species. The soils of this area are shallow and weakly developed (Harmse 1978) and derived mainly from Bokkeveld and Witteberg parent formations (Theron 1983). The site itself is underlain predominantly by shale of the Malmesbury formation, which appears to be almost vertically bedded on the slopes of the Reserve, giving rise to exposed outcrops of parent rock in places.

According to Schulze's (1947) mapped Koppen climatic regions for

southern Africa the site is within a BSks climatic region, although the mean annual temperature for this site, given in the climate diagram (Figure 4.1), indicates that it falls precisely between BSks and BShs categories.

The site was proclaimed as a reserve in 1935, after serving as commonage for the municipality of the town of Worcester, and has been protected from grazing by domestic stock since that time.

In a floristic survey of the Reserve, Olivier (1966) identified three main plant communities; dominated by the shrubs Pteronia paniculata, Ruschia caroli, and Euphorbia mauritanica respectively. However, Joubert (1968), in a survey of the whole Worcester-Robertson valley, did not distinguish between P. paniculata- and R. caroli-dominated communities, and identified instead a co-dominated P. paniculata-R. caroli community, with the relative importance of the two dominants determined largely by slope aspect. This classification was supported by Norton (1977), in her survey of the Karoo Botanic Garden situated 2km north of the study site.

The E. mauritanica community, recognised by Olivier (1966), Joubert (1968) and Norton (1977), occurs in isolated vegetation patches within the P. paniculata-R. caroli community. These patches are restricted to slightly raised circular mounds of Ca-rich soil, known locally as heuweltjies, which are possibly of zoogenic origin (Lovegrove & Siegfried 1986, Cox & Lovegrove 1987). The soil found on these mounds differs in chemical composition and depth (Joubert 1968) from soil of the surrounding community.

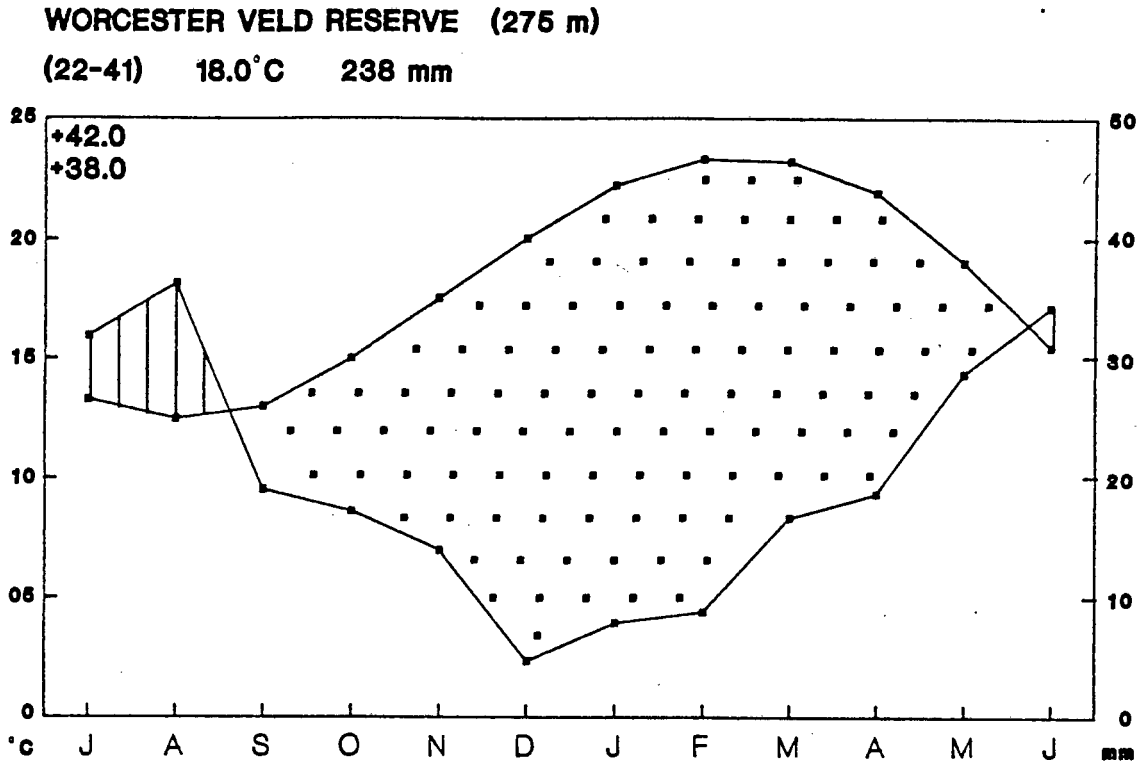


Figure 4.1 Climate diagram for the study site, Worcester Veld Reserve (using conventions of Ostendorf & Lieth 1982)

Experimental design and sampling protocol

Two sample areas, each approximately one hectare in size and encompassing both on- and off-mound substrate types, were selected on opposite, approximately equator- and pole-facing slopes of a hill situated near the southern border of the site. All measurements of soil water content and plant water potential were carried out within the borders of these areas. Similarly, all soil samples collected for analysis were taken from these areas. Details pertaining to the species selected for the study are presented in Table 4.1.

A climate station (serviced by the Winter Rainfall Region of the Department of Agriculture), situated less than 500m from both study areas, provided the environmental data required by the study.

Slope aspect and angle were calculated from a 1:50 000 map of the area (map 3319CB, Government printer, Pretoria). These data, appropriately rounded, allowed the calculation of maximal annual shortwave energy load (assuming year-round cloudless conditions) according to the method of Holland and Steyn (1975), and daily interception of shortwave radiation (assuming cloudless conditions) on equinox, midsummer and midwinter days according to the method of Schulze (1975).

Percentage plant canopy cover was measured along five 10m long line transects on both soil types on both slopes.

Shoot xylem pressure potential was measured as close to dawn as possible and at midday, using a pressure chamber (Soil Moisture Equipment Corp., California) with a 4,0 Mpa limit. Measurements

Table 4.1 Growth form grouping of selected study species, and the substrates on which they were sampled at the study site

	slope aspect, substrate type			
	equator-facing		pole-facing	
	on-mound	off-mound	on-mound	off-mound
<u>DECIDUOUS FORMS</u>				
<u>Lebeckia cytisoides</u> Thunb.			*	
<u>Osteospermum sinuatum</u> (DC.)T.Norl.	*			
<u>Rhus incisa</u> L.f.		*		*
<u>EVERGREEN FORMS</u>				
<u>Pteronia incana</u> (BURM.)DC.	*		*	
<u>Galenia africana</u> L.var. <u>africana</u>	*		*	
<u>Pteronia paniculata</u> Thunb.		*		*
<u>Dodonaea angustifolia</u> L.f.		*		*
<u>Elytropappus rhinocerotis</u> (L.f.)Less.		*		*

on the two slopes were carried out on subsequent days at approximately monthly intervals. A single shoot from each of at least three individuals of Osteospermum sinuatum, Rhus incisa, Pteronia incana, P. paniculata, Galenia africana and Elytropappus rhinocerotis was sampled. For Lebeckia cytisoides and Dodonaea angustifolia, three shoots were sampled from a single individual, due to the relative scarcity of these species on the site. For R. incisa, bark and phloem were removed a short distance from the cut face to prevent phloem exudate from obscuring the end point during pressurisation.

Deciduous species were recorded as leafless only if all individuals sampled for water potential were without leaves.

Approximate soil depth and structure was established by digging soil pits on both slopes. Depth of soil to bedrock (in the case of off-mound soil) or to a consolidated calcrete layer (in the case of on-mound soil) was then estimated by driving a metal stake into the soil until it reached a solid obstacle, at one metre intervals along transects of not less than fourteen metres in length, in each substrate type and on each slope.

Soil water content was sampled approximately monthly, on the same days as plant water potential data were collected. Using a Wehrmeyer-type auger, five replicate samples were taken at 50mm intervals from the surface to 150mm depth, in each substrate type and on each slope. These samples, weighing on average between 8g and 10g, were sealed in glass phials of known mass immediately after sampling, and were weighed within one to two hours on site, using a Mettler top-loading balance with 0.01g resolution.

Samples were dried to constant mass at 105°C within 24 - 48 hours of sampling and then reweighed. Data were combined to yield a soil water content for the profile from 0mm to 150mm. Differences in soil water content between the same soil types on the different slope aspects were tested for significance using the Wilcoxon signed rank test, with data from each slope paired in time.

Soil texture was determined using the hydrometer method (Fertilizer Society of South Africa 1974).

Soil water retention characteristics of each soil type were determined using a pressure plate apparatus (Slavik 1974). Four replicate samples of unsieved surface soil from each soil type were used for each water potential curve. Samples were saturated with distilled water, then equilibrated in the apparatus at 0,06 0,1 0,32 0,5 0,7 0,11 and 1,5 Mpa, weighed at each equilibration level, dried at 105°C to constant mass, and weighed to calculate gravimetric soil water content at each pressure.

RESULTS

Climatic parameters

Figure 4.2 summarises the weekly rainfall and monthly air vapour pressure deficit recorded at the site during the study period. Total rainfall during 1985 was 320,2mm, 101,4mm of which fell immediately prior to and during the first four months of the study period. Total annual rainfall for 1986 was 215,4mm, and occurred mainly during late autumn and winter months. Minimum daily vapour pressure deficit was relatively constant

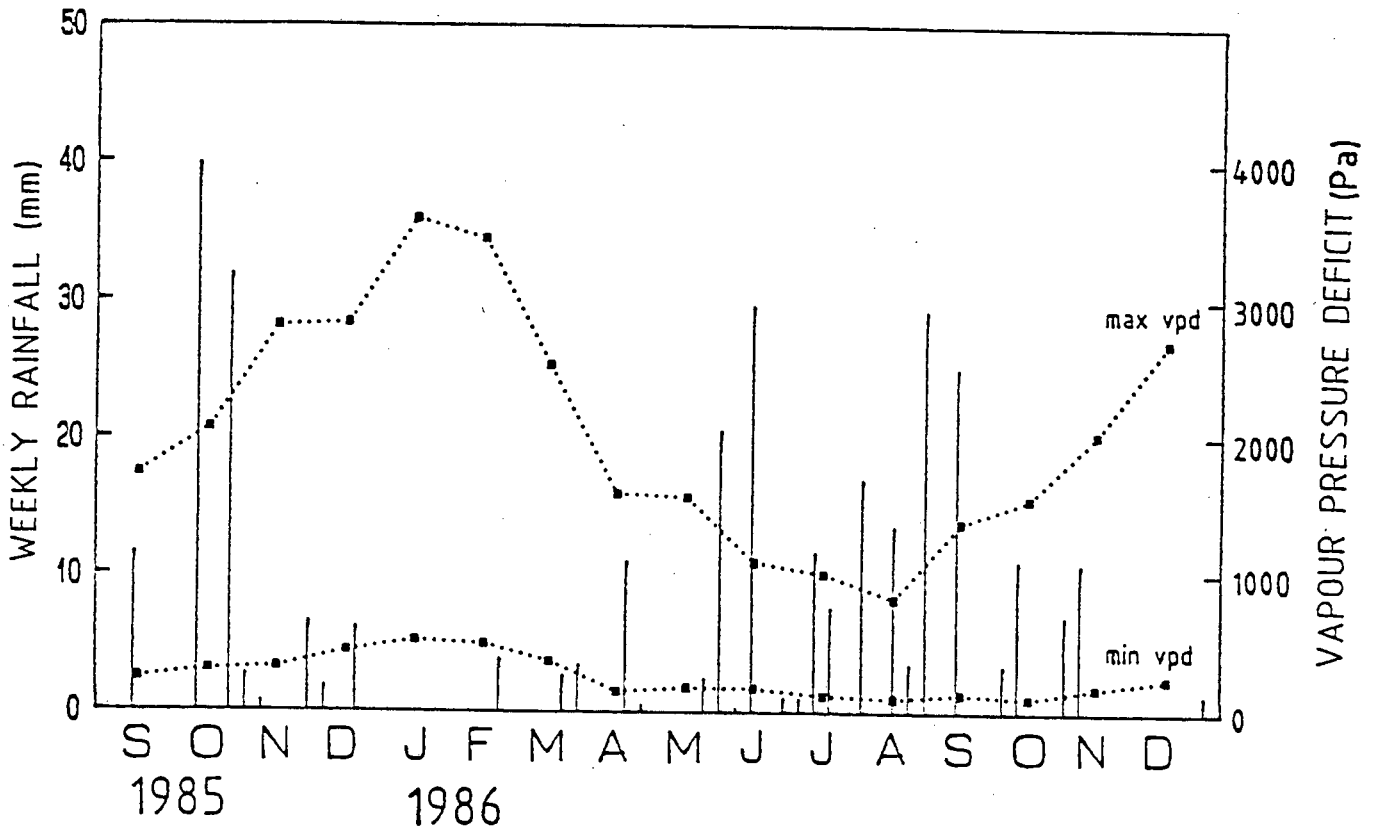


Figure 4.2 Weekly rainfall totals and mean monthly minimum and maximum vapour pressure deficit for the study site during the study period

throughout the study period, but maximum daily vapour pressure deficit increased markedly from low winter levels to high values during relatively rainless periods in late spring and summer months.

Plant canopy cover

Plant canopy cover was between 65% and 110% higher on pole- than on equator-facing slopes (Table 4.2).

Slope aspect, angle and heat load

Aspects of both slopes lay roughly 45° from the meridian (Table 4.3). The equator-facing slope was almost twice as steep as the pole-facing slope. It is likely that heat loading on the pole-facing slope did not exceed that on the equator-facing slope at any time of year, and that differences between slopes were most marked during winter than summer months. On an annual basis, heat loading on equator-facing slopes may have been in the order of 30% higher than that on the pole-facing slope.

Soil physical characteristics

All soils had a mean depth of less than 500mm (Table 4.4), but depth was highly variable, probably because of the fractured nature of the weathering, almost vertically bedded, shale parent material. On-mound soils were approximately twice as deep as those off-mound on both slopes, and soils on the pole-facing slope were roughly 25% deeper than soils of the same type on the equator-facing slope.

All soils could be classed as loamy sands (MacVicar et al. 1977), though on-mound soils had roughly 40% higher clay content than those off-mound, irrespective of slope aspect (Table 4.5). There

Table 4.2 Canopy cover (%) of on- and off-mound communities on equator- and pole-facing slopes at the study site (standard deviation given in brackets beside the mean)

Substrate	Slope aspect	
	equator-facing	pole-facing
on-mound	15,8 (6,4)	26,2 (12,2)
off-mound	18,6 (8,9)	40,2 (15,2)

Table 4.3 Characteristics of slope angle, aspect and heat load of equator- and pole-facing slopes at the study site

Substrate	Slope aspect	
	equator-facing	pole-facing
Slope angle (degrees)	21,8	12,5
Aspect (degrees)	42,5	229,5
*Radiant flux density (J/m ² /day)		
midsummer	30,9	30,9
equinoxes	27,8	21,1
midwinter	15,1	7,1
**Annual shortwave radiation (kiloangleys/year)	150	115

* Interpolated for NW- and SE-facing slopes of 200 and 150 respectively from Schulze (1975).

** Interpolated for N- and S-facing slopes of 220 and 130 respectively from Holland and Steyn (1975).

Table 4.4 Mean depth (mm) of each substrate type on each slope (standard deviation given in brackets beside the mean, sample size below the mean)

Substrate	Slope aspect	
	equator-facing	pole-facing
on-mound	308 (105) (20)	438 (114) (20)
off-mound	162 (99) (20)	203 (83) (14)

Table 4.5 Mean clay content (%) of each substrate type on each slope at the study site (sample size given in brackets beside the mean)

Substrate	Slope aspect	
	equator-facing	pole-facing
on-mound	13,3 (3)	10,0 (2)
off-mound	7,3 (3)	6,7 (3)

appeared to be relatively little difference in clay content between soils of the same type on opposite slopes, although sample size was too small to state this with certainty.

The water retention characteristics of the on- and off-mound soils clearly reflected the differences in their clay contents (Figure 4.3).

Soil water content

On- and off-mound soils showed similar, low water contents during summer months, irrespective of slope aspect (Figure 4.4). However, after late autumn rains, the water contents of the two soil types rose by different degrees. Possibly because of better water infiltration characteristics, on-mound soils on both slopes had markedly higher water contents than those off-mound during winter months. It is unlikely that the higher water contents of on- than off-mound soils during winter were reflected in greater levels of plant available water, due to the different water retention characteristics of the two soil types. Slope aspect had no significant effect on the water content of soils of the same type ($p > 0,05$; Wilcoxon Signed Rank Test).

Plant water potential

Maximum base water potential for all species was recorded during winter and early spring (Figures 4.5 a,b,c), while soil water content was above 8% in on-mound and 4% in off-mound soils. During this period, the mean base water potential of all species on both slopes fell within a wide range between -0,5 and -2,1 MPa. The water potential of all species on both slopes decreased gradually during late spring, and more rapidly during

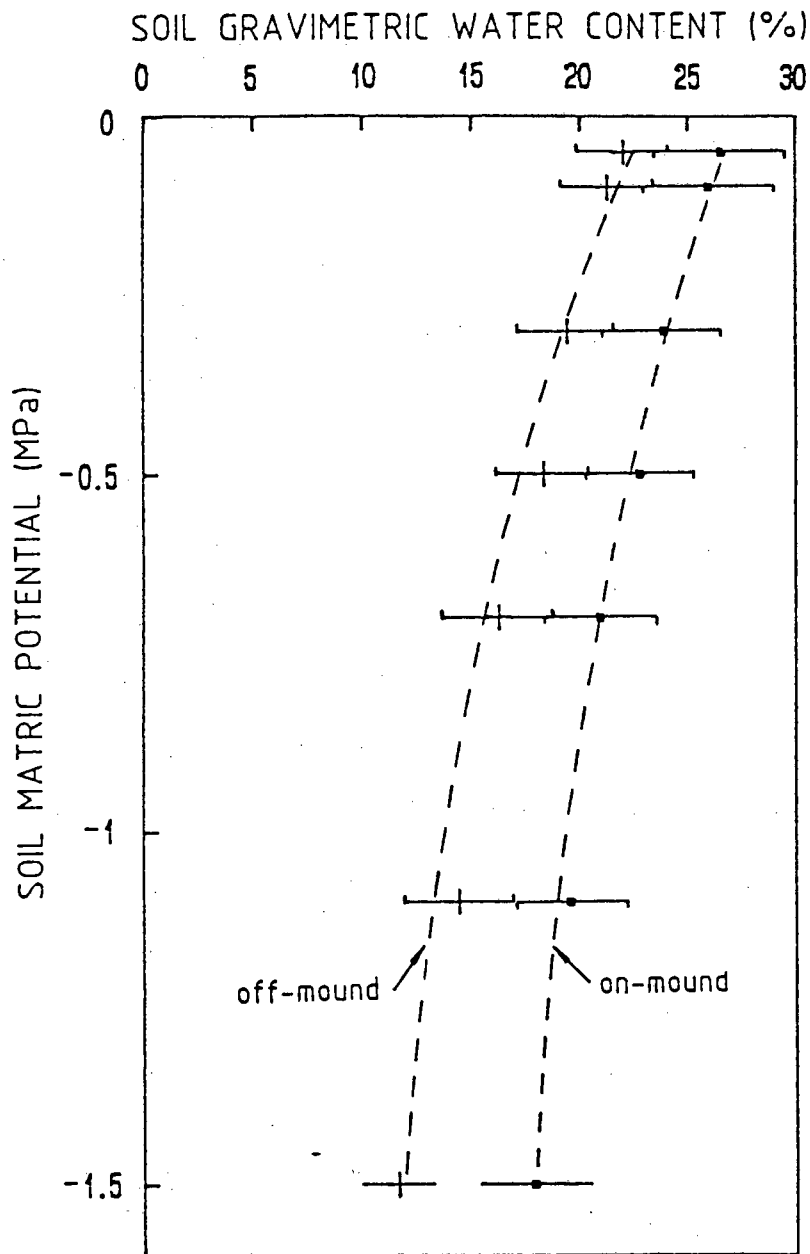


Figure 4.3 Water retention characteristics of on- and off-mound substrate types at the intensive study site (n = 4 for each sample point, standard deviations indicated by the horizontal bars)

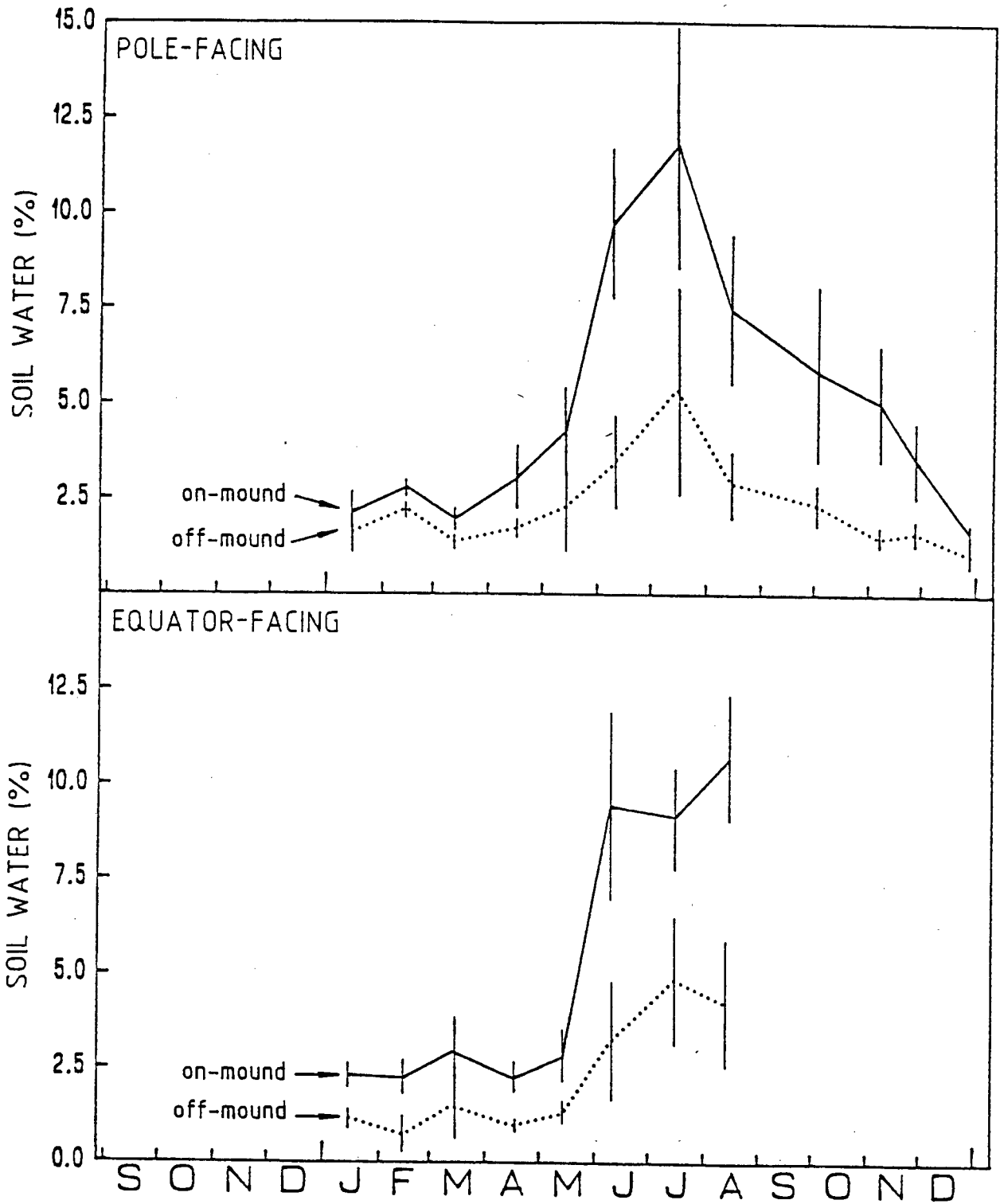


Figure 4.4 Mean soil water content (n = 5) at 0 - 150mm depth in on- and off-mound substrate types on equator- and pole-facing slopes during the study period (standard deviations indicated by vertical bars)

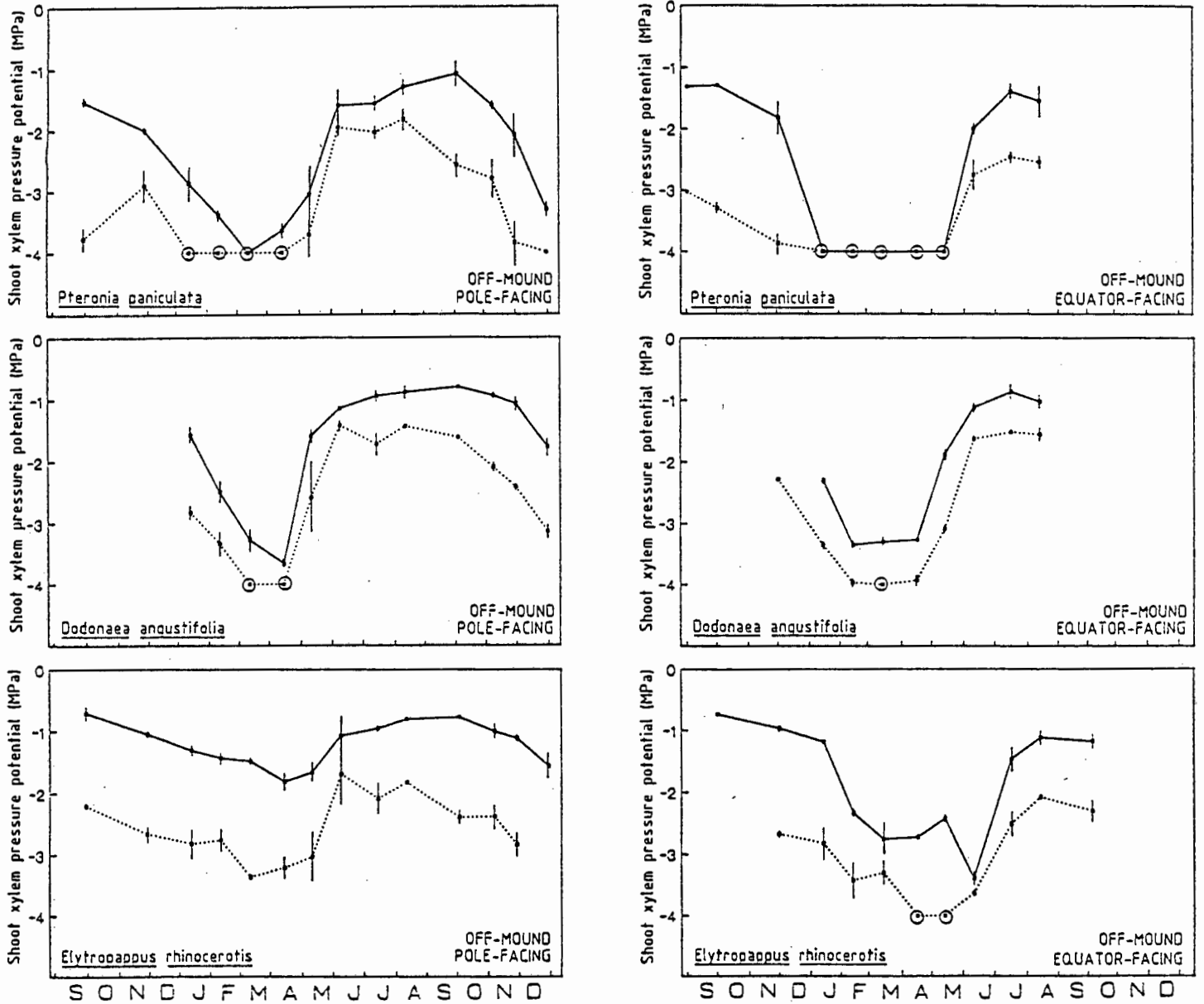


Figure 4.5a Seasonal courses of base (solid lines) and minimum (dotted lines) xylem pressure potential of selected evergreen off-mound species (standard deviations indicated by vertical bars, readings which exceeded the limits of the instrument are ringed)

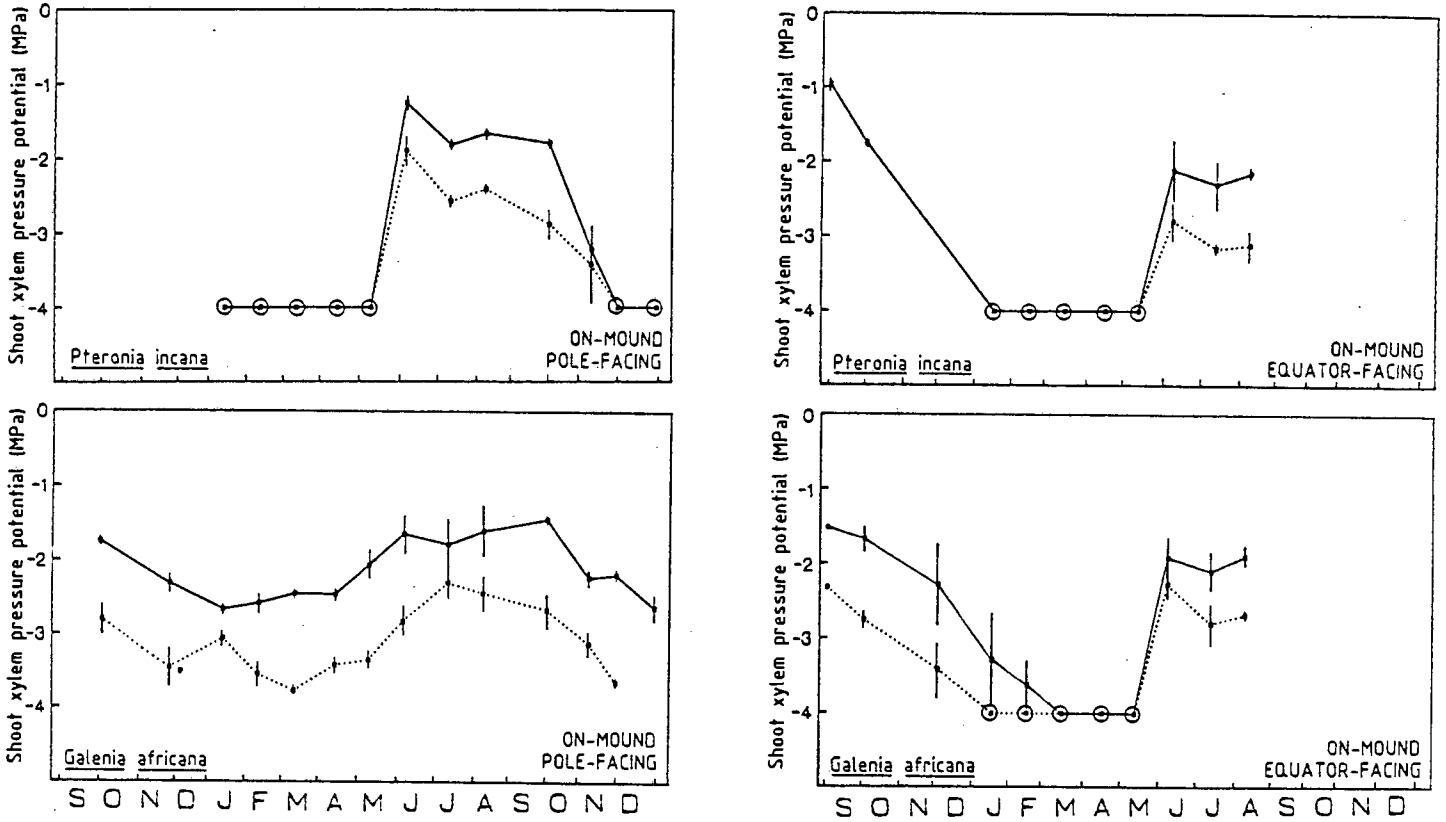


Figure 4.5b Seasonal courses of base (solid lines) and minimum (dotted lines) xylem pressure potential of selected evergreen on-mound species (standard deviations indicated by vertical bars; readings which exceeded the limits of the instrument are ringed)

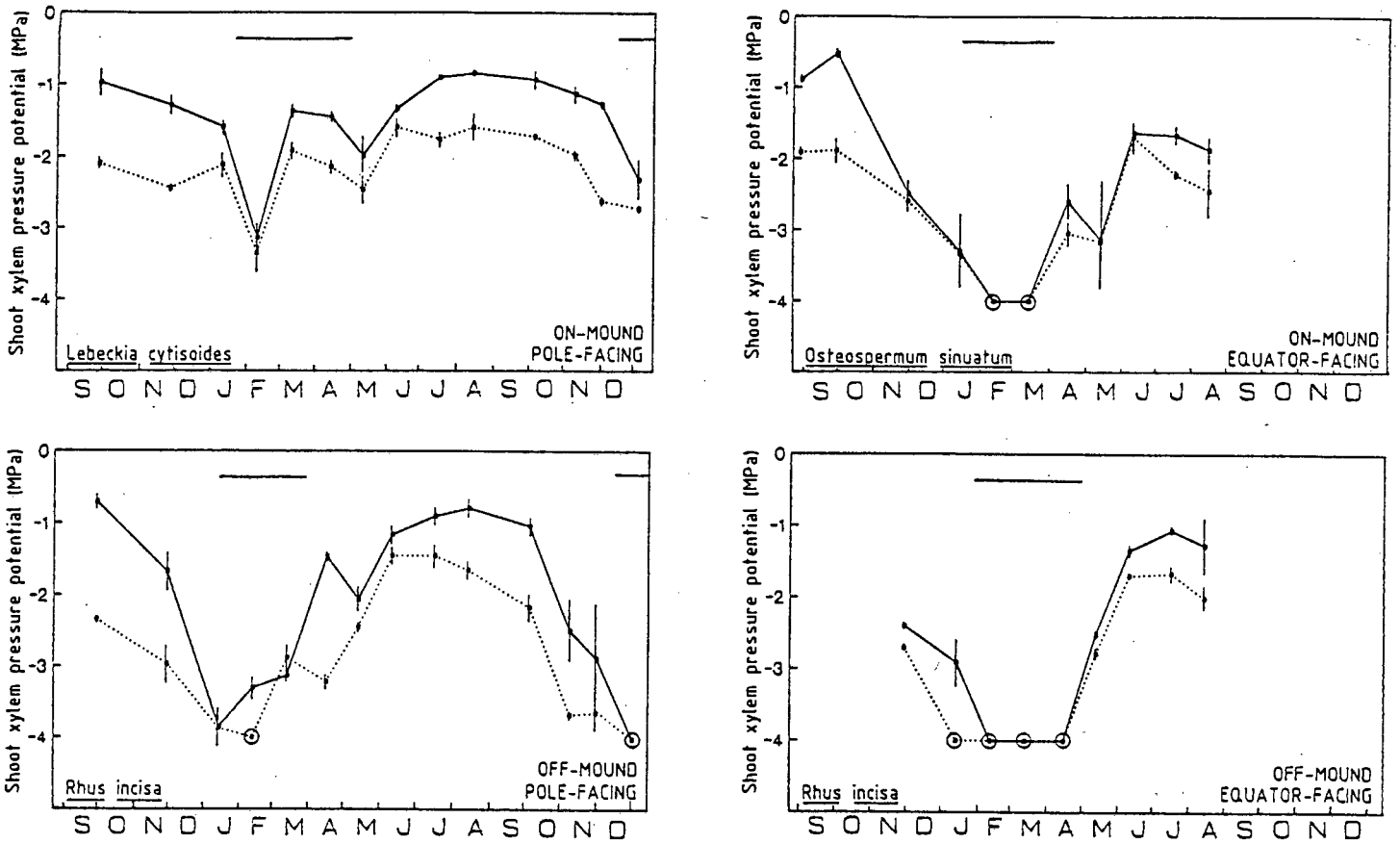


Figure 4.5c Seasonal courses of base (solid lines) and minimum (dotted lines) xylem pressure potential of selected deciduous species (standard deviations indicated by vertical bars; readings which exceeded the limits of the instrument are ringed; approximate leafless periods (+/- 2 weeks) indicated by horizontal bars)

early summer to reach minimum values during summer and autumn. Minimum base water potential for all species was recorded when soil water content was below 3% in on-mound and below 2% in off-mound soils. Due to the limitations of the pressure bomb, it was not possible to identify precisely the period of maximum water stress for some species. Some species had minimum base water potential greater than -4,0 MPa, and for these the period of maximum water stress varied from early summer to mid-autumn. Increases in base water potential were observed from mid-autumn to early winter, after mean soil water content had risen to above 5% in on-mound and above 3% in off-mound soils. The water potentials of all species except the evergreen P. incana attained low values for longer periods during summer months on the equator- than pole-facing slope, but during winter months there appeared to be no major differences between the water potentials of species occurring on both slopes. During this period there was also little apparent difference between the base water potentials of species growing on the two soil types.

DISCUSSION

Soil water content

The general trend of soil water content measured on both slopes complies with the pattern proposed by Wallen and de Blichambaut (1962, in Miller & Hajek 1981) of a three-phased water year in mediterranean-type ecosystems. These phases are:

1. High soil water content (mainly during winter), together with the greatest precipitation, and low vapour pressure deficit.

2. Relatively high soil water content (mainly during spring), with lower levels of precipitation, but higher vapour pressure deficit and greater potential evapotranspiration.
3. Low soil water content (mainly during summer), when little precipitation occurs and vapour pressure deficit is highest.

However, soil water content is likely to vary in the short term, thus short periods of high water availability could occur even in summer, after aseasonal rainfall events (Giliberto & Estay 1978). The period of low soil water contents encountered in both soil types in this study (four to five months) is of a similar duration to that found by Giliberto and Estay (1978) in matorral, and that found by Poole and Miller (1975) in chaparral vegetation. However, according to Miller and Hajek (1981), mediterranean regions generally experience dry soil for between one to four months, which suggests that the soil water characteristics of the Worcester study site represent a dry extreme for a mediterranean region.

The similarities between slopes in soil water contents of both soil types at Worcester is interesting in the light of conflicting findings from Californian chaparral and Chilean matorral vegetation. In chaparral, soil moisture contents were consistently lower on pole- than equator-facing slopes during a five year period (Miller & Poole 1979, Ng & Miller 1980), confirming the results of Poole and Miller (1975), who measured greater water stress in plants growing on pole-facing slopes. However, Giliberto and Estay (1978) reported lower soil water content and greater plant water stress on equator- than

pole-facing slopes. These apparently anomolous results have been interpreted in terms of greater vegetation cover, and consequently greater plant water use on pole- than equator-facing slopes in chaparral, and greater exposure to radiation, drying winds and lower vapour pressure deficits on equator- than pole-facing slopes in matorral vegetation. Therefore, the similar soil water contents on the two slopes obtained during the course of this study may be due to a balance between drying by greater transpiration (i.e. higher plant canopy cover) on the pole-facing slope, and higher rates of evaporation due to greater heat loading on the more exposed soil of the equator-facing slope.

Plant water potential

The range of seasonal water potential patterns observed in this study compares well with results from Chilean matorral (Giliberto & Estay 1978, Poole et al. 1981) and Californian chaparral vegetation (Poole et al. 1981). However, the extreme levels of summer stress shown by the evergreen P. paniculata and P. incana (i.e. four to five months with base water potential less than -4,0 MPa) have not been matched in other similar studies in mediterranean-type shrublands. These levels of stress would not be unexpected in a plant with a shallow-rooting habit, growing in soil with the water retention characteristics and seasonal pattern of water content observed in this study.

The surprisingly stable seasonal base and minimum water potential pattern shown by some species, including L. cytisoides and G. africana on the pole-facing slope and E. rhinocerotis on both slopes, is consistent with a deep, well-developed rooting system,

and strongly suggests that water was available year-round in sub-soil layers. This water may have been present as either a 'perched' (Crombie et al. 1988) or true water table, or may have resided in cracks in weathering parent rock. It also appears that this water source was not equally accessible on both slopes, but the reason for this is not clear.

Leaf shedding in deciduous species did not seem to preempt and ameliorate low xylem pressure potentials, but seemed rather to occur in response to the onset of water stress. This suggests either that the leaves of the deciduous species were unable to maintain turgor with decreasing xylem pressure potential through osmotic adjustment (Turner & Jones 1980), thereby losing the potential for stomatal opening and net carbon uptake (Turner & Begg 1981), or that leaf shedding was the result of an annual rhythm not determined by drought stress, as has been found in 'wet-deciduous' tropical trees of western Mexico (Fanjul & Barradas 1987). Even after leaf shedding was complete, both R. incisa and O. sinuatum on the equator-facing slope continued to show decreasing base water potential. Therefore, leaf shedding by these species cannot be viewed as a drought avoidance mechanism. Sobrado (1986) found a clear distinction between the water relations of evergreen and deciduous trees and shrubs of the tropical dry forest of Venezuela, which was ascribed to the different rooting characteristics of these forms (evergreens predominantly deep-rooted, deciduous species predominantly shallow-rooted). However, evergreen and deciduous forms sampled in this study could not be differentiated on the basis of their

seasonal water potential patterns. This suggests that there was no spatial partitioning of water resources between these forms through growth form-specific rooting depth characteristics at the study site, as has been found in more arid systems such as the Mojave desert (Yeaton & Cody 1976). In chaparral it has been shown that heterogenous soil conditions and variable soil depth may favour the development of mixed stands of vegetation (Kummerow & Wright 1988); therefore the variable soil depth and water characteristics found in this study may explain the coexistence of species with similar water requirements.

Halvorsen and Patten (1974) have proposed a qualitative functional grouping of non-succulent arid-zone perennials based on three types of response to seasonal changes in soil water availability. These groups are: (1) slightly responsive, (2) moderately responsive and (3) highly responsive. Representatives of each group could be identified in this study:

1. Relatively constant base water potentials (E. rhinocerotis on both slopes and L. cytisoides on the pole-facing slope), which suggest that these species were accessing perennially available soil water through deeply deployed rooting systems. A similar pattern has been observed in phreatophytes in the Sonoran Desert (Nilsen et. al. 1983, Nilsen et. al. 1984).
2. Relatively large seasonal water potential changes (D. angustifolia on both slopes), which suggests a fairly deeply deployed root system that does not tap soil water as effectively as in the phreatophytic species. Maintenance of cell turgor pressure and transpiration through the summer

drought is probably achieved by diurnal and seasonal osmotic adjustment, which has been found to increase plant tolerance to drought (Turner & Jones 1980).

3. Low base water potentials during the drought period, followed by abrupt recovery after autumn rains (O. sinuatum on the equator-facing and P. incana on both slopes). This pattern has been found to be typical of shallow rooted perennials (Giliberto & Estay 1978, Poole et al. 1981).

However, several species did not fit this grouping. G. africana, P. paniculata and R. incisa all showed considerably greater levels of stress on equator- than pole-facing slopes, which placed them in more than one group. It is well known that plant root systems can be extremely plastic in their form and development, and this was possibly reflected in the greater water stress experienced by individuals of these species growing on the equator-facing slope. Preliminary work has shown that the root systems of G. africana and E. rhinocerotis may penetrate soil to a depth exceeding 7m (Scott & van Breda 1937a,b) in deep soils, but that root development is highly plastic and subject to local soil water conditions.

Only two species (D. angustifolia and E. rhinocerotis) appeared to access the perennially available water source on both slopes. Both species are associated with the relatively more mesic margins of the Cape Fynbos vegetation, rather than the true semi-arid succulent Karoo vegetation type. This may explain their requirement for perennially available water, presumably at the cost of major investment in root biomass.

CONCLUSIONS

The majority of species investigated showed relatively plastic responses to different levels of seasonal water stress, the exceptions being those species with more mesic affinities. On the whole, the dominant non-succulent species of both communities appeared to be highly drought resistant evergreens.

It was not possible to differentiate between evergreen and deciduous species on the basis of their seasonal water potential patterns, and it is possible that plant rooting habit was a principle determinant of these patterns. Root system characteristics could, therefore, provide a basis for an ecologically useful functional classification of non-succulent shrub forms.

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PART 5
CONCLUSIONS

While this research was not concerned with determining the processes responsible for mound formation, it is clear that the characteristics of on-mound soils are consistent with a zoogenic origin. The neutral to high pH on-mound soils differ fundamentally from the surrounding acidic substrate, having higher concentrations of macro- and micro-nutrients, and better water infiltration characteristics.

The low nutrient status off-mound soils support vegetation dominated by evergreen perennial shrubs, while deciduous shrubs occur predominantly on-mound. Off-mound vegetation contrasts strongly with vegetation described for semi-arid mediterranean regions in California and Chile, where deciduous plant forms, better adapted to extended summer drought conditions than evergreens, are dominant. Patterns of soil water availability through the year, and seasonal water potential of some selected non-succulent evergreen shrubs from both substrate types are indicative of severe and extended drought conditions in the shallow soils of the study site during summer. Therefore the success of apparently shallow-rooted non-succulent evergreens at this site is surprising, and emphasises the overriding effect of soil chemical characteristics and nutrient status on vegetation structure and composition on these two substrate types in this area.

Soil water availability does not appear to influence differences in vegetation structure and composition in on- and off-mound situations directly. However, higher soil water content on-mound during autumn, winter and spring may be linked with greater

microbial activity and nutrient turnover in that soil type. Therefore soil water may play an indirect role, in combination with soil chemical characteristics and nutrient availability, in determining vegetation structure and composition on the two main substrate types in the study area.

Some non-succulent species appear to avoid summer drought conditions to a greater or lesser extent by tapping either a 'perched' or true water table, presumably through investment in deep, extended rooting systems, and cannot be viewed as drought resistant. However, these species tend to be associated with the relatively more mesic margins of fynbos areas, and are not common in nor characteristic of the karroid vegetation of the Worcester-Robertson valley. The success of apparently shallow-rooted evergreen perennials, which dominate off-mound vegetation together with succulent forms and are an important component of on-mound vegetation, can be partially explained by their ability to survive low soil water potential and internal water deficit. Further research on this important group of species is necessary to elucidate the mechanism by which their extreme drought resistance is achieved, and to establish their tolerance limits. It is not possible to differentiate between the selected non-succulent deciduous and evergreen forms on the basis of their seasonal water potential patterns, probably because of the importance of plant rooting characteristics in determining these patterns. Plant root system characteristics could therefore provide a basis for an ecologically useful functional

classification of non-succulent shrub forms in this semi-arid area.