STRUCTURE, DISTRIBUTION AND PHENOLOGY OF PERENNIAL PLANT SPECIES IN THE WORCESTER VELD RESERVE, IN THE ARID WINTER RAINFALL REGION OF THE SOUTHWESTERN CAPE.

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SUBMITTED IN PARTIAL FULFILMENT OF THE M.Sc.-DEGREE IN PLANT
ECOLOGY, UNIVERSITY OF CAPE TOWN

OCTOBER 1989

CONTENTS

Acknowledgements

Thanks to Barry and Fiona for the various ways in which they assisted.

Eugene Moll (supervisor) and Dick Yeaton helped to keep the study on track.

Pascale Chesselet did the anatomical illustrations in Chapter two.

Thanks to Timm Hoffman for critically commenting on and scrutinizing the entire manuscript, and to Pascale Chesselet for critical comments on Chapters two and three. Eugene Moll commented on earlier drafts.

The Botanical Research Institute (Dept. of Agriculture and Water Supply) provided meteorological data.

C.S.I.R. (F.R.D) provided financial support.

My thanks to the Department of Agriculture and Water Supply (Winter Rainfall Region) for permission to do research in the Worcester Veld Reserve.

ABSTRACT

High structural diversity amongst plant species in the arid winter rainfall region of southern Africa is common to other arid regions of the world. Details of the range and combinations of structural attributes in species, and within plant communities, are not widely known for southern African arid ecosystems. Hence little is known of how plant-form distributions vary within and between arid ecosystems, and of the environmental factors that may be responsible for any variations found. Nor is much information available on how phenological behaviour relates to the structural attributes of plant species.

This study examined structural attributes of perennial plant species on the Worcester Veld Reserve, southwestern Cape, in relation to their distribution and phenology. Species were grouped on the basis of aboveground structural and anatomical criteria. The distribution of species and plant-forms was assessed through a phytosociological survey along an environmental gradient in the area, and their phenology determined through qualitative and quantitative monitoring of species phenophases over a two year period.

The results show that species of the predefined structural groups :

i) Co-occur throughout the area, but relative abundances vary from site to site and in relation to topography, aspect and the presence of Mima-like mounds;

ii) Phenological patterns for the flora overall are strongly seasonal, but the timing and periods of phenophases differ between, but are relatively uniform within, the defined structural plant

groups.

Since phenological patterns are indicative of resource-use patterns, these results indicate that the different plant-forms have different functional responses to the conditions of limited water availability and summer drought. This conceivably facilitates the co-existence of species in this water-limited environment. Habitat variability, which can be related to land-form patterns, is also implicated as a factor facilitating the co-existence of a diversity of species and plant-forms.

Structural - functional relationships known for arid region plants help to explain the relative uniformity of behaviour within plant-form groups, and aid in understanding the ecological significance of distribution patterns of plant-forms in the arid landscape. The conclusion is reached that because of the close coupling between photosynthesis and water-use, the water storage potential and photosynthetic organ type are plant attributes which can serve as useful criteria by which arid region species can be grouped into ecologically meaningful categories or functional guilds. The formulation of a practical and meaningful functional classification is necessary to facilitate the understanding of complex vegetation patterns and processes within arid ecosystems, and allow for meaningful inter-ecosystem comparisons.

1 GENERAL INTRODUCTION

The vegetation of the Succulent Karoo (sensu Rutherford and Westfall 1986) in southern Africa is described as a dwarf shrubland (see Acocks 1953; Cowling 1986; Hoffman and Cowling 1987). However, a great variety of species and plant-forms are present in what appears superficially to be a structurally uniform shrubland. Some plant-forms (e.g. succulents) are not restricted to arid regions, but in these regions they may occur in great abundance. Other forms are unique to water-limited environments (Solbrig 1986). It is widely suggested that low rainfall, and in some arid regions, the unpredictability of rainfall, is the main ecological driving force in these systems (Noy-Meir 1973; Westoby 1980; Hoffman and Cowling 1987). Thus, the physical structure of plants in arid-lands is assumed to be an expression of adaptations to survival under conditions of limited and sporadic water availability. Although it is believed that certain structural adaptations are always present in arid region plants (xeromorphy) available evidence suggests that this is not necessarily so (Mooney 1974; Seddon 1974; Solbrig et al.1977). Indeed, certain structural features are confined to or abundantly present in plants of arid regions (Fahn 1964), but many species do not have "unusual" features relative to species in non-arid regions. This suggests that there has been no simple or uniform structural adaptive response to conditions of aridity which could lead to competitive superiority (Mooney 1974). The fact that many arid regions have a great diversity of plant-forms, co-existing successfully within the same environment, supports this deduction (Solbrig 1986). The central questions arising are whether, and how, limited available water is partitioned amongst species, and what, if any, are the stuctural attributes which enable or improve such partitioning and hence, co-existence. Within the context of plant community ecology in arid ecosystems, these are the main questions being addressed in this thesis.

This study examines both temporal and spatial aspects in relation to plant structural characteristics in 39 co-occuring perennial species in an arid area protected from utilization by domestic stock. These 39 species were grouped according to leaf and stem structural criteria (Chapter 2). A phytosociological survey of species and of plant-forms examines spatial aspects (Chapter 3), and a phenological study over a two year period is used to investigate temporal aspects (Chapter 4). Results are examined for any associations in behaviour and distribution between the predetermined groups. These were interpreted in terms of the functional significance of any such relationships. The results are furthermore interpreted in the context of current ideas and concepts of structural-functional relationships of plant species in arid ecosystems, and how these relate to plant community patterns and processes.

1.1. REFERENCES

Acocks, J.P.H., 1953. Veld types of South Africa. Mem. Bot. Surv. S.A. 28 : 1-128.

Cowling, R.M., 1986. A description of the Karoo Biome Project. S.A. Nat. Sci. Prog. Report no. 122, F.R.D., C.S.I.R., Pretoria.

Fahn, A., 1964. Some anatomical adaptations of desert plants. Phytomorphol. 14 : 93 -102.

Hoffman, M.T. and Cowling, R.M., 1987. Plant physiognomy, phenology and demography. Ch. 1 in : Cowling,R.M. and Roux, P.W. (eds.). 1987. The karoo biome - a preliminary synthesis part 2 - vegetation and history. S.A. Nat. Sci. Progr. no. 142, C.S.I.R., Pretoria.

Mooney, H.A., 1974. Plant forms in relation to environment. Ch. 7 in : Strain, B.R. and Billings, W.D., (eds.), 1974. Vegetation and environment. Dr. W. Junk, The Hague.

Noy-Meir, I., 1973. Desert Ecosystems : Environment and producers. Ann. Rev. Ecol. Syst. 4 : 25-51

2 STRUCTURAL AND ANATOMICAL CHARACTERISTICS OF PERENNIAL PLANT SPECIES IN THE WORCESTER VELD RESERVE

2.1 Introduction

There is great structural diversity amongst plant species in desert and arid ecosystems. Many plant-forms are unique to, or abundant in these regions (Solbrig *et al.*1977; Solbrig 1986). However, there appears to be no universally accepted system by which arid region plants can be classified into ecologically meaningful structural groups. This problem is exacerbated by a lack of uniformity in relevant terminology (see Seddon 1974). Because structural attributes represent the phenotypic expression of a plant's adaptive strategy (Ayyad 1981), and because form is a partial expression of niche (Root 1967), the use of any particular structural classification in ecological studies warrants careful consideration.

Raunkiaer's (1934) classification of life-forms, based on leaf-type and the position of the perennating buds, is widely used in ecological studies. However, it is thought to be ecologically relatively meaningless in grouping arid region plants (Orshan 1953; Schulze 1982; Hoffman and Cowling 1987). The critical environmental factor on which Raunkiaer's system is based, namely severe seasonal snowfall, is largely absent from arid environments. Instead, the most critical limiting factor in arid ecosystems is the low and sporadic amounts of available moisture, and major structural attributes should reflect adaptations to this selective agent. For example, many species of arid regions can be classed as chaemaphytes according to Raunkiaer's system, but would in fact contain a diversity of structural types, including leaf succulents, sclerophylls and mesophylls (also see Hoffman and Cowling 1987). The functional significance of the structural diversity amongst arid region plants is not explicit in this classification.

Since Raunkiaer's classification (1934), several ecological classifications have been proposed for arid region vegetation. Some of these are based on life-history characteristics alone (e.g. drought avoiders, drought tolerators and drought endurers - after Shantz 1956,in McGinnies 1979; see also Noy-Meir 1973; Gupta 1979; Solbrig 1986) and give no indication of how structural attributes are related to these types. Other proposals include both structural and life-history traits, notably those of Shreve (1942, in McGinnnies 1979) and Orshan (1953), where type and behaviour of the photosynthetic organs are the major criteria. Although more detailed and meaningful, the structural-functional relationships pertaining to survival in conditions of aridity are not clearly enunciated by these authors. In southern Africa, none of these classifications have been formally accepted or are in general use (see Hoffman and Cowling 1987).

A further problem is the ambiguity that has evolved around terms and concepts which define structural adaptations to conditions of aridity (Seddon 1974). For instance, "xerophytes" (drought-loving plants) are not necessarily confined to arid regions since particular species may occupy xeric niches in an otherwise mesic environment (see Seddon 1974; Solbrig 1986). Furthermore, structural and anatomical characteristics associated with water-limited conditions are not necessarily confined to arid region species, and classical xeromorphic features (e.g. sunken stomata, thick cuticle, pubesence, succulence, and small thick-walled cells) may in fact be absent in some arid region species (Kummerow 1973, Seddon 1974; Solbrig et al. 1977). Also, "xeromorphosis", which is the plastic and often seasonal structural response to decreasing moisture availability, is known for plants in mesic and xeric environments (Kummerow 1973). Since these terms are ambiguously used in the literature, I largely avoid their use in this paper. Here I will simply refer to "plant-form" which is defined to mean the aboveground structure of a plant without implying any adaptive significance. Anatomical and micro-structural features were assessed as a separate aspect in this study, with the aim of determining the range and combination of these features present in any particular structural type or plant-form. This affords the opportunity to determine to what extent species of an arid region have "xeromorphic" features, and how anatomical and micro-structural characteristics relate to the gross morphology and life-history of species.

To date, basic aspects of vegetation form and function have not received much attention in southern Africa's arid ecosystems. The aim of this study is to determine the range of plant-forms, and the structural and anatomical attributes associated with them, for perennial plant species in a part of the Succulent Karoo (sensu Rutherford and Westfall 1986). The study is a preliminary assessment of the structural and anatomical attributes for species of this region, and which could serve as a basis for the investigation of these aspects in other arid ecosystems of southern Africa. Comprehensive assessment of form and structural diversity throughout these regions will contribute significantly towards the definition of plant functional guilds which form meaningful ecological units (Root 1967; Cowling 1986). Such definition may help to interpret complex vegetation patterns and processes in arid lands.

2.2 Methods

2.2.1. Plant-forms

The aboveground form of 39 co-occurring perennial species was assessed throughout the Worcester Veld Reserve (WVR), a protected area in the arid winter rainfall region of the southwestern Cape. The consistency of leaves and stems, and the type of primary photosynthetic organ (whether leaf or stem) was noted. Because of an apparent relationship between the annual behaviour of the photosynthetic organ and its consistency (see for instance Chapter 4; Orshan 1989) I included leaf behaviour (a life-history trait) as an additional criterion for the classification of species.

The consistence categories used were succulent, semi-succulent, mesophyllous, and sclerophyllous for leaves, and woody or succulent for stems. Succulence is taken as a relative measure of the internal water-storage potential of a species. Although the exact boundaries between these classes are debatable (see Cowling and Campbell 1983), I believe that most of the leaves and stems of the different species fall clearly into one or other of these categories. Evergreeness and deciduousness were used as leaf-behaviour classes. Again the delimitation is debatable (facultative deciduous species are known for certain arid regions - Miller 1988), but most species of this study can be unambiguously defined as evergreen or deciduous.

2.2.2 Leaf anatomy

22 of these 39 species were selected for the purpose of anatomical investigation. Mature leaf specimens were obtained during the early spring of 1987, and were fixed in FAA for several weeks. Standard histological techniques (Clayden 1955; Duddington 1960) were used to produce permanently mounted transverse sections of leaves and stems. Sections were stained with Fast Green and Safronin O (Johansen 1940). Sections were photomicrographed, and used for inter- and intra-specific comparison of anatomical and micro-structural features of photosynthetic organs. Xylem vessel diameters and wall thicknesses were measured with the aid of a graticule (micrometer).

A character matrix for the 22 species was constructed. This was used to assess patterns and trends in anatomical features. A representative sample of the defined structural groups was illustrated.

2.3 Results

2.3.1 Plant-forms

Six distinct groups were recognized on the basis of leaf and stem consistency, leaf anatomy and leaf or stem behaviour classes, and are described below. Height classes are adopted from Cowling 1986 :

1. EVERGREEN SCLEROPHYLLS (ESC). Mid-high (1 - 2 m), woody-stemmed shrubs with relatively small (5 - 30 mm long) and hard leaves, and no water-storage potential.
2. EVERGREEN LEAF SUCCULENTS (ELS). Dwarf (0 - 0.25 m) and low (0.25 - 1 m), woody-stemmed shrubs with relatively large (15 - 60 mm long) but true succulent leaves. Leaf shape is generally globose or cylindrical. Water-storage in leaves only.
3. EVERGREEN STEM SUCCULENTS (ESS). Mid-high shrubs with numerous (5 - 100 +) slender and cylindrical succulent stems. Stems are the primary photosynthetic organs, and are evergreen. Small (2 - 25 mm long), semi-succulent leaves are produced seasonally. Water-storage potential is in the stems and is relatively high.
4. DECIDUOUS MESOPHYLLS (DM). Dwarf and low to mid-high woody-stemmed shrubs with soft leaves and no water-storage potential.
5. DECIDUOUS LEAF SUCCULENTS (DLS). Dwarf and low woody-stemmed shrubs with semi-succulent leaves which are deciduous. No stem water-storage, but some water-storage

Table 2.1. List of defined plant-form categories and perennial plant species of the WVR assigned to these (see Methods)

EVERGREEN SCLEROPHYLL : *Chrysocoma coma-aurea* L.; *Euclea undulata* Thunb.; *Felicia filifolia* (Vent.) Burtt Davy; *Galenia africana* L.; *Passerina obtusifolia* Thoday; *Pteronia incana* (Burm.) Dc.; *Pteronia fastigiata* Thunb.; *Pteronia paniculata* Thunb.; *Relhania squarrosa* (L.) L'Herit.

EVERGREEN LEAF SUCCULENT : *Adromischus filicaulus* (Eckl. & Zeyh.) C.A. Sm.; *Aloe microstigma;* *Aridaria* sp. N.E. Br.; *Crassula atropurpurea* (Haw.) Dietr.; *Crassula rupestris* Thunb.; *Crassula subaphylla* (Eckl. & Zeyh.) Harv.; *Crassula tetragona* L.; *Drosanthemum speciosum* (Haw.) Schwant.; *Haworthia* sp. Duval; *Kleinia radicans* (L.f.) Harv.; *Lampranthus haworthii* (Donn.) N.E. Br.; *Ruschia caroli* (L.Bol.) Schwant.; *Ruschia multiflora* (Haw.) Schwant.

EVERGREEN STEM SUCCULENT : *Euphorbia burmannii* E. Mey. Ex Boiss.; *Euphorbia mauritanica* L.; *Psilocaulon* sp. N.E. Br.; *Sarcostemma viminale* (L.) R. Br.; *Senecio junceus* (DC.) Harv.

Table 2.1. (continued)

DECIDUOUS MESOPHYLL : *Hirpicium integrifolium* (Thunb.) Less.; *Lightfootia tenella* Lodd.; *Pentzia incana* (Thunb.) Kuntze; *Rhus incisa* L.

DECIDUOUS LEAF SUCCULENT : *Delosperma pageanum* (L. Bol.) L. Bol.; *Drosanthemum hispidum* (L.) Schwant.; *Lycium* sp. L.; *Osteospermum sinuatum* (DC.) T. Norl.; *Tetragonia fruticosa* L.; *Tetragonia sarcophylla* Fenzl.

STEM STORAGE SUCCULENTS : *Othonna arbuscula* (Thunb.) Sch. Bip.; *Pelargonium alternans* Wendl.; *Senecio corymbiferus* Dc.; *Tylecodon paniculatus* (L.F.) Toelken in leaves.

6. STEM STORAGE SUCCULENTS (SSS). Dwarf and low to mid-high shrubs with relatively large and "swollen" succulent stems. Stems are non-photosynthetic, and with seasonal semi-succulent or succulent leaves, which are deciduous.

Species assigned to the various groups are listed in Table 2.1. The taxonomy of Gibbs Russell *et al*. (1985) was followed. Most species could unambiguously be classed into the respective structural classes, with perhaps the exception of *Galenia africana*. This species behaves and looks like a typical evergreen sclerophyll, but the leaves are not sclerophyllous and also possess bladder cell idioblasts as in other succulents.

2.3.2 *Leaf anatomy*

Anatomical features are summarized in table 2.2 and are discussed below. Anatomical features of some species, representative of the different plant-form groups, are illustrated in Figures 2.2 to 2.7.

Only two species have true sunken stomata (*Euphorbia mauritanica*, *Euphorbia burmannii*) whereas *Sarcostemma viminale* has partly sunken stomata. These are all evergreen stem succulents and have milky latex. In three species of Mesembryanthemaceae stomata are not superficial in the sense that they are level with the outermost layer of cells, but are situated at the base of bladder-cell idioblasts. This could be viewed as a special type of sunken stomata

Table 2.2. Summary of anatomical characteristics for 22 perennial plant species of the Worcester Veld Reserve

SPECIES	1	2	3	4	5	6	7	8	9	10	11	12
P. paniculata	L	C	S	P	1	R	-	-	-	VT	+	S
P. fastigiata	L	C	S	P	1	R	-	-	-	VT	-	S
P. incana	L	C	S	P	1	R	-	U	-	-	-	-
G. africana	L	CM	S	PH	1	?	B	-	D	-	-	-
H. integrifolium	L	M	S	PS	1	?	-	UM	-	-	-	P
T. fruticosa	L	o	P	PH	1	?	B	-	?	-	-	-
T. sarcophylla	L	o	P	H	1	?	B	-	D	-	-	P
O. sinuatum	L	o	P	H	1	F	-	-	-	-	-	-
T. paniculatus	L	o	P	H	1	F	-	-	R	-	-	-
S. corymbiferus	L	S	P	H	1	F	-	-	-	-	-	-
O. arbuscula	L	o	P	H	1	F	-	-	-	-	-	-
A. filicaulus	L	S	P	H	1	F	-	-	RG	-	-	-
D. speciosum	L	S	P	H	1	?	B	-	P	-	-	-
R. caroli	L	S	P	H	1	n	b	-	RPG	-	-	P
K. radicans	L	S	P	H	2	F	-	-	-	-	+	-
R. multiflora	L	S	P	H	1	F	-	-	-	-	-	-
L. haworthii	L	S	P	PH	1	n	b	-	RPG	T	-	-
C. subaphylla	L	S	P	H	1	?	-	-	R	-	-	-
S. viminale	S	S	P	PH	3	n	-	-	RD	P	-	-
E. mauritanica	S	S	P	H	3	S	-	-	-	-	-	-
Psilocaulon sp.	S	S	P	H	2	?	-	-	R	T	-	-
E. burmannii	S	S	P	H	3	S	-	-	D	P	-	-

Key :

? - Not determined
- Feature absent

1. Photosynthetic organ type: L - leaf; S - stem
2. " " consistency : C - sclerophyll; M - mesophyll; o - semi - succulent; S - succulent
3. Quantity of parenchyma : S - small; P - large
4. Photosynthetic tissue types : P - palisade-like; S - spongy mesophyll; H - homogenous parenchyma
5. Epidermis : 1 - single layer; 2 - one hypodermal layer; 3 - two hypodermal layers
6. Stomata : R - raised; F - superficial; n - slightly sunken; S - sunken
7. Bladder cell idioblasts : b - small; B - large
8. Pubesence : U - unicellular hairs; M - multicellular hairs
9. Crystals : R - red rhomboidal; D - druses; P - raphides; G - granular
10. Sclerification : V - vascular bundle; T - support bundles; P - phloem
11. Ducts : + - present
12. Bundle sheath : S - sclerified; P - parenchymatous

(Ihlenfeldt 1983). Stomata are superficial in the other succulent taxa. Raised stomata are present in sclerophyllous species (*P. paniculata*, *P. fastigiata*, *P. incana*). This has also been found for certain other evergreen shrubs in the Karoo region (H. Kruger, unpubl.).

Three of the four photosynthetic stem succulents have two hypodermal layers (*E. mauritanica*, *E. burmanni*, *S. viminale*) and one leaf succulent species has one hypodermal layer (*Kleinia radicans*). Other species investigated lack the hypodermal layer(s), but epidermal cells show large variation in size and shape amongst species. Two species are pubescent (*P. incana*, *H. integrifolium*), the latter species having both multi- and unicellular hairs. A sticky resin is secreted seasonally by *P. paniculata* onto the leaf-surface.

Organization and type of photosynthetic tissue varies in relation to leaf consistency. In all succulents, including the semi-succulent *T. paniculatum*, only homogeneous chlorenchyma is present. However, there is some differentiation of cells peripherally in at least three leaf succulent species. These chlorenchyma cells, and the water-storage parenchyma, are all thin-walled and elastic and are able to withstand considerable shrinkage and expansion in relation to water status (pers. obs.). Only one species has true palisade and spongy mesophyll tissue (*H. integrifolium*). Palisade-like tissue without spongy mesophyll is present in the three sclerophyllous species (*P. paniculata*, *Pteronia incana*, *P. fastigiata*). *G. africana* also have palisade-like tissue but have a small quantity of central parenchymatous tissue as well.

No evidence of Krantz anatomy, indicative of the C4 photosynthetic mode, was evident in any of the species investigated.

Except for the stem succulents and K. radicans, A. filicualus (ELS) and S. corymbiferous (SSS), all species have a central primary vascular bundle in the leaves, with scattered secondary and tertiary bundles. The latter three species have no central bundle but have bundles situated towards the periphery of the leaves.

A scattergram of xylem vessel diameters against wall thicknesses (Fig. 2.1) show a range from : (1) small diameter vessels with thick walls to; (2) large diameter vessels with relatively thin walls. Sclerophylls are associated with (1), and evergreen stem succulents with (2). Stem storage and leaf succulents are clumped as a group between these two extremes. H. integrifolium, the deciduous mesophyll, appears transitional between sclerophylls and the leaf succulent group. There are three exceptions to this trend, viz. C. rupestris is grouped closer to sclerophylls than leaf succulents; T. fruticosa is grouped with the evergreen stem succulents and not with other mesophylls; and the evergreen stem succulent, Psilocaulon sp. is grouped with the leaf succulent group.

Lacunae, presumably lined with secretory cells, are present in K. radicans, and ducts are present in P. paniculata. The function of the former is not known, but the latter are probably resin ducts since this species seasonally excretes

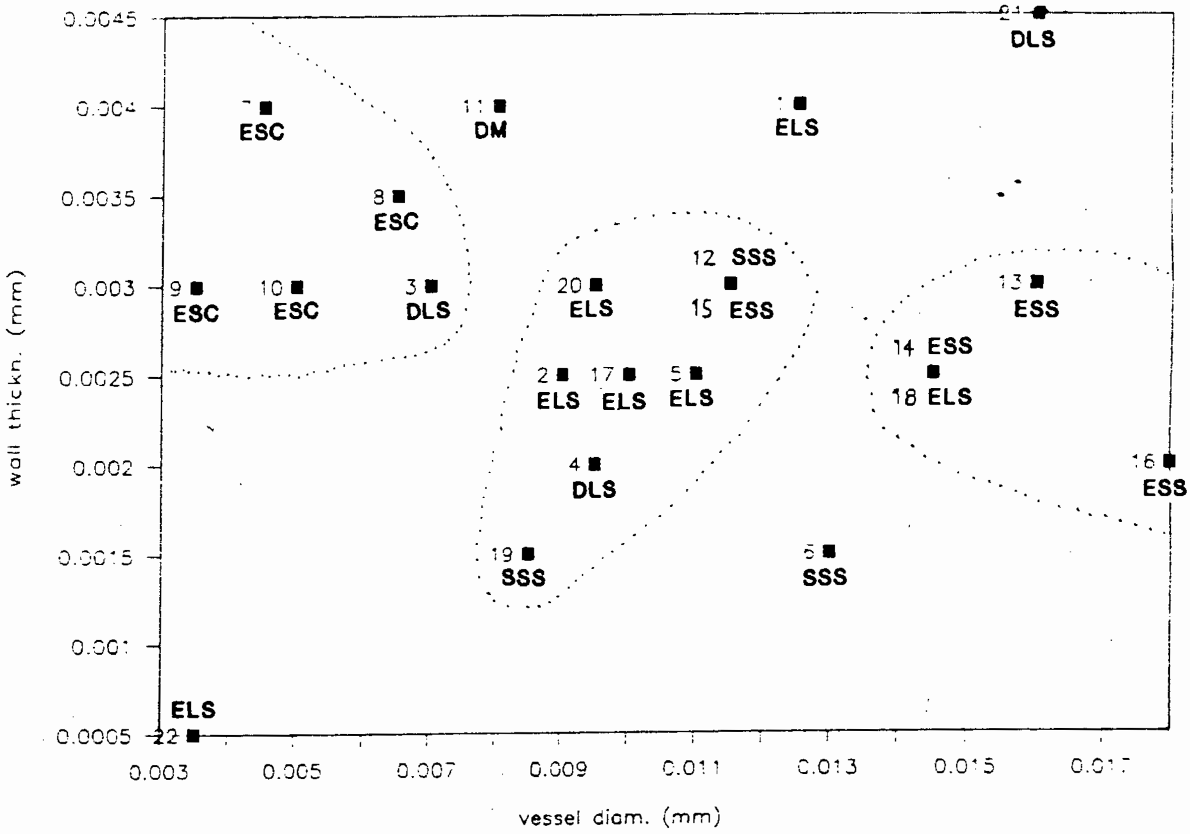
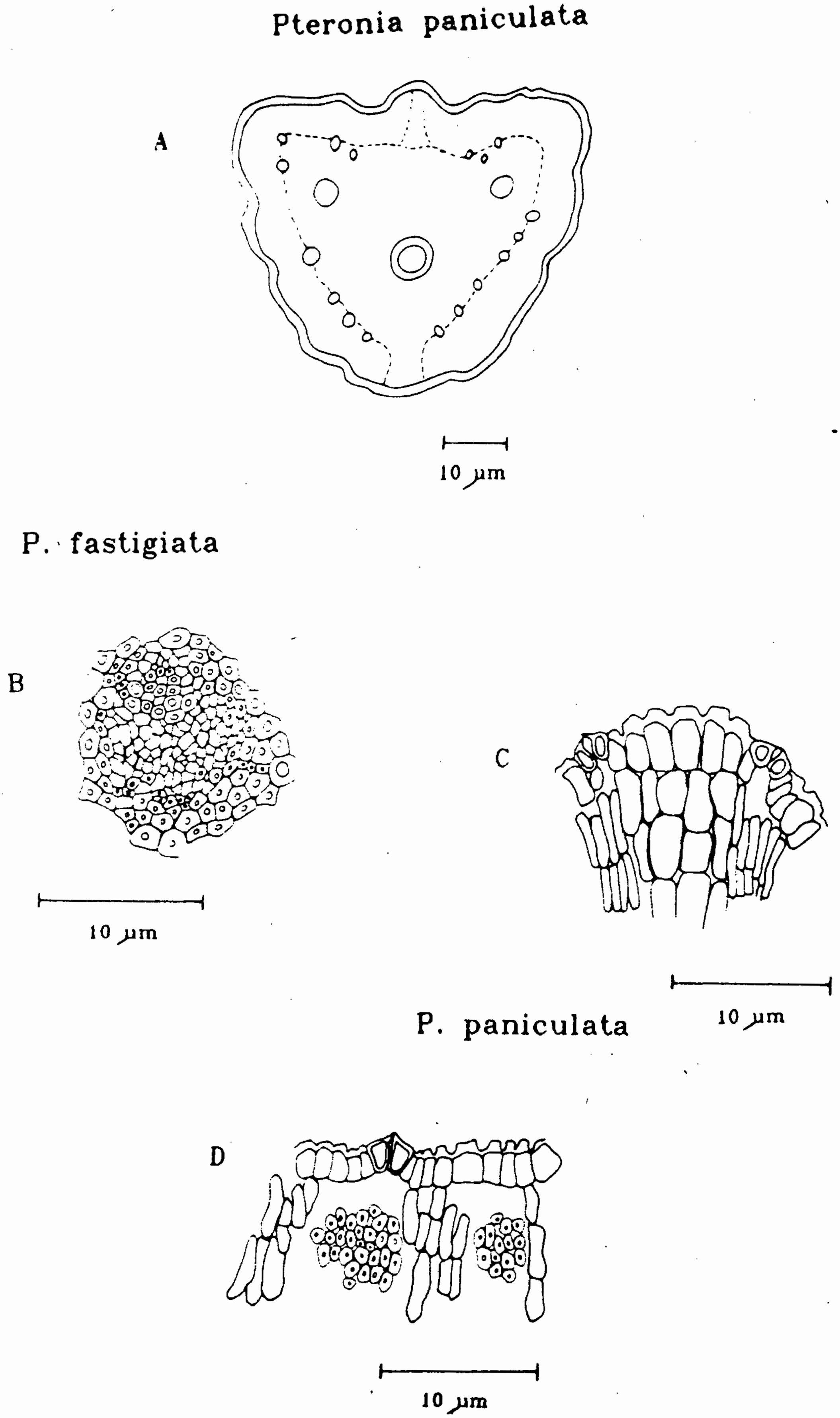


Fig.2.1. Scattergram of xylem vessel diameters vs. xylem vessel wall thicknesses for 22 perennial plant species of the Worcester Veld Reserve. KEY :(1) A. filicaulus (2) D. speciosum (3) T. sarcophylla (4) O. sinuatum (5) R. caroli (6) T. paniculatus (7) P. fastigiata (8) P. paniculata (9) G. africana (10) P. incana (11) H. integrifolium (12) S. corymbiferus (13) S. viminale (14) E. mauritanica (15) Psilocaulon sp. (16) E. burmannii (17) K. radicans (18) R. multiflora (19) O. arbuscula (20) L. haworthii (21) T. fruticosa (22) C. subaphylla. SSS - Stem-storage succulent ; DLS - Deciduous leaf succulent ; DM - Deciduous mesophyll ; ESS - Evergreen stem succulent ; ELS - Evergreen leaf succulent ; ESC - Evergreen sclerophyll



Pteronia paniculata

P. fastigiata

P. paniculata

Fig. 2.2. Leaf anatomical features of evergreen sclerophyll species (ESC). a) Plan of leaf section; b) detail of vascular bundle; c) detail of parenchyma and palisade tissue; d) detail of stoma and sclereid bundles

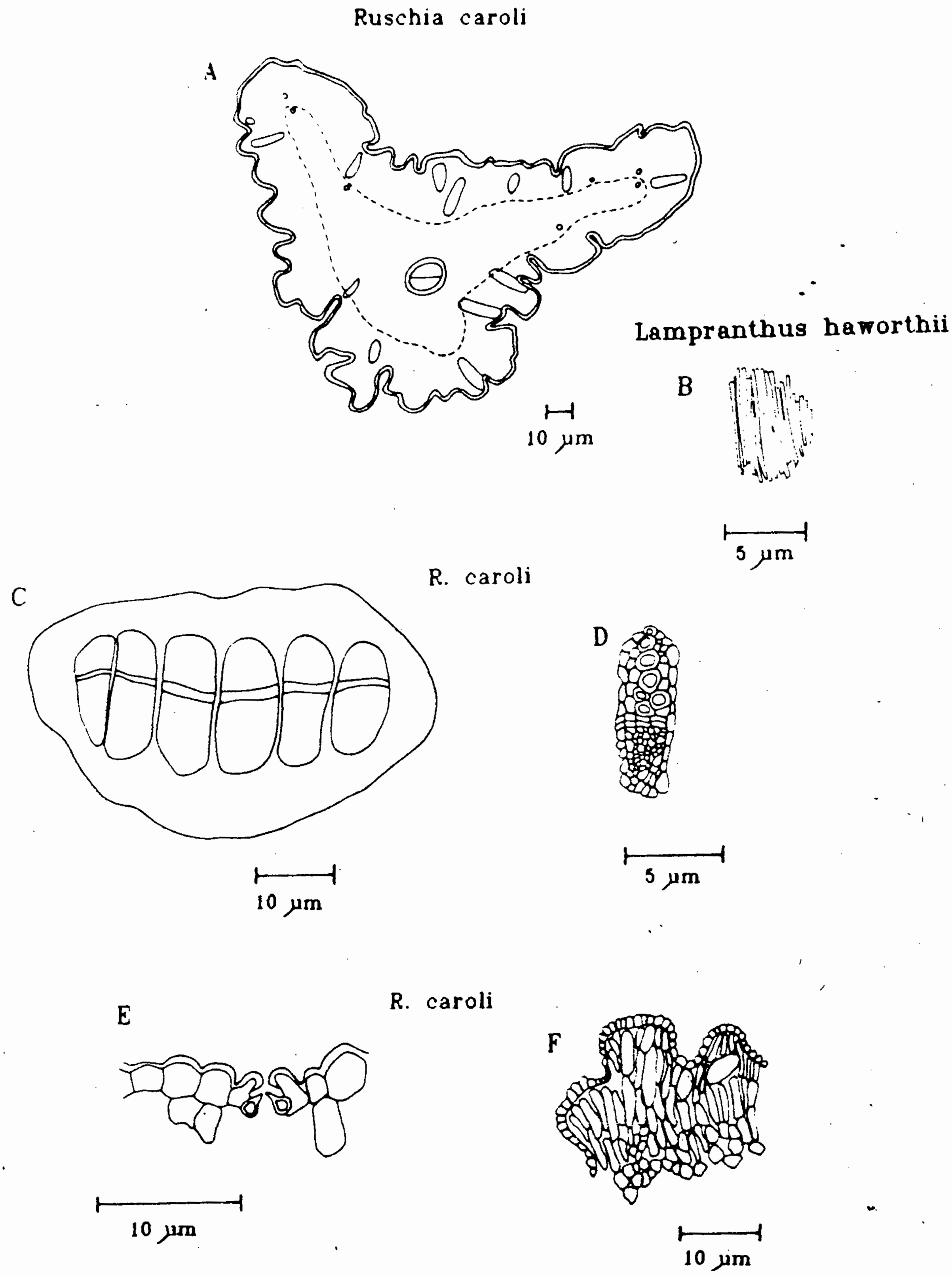


Fig. 2.3. Leaf anatomical features of evergreen leaf succulent species (ELS). a) Plan of leaf section; b) raphide crystals; c) plan of vascular bundle; d) detail of part of vascular bundle; e) detail of stoma; f) detail of photosynthetic tissue

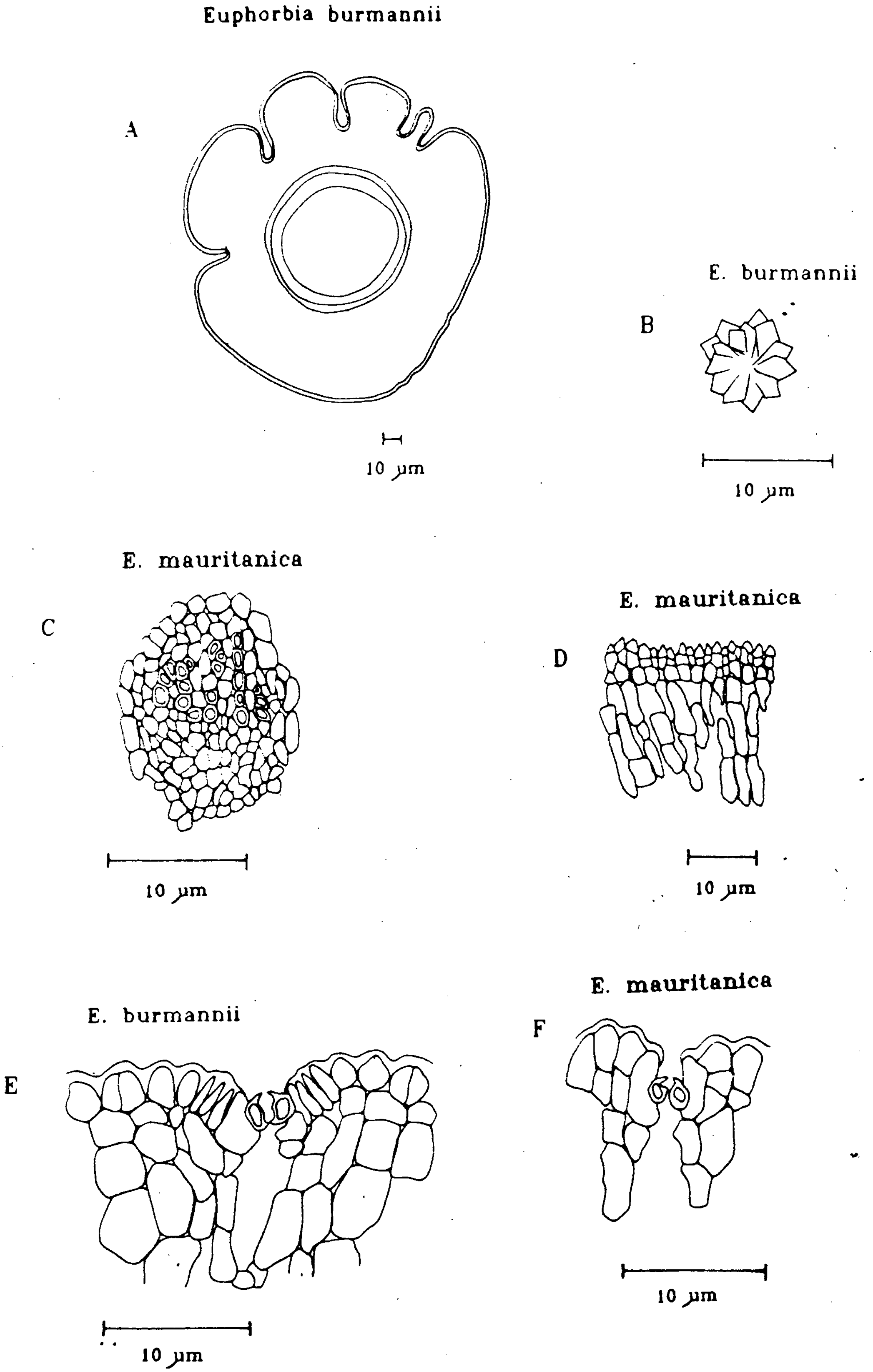


Fig. 2.4. Stem anatomical features of evergreen stem succulent species (ESS). a) Plan of stem section; b) druse crystal; c) detail of vascular bundle; d) detail of epidermis and photosynthetic tissue; e) detail of stoma; f) detail of stoma

Hirpicium integrifolium

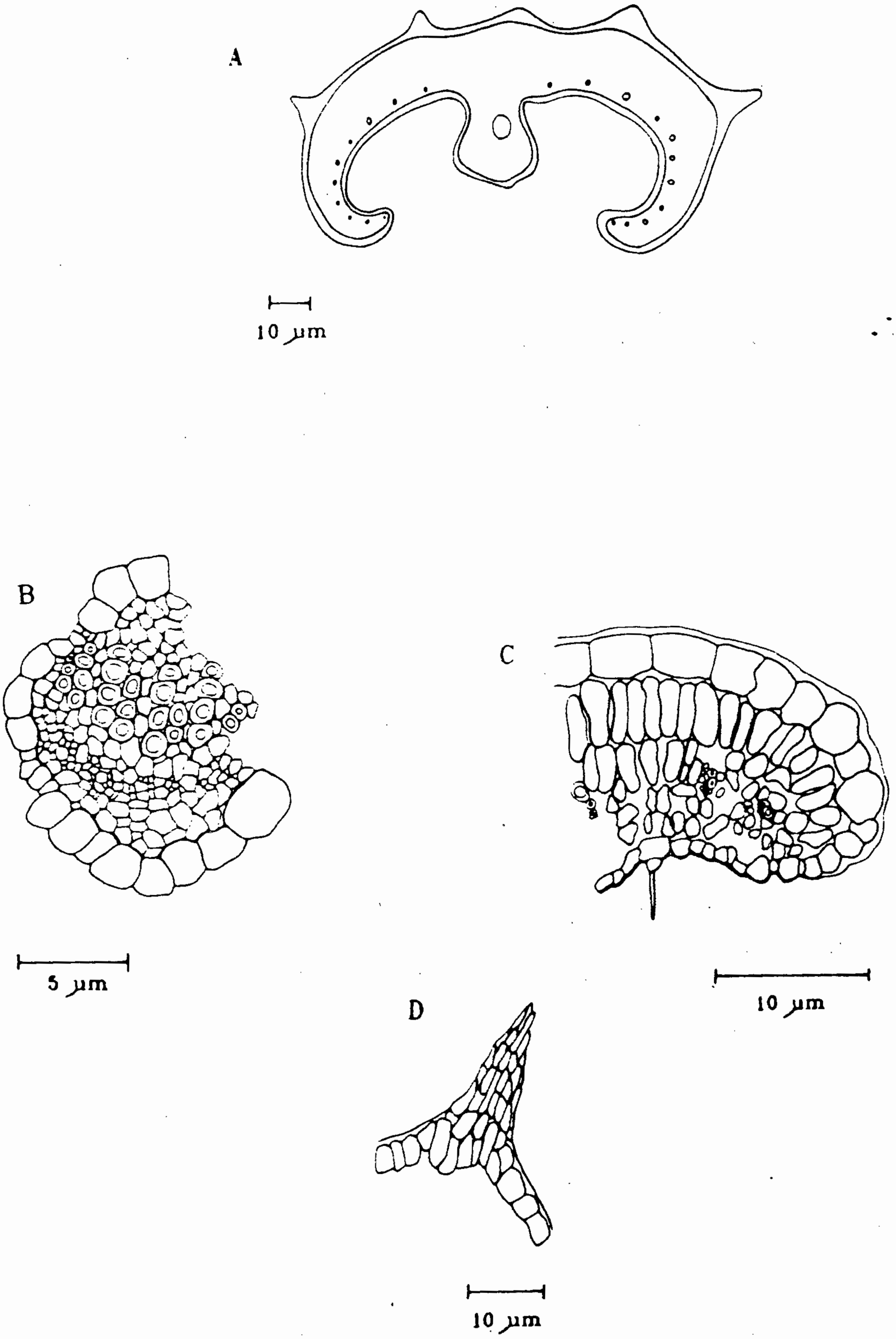


Fig. 2.5. Leaf anatomical features of a deciduous mesophyll (DM). a) Plan of leaf section; b) detail of vascular bundle; c) detail of epidermis, palisade and spongy mesophyll tissue; d) detail of adaxial multi-cellular hair

Osteospermum sinuatum

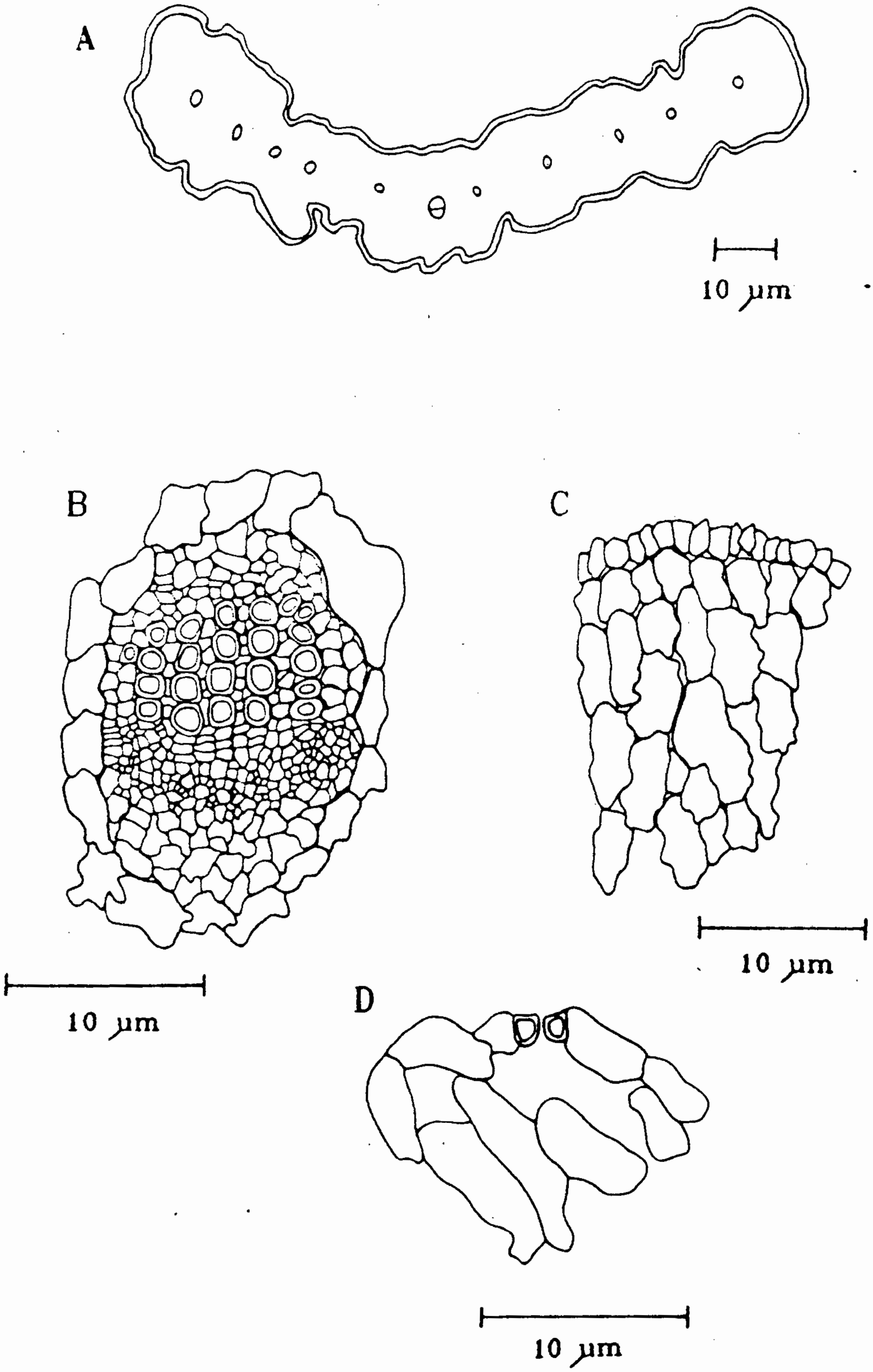


Fig. 2.6. Leaf anatomical features of a deciduous leaf succulent (DLS). a) Plan of leaf section; b) detail of vascular bundle; c) detail of photosynthetic tissue; d) detail of stoma

Othonna arbuscula

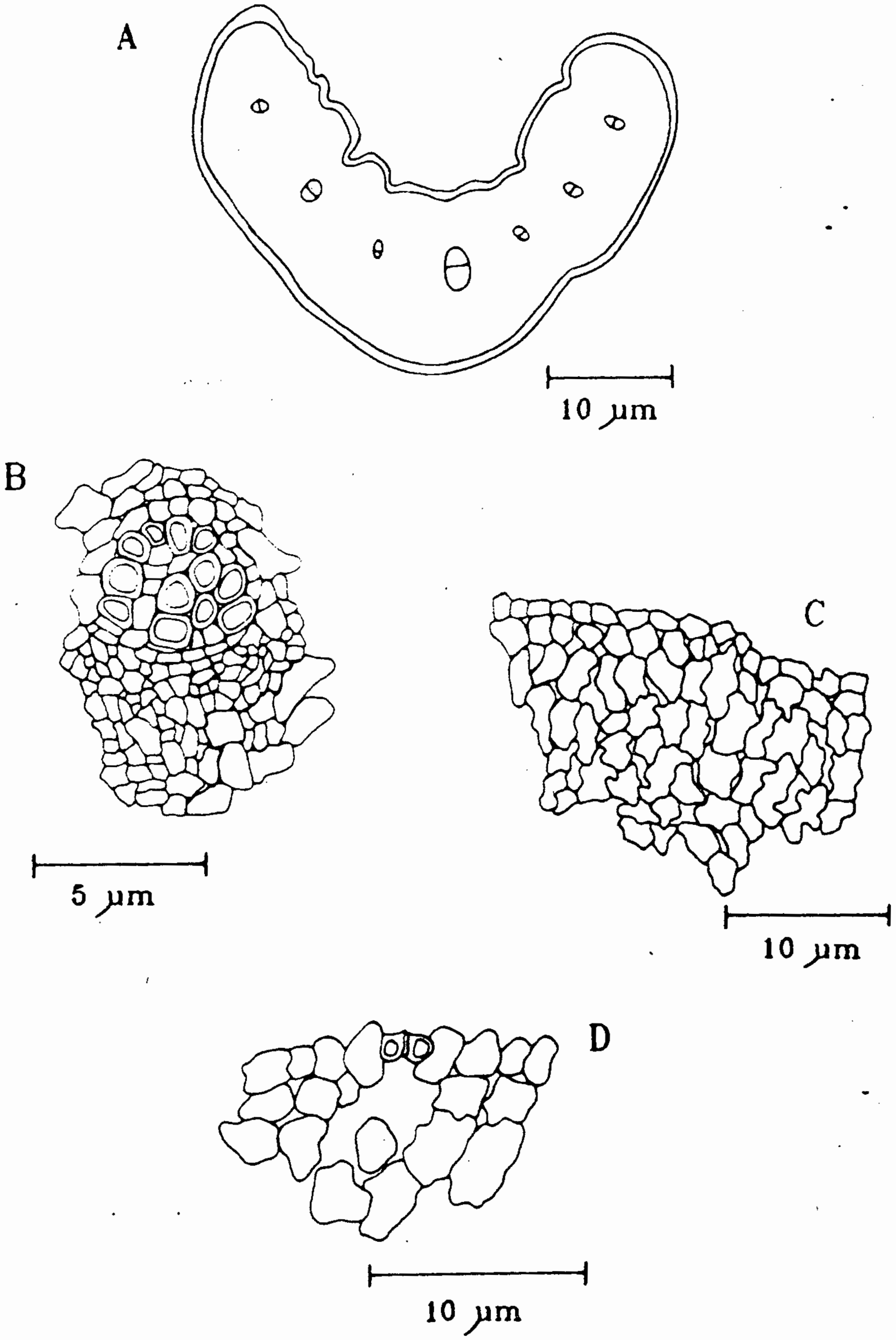


Fig. 2.7. Leaf anatomical features of a stem storage succulent (SSS). a) Plan of leaf section; b) detail of vascular bundle; c) detail of photosynthetic tissue; d) detail of stoma

resin onto the leaf-surface.

Different types of crystals were present in some species. Red rhomboidal crystals were the most common, and were numerous in some of the species in which they occured. Crystals were confined to species with succulent characteristics.

2.4 Discussion

2.4.1 Plant forms

The results show that six distinct groups of plants can be defined on the basis of leaf and stem consistency, and the longevity and nature of the primary photosynthetic organ. The primary dichotomy between groups is based on evergreeness or deciduousness, and within these on the nature (i.e. whether leaf or stem) and consistency of the primary photosynthetic organ. There appears to be a consistent interrelationship between the presence of specific attributes, viz. species with sclerophyllous leaves are all woody-stemmed and evergreen, without any water-storage potential, whereas mesophyllous species are woody-stemmed but deciduous. Among succulents, in species with slender succulent stems, the stems are the primary photosynthetic organ and are evergreen. Three out of four of these species also have secondary deciduous leaves. Species with a single, massive succulent stem are all deciduous with semi-succulent to succulent leaves. This is suggestive of functional interrelationships between the various attributes used in classifying the species. In other words, possesion of a particular attribute necessitate the co-occurence of other specific attributes, and these combinations may be relatively constant for arid region species because of the physical and developmental constraints imposed by the environment. It may also include consistent relationships between the root-type and aboveground plant-form (see Noy-Meir 1973, Drew 1979). This concept is developed further in later chapters of this thesis (Chapter 4 and 5).

2.4.2 Anatomical features in relation to plant-forms

Anatomy provide a view of the internal structure of plants, and the anatomical structure of the photosynthetic organs must thus partially contribute to the overall structure and form of a species. The results from this study show that there is relative uniformity in the anatomical characteristics amongst species within the respective predefined plant-form groups. Common features and exceptions for the different groups are summarized below :

i) ESC : Photosynthetic tissue (PT) is palisade-like, with no or little spongy mesophyll or parenchymatous tissue. Stomata are raised. Sclerification may be present in the form of vascular and support bunbles. Crystals are absent. Xylem vessels are of small diameter and thick-walled relative to species of other groups.

ii) ELS : PT is homogeneous chlorechyma, with spongy mesophyll and palisade-like tissue absent. Stomata are superficial, but in members of the Mesembryanthemaceae are shielded by bladder-cell idioblasts. There is relatively large amounts of parenchymatous tissue, with the cells large and thin-walled and capable of expansion and contraction. Crystals are present, and may be conspicuous and abundant. Xylem vessels are intermediate in diameter and wall-thickness relative to members of other groups. An exception is C. rupestris which have vessels of diameter similar to ESC species, but which are very thin.

iii) ESS : Primary photosynthetic organ is the stem, and PT is homogenous parenchyma. In S. viminale there is some differentiation of PT into palisade-like cells. Hypodermal layer(s) present. Stomata sunken or partially so (S. viminale). Crystals may be present. Sclerification of the vascular bundle or support bundles may be evident. Xylem vessel diameters are large relative to other groups, but wall-thicknesses are similar to species of the ELS. An exception is Psilocaulon sp. which have vessel diameters similar to those of ELS species.

iv) DM : PT differentiated into palisade-like and spongy mesophyll tissue. Parenchymatous tissue present in small amount. Stomata abaxially only. Xylem vessel characteristics similar to that of ESC species. Crystals absent.

v) DLS : PT is homogeneous clorenchyma, and in one species palisade-like tissue is also differentiated. Stomata superficial, but may be shielded by bladder-cell idioblasts in members of the Aizoaceae and Mesembryanthemaceae. Crystals may be present. There is no clear trend in xylem vessel features : One species is similar to the ESC, one to the ELS, and the other exceptional in having wide vessel diameters and thick walls relative to other species.

vi) SSS : Leaf anatomical features of this species is similar to those of the DLS, except that bladder-cell idioblasts are not present in any of the species. Xylem vessel characteristics are similar to the ELS.

There are perhaps too few species per plant-form group to make any definitive statements about anatomical patterns amongst the species investigated, nor about the functional significance of the particular anatomical characteristics of species and groups. However, the consistent co-occurence of particular features in species of the same plant-form may indicate that these constitute "adaptive character syndromes" (sensu Rury and Dickison 1984) and which may reflect ecological preferences of individual species or groups of species. For instance, the relative simplicity of structures and organization of deciduous succulent leaves stand in contrast to that of evergreen succulent leaves (compare Fig.'s 2.3, 2.6 and 2.7). Functionally this can be explained in terms of the costs involved relative to the benefits derived, where for instance it does not "pay" a species to expend energy and materials on elaborate or complex structures when the organ is ephemeral (see also Orians and Solbrig 1977).

The abundance of species with crystals in the photosynthetic tissue was unexpected. In general, the function of crystals is not clear, but they are assumed to be waste products of metabolism , and may be important in maintaining the ionic balance of plant cells (Franceschi and Horner 1980). The most common are red rhomboidal crystals, which are perhaps the product of tannin accumulation (Esau 1977). Crystal druses, raphides and granular forms are also present, and are possibly composed of calcium oxalate (Esau 1977). All crystals are contained in specialized idioblast cells, and none are interstitial. In two species (*Psilocaulon sp.* and *L. haworthii*) rhomboidal crystals are closely associated with vascular tissue. This high incidence of crystals amongst species is perhaps an indication that they constitute an exaptation (*sensu* Gould and Vrba 1982) in that they may have an anti-herbivory function beside their primary function in waste metabolism and ionic balance (Franseschi and Horner 1980). This may explain the predominance of species of the Mesembryanthemaceae and Crassulaceae, among which the crystals largely occur, in the Succulent Karoo, which has a long history of grazing pressure.

2.4.3 Photosynthetic mode

No evidence of Kranz anatomy (Esau 1977; Vogel and Fuls 1974), which would possibly indicate C4 photosynthetic mode, was found amongst species investigated. It is thus assumed that all non-succulent taxa are of the C3 photosynthetic mode. Many of the succulent genera to which species in this study belong are known to photosynthesize using CAM (Mooney *et al.*1977; Werger and Ellis 1981). There is speculation that in *E. mauritanica* the stem exhibits CAM but the seasonally produced leaves are C3 (E.J. Moll pers. comm.). Other studies (e.g. Earnshaw *et al.* 1985; Von Willert *et al.* 1985; Jimenez and Morales 1987) have shown that CAM is facultative in some species, changing from CAM to C3 modes depending on prevailing environmental conditions. The degree to which species of this study are obligate or facultative CAM plants is not known, but the seasonally aquired C3 leaves of *E. mauritanica* presumably enhance production potential during the optimal growth period of the year.

2.4.4 Conclusions

The classification as defined was used during investigation of ecological aspects in the WVR (Chapters 3 and 4), which themselves served to test the validity of this classification. The similarity to the classification of Shreve (1942, in McGinnies 1979) is some indication of similarity of plant-forms between the vegetation of the Succulent Karoo and some North American arid ecosystems. However, the validity of the present system may be limited to the arid winter rainfall regions of southern Africa because of the relatively low diversity of succulent forms in autumn and summer rainfall arid regions.

Moreover, it can be concluded that all species of this study possess some attributes classically defined as xeromorphic (see Fahn 1964; Seddon 1974). However, it is evident that only certain combinations of xeromorphic features are present in any one species, with none possessing all of the classically defined xeromorphic characteristics. This indicates that within a particular arid-adaptive syndrome, as defined from gross morphology, there are what could be termed "secondary" structural adaptive options with which the water-use characteristics of a species is enhanced and optimized. These secondary characteristics do not detract from the validity of grouping species along functional lines according to gross morphological and behavioural criteria. They may, however, account for apparently anamolous behavioural and distributional characteristics of species within defined functional guilds. Further research may reveal consistent relationships between overall plant-form (gross morphology) and secondary structural adaptations with which existing structural-functional classifications can be refined.

2.5 References

Ayyad, M.A., 1981. Soil - vegetation - atmosphere interactions. Ch. 2 in : Goodall, D.W. and Perry, R.A., (eds.), 1981. Arid-land ecosystems : structure, functioning and management. Vol. 2. Cambridge University Press, Cambridge.

Cowling, R.M., 1986. A description of the Karoo Biome Project. S.A. Nat. Sci. Prog. Report no. 122, F.R.D., C.S.I.R., Pretoria.

Cowling, R.M., and Campbell, B.M., 1983. The definition of leaf consistency categories in the Fynbos Biome and their distribution along an environmental gradient in the southeastern Cape. J. S.A. Bot. 49 (2) : 87-101.

Clayden, E.C., 1955. Practical section cutting and staining. J.& A. Churchill Ltd., London.

Duddington, C.L., 1960. Practical Microscopy. Sir Isaac Pitman and Sons, Ltd, London.

Drew, M.C., 1979. Root development and activities. Ch. 23 in : Goodall, D.W. and Perry, R.A., (eds.), 1979. Arid-land ecosystems : structure, functioning and management. Vol 1. Cambridge University Press,Cambridge.

Esau, K., 1977. Anatomy of seed plants. Second edition. John Wiley and Sons, New York.

Franseschi, V.R., and Horner Jr.,H.T., 1980. Calcium oxalate crystals in plants. Bot. Review 46 (4) : 361-427.

Gould, S.J. and Vrba, E.S., 1982. Exaptation - a missing term in the science of form. Paleobiol. 8 (1) : 4-15.

Earnshaw, M.J., Carver, K.A. and Lee, J.A., 1985. Changes in leaf water potential and CAM in Sempervivum montanum and Sedum album in response to water availability in the field. Oecologia 67 : 486-492.

Gibbs Russell, G.E., Reid, C., Van Rooy,J., and Smook, L. 1985. List of species of southern African plants Edition 2 Part 2. Mem. Bot. Surv. S. Afr. 56. B.R.I., Dept. of Agric., Pretoria.

Gupta, R.K., 1979. Integration. Ch. 27 in : Goodall, D.W. and Perry, R.A., (eds.), 1979. Arid-land ecosystems : structure, functioning and management. Vol 1. Cambridge University Press, Cambridge.

Ihlenfeldt, H.D., 1983. Epidermis structure in the Mesembrymthemaceae. Bothalia 14 (3&4) : 931-937

Jimenez, M.S. and Morales, D., 1987. Kleinia neriifolia - a facultative CAM plant. Photosynthetica 21 (3) : 329-332.

Johansen, D.A., 1940. Plant microtechnique. McGraw-Hill, London.

Kruger, H. and Jordaan, A., 1989. Anatomical structure of the leaves of a few drought-resistant plants. Paper, 3rd Annual Research Meeting, Karoo Biome Project, C.S.I.R., Pretoria.

Kummerow, J., 1973. Comparative anatomy of sclerophylls of the Mediterranean climatic areas. Ch. 4, section 3 in : Di Castri, F. and Mooney, H.A. (eds.). 1973. Mediterranean type ecosystems : Origin and structure. Chapman and Hall, London.

McGinnies, W.G., 1979. Arid-land ecosystems - common features throughout the world. Ch. 8 in : Goodall, D.W. and Perry, R.A., (eds.), 1979. *Arid-land ecosystems : structure, functioning and management. Vol 1*. Cambridge University Press, Cambridge.

Miller, D.F., 1988. Comparison of water use by *Artemisia tridentata* spp. *wyomingensis* and *Chrysothamnus viscidiflorus* spp *viscidiflorus.* J. *Range Mangmt. 41 (1)* : 58-62.

Mooney, H.A., Troughton, J.H. and Berry, J.A., 1977. Carbon isotope ratio measurements of plants in southern Africa. *Oecologia 30* : 295-305.

Noy-Meir, I., 1973. Desert Ecosystems : Environment and producers. *Ann. Rev. Ecol. Syst. 4* : 25-51.

Orians, G.H. and Solbrig, O.T., 1977. A cost-income model of leaves and roots with special reference to arid and semi-arid areas. *Am. Nat. 111 (980)* : 677-690.

Orshan, G., 1953. Notes on the application of Raunkiaer's life forms in arid regions. *Palestine J. Bot., Jerusalem Series 6* : 120-122.

Orshan, G., 1989. Plant pheno-morphological studies in Mediterranean type ecosystems. Kluwer Academic Publishers, Dordrecht.

Raunkiaer, C., 1934. The life forms of plants and statistical plant geography. Clarendon, Oxford.

Root, R.B., 1967. The niche exploitation pattern of the blue-grey gnatcatcher. Ecol. Monogr. 37 (4) : 317 - 350.

Rury, P.M. and Dickison, W.C., 1984. Structural correlations among wood, leaves and plant habit. pp. 495-539 in : White, R.A. and Dickison, W.C., (eds.), 1984. Contemporary problems in plant anatomy. Academic Press Inc., Orlando.

Rutherford, M.C. and Westfall, R.H., 1986. The biomes of southern Africa - an objective categorization. Mem. Bot. Surv. S.A. 54 : 1-98.

Schulze, R., 1982. Plant life forms and processes. In : Lange, I., Nobel, P.S. and Osmond, C.B., (eds.), 1982. Physiological plant ecology 2 : Water and carbon-dioxide assimilation. Springer-Verlag, New York.

Scott, J.D. and Van Breda, N.G., 1937 (a). Preliminary studies on the root system of the rhenosterbos (*Elytropappus rhinocerotis*) on the Worcester Veld Reserve. *S.A. J. Sci. 33* : 560-569.

Scott, J.D. and Van Breda, N.G., 1937 (b). Preliminary studies on the root system of *Galenia africana* on the Worcester Veld Reserve. *S.A. J. Sci. 34* : 268-274.

Scott, J.D. and Van Breda, N.G., 1938. Preliminary studies on the root systems of *Pentzia incana-forma* on the Worcester veld reserve. *S.A. J. Sci. 35* : 280-287.

Scott, J.D. and Van Breda, N.G., 1939. Preliminary studies of the root systems of *Euphorbia mauritanica, E. burmannii* and *Ruschia multiflora* on the Worcester Veld Reserve. *S.A. J. Sci. 36* : 227-235.

Seddon, G., 1974. Xerophytes, xeromorphs and sclerophylls : The history of some concepts in ecology. *Biol. J. Linn. Soc. 6* : 65-87.

Solbrig, O.T., Barbour, M.A., Cross, J., Goldstein, G., Lowe, C.H., Morello, J. and Yang, T.W., 1977. The strategies and community patterns of desert plants. Ch. 4 in : Orians, G.H. and Solbrig, O.T. (eds.). 1977. Convergent evolution in warm deserts. Dowden, Hutchinson and Ross, NY.

Solbrig, O.T., 1986. Evolution of life-forms in desert plants. Ch. 4 in Polunin, N. (ed.). 1986. Ecosystem theory and application. John Wiley and Sons, New York.

Vogel, J.C. and Fuls, A., 1978. The geographical distribution of Kranz grasses in South Africa. S.A. J. Science 74 : 209-215.

Von Willert, D.J., Brinckmann, E., Scheitler, B. and Eller, B.M., 1985. Availability of water controls crassulacean acid metabolism in succulents of the Richtersveld (Namib desert, South Africa). Planta 164 : 44-55.

Werger, M.J.A. and Ellis, R.P., 1981. Photosynthetic pathways in the arid regions of South Africa. Flora 171 : 64-75.

Yeaton, R.I., Travis, J. and Gilinsky, E., 1977. Competition and spacing in plant communities : The Arizona upland association. J. Ecol. 65 : 587 - 595.

3 PLANT SPECIES AND PLANT-FORM DISTRIBUTIONS ACROSS MICROHABITATS IN THE WORCESTER VELD RESERVE

3.1 Introduction

The limited, and in some instances sporadic, availability of water in arid regions, and the uneven distribution of soil moisture both in space and time (Kovda *et al*. 1979), are primary determinants of plant community composition and structure in these regions (Noy-Meir 1973; MacMahon 1979; Ludwig and Whitford 1981). Diversity of plant-form is high in arid and desert regions (Solbrig 1986). The variation in structural diversity and co-occurence of particular forms can be related to the abovementioned environmental characteristics (Ayyad 1981; Bowers and Lowe 1986). These aspects have received little attention in southern African research (Cowling 1986) despite the large arid zone in this region and the high diversity of plant-forms present (Hoffman and Cowling 1987; pers. obs.). However, several phytosociological surveys do exist for various parts of the Karoo (e.g. Olivier 1966; Joubert 1968; Norton 1977; Werger 1978; Skarpe 1986), but in few (e.g. Palmer 1981; Hoffman 1989) are species distribution patterns interpreted beyond taxanomic or broad life-form groupings. Thus little is known about the distribution patterns of plant-forms in southern African arid regions, nor of the way in which primary environmental factors determine these patterns.

Excluding meteorological considerations, the spatial and temporal variability of moisture content is related primarily to inherent soil characteristics (Kovda et al.1979), including soil depth, soil texture and horizontal differentiation of soil layers. In general, these soil variables, and hence soil moisture content, are correlated with topographical and geomorphological changes in the landscape (Ayyad 1981). It is therefore not surprising that community composition and structure have been found to vary in relation to landform patterns (Ayyad 1981; Ludwig and Whitford 1981), and to soil depth and soil textural changes (see Werger 1978; Ludwig and Whitford 1981; Bowers and Lowe 1986; Skarpe 1986). Furthermore, several studies show that plant cover, and species and plant-form diversity increase up-slope with concomitant increase in soil particle size (Whittaker and Niering 1965; Solbrig et al.1977; Bowers and Lowe 1986). Since flats and low-lying areas have higher soil moisture content but lower species and plant-form diversity than slopes, these findings are interpreted as evidence for an increase in the variability of soil moisture content with increasing aridity within the landscape (Solbrig 1986). This allows for greater species "packing" (Whittaker 1972; Wuenscher 1974), since any individual adaptive strategy enables a species the optimal use of only a portion of the available moisture, temporally and spatially (Mooney 1974). This is due to structural and physiological constraints (Orians and Solbrig 1977; Solbrig 1986).

Knowledge of the functional significance of particular plant-forms, and of their associated structural attributes, can be invoked to explain the habitat preference and pattern of distribution of many species (Solbrig et al.1977). Orians and Solbrig (1977), Solbrig et al.(1977), and Solbrig (1986) have elucidated many structural-functional relations in plants, and have developed a predictive model based on the assumption that there are definitive trade-offs between optimization of photosynthesis and water-use under conditions of limited and sporadic availability of water. For instance, the energetic costs of constructing sclerophyllous leaves relative to mesophyllous leaves are high, but are compensated for by the plant's ability to photosynthesize and grow when evaporative demand and soil water tensions are high. Conversely, the inherently low internal resistances to vapour, in mesophyllous species, allow for high photosynthetic rates when adequate moisture is available. This is off-set by the inherent inability of these plants to photosynthesize and grow when soil moisture tensions are high. Data from many studies provide evidence for such relationships (see DePuit 1979; Chapter 4).

In this study, the distribution patterns of perennial plant-forms and species were determined in an area of the Succulent Karoo, and are related to topography and soil characteristics. This was achieved through a phytosociological survey of species and plant-forms across a shale ridge with north- and south-facing slopes, and pock-marked by mima-like mounds (circular, slightly raised patches up to 10 m in diameter). The soils of these mounds differ in texture and nutrient content from the surrounding soils (Midgley and Musil in prep.) and can be viewed as distinct habitats, irrespective of their position in the landscape. Data collected in this study were examined for species and plant-form diversity patterns. The impact that mounds have on the diversity characteristics of this area was assessed. Furthermore, the dominance or scarcity of particular plant-forms were interpreted in relation to structural-functional relationships.

3.2 Site Description

The study was conducted in the Worcester Veld Reserve (WVR) (33^o 41' S 19^o 31' E; altitude 150 - 220 m), 110 km north-east of Cape Town.

The reserve is situated on a ridge of Malmesbury shale in the Breede River Valley, and is surrounded by quartzite mountains of the Table Mountain Group. These mountains create a rainshadow, resulting in a mean annual rainfall of approximately 238 mm in the valley relative to the 1200-2000 mm annual mean in the mountains. Rain occurs mainly as winter frontal storms, starting during late autumn (March, April) and ending in early- to mid-spring (September, October). (see Ch. 4).

Commonly known as the Worcester-Robertson Karoo, the vegetation is classified as a succulent form of Karroid Broken Veld by Acocks (1953). The vegetation is typically a sparse, dwarf shrubland. This vegetation is included in the Succulent Karoo Biome recently defined by Rutherford and Westfall (1986). Mima-like mounds or "heuweltjies" are characteristic of the area, as they are throughout the arid winter rainfall region of southern Africa (Lovegrove and

Siegfried 1986). These mounds are concentric, and physiognomically and floristically distinct from the surrounding vegetation (Darlington 1985; Midgley and Musil in prep.) and have a regular distribution in the landscape (Lovegrove and Siegfried 1986).

The soils are derived from shale, have a fine texture and a high clay content. They are poorly drained. The soils are shallow (less than 50 cm) and weakly developed, particularly on the ridges. They attain depths of two meters or more in valley bottoms and alluvial plains (see Scott and van Breda 1938). A and B horizons may be differentiated in the deeper soils of mounds and run-on areas. Bedrock protrudes frequently on the ridges and north-facing slopes.

3.3 Methods

Four plots of 49 m^2 each were sampled at each of five sites. At each site, two of the four plots were on the mounds.Two sites were located on the north slope, two on the south slope, and one was located on the ridge. The approach was thus essentially that of a gradient analysis, with sites located from the warmer and drier north-facing slopes to the cooler and wetter south-facing slopes (see Armesto and Martinez 1978).

Cover-abundance values were assigned to all perennial species present in each plot according to the Braun-Blanquet method of phytosociological survey (see Werger 1974). Relevant observable environmental features, including open ground, exposed bedrock, and aspect, were recorded at each plot.

Soil depth was measured by driving in a metal stake until bedrock was encountered along a transect spanning the ridge. Five replicates were obtained at 20 m intervals, and seven replicates where mounds were encountered along the transect. Rainfall, and minimum and maximum temperature data for the north- and south-facing slopes, and the ridge top respectively, were obtained for a period of 18 months from thermometers and raingauges. Data were not obtained for November 1986 and January 1987.

3.4 Analytical Methods

Cover-abundance values for all species in all plots were ordered in a phytosociological table according to the method of Braun-Blanquet (see Werger 1974). Except for species with the value "r" (species present but outside plot) and "+" (single small individual present or cover less than 1%) all data were entered into a data matrix upon which detrended correspondence analysis was performed (Decorana : Hill 1979). Detrended correspondence analysis was also performed on plant-form cover-abundance data. The relative contribution of each plant-form at each plot was further determined by adding the cover-abundance values of each species in each plant-form group, and tabulating these values. A Simpson's dominance index (see Whittaker 1972) was calculated for the various forms at all plots, and from which variation in plant-form dominance patterns could be assessed.

3.5 Results

The variation in total monthly rainfall at the three sites is shown in Fig. 3.1. Total rainfall for the 18 months indicate that the ridge top received the least rain (478.1 mm), the north slope 520.7 mm, and the south slope received the largest amount at 616.7 mm. The area has a lengthy annual rainy season, which starts as early as March and continuing until September. This confirms the winter seasonality of rainfall for the region.

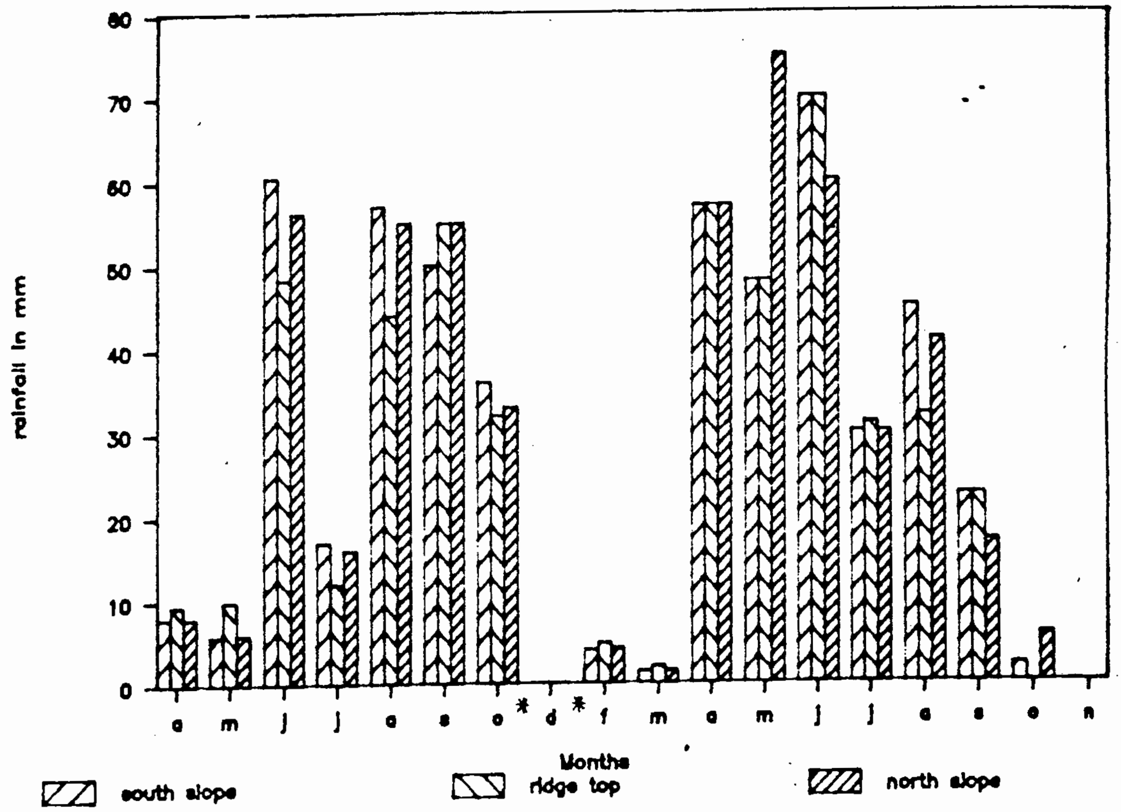


Fig.3.1. Distribution of monthly rainfall for different sites in the Worcester Veld Reserve, March 1986 to November 1987

Monthly minimum and maximum temperatures varied between sites, but the south slope generally remained coolest and is the only slope at which sub-zero temperatures were recorded (Fig.'s 3.2 and 3.3). These cooler conditions, coupled with a shorter period of irradiance and reduced evaporation, should result in greater moisture availability relative to the top and the north-facing slopes from any given rainfall event.

Mound soils were consistently deeper than the soil surrounding any particular mound (Fig. 3.4). However, the soil depth of the mound at the base of the southern slope slope was the same as the surrounding soil. This is the result of run-on of water at the base of the slope, where transported soil is deposited. A typical erosion profile was evident across the ridge. Soil is eroded away from the ridge top and increasingly deposited further down the slope on either side of the ridge. Thus the ridge top has the least soil for the retention of water.

In the ordered phytosociological table (Table 3.1), very little ordering of plots (vertical columns) took place. The mound plots were sequentially arranged as they were sampled from south to north on the left of the table, with the remainder also sequentially arranged to the right. Only horizontal shuffling was then needed to group species.

Mound communities are distinguished from the surrounding vegetation on the basis of their species compliment (Table 3.1; block A), which include Euphorbia mauritanica,

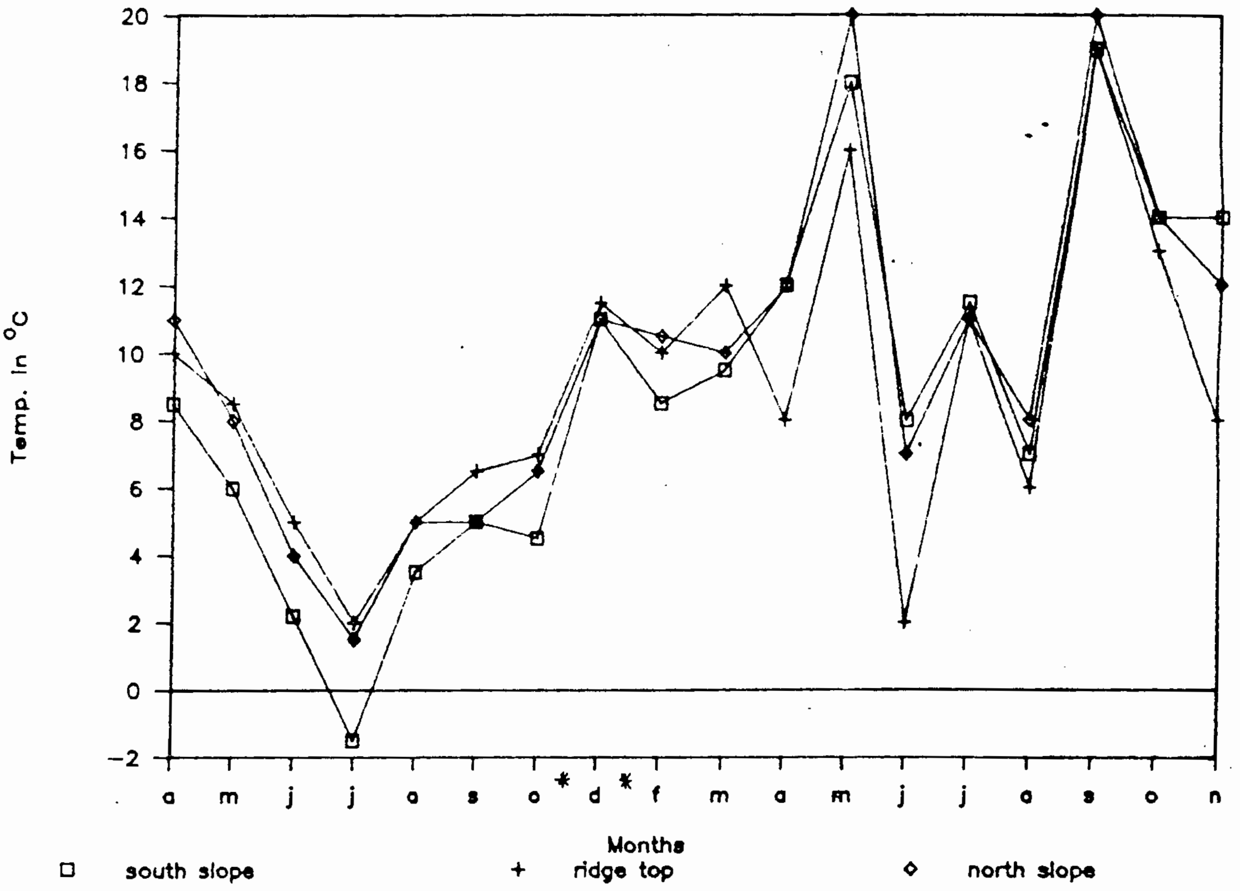


Fig.3.2. Minimum monthly temperatures for different sites in the Worcester Veld Reserve, March 1986 to November 1987

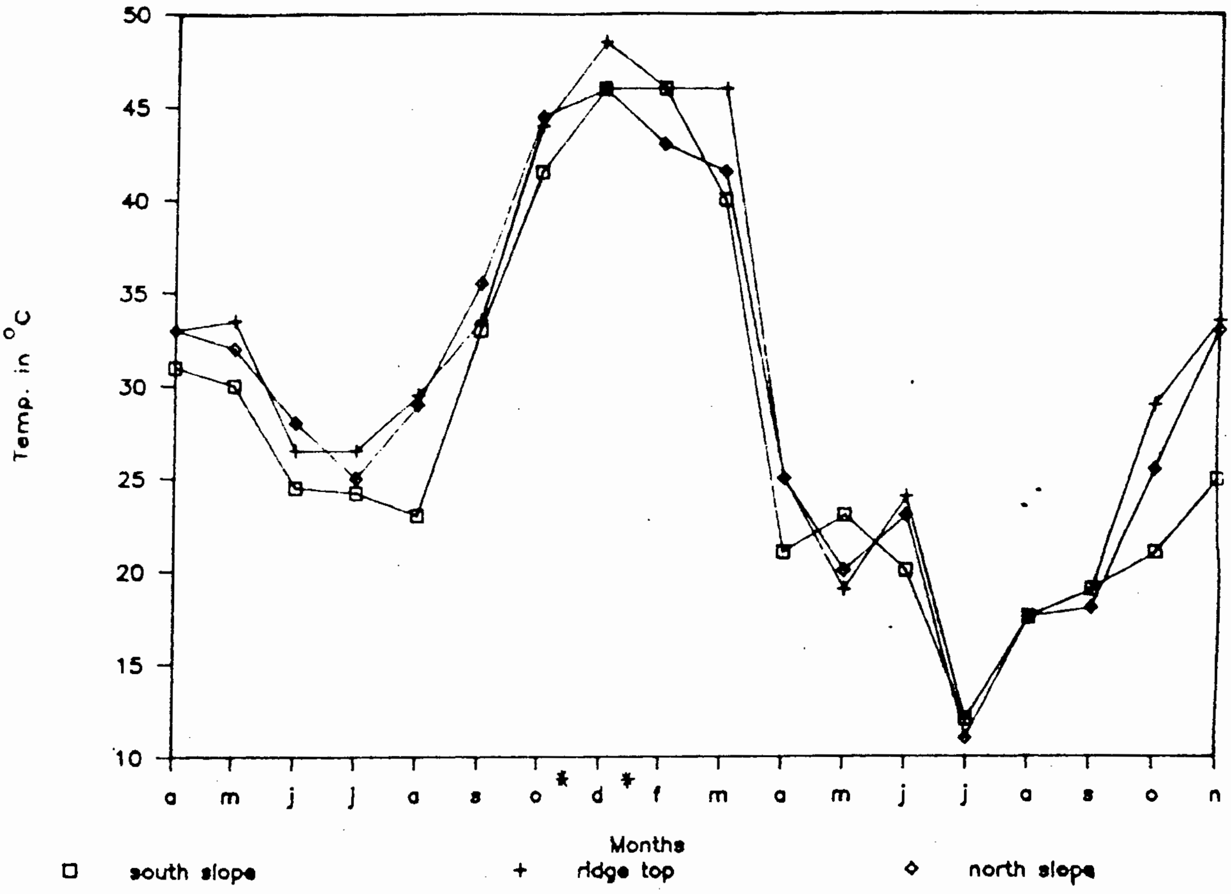


Fig.3.3. Maximum monthly temperatures for different sites in the Worcester Veld Reserve, March 1986 to November 1987

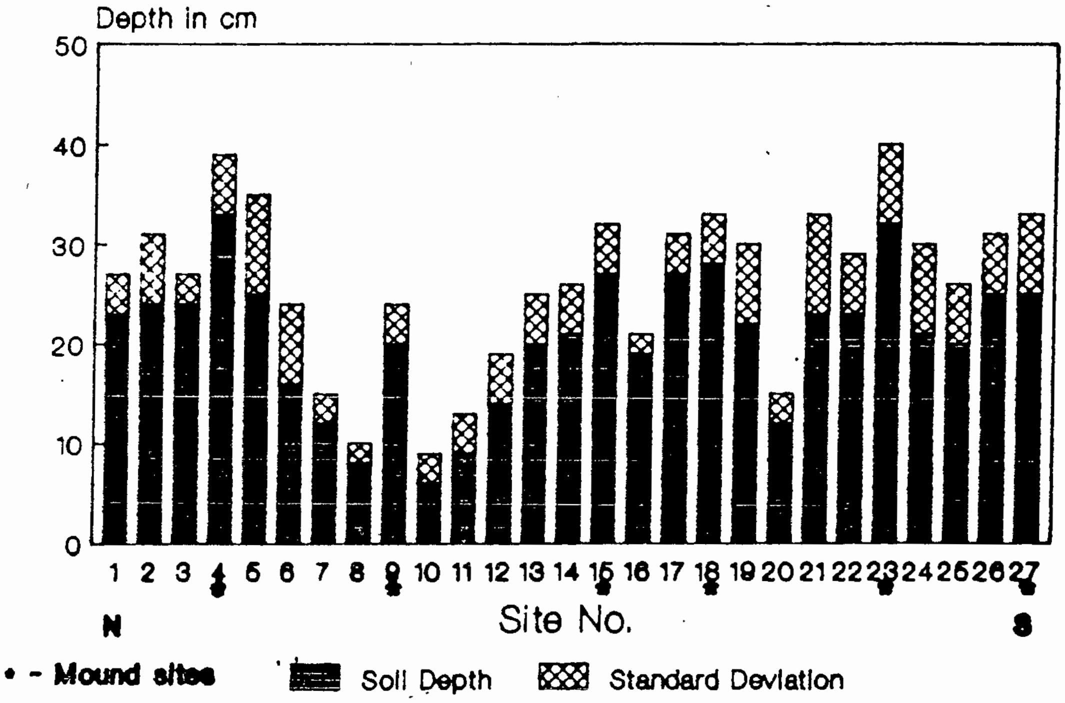


Fig.3.4. Soil depth along a transect from the north to south slope over a ridge in the Worcester Veld Reserve. n = 5 at each site off-mound, n = 7 at each site on-mound

Table 3.1. Phytosociological ordination of perennial plant species in the Worcester Veld Reserve. See text for description of blocks A - H

Plots Species	3	4	6	7	10	11	16	17	18	20	1	2	5	8	9	12	13	15	14	19	21
Euphorbia mauritanica	4	3	2	3	2	2		2	2	1		A							+		
Pteronia incana	3	3	2	3	3	3	2		+	1								+			
Lycium sp.		1	+		r	+		1	+	+											
Protasparagus sp.	+				+	+	+	+		+											
Tylecodon paniculatus	1	2	2	2	1				2												
Galenia africana	+	1	1	+			+	+	2		+										
Delosperma pageanum	1	2	+	1	2	+				+											
Drosanthemum hispidum			2	1		1															
Crassula subaphylla					1		1	1	2	2		+	+								
Psilocaulon sp.					1	1															
Pentzia incana	+							3	3												
Pteronia paniculata							2	r				2	3	2	2	3	2	3		3	2
Acromiscus filicaulus							+	+		+			+	1	1	1	1	2	2	1	1
Crassula tetragona	r									+	1	+		+	+		C				
Haworthii sp.														1	+	+	+	+			
Aridaria sp.														2	+	1	1				
Reihania squarrossa											r			1	2	1	1				+
Lampranthus haworthii												r		1	1		1				1
Lightfootia tenella														1	+	D	+				
Chrysocoma coma-aurea														1	1						+
Restio gaudichaudianus															r	r	2				
Tetragonia fruticosa																2	+				+
Drosanthemum speciosum									B							2	2	E			
Passerina obtusifolia																1	1				
Felicia filifolia																2	1				
Rhus incisa					+		1						+			r		+		1	+
Crassula atropurpurea																+	1	2	2	2	+
Pelargonium alternans																+	+	2	2	F	
Crassula rupestris																	+	1	1		
Tetragonia sarcophylla																		+	+	+	1
Othonna arbusculla													+				G	1		2	1
Ruschia multiflora		H					3	2	+	1		r						2	3	2	1
Osteospermum sinuatum	+				+	+	+	1					+					+	+	+	+
Euphorbia burmannii	3	1	+	2	2	1		2	2	3	r	+	2		r	+	+		+	2	
Aloe microstigma	1	1	+	r	2	2	1	2	2	2	r	+		+	+			+	2		+
Ruschia caroli	1	1	+	r	+	2		1	2	3	5	5	2	3	4	2	1			3	2
Annuals	3	3	3	2	1	+	1	+	1	+	1		+	+	1	+	+			1	
Geophytes	+	+	1	1	+		+			+			1	+	+				+	1	
Open Ground	1	1	2	1	2	1	2	1	1	1	2	1	2	1	1	3	2	3	3	3	3
Exposed Bedrock					+	+	+							2	2	1	2	1	1	+	
Aspect	S	S	S	S	T	T	N	N	N	N	S	S	S	S	S	T	T	N	N	N	N

Pteronia incana, Tylecodon paniculatus and Galenia africana. Few of these characteristic species are present elsewhere in the vegetation (only five recorded as "+" elsewhere). Off-mound vegetation was characterized by the consistent presence and high abundance of Pteronia paniculata (evergreen sclerophyll) and Adromischus filicaulus (a small, prostrate, evergreen leaf succulent; block B). The remainder of Table 3.1 illustrates that certain species were confined to the south and ridge top (block C), some to the ridge top alone (block D), some to the ridge top and north slope (block E), and certain species to the north slope alone (block F).

Three species were consistently present in both mound and surrounding communities (block G). However, Euphorbia burmannii and Aloe microstigma predominate on the mounds, and Ruschia caroli at sites in off-mound situations. The south slope did not have a compliment of species unique to this aspect (as is the case for the top and the north slope) but which is characterized by the very high cover-abundance values of R. caroli.

The species ordination (Fig. 3.6) obscures some details but reinforces the conclusion that mound communities are distinct on the basis of species presence and abundance. Furthermore, the ridge top plots (12 & 13), and south and north slope plots (1,2,5,8,9 vs. 14,15,19,21) were grouped separately. The looser grouping of the communities in off-mound situations is attributed to fewer characteristic species confined to any one of these areas (see Table 3.1). On both the vertical and horizontal axes the north slope mound

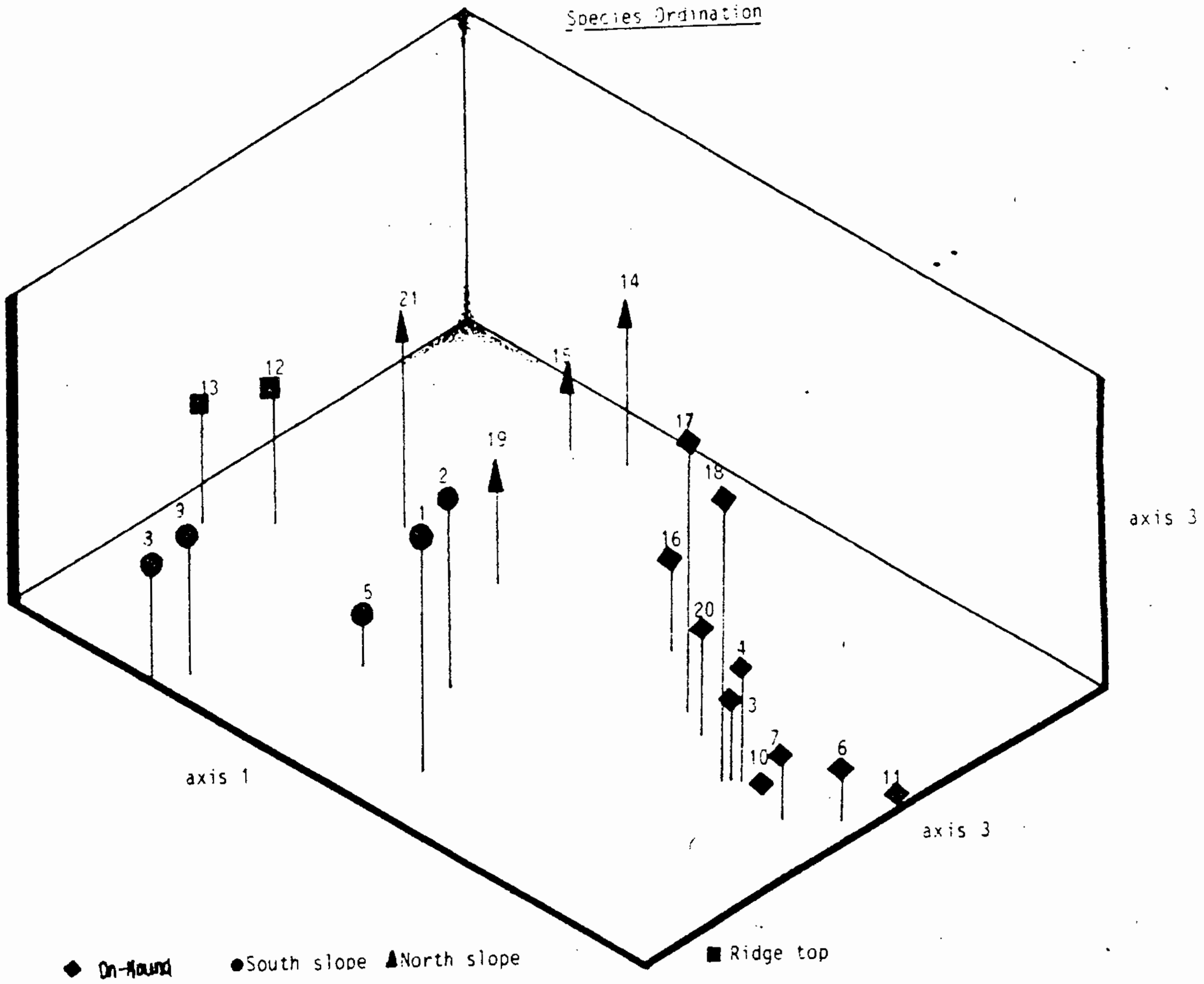


Fig.3.6. Multi-dimensional ordination of vegetation plots on the basis of plant species cover-abundances (Decorana; Hill 1979)

communities (plots 16,17,18,20) were separated out from the top and south mound plots, indicating that within the mound communities there were differences in species distribution between south and north sites. These differences can be ascribed to the higher cover-abundance values of *E. mauritanica*, *P. incana* and *T. paniculatus*, and the presence of *Delosperma pageanum* on the south and ridge top plots, with *Crassula subaphylla* and *Pentzia incana* largely confined to the north slope mounds (see Table 3.1). This further emphasizes the existence of an environmental gradient from the north to the south slope.

Mound communities were distinct from the surrounding vegetation on the basis of the plant-form ordination, with the exception of plot 16 (Figure 3.7). Summated cover-abundance values for the six plant-form groups in each plot (Table 3.2) show absence or poor representation of three or more groups in off-mound situations at the lower south slope sites off-mound. Other patterns evident from Table 3.2 can be summarized as follows :

i) Mound communities, in all sites but one, were co-dominated by ESS and ESC, and both co-dominated with ELS in ridge top and north slope sites;
ii) DLS and SSS were associated with south slope mound sites, and SSS was relatively well-represented in north slope off-mound sites;
iii) ELS dominated throughout almost all of the off-mound sites with the exception of the ridge top and one south slope site where they co-dominated with ESC. ESS species were virtually absent off-mound.

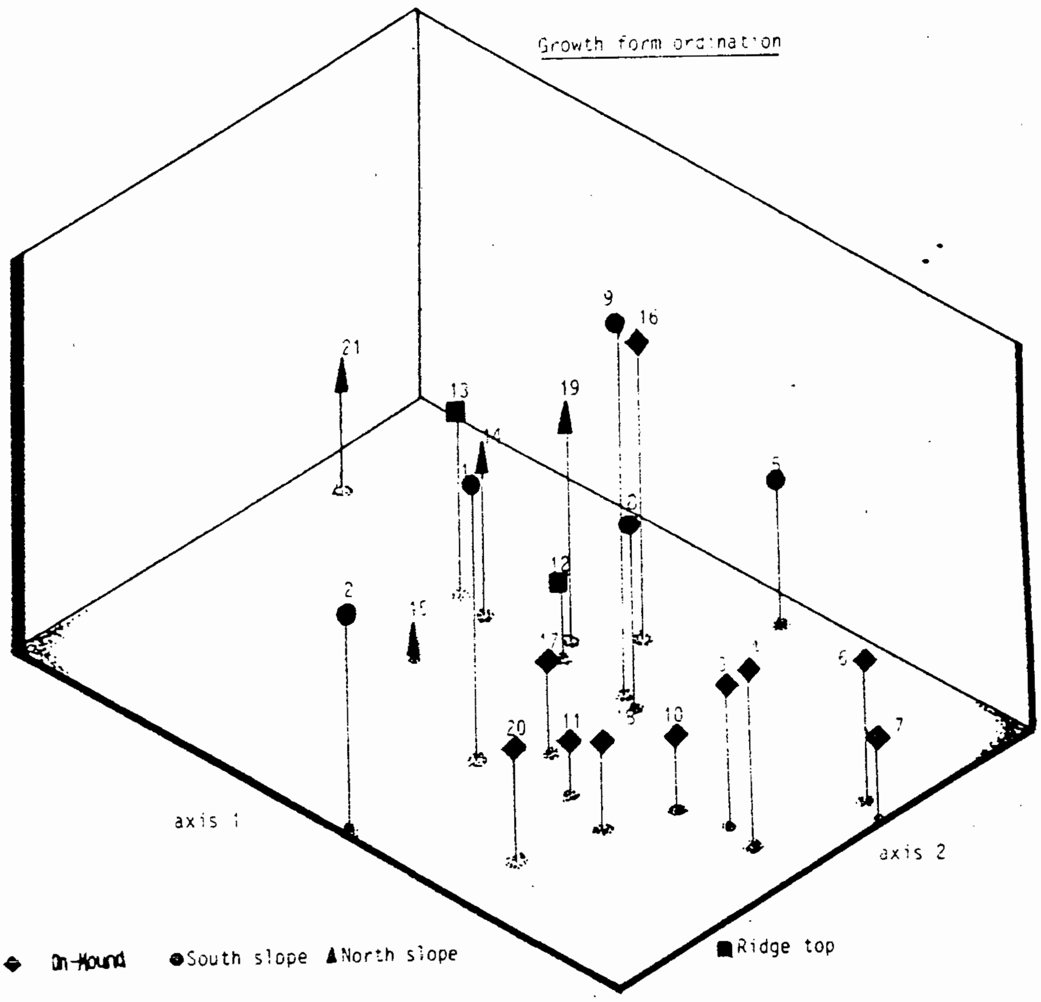


Fig.3.7. Multi-dimensional ordination of vegetation plots on the basis of structural guild cover-abundances (Decorana; Hill 1979)

Table 3.2. Summated cover-abundance values for the respective plant-forms in the various plots. KEY : ESC - evergreen sclerophyll; ELS - evergreen leaf succulent; ESS - evergreen stem succulent; DM - deciduous mesophyll; DLS - deciduous leaf succulent; SSS - stem storage succulent

	On - Mound Plots										Off - Mound Plots										
FORM	3	4	6	7	10	11	16	17	18	20	1	2	5	8	9	12	13	15	14	19	21
ESC	8	8	6	7	6	6	5	7	11	2	1	4	6	8	10	14	14	7	0	6	6
ELS	4	4	2	1	7	8	11	13	13	16	12	13	6	18	16	14	16	16	20	16	12
ESS	14	8	5	10	10	8	0	8	8	8	0	1	4	0	0	1	1	0	1	4	0
DM	1	0	0	0	2	1	3	1	0	1	0	0	1	2	1	0	1	1	0	2	1
SSS	2	4	4	4	2	0	0	0	4	0	0	0	1	0	0	1	1	6	4	4	2
DLS	3	6	6	4	5	5	1	4	1	2	0	0	1	0	0	4	1	2	2	2	4
Aspect	S	S	S	S	T	T	N	N	N	N	S	S	S	S	S	T	T	N	N	N	N

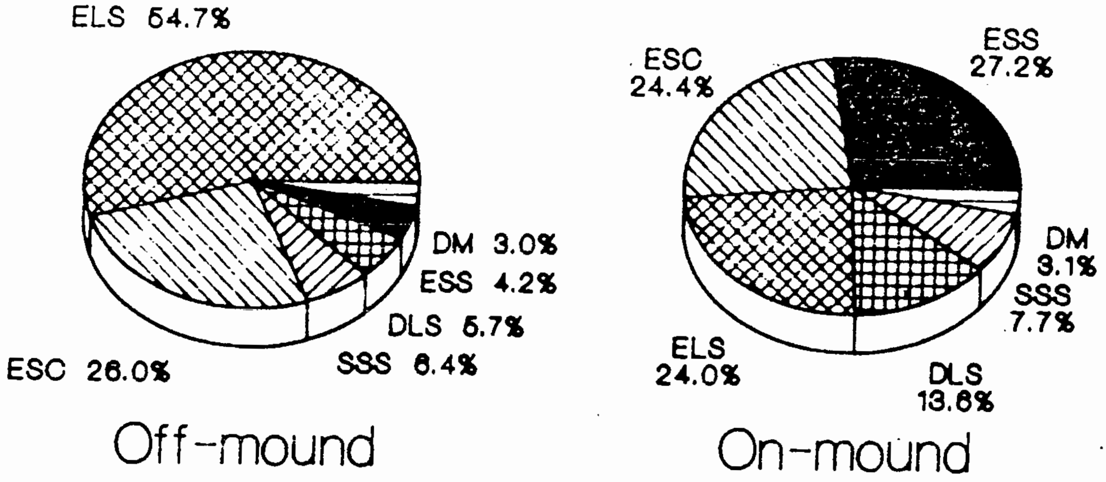


Fig. 3.5. Average proportional cover-abundance of plant-forms in mound and off-mound situations. KEY : ESC - evergreen sclerophyll; ELS - evergreen leaf succulent; ESS - evergreen stem succulent; DM - deciduous mesophyll; DLS - deciduous leaf succulent; SSS - stem storage succulent

iv) DM were scarce overall and occurred scattered amongst mound and off-mound sites.

A greater diversity in plant-form and total cover-abundance values was evident for the mound communities.

Calculation of Simpson's dominance index (see Whittaker 1972) for plant-forms showed the following characteristics :

1) The average of index values for mound communities is 0.33 (S.D. = 0.08, n = 10), compared to an average of 0.50 (S.D. = 0.19, n = 11) for the surrounding vegetation.

2) The range is 0.24 - 0.45 for mounds and 0.26 - 0.95 for the surrounding communities.

3) The highest value (0.95) was for the off-mound plot at the base of the south slope.

These observations indicate that there is less dominance of any particular plant-form in mound communities. The greater dominance values for the surrounding communities can be attributed to the predominance of evergreen leaf succulents at many of the sites (see Table 3.2).

Proportional representation of the different plant-forms, based on the averaged summated cover-abudance values for mound and off-mound situations, are illustrated in Fig. 3.5.

3.6 Discussion

The data indicate a differential plant species and plant-form distribution across microhabitats in an arid winter rainfall region of the southwestern Cape. Differences in community composition and structure were associated with variations in soil depth, which is related to topography and the presence of mounds. A trend of increasing species diversity up-slope is evident, a phenomenon reported for other arid regions (Whittaker and Niering 1965; Orians et al.1977; Bowers and Lowe 1986). There was no discernable increase in plant-form diversity up-slope, but a general increase from the south slope to the north slope is apparent. Community composition changes were also associated with aspect, it being clear that the north- and south-facing slopes, and the ridge top, have different species and plant-form compliments. Thus these results support the view that those physical environmental factors which directly influence the variability of soil moisture availability in arid regions are primary determinants of plant community structure and composition.

The results also show that the mima-like mounds support unique species and plant-form compliments relative to the surrounding vegetation, irrespective of topographical location, and contribute greatly towards the total species diversity. They contribute to a lesser extent to total plant-form diversity. These mounds are thought to be of zoogenic origin and have a regular distribution in the landscape (Lovegrove and Siegfried 1986). This suggests that they should be viewed as distinct habitats which do not share the usual relationships with topographical and geomorphological factors in the environment. However, there is some indication that within mounds, species composition varies with aspect similar to, but to a lesser extent, than the surrounding communities.

The definitions and number of plant-form groups are confounding factors in any analysis of the distribution of plant-forms. Coupled with the uncertainty of the real functional significance of particular forms and structural attributes, patterns and trends evident in the results warrant careful interpretation. For instance, this study did not show a clear increase in plant-form diversity up-slope. This may, however, become evident with more detailed groupings of species and a larger data-base. Also, this study shows that evergreen stem succulents are predominant in mound communities. This observation contradicts the findings of a previous analysis (Midgley and Musil 1989). These authors claim that deciduous forms predominate in mound communities. This discrepancy is due to their grouping _E. mauritanica_ as a deciduous form, when, arguably, the small seasonally produced leaves are secondary in their contribution to optimize carbon-gain and water-use in relation to the numerous, photosynthetically active and succulent evergreen stems. Therefore it is classified as an evergreen stem succulent in this study. Within this context, interpretation of the functional significance of the distribution of plant-forms in the Worcester Veld Reserve remains largely speculative.

Succulents, in their various forms, predominate throughout the area. This supports the inclusion of this vegetation as a dwarf succulent shrubland in the various vegetation classifications for southern Africa (see Acocks 1953;

Rutherford and Westfall 1986). Although succulence is an obvious adaptation to conditions of drought, the high diversity and abundance of succulents compared to arid regions to the east and north is not fully understood (Hoffman and Cowling 1987). Occurrence of frost is one factor known to limit the distribution of succulents (Werger and Ellis 1981; Werger 1983), although the predictability and seasonality of rainfall is expected to play a major role in their distribution (Hoffman and Cowling 1987). The prevalence of leaf succulents is also phylogenetically related, since most leaf succulent species belong to the Mesembryanthemaceae and Crassulaceae (see Hilton-Taylor 1987). However, structural attributes such as the reduced volume to surface ratio of succulent leaves relative to succulent stems, and lower total storage capacity, is some indication that they may not have adequate water reserves for extended drought periods (e.g. longer than six months). This view is supported by work in the Richtersveld by Von Willert <u>et</u> <u>al</u>.(1985) who found that the majority of leaf succulents species did not survive an unusually long drought period. The leaf succulent habit is perhaps an adaptation to intense, but short and predictable periods of drought as occurs for instance in the Worcester Veld Reserve. The scarcity of stem succulents off-mound in the study area is some indication that they are not functionally equivalent to leaf succulents, but I cannot explain the functional significance of their predominance in mound communities. However, the incidence of stem succulence is positively correlated with certain soil nutrients in the eastern Karoo, particularly phosphorus (Hoffman 1989). The higher nutrient status of mound soils relative to off-mound soils in the WVR (Midgley and Musil 1989), may account for this predominance.

Sclerophylls were represented approximately equally on mounds and in the surrounding vegetation, and in off-mound situations were more abundant on the ridge top. Since these species are known to grow throughout the year (see Chapter 4), and usually have deep or extensive root systems (see Chapter 2) their presence and relative abundance is some indication that soil moisture is available for extended periods of time at most sites in the area. However, the data show that in few places the soil is deeper than 30 cm, which suggests that roots of these species grow down cracks and passages in the bedrock (see Noy-Meir 1973), where they can tap water which has infiltrated after heavy rainfall. In this regard, Scott and Van Breda (1938) found that in deep-rooted species, tap roots commonly grow down termite burrows and other passages to great depths. The finely laminar nature and the orientation of layers of the shale bedrock could conceivably facilitate infiltration and storage of moisture at great depth. Further research is needed to substantiate this postulate.

Deciduous leaf succulents and deciduous mesophylls are conspicuously scarce throughout the area. This may be related to a relatively short optimum period of growth for species with mesophyllous leaf characteristics; viz. growth is only possible for them when low negative water potentials prevail (Orians and Solbrig 1977; Solbrig 1986), but growth processes would be relatively slow due to low temperatures in the winter rainy season. Conceivably the optimum period for growth is in the early spring months when temperatures increase and before soil moisture is depleted. Furthermore, the deciduous habit may prevent the maintenance of deep and/or extensive root systems as in the case of evergreen forms, whereas the water availability characteristics of shallow soils may be more effectively exploited by succulent forms.

There are, however, few sites at which a single plant-form dominates, with most sites shared by several or all of the plant-forms. This observation supports the view that any one plant type can capture only a part of available resources (Mooney 1974), and that co-existence is facilitated by structural diversification. It can be concluded that the vegetation of the WVR show low alpha, but high beta species diversity (sensu Whittaker 1972) which implies high habitat diversity in the landscape (Whittaker 1972; Pianka 1979). This is indicated by rapid species turnover, and by associated changes in plant-form composition, with changes in the landscape. The study provides further evidence of high structural diversity in plant communities of the arid winter rainfall Karoo, and implicates land-form pattern, and it's effect on soil moisture availability, as a primary determinant of community structure and composition.

3.7 References

Acocks, J.P.H., 1953. Veld types of South Africa. Mem. Bot. Surv. S.A. 28 : 1-128.

Ayyad, M.A., 1981. Soil - vegetation - atmosphere interactions. Ch. 2 in : Goodall, D.W. and Perry, R.A., (eds.), 1981. Arid-land ecosystems : structure, functioning and management. Vol. 2. Cambridge University Press, Cambridge.

Bowers, M.A. and Lowe, C.H., 1986. Plant-form gradients on Sonoran desert bajadas. Oikos 46 : 284-291.

Cowling, R.M., 1986. A description of the Karoo Biome Project. S.A. Nat. Sci. Prog. Report no. 122, F.R.D., C.S.I.R., Pretoria.

DePuit, E.J., 1979. Photosynthesis and respiration of plants in arid ecosystems. Ch. 21 in : Goodall, D.W. and Perry, R.A., (eds.), 1979. Arid-land ecosystems : structure, functioning and management. Vol 1. Cambridge University Press, Cambridge.

Darlington, J.P.E.C., 1985. Lenticular soil mounds in the Kenya highlands. Oecologia 66 : 116-121.

Hill, M. O., 1979. Decorana. Cornell University, Ithaca, New York.

Hilton-Taylor, C., 1987. Phytogeography and origins of the karoo flora. Ch.4 in : Cowling, R.M. and Roux, P.W. (eds.)., 1987. The karoo biome : A preliminary synthesis part 2 - vegetation and history. S. Afr. Nat. Sci. Progr. Report no. 142, C.S.I.R., Pretoria.

Hoffman, M.T. and Cowling, R.M., 1987. Plant physiognomy, phenology and demography. Ch. 1 in : Cowling, R.M. and Roux, P.W. (eds.). 1987. The karoo biome - a preliminary synthesis part 2 - vegetation and history. S.A. Nat. Sci. Progr. no. 142, C.S.I.R., Pretoria.

Hoffman, M.T., 1989. A preliminary investigation of the phenology of sub-tropical thicket and karroid shrubland in the lower Sundays River Valley, South Africa. S. Afr. J. Bot. 55 (6). (In Press).

Joubert, J.G.V., 1968. Die ekologie van die weiveld van die Robertson Karoo. Unpubl. Ph.D.-thesis, University of Stellenbosch.

Kovda, V.A., Samoilova, E.M., Charly, J.L. and Skujins, J.J., 1979. Soil processes in arid lands. Ch. 17 in : Goodall, D.W. and Perry, R.A., (eds.), 1979. Arid-land ecosystems : structure, functioning and management. Vol 1. Cambridge University Press, Cambridge.

Lovegrove, B.G. and Siegfried, W.R., 1986. The distribution and formation of Mima-like earth mounds in the western Cape region of South Africa. S. Afr. J. Sci. 82 : 412-436.

Ludwig, J.A. and Whitford, W.G., 1981. Short-term water and energy flow in arid ecosystems. Ch. 11 in : Goodall, D.W. and Perry, R.A., (eds.), 1981. Arid-land ecosystems : structure, functioning and management. Vol. 2. Cambridge University Press, Cambridge.

Midgley, G.F. and Musil, C.F., 1989. Substrate effects of zoogenic soil mounds on vegetation composition in the Worcester-Robertson valley, Cape Town, South Africa. S. Afr. J. Bot. (In Prep.).

Mooney, H.A., 1974. Plant forms in relation to environment. Ch. 7 in : Strain, B.R. and Billings, W.D., (eds.), 1974. Vegetation and environment. Dr. W. Junk, The Hague.

Norton, J., 1977. Vegetation survey of the Worcester Botanic Gardens. Unpubl. B.Sc.-project, University of Cape Town.

Noy-Meir, I., 1973. Desert Ecosystems : Environment and producers. Ann. Rev. Ecol. Syst. 4 : 25-51

Olivier, M.C., 1966. Die plantegroei en flora van die Worcesterse Veldreserwe. Unpubl. Ph.D.-thesis, University of Stellenbosch.

Orians, G.H. and Solbrig, O.T., 1977. A cost-income model of leaves and roots with special reference to arid and semi-arid areas. Am. Nat. 111 (980) : 677-690.

Palmer, A.R., 1981. A study of the vegetation of the Andries Vosloo Kudu Reserve, Cape Province. Unpublished M.Sc.-thesis, Rhodes University. Ch 4.

Pianka, E.R., 1979. Diversity and niche structure in desert communities. Ch. 10 in : Goodall, D.W. and Perry, R.A., (eds.), 1979. Arid-land ecosystems : structure, functioning and management. Vol 1. Cambridge University Press, Cambridge.

Rutherford, M.C. and Westfall, R.H., 1986. The biomes of southern Africa - an objective categorization. Mem. Bot. Surv. S.A. 54 : 1-98.

Skarpe, C., 1986. Plant community structure in relation to grazing and environmental changes along a north-south transect in the western Kalahari. Vegetatio 63 : 3 - 18.

Scott, J.D. and Van Breda, N.G., 1938. Preliminary studies on the root systems of Pentzia incana-forma on the Worcester veld reserve. S.A. J. Sci. 35 : 280-287

Solbrig, O.T., Barbour, M.A., Cross, J., Goldstein, G., Lowe, C.H., Morello, J. and Yang, T.W., 1977. The strategies and community patterns of desert plants. Ch. 4 in : Orians, G.H. and Solbrig, O.T. (eds.). 1977. Convergent evolution in warm deserts. Dowden, Hutchinson and Ross, NY.

Solbrig, O.T., 1986. Evolution of life-forms in desert plants. Ch. 4 in Polunin, N. (ed.). 1986. Ecosystem theory and application. John Wiley and Sons, New York.

Von Willert, D.J., Brinckmann, E., Scheitler, B. and Eller, B.M., 1985. Availability of water controls crassulacean acid metabolism in succulents of the Richtersveld (Namib desert, South Africa). Planta 164 : 44-55.

Werger, M.J.A., 1974. On concepts and techniques applied in the Zurich-Montpellier method of vegetation survey. Bothalia 11 (3) : 309-323.

Werger, M.J.A., 1978. Vegetation structure in the southern Kalahari. J. Ecol. 66 : 933 - 941.

Werger, M.J.A., 1983. Vegetation geographical patterns as a key to the past, with emphasis on the dry vegetation types of South Africa. Bothalia 14 (3 & 4) : 405-410.

Werger, M.J.A. and Ellis, R.P., 1981. Photsynthetic pathways in the arid regions of South Africa. Flora 171 : 64-75.

Whittaker, R.H. and Niering, W.A., 1965. Vegetation of the Santa Catalina Mountains, Arizona : A gradient analysis of the south slope. Ecology 46 (4) : 429 - 452.

Whittaker, R.H., 1972. Evolution and measurement of species diversity. Taxon 21 (2/3) : 213 - 251.

Wuenscher, J.E., 1974. The ecological niche and vegetation dynamics. Ch. 3 in : Strain, B.R. and Billings, W.D., (eds.), 1974. Vegetation and environment. Dr. W. Junk, The Hague.

4 PHENOLOGY OF PLANT-FORMS AND PLANT SPECIES IN THE WORCESTER VELD RESERVE

4.1 Introduction

Few studies have investigated the phenology of plant species in the various arid ecosystems of southern Africa (see Hoffman and Cowling 1987), and there is little long-term information (two years or longer) available for phenological events in these regions. The approach and level of investigation varies widely between the existing studies (see Van Rooyen *et al.* 1979 a, b; Le Roux *et al* 1989) and the various results are not readily comparable. Few studies (Palmer 1981; Hoffman 1989) interpret results relative to existing or proposed ecological models and concepts for arid ecosystem functioning (Noy-Meir 1973; Westoby 1980; Hoffman and Cowling 1987). There is hence a poor understanding of the range of phenological patterns possible and the significance of these in the ecology of local arid regions.

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Phenological studies in North American deserts show that phenological behaviour can be used as a good indicator of the timing of resource use, and that meaningful insights can be gained by relating phenophases not only to environmental variables but also to the structural attributes of plants (Beatley 1974; Kemp 1983; Jackson and Bliss 1984). It is clear from these studies that temporal partitioning of resources, particularly water, occurs amongst co-occurring species. Furthermore, these differential patterns of water-use are related to above-ground plant-form (Ayyad 1981; Jackson and Bliss 1984). There appears to be uniformity in the timing of phenophases within broadly definable structural groups (Roux 1968; Hoffman 1989).

The basis for direct structural-functional relationships amongst arid region plants is evident from results of several ecophysiological studies : For example, seasonal periods and diurnal rates of photosynthesis and evapotranspiration are directly related to effective moisture availability (Halvorson and Patten 1974; Lange *et al.*1975; Lange *et al.* 1978; Sammis and Gay 1979; Von Willert *et al.*1984; Earnshaw *et al.*1985; Farris 1987; Von Willert *et al.*1985; Thomas and Andre 1987). Carbon gain and water-use efficiency (WUE), as measures of growth, are in turn directly related to periods and rates of photosynthesis and evapotranspiration (Nilsen and Miller 1981; Werk *et al.*1983; Noble and Hartsock 1986; Nobel 1987; Thomas and Andre 1987; Kuppers *et al.*1988). Variation in patterns of these processes is associated with differences in photosynthetic organ structure and internal water-storage potential (Halvorson and Patten 1974; Odening *et al.*1974; Orians and Solbrig 1977; Monson and Smith 1982; Forseth *et al.*1984; Von Willert *et al.*1985). This suggests that above-ground plant structural attributes are indicative of the potential water-use characteristics of a species.

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I investigated growth and reproductive activities as indicators of temporal resource-use patterns, and used these results to explore the concept of temporal partitioning of water for the structurally and floristically diverse vegetation of the Worcester-Robertson Karoo in the southwestern Cape, South Africa. The validity of the relations outlined above was examined for co-occurring perennial species. The primary aim was to determine whether the structurally defined plant groups (Chapter 2) are similar in phenological patterns. This was done to determine if leaf consistency characteristics, photosynthetic organ type and water storage potential are meaningful ecological criteria for the functional grouping of arid region plants.

4.2 Study Area

The study was conducted in the Worcester Veld Reserve in the southwestern Cape, South Africa. Characteristics of the vegetation and environmental variables are described elsewhere (Chapter 3, Midgley and Musil in prep.). Here I discuss the meteorological variables during the two years of phenological monitoring.

The monthly distribution of rainfall was dissimilar between the two years (Fig. 4.1). In 1986, the main rainfall period started later and extended for two months longer than in 1987 (from June to November vs. April to September). Total annual rainfall was higher in 1987, and cumulative rainfall was high for the early part of the year in 1987 (Fig. 4.2).

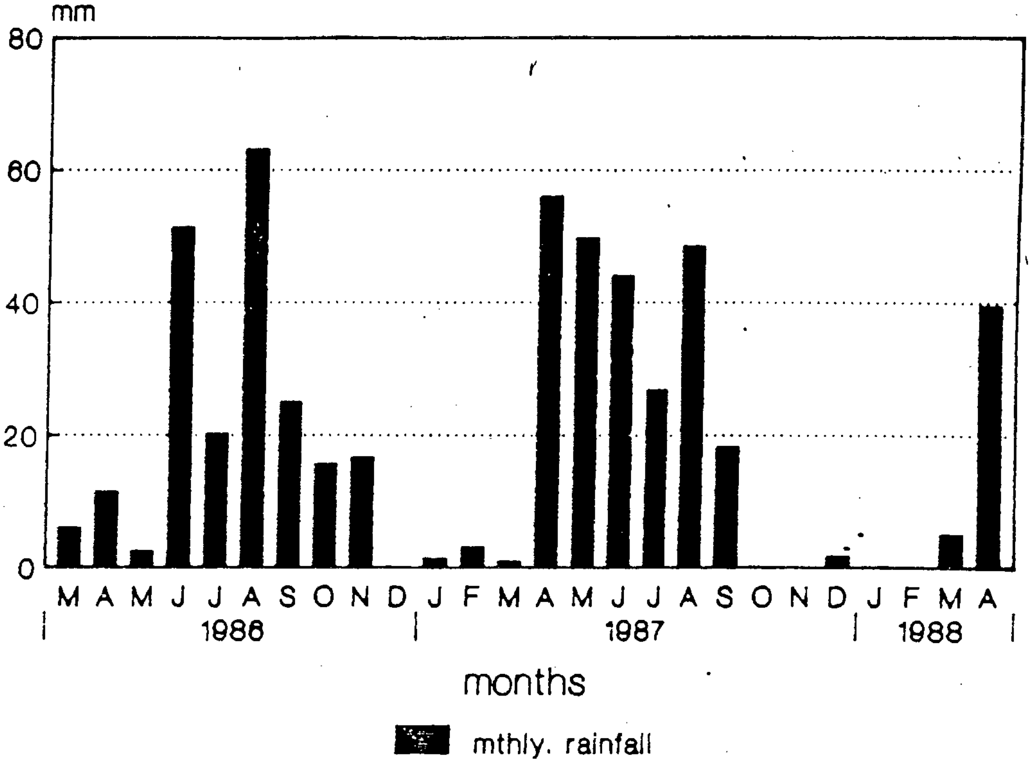


Fig.4.1. Monthly distribution of rainfall in the Worcester Veld Reserve from March 1986 to April 1988

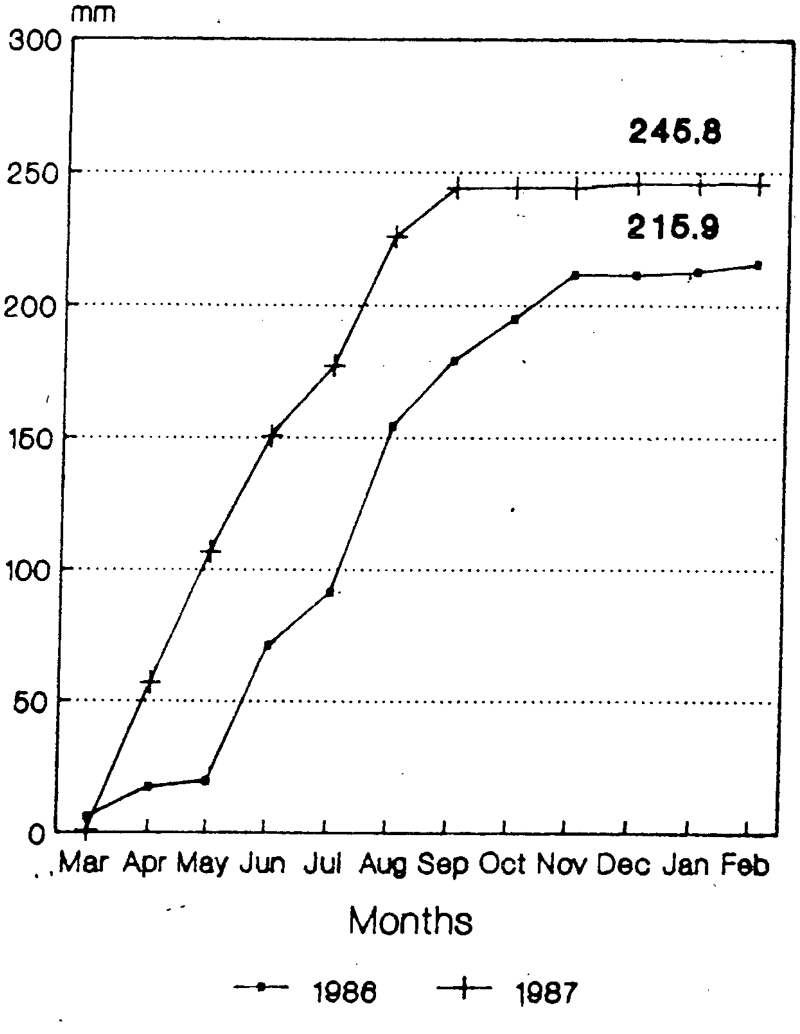


Fig.4.2. Cumulative monthly rainfall for the 1986 and 1987 seasons in the Worcester Veld Reserve

Monthly average minimum and maximum diurnal temperatures show consistent seasonal variation (Fig. 4.3). The coldest months were June, July, and August (min. = 6 - 7 °C) in both years. The hottest months were December, January and February in 1986, though December of 1987 was relatively cool. The maximum temperature for this two year period was during February 1988.

Variation in monthly evaporation was strongly seasonal (Fig. 4.4), and was positively related to diurnal temperatures (see Fig. 4.3). To a lesser extent this is also correlated with rainfall. Daily evaporative maxima of between 11 and 13 mm occurred during December, January and February of both years; minima of between 3 and 4 mm occurred during June, July and August of both years.

Monthly maximum relative humidity showed little seasonal fluctuations whereas minimum relative humidity is strongly seasonal (Fig. 4.5). Maximum relative humidity values ranged between 75 and 95 %, but a sharp decrease occurred during October and November of 1987. Minimum relative humidity values ranged from 38 to 61 % with minima in summer and maxima in winter.

On the basis of these meteorological data, the seasons for this area are defined as follows :

Autumn - March, April, May
Winter - June, July, August
Spring - September, October, November
Summer - December, January, February

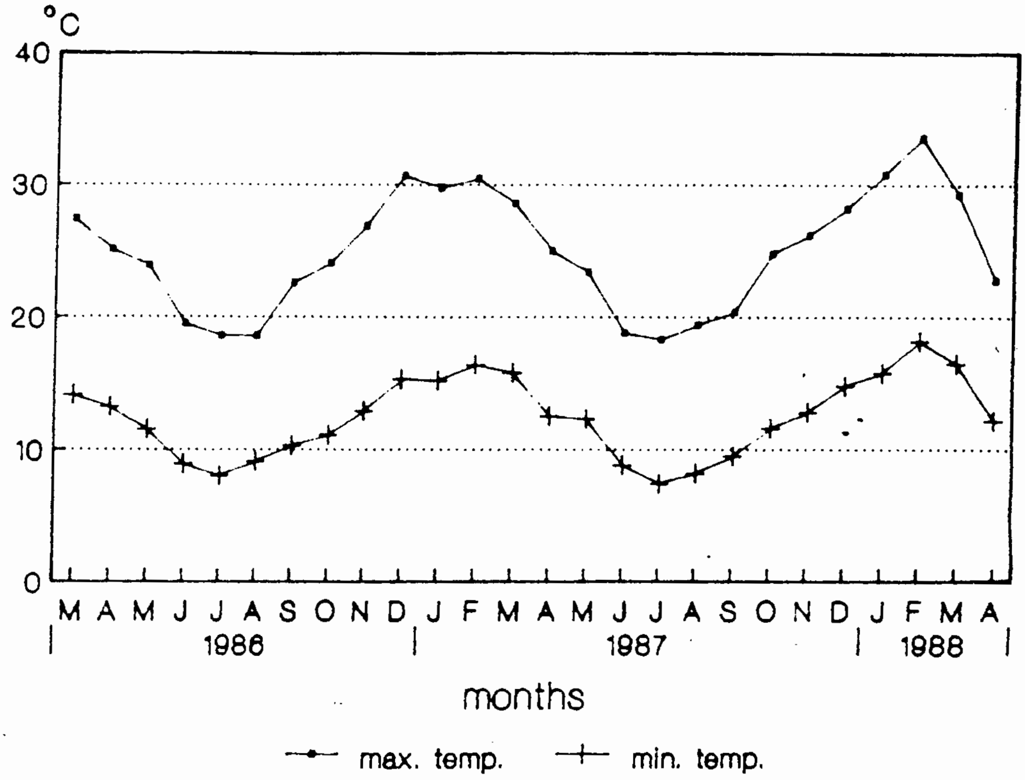


Fig.4.3. Monthly distribution of average daily minimum and maximum temperatures for the Worcester Veld Reserve, March 1986 to April 1988

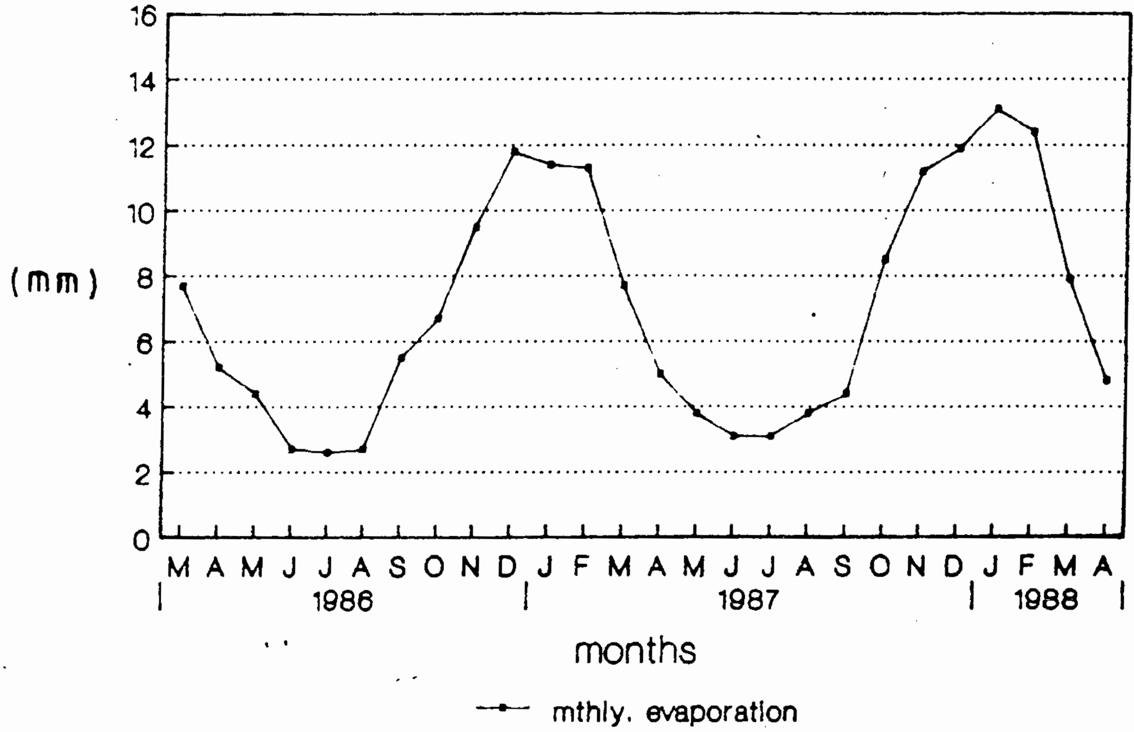


Fig.4.4. Monthly distribution of average daily pan evaporation in the Worcester Veld Reserve, March 1986 to April 1988

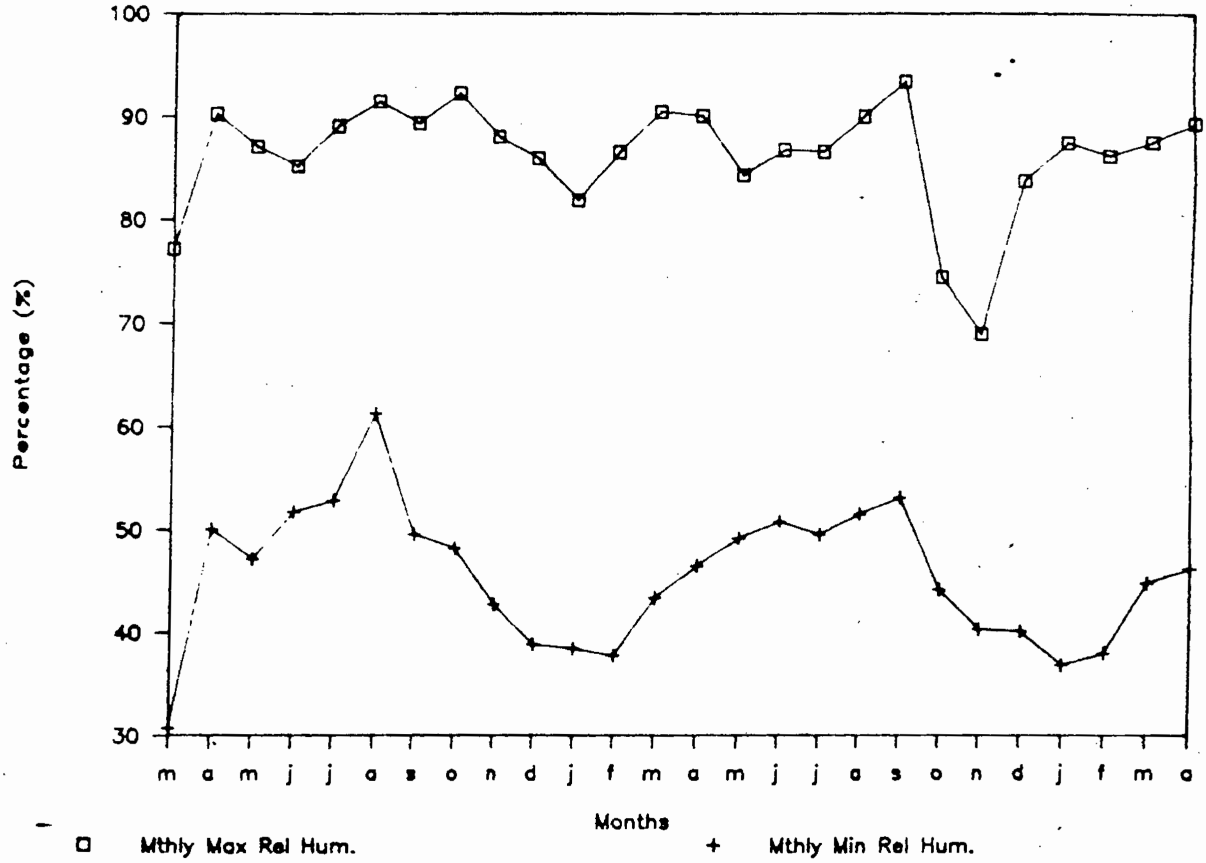


Fig.4.5. Monthly distribution of average daily minimum and maximum relative humidity for the Worcester Veld Reserve, March 1986 to April 1988

4.3 Methods

i) Community phenology

Five one hectare sites were selected so as to represent different topographic features, and include mima-like mounds of the area. These sites were represented by a south-facing slope, a north-facing slope, a ridge top, an alluvial plain, and mounds throughout the area.

Phenophases for 39 perennial species were monitored monthly for a period of 25 months (March 1986 to April 1988). Phenophases recorded included presence of immature leaves, presence of mature leaves, shoot growth, presence of flower buds and flowers, presence of fruiting structures and mature seed, and leaf shedding. Phenophases for at least five individuals or more per species per site at each sampling date were recorded. The duration of phenological states for each species was determined by those periods where more than one individual of a species exhibited a particular phenological state.

Phenodiagrams were constructed for all species. From these, overall patterns of behaviour were determined, and intra- and interspecific comparisons of phenophases made to establish similarities and differences in phenological patterns.

ii) Detailed phenology

Ten individuals of five species were selected and marked in a three hectare north slope site. Species selected represented different plant-form groups as defined in section 3.3.1. The species and corresponding groups were :

1. *Ruschia caroli* - Evergreen Leaf Succulent
2. *Tylecodon paniculatus* - Stem Storage Succulent
3. *Rhus incisa* - Deciduous Mesophyll
4. *Pteronia paniculata* - Evergreen Sclerophyll
5. *Euphorbia mauritanica* - Evergreen Stem Succulent

Five shoots per individual, each on a different main branch, were selected and labelled. At approximately monthly intervals from March 1986 to April 1988 the following measures for each shoot were made :

1. Length
2. Number of leaves
3. Median length of leaves
4. Number of flowers
5. Number of seed or seedheads

Data were not obtained for October 1986, January and December 1987, and January and March 1988.

Shoot and leaf lengths were measured with dividers. The number of leaves, flowers and seed or seedheads were determined by absolute counts. Other variations in physical appearance were noted.

4.4 Results

i) Community phenology

just to give an example from Boshoff's studies.

Growth

Monthly distribution of percentage species in the various phenophases show definite seasonal peaks (Fig. 4.6 a-c) The growing season in both years was from March/April till November. During the three summer months of the year some 65 % of the species did not show either shoot or leaf growth. Approximately 35 % of the species showed some growth throughout the summer months. The period during which all species grew was longer by several months in 1987 relative to 1986. This was probably a response to the high sustained and earlier rainfall during April and May of 1987.

(+)L

flow.

A peak in the percentage of species flowering (Fig. 4.6 b)

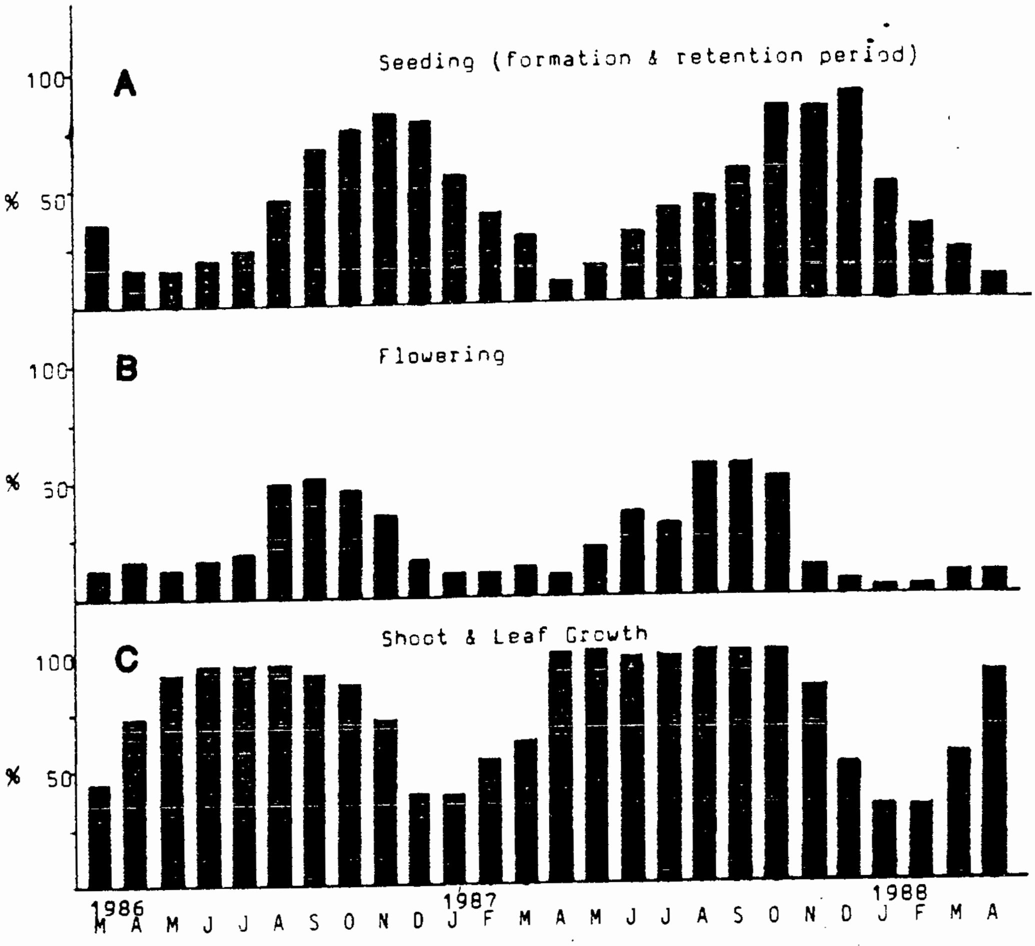


Fig.4.6. (a), (b), (c). Monthly distribution of seeding, flowering and growth phases respectively in perennial plant species on the Worcester Veld Reserve (Y-axis = % of species, n = 39)

occurred during August, September and October in both years, but this peak comprised only about 50 % of all species. This was due to the temporal spread in flowering amongst species (see Fig. 4.8). Seed production peaked about two months after the flowering peak and was greatest in October, November and December (Fig. 4.6 a).

Combined individual species growth patterns (Fig. 4.7) show that several species grew all year long. It is evident that despite minor variation the remainder grew from March till November in both years. The shorter period of inactivity during the summer of 1987/88 is again indicative of an increased growth period in 1987 as suggested above (see Fig. 4.6).

There was temporal spread in the flowering periods amongst species (Fig. 4.8). The trend was similar for both years. One group flowered twice annually. Some species also had extended flowering periods in 1987 relative to 1986. This may be related to the increased rainfall and hence increased growth in 1987.

Species exhibited a similar temporal staggering in seeding as in flowering (Fig. 4.9), but this trend was obscurred by species of Mesembryanthemaceae with serotinous seed structures. In some instances, species which flowered more than once per year maintained seed from one flowering period to the next, obscurring the separate production of these two crops of seeds.

Individual species phenopatterns (growth + flowering + fruiting) are presented in the appendix (Fig. 4.16).

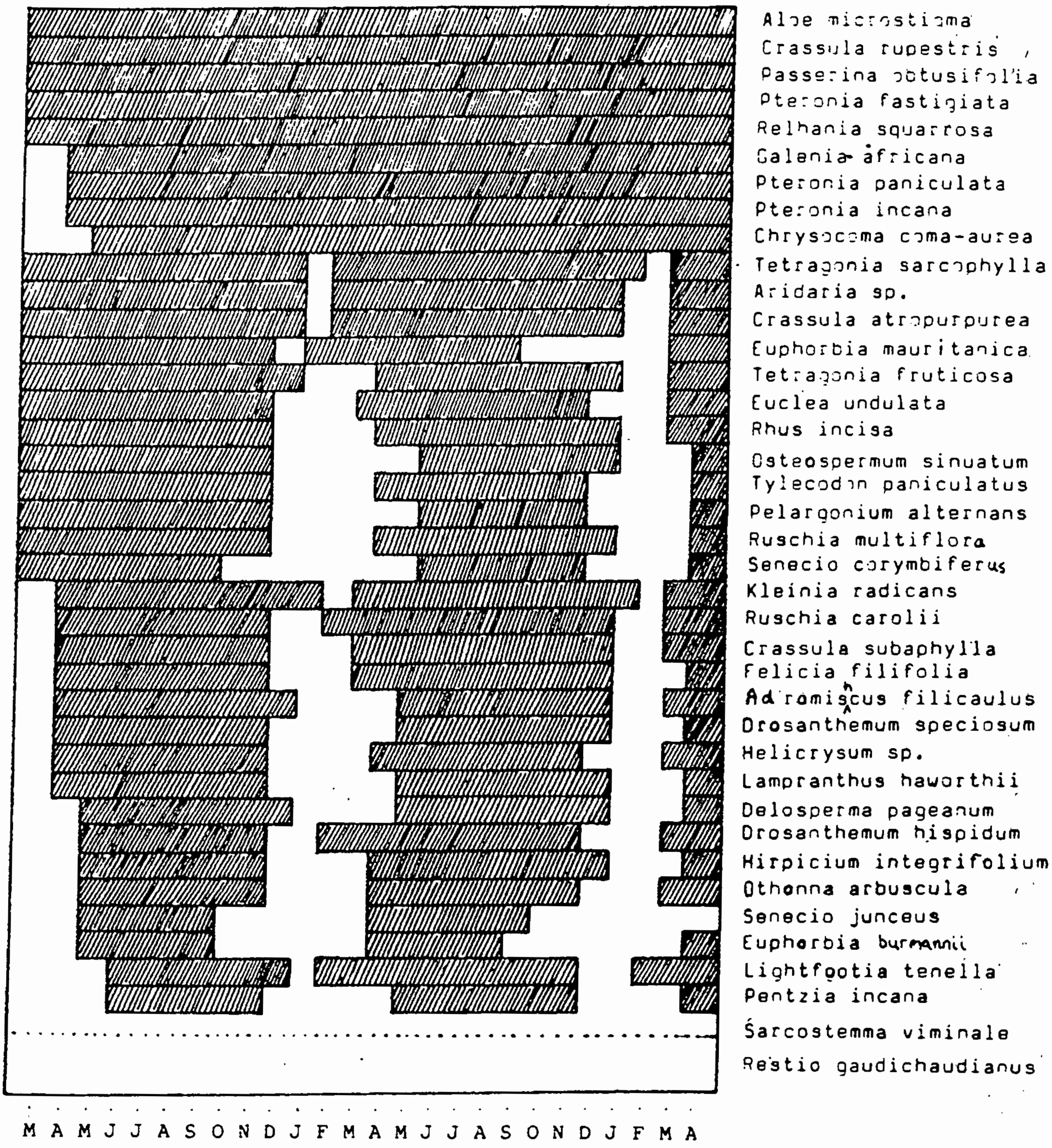


Fig.4.7. Combined phenodiagrams of growth in 39 perennial plant species in the Worcester Veld Reserve, March 1986 to April 1988. Month-symbols indicate end of months

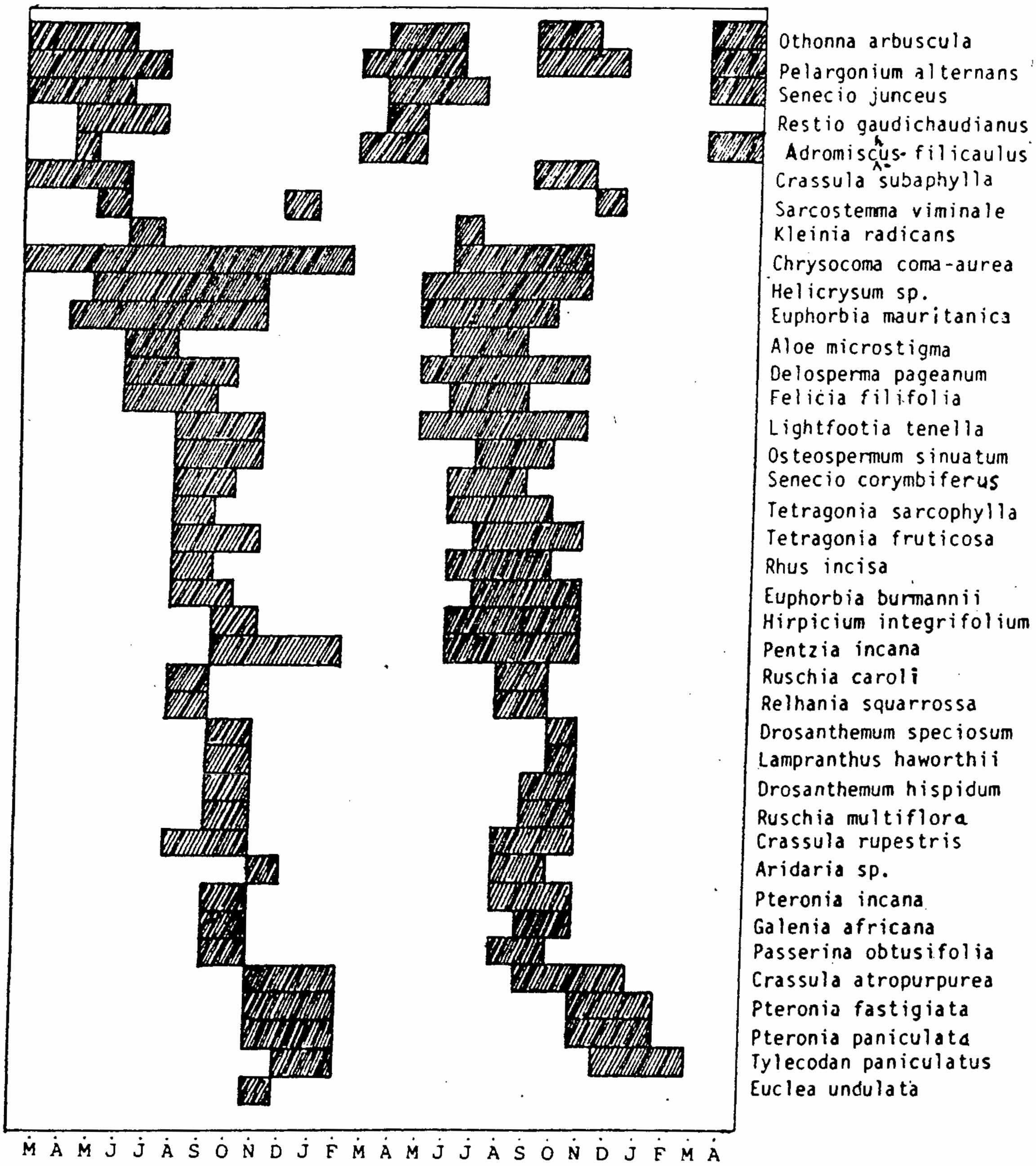


Fig.4.8. Combined phenodiagrams of flowering in 39 perennial plant species in the Worcester Veld Reserve, March 1986 to April 1988

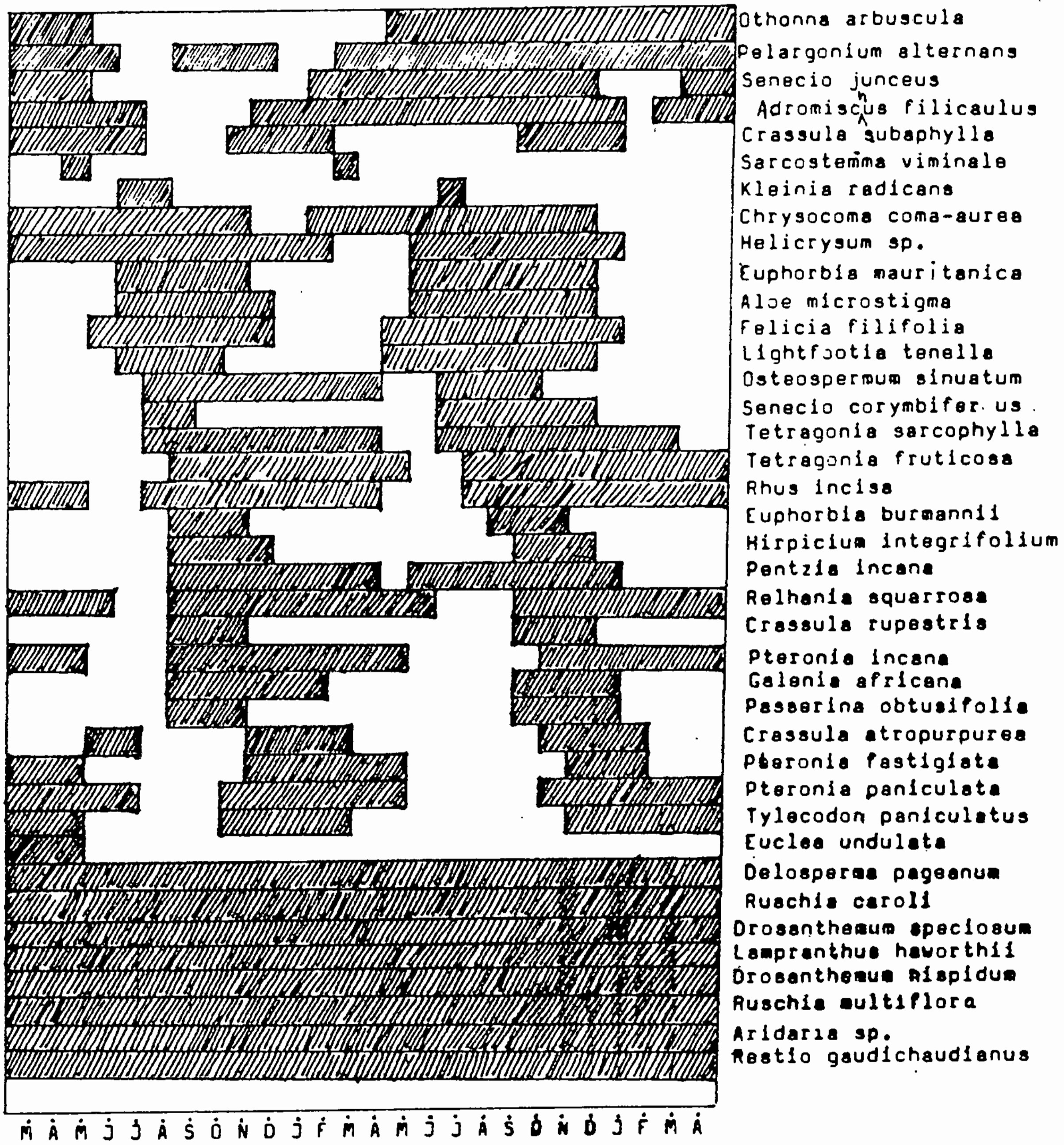


Fig.4.9. Combined phenodiagrams of seeding (maturation and retention periods) of 39 perennial plant species in the Worcester Veld Reserve, March 1986 to April 1988

The growth behaviour of species as analyzed within the predefined stuctural groups (Fig. 4.10 a-f) show that those species that maintained growth throughout the year were mostly evergreen sclerophylls (e.g. Pteronia paniculata, Relhania squarrosa). In addition, the ESC species had the longest periods of growth relative to all other structural groups (see Table 4.1).

There were distinct differences in the flowering behaviour of the various groups (Fig. 4.11 a-f). The patterns for ESS and SSS showed no distinct seasonal peak, indicating that members of these two groups flower independently of each other and from any particular season. In contrast, the remaining four groups had distinct seasonality with respect to reproductive activity. The shape of the curves for the two evergreen leaf groups (ESC and ELS) was similar, with the sclerophyll species having longer flowering times on average than leaf succulents. Flowering in the latter two groups peaked in August/September of both years. The flowering curves for the two deciduous groups were more similar to each other than for any other group. This was especially so for the deciduous mesophylls, and suggests that the optimal flowering period is short for these species.

Absolute phenophase lengths, irrespective of season, and averaged between years and species within a structural group, show that ESC had the longest period of growth, and SSS the shortest (Table 3.1). ELS also had a relatively long growth period. The remaining groups were similar in growth period. Flowering is longest in ESS and DM, followed by SSS. These

Table 4.1. Average lengths and standard deviation (in months) of phenophases for the defined plant-form groups, 1986 and 1987.

FORM	Growth	Leafless	Flowering	Seed
ESC	11.2	0.0	2.4	6.3
	(1.1)	(0.0)	(2.1)	(2.9)
ELS	9.8	0.5	2.4	7.9
	(1.7)	(1.0)	(1.3)	(4.4)
ESS	7.3	6.9	4.2	5.0
	(2.2)	(4.1)	(1.1)	(2.3)
DM	8.0	3.8	4.1	6.0
	(1.4)	(1.7)	(1.0)	(1.2)
DLS	8.8	3.7	2.6	8.9
	(1.2)	(1.5)	(0.3)	(2.4)
BSS	6.6	6.6	3.9	6.0
	(0.9)	(0.3)	(2.3)	(2.0)

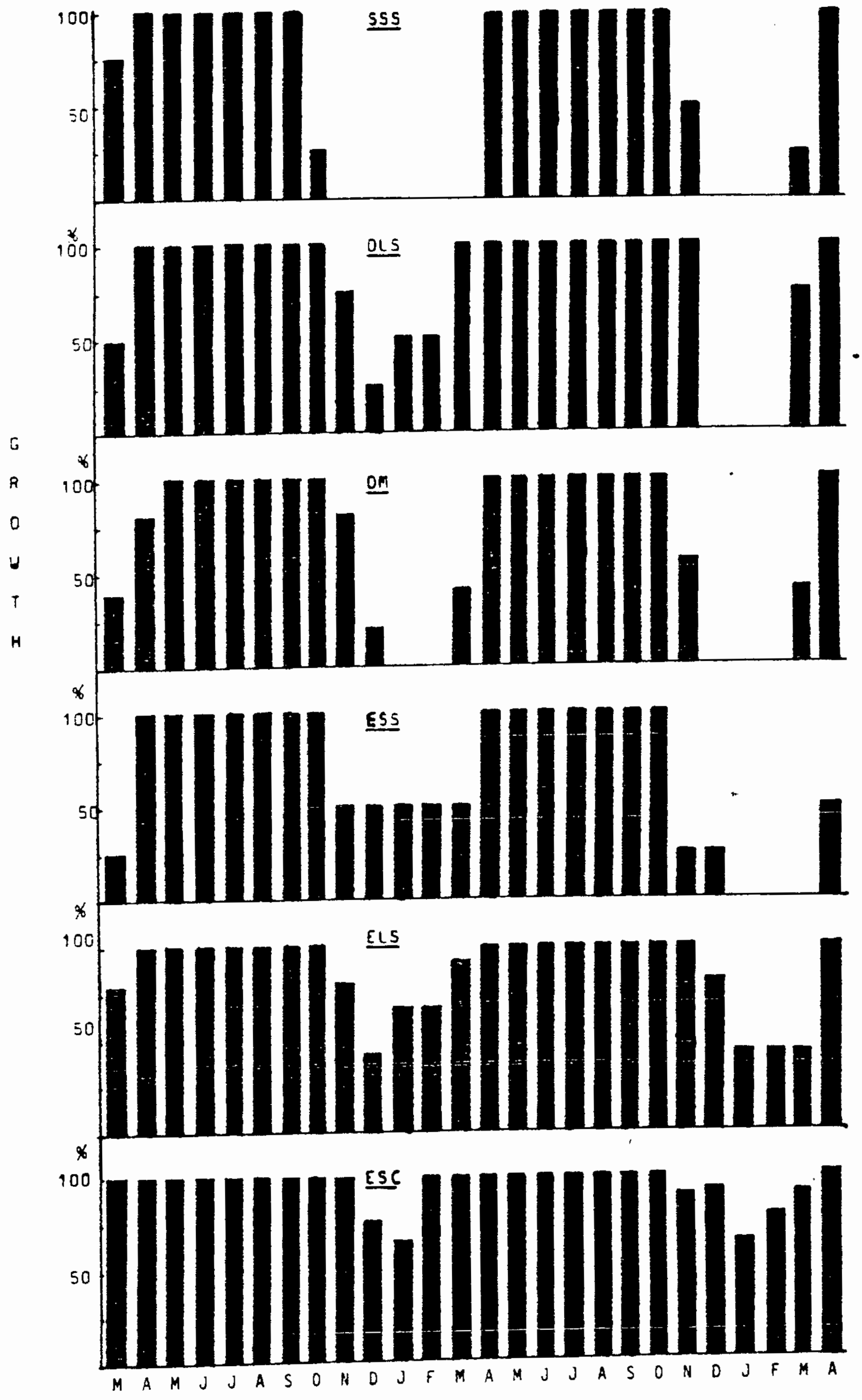


Fig.4.10. Growth patterns in six structural guilds on the Worcester Veld Reserve from March 1986 to April 1988 : KEY : ESC - evergreen sclerophyll; ELS - evergreen leaf succulent; ESS - evergreen stem succulent; DM - deciduous mesophyll; DLS - deciduous leaf succulent; SSS - stem storage succulent

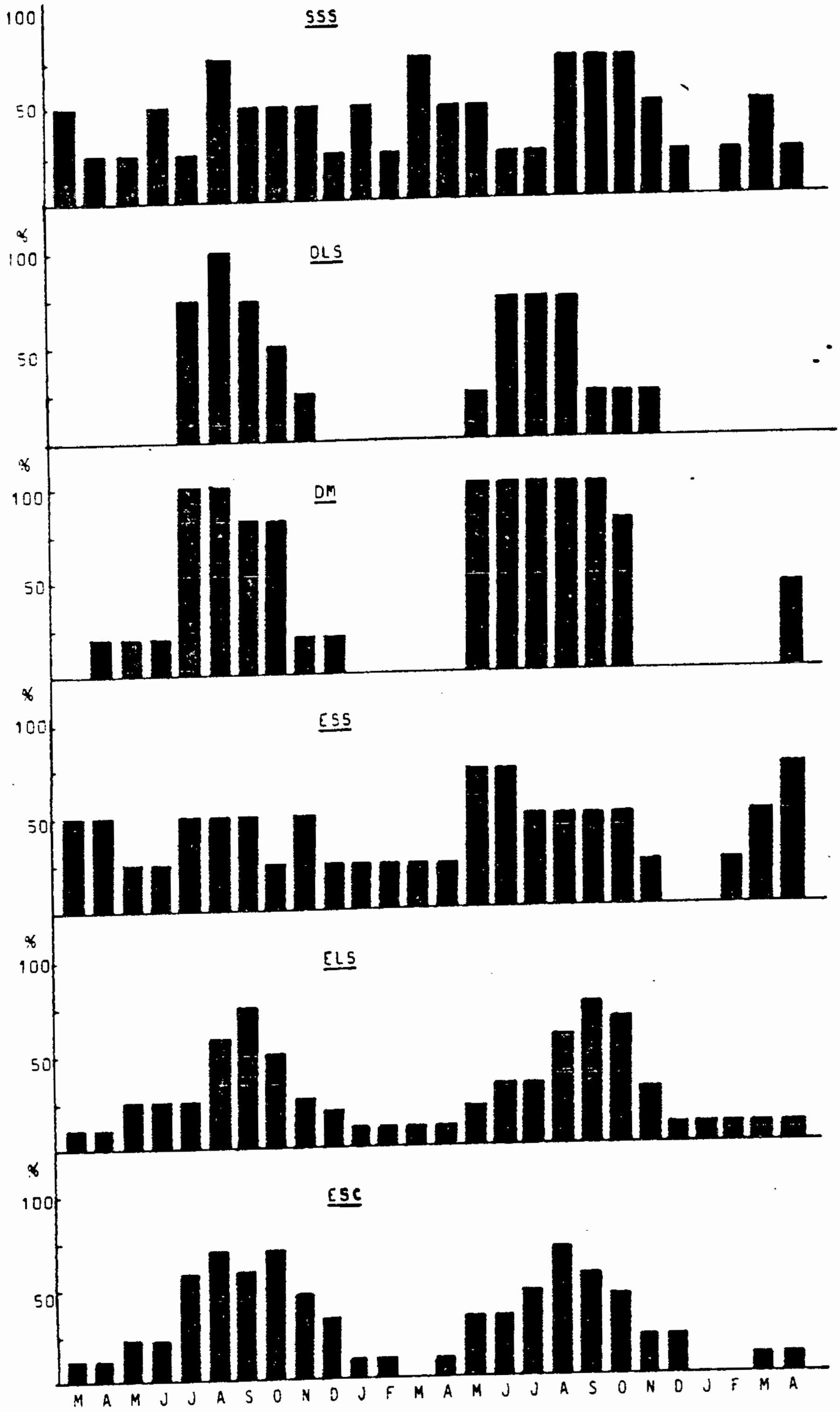


Fig.4.11. Flowering patterns in six structural guilds on the Worcester Veld Reserve from March 1986 to April 1988 : Key as in Fig.4.10

were approximately twice as long as for the other three groups. Seed maintenance was longest in DLS. Other groups retained seed for approximately six to seven months.

Many species did not have periods of distinct shoot growth. In many species there were seasonal changes in leaf or stem consistency and colour. This may be indicative of true functional responses. For instance, in some ELS species leaves turned reddish, and in ESC species, yellow-green, during the drier periods. This suggests that certain physiological processes may be activated during summer, presumably to buffer leaves against increased water tensions, temperature and illumination.

ii) Detailed phenology

Detailed aspects of phenological activity for the five species monitored are depicted in Figures 4.12 to 4.15, and salient features discussed below :

1. Leaf gain and loss (Fig. 4.12) :

There is little similarity in leaf production and leaf loss patterns amongst the five species. The curve for Euphorbia mauritanica indicates that individual shoots behaved independently of each other in terms of leaf gain. Leaf gain was spread amongst shoots over a period of five to six months in the middle part of the year. Rhus incisa and Tylecodon paniculatus (2nd yr) show two distinct peaks in leaf gain (autumn and spring) with leaf loss in June/July or July. Leaf gain and loss in R. incisa appeared positively

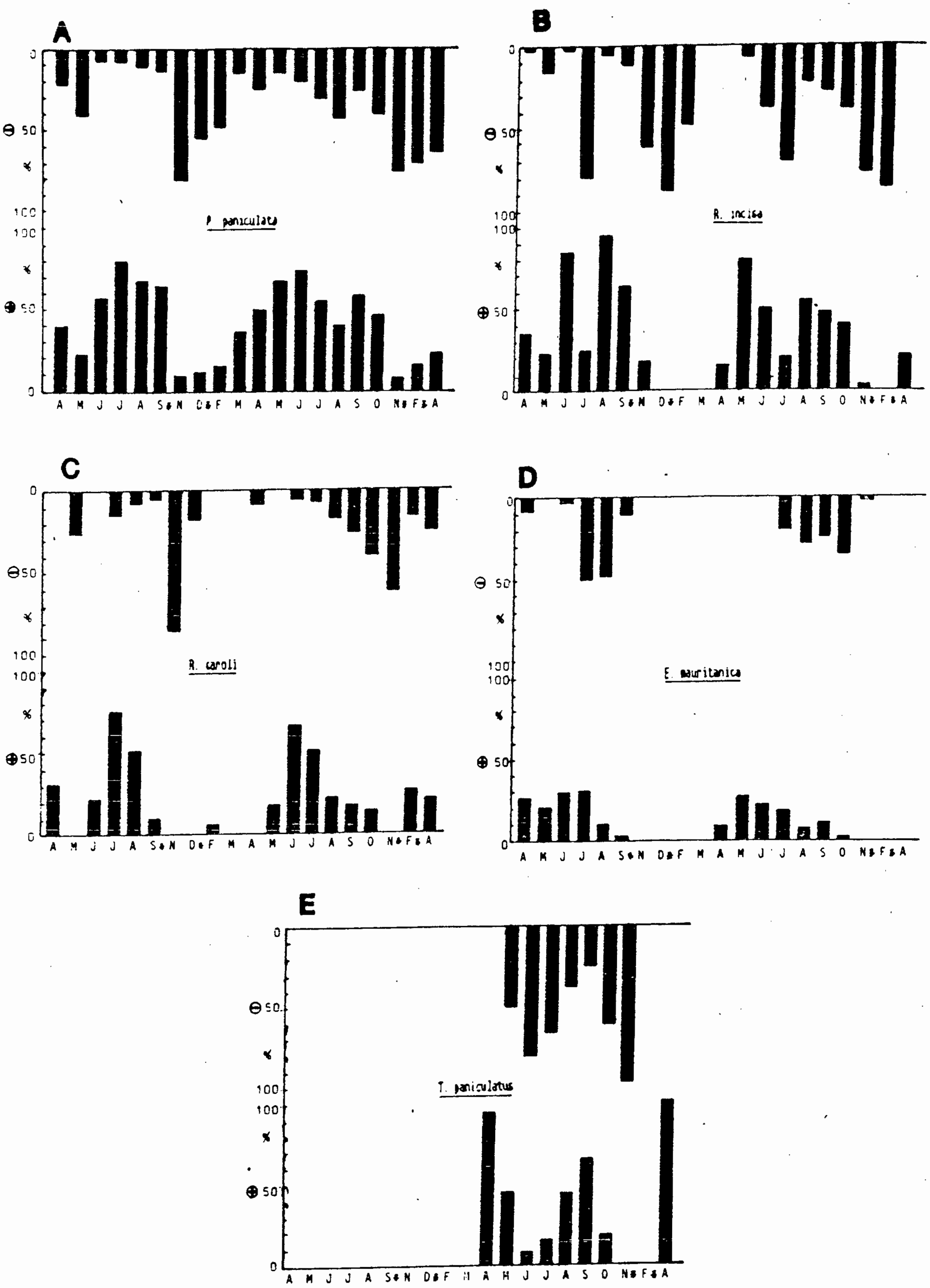


Fig.4.12. Leaf gain and loss for five perennial plant species in the Worcester Veld Reserve, March 1986-April 1988; (a) Pteronia paniculata (b) Rhus incisa (c) Ruschia caroli (d) Euphorbia mauritanica (e) Tylecodon paniculatus (Y-axis = % shoots with positive and negative increment in no. of leaves over the previous month)

correlated with rainfall events in both years. This correlation was also evident for *T. paniculatus* in the second year. *R. incisa* had only one peak of leaf flush in about mid-winter, whereas *Pteronia paniculata* accumulated leaves steadily throughout a large proportion of the year.

Leaf loss was negatively correlated with leaf gain. *R. incisa*, *T. paniculatus* and *P. paniculata* showed greatest leaf loss during November. *T. paniculatus* had high leaf loss in mid-winter. *R. incisa* also showed mid-winter leaf loss, but greatest leaf loss was in December. Leaf loss in *E. mauritanica* was considerable from early on in the year (July/August) but like leaf gain, was spread amongst shoots over several months ending in November/December.

2. Shoot growth (Fig. 4.13) :

Distinct peaks in shoot growth were evident for *Ruschia caroli*, *T. paniculatus* and *P. paniculata*. These peaks were either in September, October or November. For the second year *E. mauritanica* exhibited a peak in June. Note that *R. caroli* and *T. paniculatus* did not have such clear peaks in the second year relative to the first, whereas the contrary was true for *P. paniculata*.

3. Flowering (Fig. 3.14) :

Peak flowering in *R. incisa*, *E. mauritanica* and *R. caroli* was in August the first year, two months before *T. paniculatus* and *P. paniculata*. *E. mauritanica* and *R. incisa* peaked a month earlier (July) in the second year, but *R. caroli* a month later (September). No shoots of *P. paniculata*, and very few in *R. caroli*, flowered in the second year. It may be significant that these are both evergreen species.

There are few consistent correlations of flowering with other phenophases. Peak flowering in *P. paniculata* and *E. mauritanica* corresponds with periods of greatest shoot growth, which in turn correspond to periods of greatest leaf loss. *T. paniculatus* also showed this tendency (1987). Peak flowering in *R. carolii* was between peak leaf gain and leaf loss, but for *R. incisa* there were no discernible correlates.

Flowering periods, and especially peak periods, were generally short (one to two months) with the exception of *E. mauritanica*.

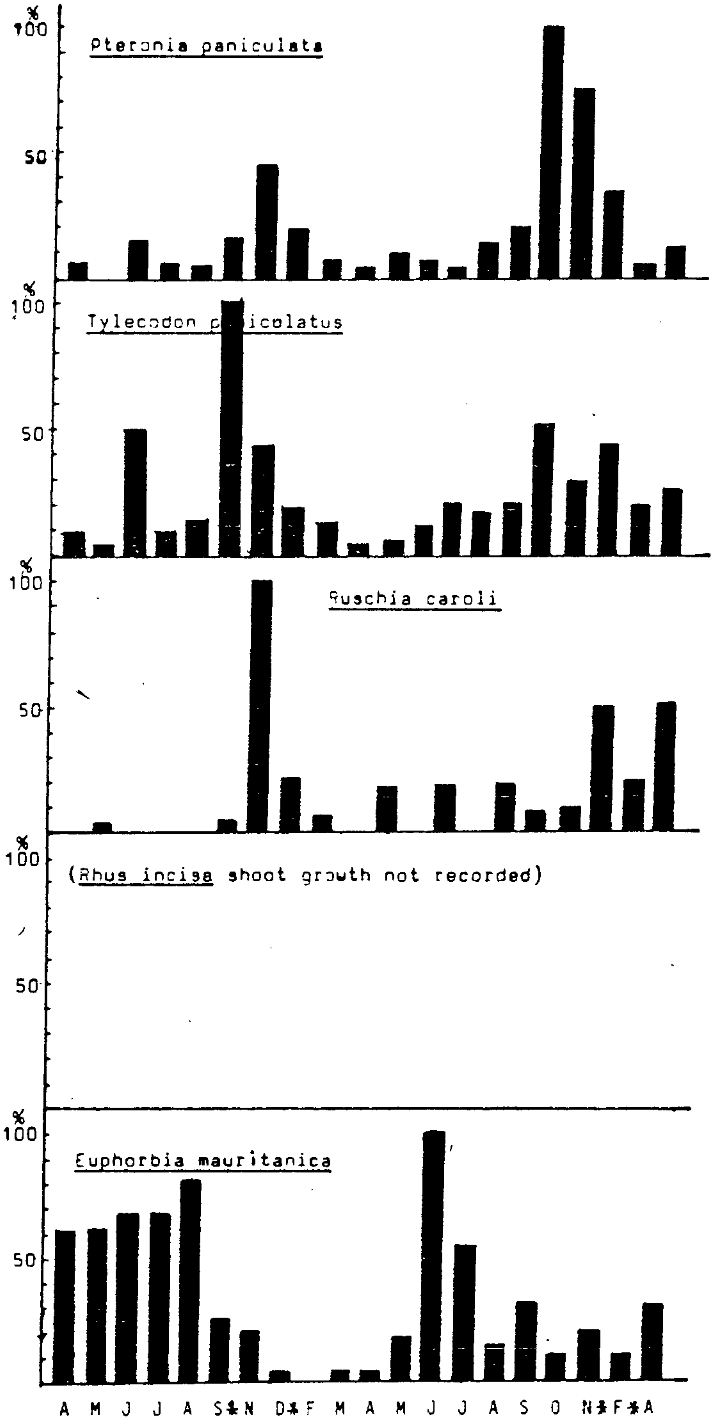


Fig.4.13. Distribution of monthly shoot growth activity of five perennial plant species in the Worcester Veld Reserve, March 1986-April 1988. (Y = % of shoots with positive increment >1.5 mm over previous month)

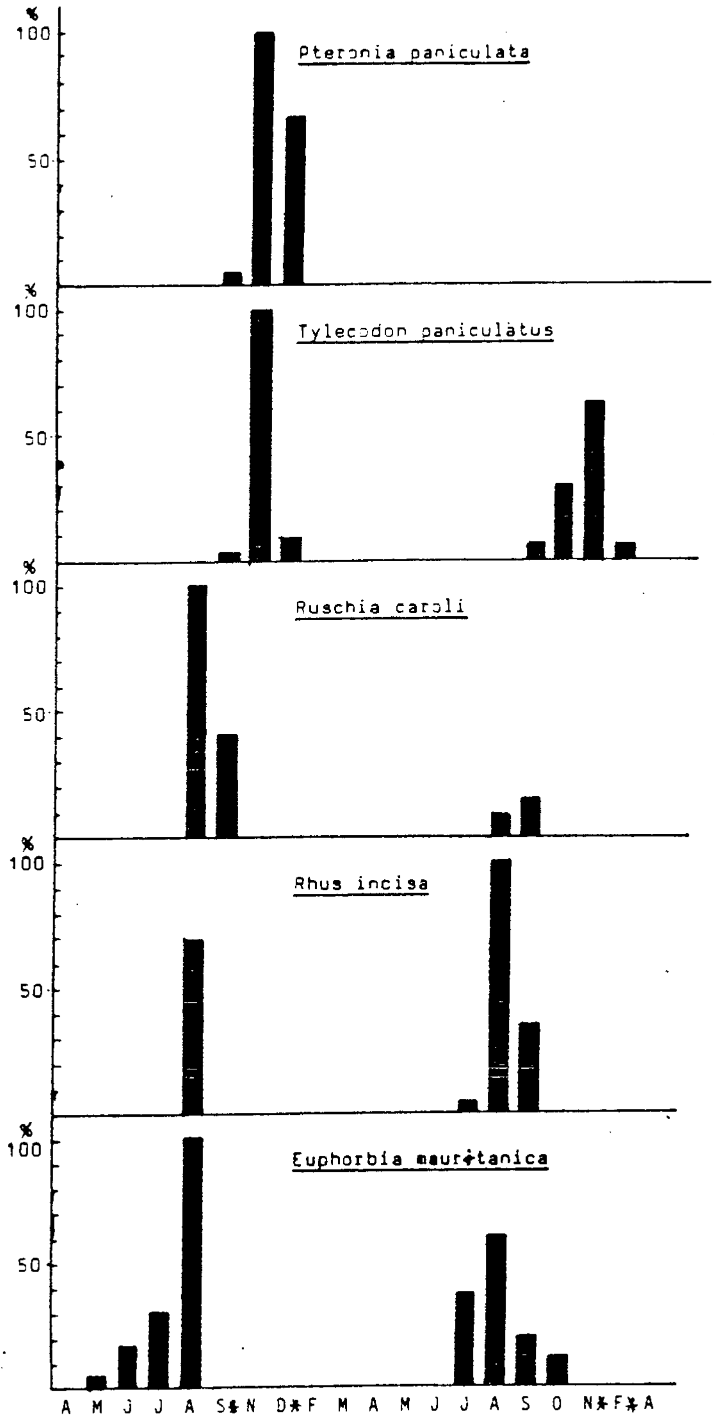


Fig.4.14. Distribution of monthly flower production of five perennial plant species in the Worcester Veld Reserve, March 1986-April 1988 (Y = % flowers of maximum flower production for monitoring period)

4. Seeding (Fig. 3.15) :

There was little similarity in the time of maturation and maintenance of seed between the five species. R. carolii maintained a seed store all-year round, with the maturation of new crops in September (both years). There was a steady decline in seed capsules with time. T. paniculatus seed matured at the beginning of the hottest and driest months, with some seed being present till May. Quantities of seed produced during the 1987 season by this species is not accurately reflected here due to vagaries in monitoring during December and January. Many P. paniculata seed were present from the 1985 crop. The 1986 flowering resulted in a small crop of seeds, with no flowering and hence seeds in the 1987 season. E. mauritanica seed production peaked in August of both years. Some E. mauritanica seed remained till the beginning of the dry season. Few seed were produced by R. incisa in 1986 relative to 1987. Seed was maintained in the 1987 season for at least seven months. Seed maturation time was the longest for this species, if the distance in the seed peak from the flowering peak is taken as a measure of this.

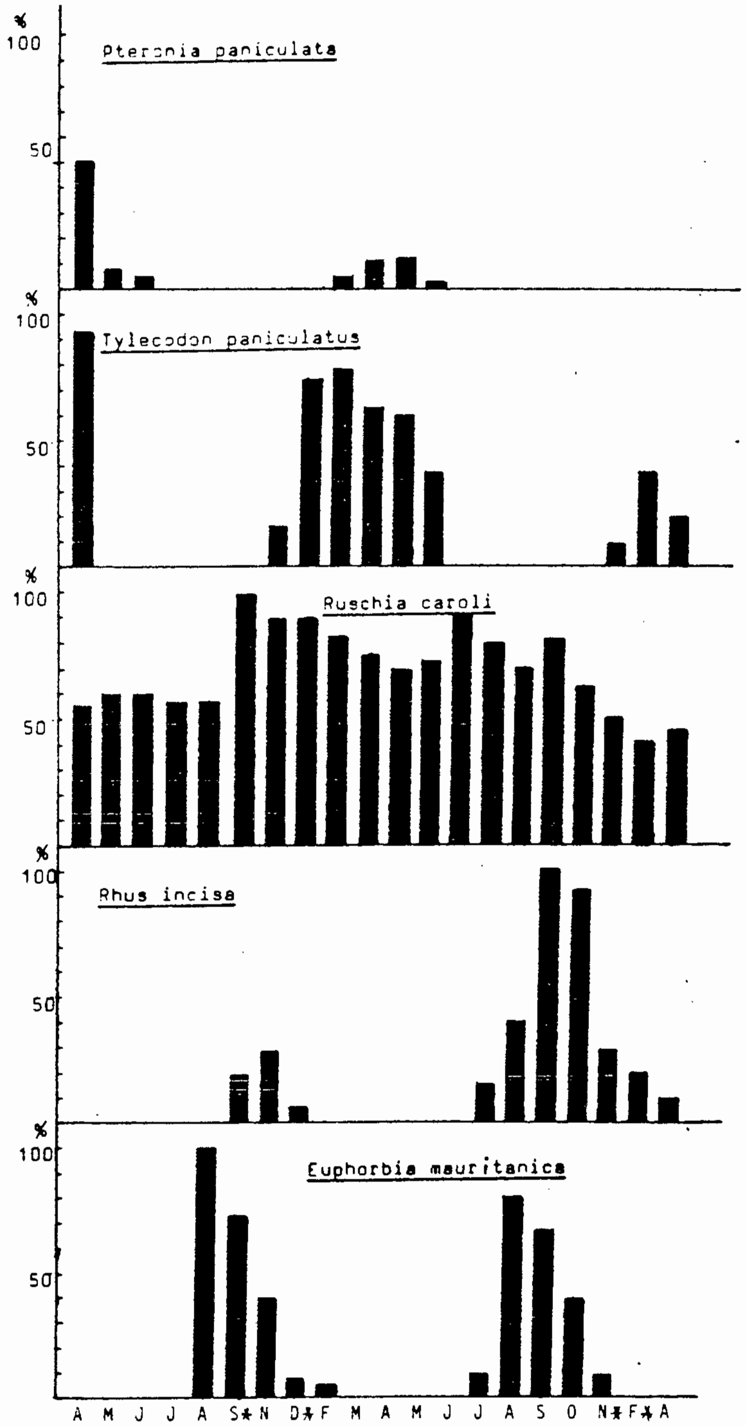


Fig.4.15. Distribution of monthly seed production of five perennial plant species in the Worcester Veld Reserve, March 1986-April 1988 (Y-axis = % seed or seedheads of maximum production during period of monitoring)

4.5 Discussion

The results of this study show that the majority of species are strongly seasonal in phenological behaviour, which for the most part can be related to the strong seasonality of optimal rainfall and temperature conditions. Divergence from a strict seasonal pattern in some species can be related to the possession of certain structural attributes, notably succulence. This study also show that although conclusions can be drawn at the ecosystem level regarding the distribution of phenophases amongst species, a more detailed level of investigation of phenophases reveal finer patterns of behaviour not readily explicable in broad ecological terms, and may even contradict statements derived from less detailed phenology. For instance, the community phenology of this study supports previous findings that the main growth season is from late autumn, through winter and early spring in the Succulent Karoo (Van Rooyen et al.1979 a, Le Roux et al.1989). However, Le Roux et al.(1989) and Hoffman and Cowling (1987) contend that a definite depression in growth is evident during mid-winter months in the Succulent Karoo, but this was evidenced in only two out of five species selected for detailed investigation in the present study. The strong variability both within and among species, and between various regions, suggest extreme caution should be taken when making general statements regarding phenological patterns and their ecological significance (also see Pierce 1984; Turner and Randall 1987).

However, despite these seasonal trends the timing and recurrence of particular phenopatterns is variable amongst species within the broader definitions of season. The present study showed that sclerophyll species are evergreen in the WVR, and maintained some growth throughout the dry summer months. This has been found for sclerophyll species elsewhere (Ackerman and Bamberg 1972; Oechel _et_ _al._ 1972; Halvorson and Patten 1974; Odening _et_ _al._1974; Monson and Smith 1982). These species usually have deep and extensive rooting systems which enable the utilization of water over a long period at depth not accessible to other forms (Noy-Meir 1973; Mooney 1974; Gupta 1979). Sclerophyllous species are furthermore the only species known to be capable of growth and or leaf expansion under conditions of severe negative internal water potentials and of extracting and using water against high negative soil water potentials (Orians and Solbrig 1977; Solbrig 1986). This implicates the structure of their photosynthetic organs, namely the leaves, of setting the potential for nett water use, and hence growth and reproduction, under water-stressed and apparently non-optimal conditions.

That the consistency and structure of the photosynthetic organ largely dictate a species' behaviour in arid environments can be further argued with examples from other structural groups as defined in the present study. Mesophyll species, for instance, are known to have an inherently higher photosynthetic capacity and water-use than sclerophylls (Orians and Solbrig 1977; DePuit 1979). Conversely, they have an inherently lower capacity to grow and maintain leaves when soil or internal water potetials are low (Halvorson and Patten 1974). This relation dictates that mesophyllous species can be photosynthetically active and grow only during those parts of the year when enough rain falls to raise soil-water levels above a certain minimum for a long enough period. Growth outside of the latter conditions will only be possible if the plant is in possession of deep roots or a water-storage system. This has been shown for phreatophytes which have roots tapping sources of permanent ground-water (Odening et al.1974; Nilsen et al.1987). Thus it is again the structure of the main photosynthetic organ which appears important in determining phenological behaviour.

Succulence is an obvious adaptation for water storage, and hence the potential for photosynthesis and evapotranspiration when soil water sources are inadequate (Kluge and Ting 1978). Certain attributes are common to many succulent species. For instance, crassulacean acid metabolism (CAM) is largely associated with succulence, which ensure some of the highest water-use efficiencies (WUE) known in plants (see Chapter 2). However, it does impose very low rates of photosynthesis and hence primary production. Despite the obvious ecological benefits of high WUE in arid regions, CAM could be viewed as an adaptation not only because of improved WUE relative to C3 and C4 modes, but as one that enables plants to accumulate water reserves under conditions of limited soil water availability and high evaporative demand. Water reserves then become available for maintenance and growth when soil water is depleted. Succulent species are generally shallow rooted (Werger 1983; Drew 1979; Jordan and Noble 1984) which enable them to use small rainfall events. Such minor events, especially during the hotter parts of the year, could not reliably sustain a species with a low WUE (e.g. a mesophyll), or with a deep root system (e.g. a sclerophyll). This implies that without the reserve capacity and shallow roots of succulents, such rain would be largely lost to the plant kingdom. Despite these common features, different succulent species take on a variety of forms. The succulents in the study area comprised four of the recognizable groups, the definition of which was based on the degree of succulence of leaves and the water-storage and photosynthetic capacity of the stem. The phenopatterns of these species suggest that these groups are indeed functionally different. For instance, all the stem-storage stem succulents were deciduous, and leaves were relatively large and semi-succulent or mesophyllous. Their main growth period was similar to that of the mesophyll group, with the abscision of leaves during the onset of summer drought. This implies that relatively high production for them is possible only during the optimal period of water availability. The function of the relatively large and "swollen" stem is realized when noting that all species of this group do reproduce outside of the optimal period of spring. That is, the stem reserve enables these species to produce flowers and seeds when impossible for other forms, since resources do not have to be partitioned between ongoing photosynthetic activity and reproduction. A further apparent adaptive advantage of this form lies in the potential to initiate and sustain leaf growth prior to the onset of winter seasonal rains. This is identical to the adaptive capabilities of "perennial ephemeroids" defined by Gupta (1979), the latter which have largely underground storage organs.Species with semi-succulent leaves and woody stems are also all deciduous but have their reproductive period confined to the optimal period of early spring. Similarly, the uniform behaviour amongst species of the other two succulent categories can be explained in terms of the inherent characteristics of true succulent leaves or stems and other structural features of theirs.

The more detailed patterns of behaviour as determined for the five species selected on the basis of their different form, generally corroborate the preceding argument, but reveal finer patterns of behaviour which are not readily explicable in terms of broad ecosystem concepts. Detailed phenopatterns are known for several other arid region species (e.g. Nilsen et al.1987), including many species described by Orshan (1989) and co-workers. From these it is evident that within broadly definable groups individual species have adaptive characteristics unique to them, presumably evolved in response to the finer and subtler selective agents of the arid environment, and which are suited to the particular characteristics of the ecological niche available to them.

It can be concluded that the structure of photosynthetic organs and water-storage potential are meaningful criteria in the formulation of functional plant groups which reflect uniformity in the timing of phenophases and hence of resource-use patterns. The results support the validity of the concept of temporal resource partioning amongst co-occuring species in arid regions (Noy-Meir 1973; Kemp 1983; Jackson and Bliss 1984) and the formulation of plant functional guilds (Root 1967, Cowling 1986) as meaningful ecological units which would aid in analysis of complex plant community patterns and processes. There is, however, the real danger of misinterpretation of phenological results due to differences in the scale of investigation and degree of variability in phenophases amongst species and ecosystems. Future phenological studies should concentrate on finding a common framework within which information can be assessed.

4.6 Appendix

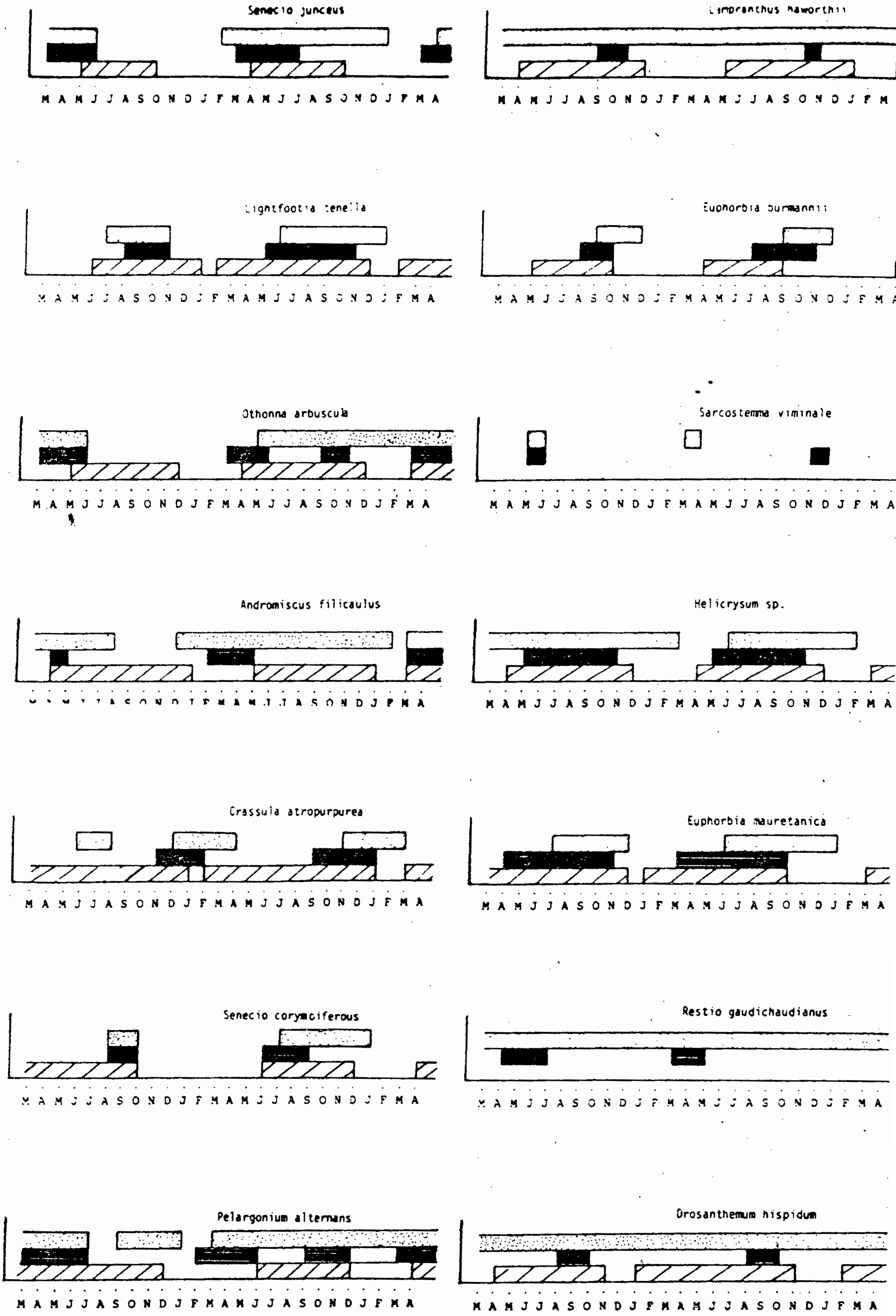
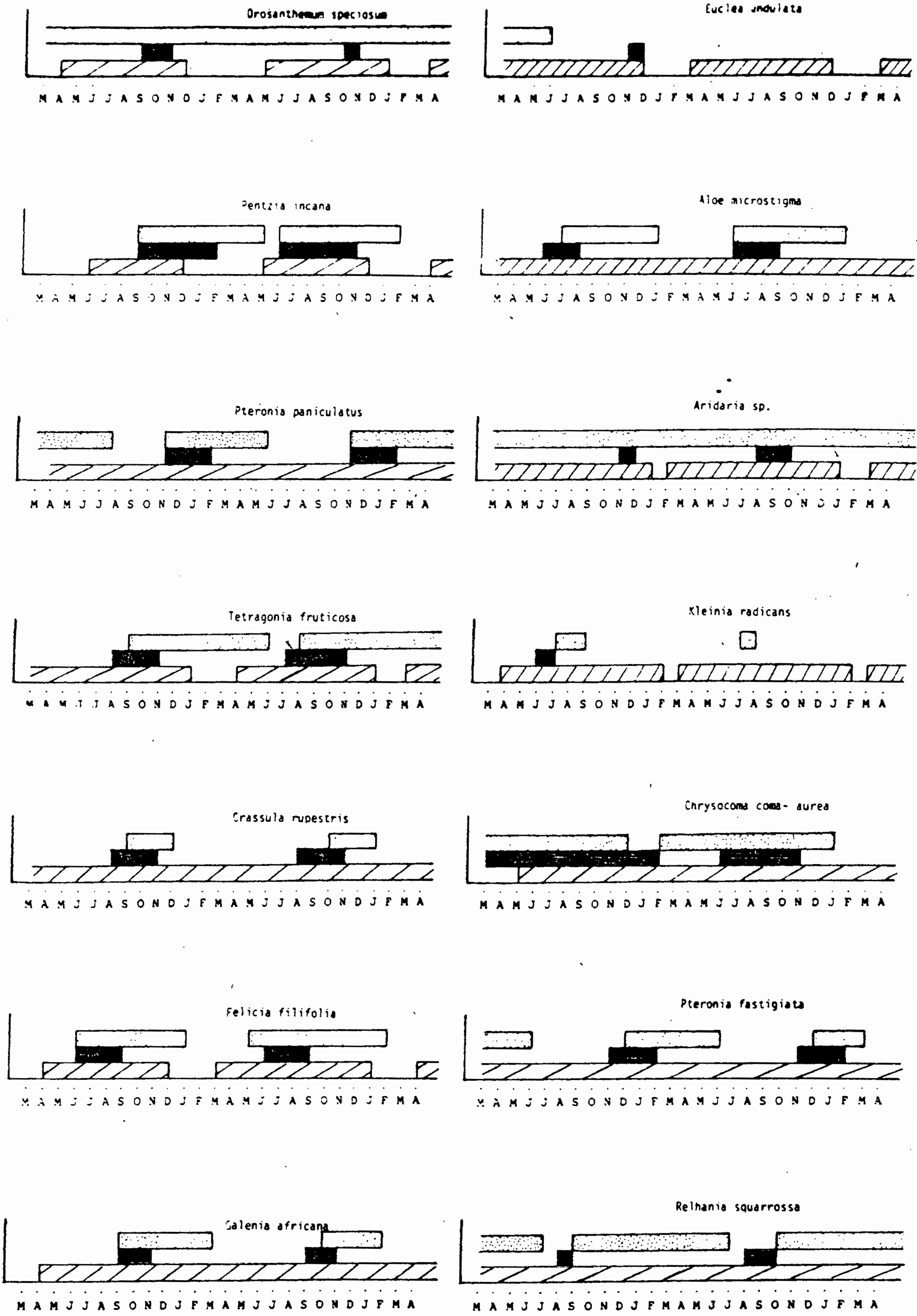


Fig.4.16. Phenograms of 39 perennial plant species in the Worcester Veld Reserve, March 1986 to April 1988.
KEY: = shoot and leaf growth; = flower buds and flowering; = seeding



Orosanthemum speciosum

Euclea undulata

Pentzia incana

Aloe microstigma

Pteronia paniculatus

Aridaria sp.

Tetragonia fruticosa

Kleinia radicans

Crassula rupestris

Chrysocoma coma- aurea

Felicia filifolia

Pteronia fastigiata

Galenia africana

Relhania squarrossa

Fig.4.16. (contd.)

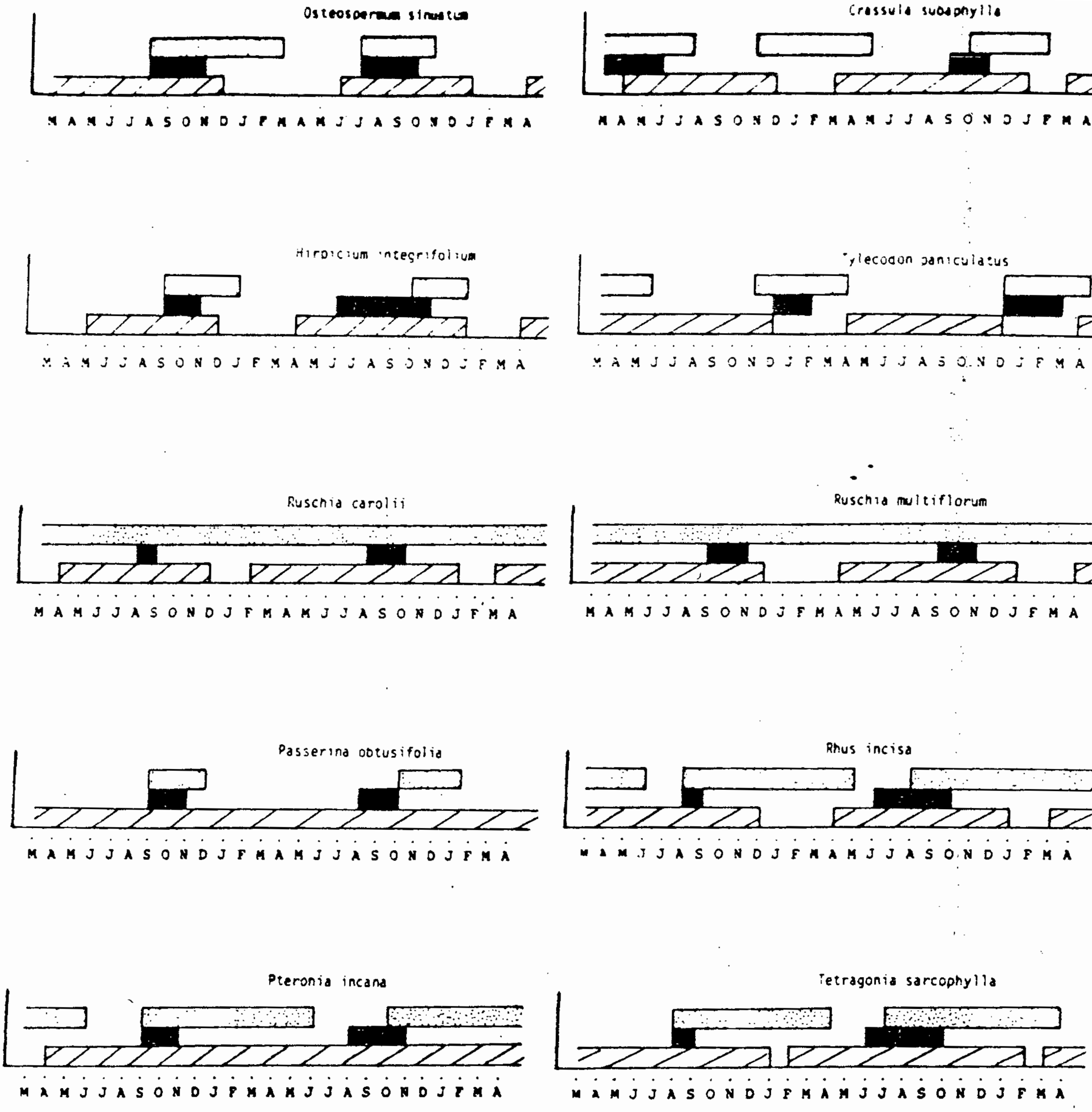


Fig.4.16. (contd.)

4.7 References

Ackerman, T.L. and Bamberg, S.A., 1974. Phenological studies in the Mojave desert at Rock Valley (Nevada Test Site). Ch. 2 in : Lieth, H. (ed.)., 1974. Phenology and seasonality modelling. Springer-Verlag, New York.

Ayyad, M.A., 1981. Soil - vegetation - atmosphere interactions. Ch. 2 in : Goodall, D.W. and Perry, R.A., (eds.), 1981. Arid-land ecosystems : structure, functioning and management. Vol. 2. Cambridge University Press, Cambridge.

Beatley, J.C., 1974. Phenological events and their environmental triggers in the Mojave desert ecosystem. Ecology 55 : 856-863

Cowling, R.M., 1986. A description of the Karoo Biome Project. S.A. Nat. Sci. Prog. Report no. 122, F.R.D., C.S.I.R., Pretoria.

DePuit, E.J., 1979. Photosynthesis and respiration of plants in arid ecosystems. Ch. 21 in : Goodall, D.W. and Perry, R.A., (eds.), 1979. Arid-land ecosystems : structure, functioning and management. Vol 1. Cambridge University Press, Cambridge.

Drew, M.C., 1979. Root development and activities. Ch. 23 in : Goodall, D.W. and Perry, R.A., (eds.), 1979. Arid-land ecosystems : structure, functioning and management. Vol 1. Cambridge University Press, Cambridge.

Earnshaw, M.J., Carver, K.A. and Lee, J.A., 1985. Changes in leaf water potential and CAM in Sempervivum montanum and Sedum album in response to water availability in the field. Oecologia 67 : 486-492.

Farris, M.A., 1987. Natural selection on the plant-water relations of Cleome serrulata growing along natural moisture gradients. Oecologia 72 : 434-439.

Forseth, I.N., Ehrlinger, J.R., Werk, K.S. and Cook, C.S., 1984. Field water relations of Sonoran desert annuals. Ecology 65 (5) : 1436-1444.

Gupta, R.K., 1979. Integration. Ch. 27 in : Goodall, D.W. and Perry, R.A., (eds.), 1979. Arid-land ecosystems : structure, functioning and management. Vol 1. Cambridge University Press, Cambridge.

Halvorson, W.L. and Patten, D.T., 1974. Seasonal water potential changes in Sonoran desert shrubs in relation to topography. Ecology 55 : 173-177.

Hoffman, M.T. and Cowling, R.M., 1987. Plant physiognomy, phenology and demography. Ch. 1 in : Cowling, R.M. and Roux, P.W. (eds.). 1987. The karoo biome - a preliminary synthesis part 2 - vegetation and history. S.A. Nat. Sci. Progr. no. 142, C.S.I.R., Pretoria.

Hoffman, M.T., 1989. A preliminary investigation of the phenology of sub-tropical thicket and karroid shrubland in the lower Sundays River Valley, South Africa. S. Afr. J. Bot. 55 (6) (In Press).

Jackson, L.E. and Bliss, L.C., 1984. Phenology and water relations of three plant life forms in a dry tree-line meadow. Ecology 65 (4) : 1302-1314.

Jordan, P.W. and Nobel, P.S., 1984. THermal and water relations of roots of desert succulents. Ann. Bot. 54 : 705-717.

Kemp, P.R., 1983. Phenological patterns of Chihuahuan desert plants in relation to the timing of water availability. J. Ecol. 71 : 427-436.

Kuppers, B.I., Kuppers, M. and Schulze, E.D., 1988. Soil drying and its effects on leaf conductance and CO2 assimilation of Vigna uniculata (L) Wals. 1. The response to climatic factors and to the rate of soil drying in young plants. Oecologia (Berl) 75 : 99-105.

Kluge, M. and Ting, I.P., 1978. Crassulacean acid metabolism. Springer-Verlag, Berlin.

Lange, O.L., Schulze, E.D., Evenari, M., Kappen, L. and Buschbom, U., 1978. The temperature related photosynthetic capacity of plants under desert conditions. Oecologia 34 : 89-100.

Lange, O.L., Schultze, E., Kappen, L., Buschbom, U. and Evenari, M., 1975. Photosynthesis of desert plants as influenced by internal and external factors. Ch.8 in : Gates, D.M. and Schmerl, R.B. (eds.). 1975. Perspectives of biophysical ecology. Springer-Verlag, Berlin.

Le Roux, A., Perry, P. and Kyriacou, X., 1989. South Africa. Ch. 2.3 in : Orshan, G. (ed.). 1989. Plant phenomorphological studies in Mediterranean type ecosystems. Kluwer Academic Publishers, Dordrecht.

Midgley, G.F. and Musil, C.F., 1989. Substrate effects of zoogenic soil mounds on vegetation composition in the Worcester-Robertson valley, Cape Town, South Africa. S. Afr. J. Bot. (In Prep.)

Monson, R.K. and Smith, S.D., 1982. Seasonal water potential components of Sonoran desert plants. Ecology 63 (1) : 113-123.

Mooney, H.A., 1974. Plant forms in relation to environment. Ch. 7 in : Strain, B.R. and Billings, W.D., (eds.), 1974. Vegetation and environment. Dr. W. Junk, The Hague.

Nilsen, E.T. and Muller, W.H., 1981. Phenology of the drought-deciduous shrub *Lotus scoparius* : Climatic controls and adaptive significance. Ecol. Monogr. 51 (3) : 323-341.

Nilsen, E.T., Sharifi, M.R., Virginia, R.A. and Rundel, P.W., 1987. Phenology of warm desert phreatophytes : seasonal growth and herbivory in *Prosopis glandulosa* var. *torreyana* (honey mesquite). J.Arid Env. 13 : 217-229.

Nobel, P.S., 1977. Water relations and photosynthesis of a barrel cactus, *Ferocactus acanthodes*, in the Colorado desert. Oecologia 27 : 117-133.

Nobel, P.S. and Hartsock, T.L., 1986. Temperature, water, and PAR influences on predicted and measured productivity of Agave desertii at various elevations. Oecologia 68 : 181-185.

Noy-Meir, I., 1973. Desert Ecosystems : Environment and producers. Ann. Rev. Ecol. Syst. 4 : 25-51.

Odening, W.R., Strain, B.R. and Oechel, W.C., 1974. The effect of decreasing water potential on net carbon-dioxide exchange of intact desert shrubs. Ecology 55 : 1086-1095.

Oechel, W.C., Strain, B.R. and Odening, W.R., 1972. Tissue water potential, photosynthesis, carbon-14 labelled photosynthate utilization and growth in the desert shrub Larrea divaricata CAV. Ecol. Monogr. 42 (2) : 127-141.

Orians, G.H. and Solbrig, O.T., 1977. A cost-income model of leaves and roots with special reference to arid and semi-arid areas. Am. Nat. 111 (980) : 677-690.

Orshan, G., 1989. Plant pheno-morphological studies in Mediterranean type ecosystems. Kluwer Academic Publishers, Dordrecht.

Palmer, A.R., 1981. A study of the vegetation of the Andries Vosloo Kudu Reserve, Cape Province. Unpublished M.Sc.-thesis, Rhodes University. Ch 4.

Pierce, S.M., 1984. A synthesis of plant phenology in the Fynbos Biome. S.A. Nat. Sci. Prog. Report no. 88, F.R.D., C.S.I.R., Pretoria.

Root, R.B., 1967. The niche exploitation pattern of the blue-grey gnatcatcher. Ecol. Monogr. 37 (4) : 317 - 350.

Roux, P.W., 1968. Principles of veld management in the Karoo and adjacent dry sweet-grass veld. Ch. 19 in : Hugo, W.J. (compiler) 1968. The small livestock industry in South Africa. Dept. of Agric. Technical Services, Pretoria.

Sammis, T.W. and Gay, L.W., 1979. Evapotranspiration from an arid zone plant community. J. Arid Env. 2 : 313-321.

Solbrig, O.T., 1986. Evolution of life-forms in desert plants. Ch. 4 in Polunin, N. (ed.). 1986. Ecosystem theory and application. John Wiley and Sons, New York.

Thomas, D.A. and Andre, M. 1987. Oxygen and Carbon dioxide exchanges in crassulacean acid metabolism plants : I. Effect of water stress on hourly and daily patterns. Plant Physiol. Biochem. 25 : 85-93.

Turner, N.B. and Randall, D.C., 1987. The phenology of desert shrubs in southern Nevada. J.Arid. Env. 13 : 119-128

Van Rooyen, M.W., Grobbelaar, N. and Theron, G.K., 1979 (a). Phenology of the vegetation in the Hester Malan Nature Reserve in the Namaqualand Broken Veld : 2. The therophyte population. J. S.A. Bot. 45 (4) : 433-452.

Van Rooyen, M.W., Theron, G.K. and Grobbelaar, N., 1979 (b). Phenology of the vegetation in the Hester Malan Nature Reserve in the Namaqualand Broken Veld : 1. General observations. J. S.A. Bot. 45 (3) : 279-293.

Von Willert, D.J., Brinckmann, E., Eller, B.M. and Scheitler, B., 1984. Water loss and malate fluctuations during the day for plants in the southern Namib desert. Oecologia 61 : 393-397.

Von Willert, D.J., Brinckmann, E., Scheitler, B. and Eller, B.M., 1985. Availability of water controls crassulacean acid metabolism in succulents of the Richtersveld (Namib desert, South Africa). Planta 164 : 44-55.

Werger, M.J.A., 1983. Vegetation geographical patterns as a key to the past, with emphasis on the dry vegetation types of South Africa. Bothalia 14 (3 & 4) : 405-410.

Werk, K.S., Ehrlinger, J., Forseth, I.N. and Cook, C.S., 1983. Photosynthetic characteristics of Sonoran winter annuals. Oecologia 59 : 101-105.

Westoby, M., 1980. Elements of a theory of vegetation dynamics in arid rangelands. Isr. J. Bot. 28 : 169-194.

5 GENERAL DISCUSSION AND SUMMARY

Many publications suggest that partitioning of limited resources is a means by which species are able to successfully co-exist in water-limited environments. This concept has been defined for arid ecosystems where water is clearly the primary limiting factor (Noy-Meir 1973; Westoby 1980). Furthermore, the general form and structural attributes of plant species are implicated as major factors enabling resource partioning to take place (Mooney 1974; Orians and Solbrig 1977; Solbrig *et al*. 1977; Solbrig 1986), although physiological (Noy-Meir 1973; Mooney 1974), and reproductive and recruitment strategies (Hoffman and Cowling 1987) must also be contributory factors. Few arid region studies have, however, investigated finer details of resource partitioning at the plant community level (Sammis and Gay 1979; Kemp 1983), and structural-functional relationships are rarely used to explain the mechanisms by which temporal and spatial resource partioning amongst co-occurring species are likely to take place (Orians and Solbrig 1977; Solbrig 1986).

A review of ecophysiological studies in arid systems indicates that there is a direct relationship between the consistency and type of photosynthetic organ and growth-activity of plants in water limited environments. For instance, all sclerophyllous species appear to have the ability to photosynthesize and grow despite the presence of high negative water potentials. Also, these species have an inherently low maximum photosynthetic rate and hence rate of biomass accumulation. Conversely, mesophyllous species can maintain photosynthesis and photosynthetic organs only when water potentials are relatively low, but have an inherently high maximum rate of photosynthesis and hence rate of growth. The type and consistency of a plant's photosynthetic organ is thus a good indicator of it's potential water-use abilities since water-use is directly coupled to rates of photosynthesis and carbon gain (Chapter 4). The consistency of the photosynthetic organ and the potenial for water storage should therefore be meaningful criteria by which arid region species can be functionally grouped.

In the Worcester Veld Reserve, a variety of plant-forms co-occur successfully in a range of microhabitats (Chapter 3). Their phenology (Chapter 4) shows that groups defined on the basis of photosynthetic-organ consistency and water storage potential have varying periods of growth, and different patterns of flowering and seeding. There is however an obvious optimal period for growth during winter and early spring when for some time all species from all groups were found to grow. Mesophylls and leaf semi-succulents were invariably deciduous with shorter growth periods than other groups. Sclerophylls and leaf succulents were invariably evergreen with longer periods of growth than the other groups. This substantiates the proposed relationship between photosynthetic organ type and leaf consistency and phenological behaviour.

The phytosociological survey (Chapter 3) shows that in no site was only one plant-form present, and that all plant-forms were present in many of the sites. Comparison with previous surveys indicate that patterns of co-occurence have not changed discernibly for at least 23 years - thus there is little if any competitive exclusion taking place. The likely stratification or diversification of roots amongst plant-form groups (Chapter 2), coupled with the differential growth activity (Chapter 4) support the concept that particular forms occupy distinct spatial and temporal water-available niches in this water-limited region.

Topography, with concomitant erosion and drainage characteristics, imposes further variation in effective moisture availability in any given area (Chapter 3). I suggest that there is both "passive" and "active" resource partitioning:

i) Passive in the sense that various microsites have different effective moisture availabilities over time which are determined by characteristics of soil and geomorphology. The spatial heterogeneity will determine the range and densities of forms that can co-occur within any one particular area. In this regard Noy-Meir (1981) suggests that strong small scale spatial heterogeneity is the norm in arid ecosystems.

ii) Active in the sense that, where soil conditions allow, co-occurring species may develop roots to varying depths and extent depending on their form, and further through the differential timing of water-use. Competition as such would be limited to species with similar space-time niche-axes.

I conclude from the various considerations in this thesis that the photosynthetic organ structure per se and water storage potential of arid region plants are ecologically meaningful attributes with which to help define functionally similar groups in arid environments. This is based on the critical role of water in arid environments and the direct link between photosynthesis, evapotranspiration and structural plant attributes. This supports the view that water-limited environments set definitive limits to the adaptive options available to plants. I further suggest that selection of primary photosynthetic-organ structure restricts a species to a particular life-history strategy, and to particular secondary structural and perhaps physiological adaptations. This also indicates that there is no single adaptive syndrome to conditions of limited water that may lead to competitive superiority, hence the diversity of plant-forms and species in the Succulent Karoo and other arid regions of the world.

The implications of these considerations can be summarized as follows:

1) The likely behaviour of a species (e.g. the timing and period of growth) can be predicted from knowledge of the nature of the photosynthetic organ and the effective moisture availability in the environment.

2) The type of soil moisture used by a species can be

predicted on the basis of the growth behaviour of a species with a particular leaf type, given knowledge of certain soil and effective moisture availability characteristics. Growth behaviour may also indicate the nature of the root structure present. For instance, a mesophyllous species found to maintain leaves and high photosynthetic rates under conditions of drought must have a rooting system deep enough so as to have access to permanent sources of moisture. Studies on phreatophytes support this postulate.

3) The diversity and combinations of co-occuring plant-forms at any one locality may be good indicators of the degree of niche variability. Alternatively, the absence of particular forms may be a good indicator as to the absence of particular water-available niches, or indicate management practices which have put pressure on survival in particular niches. For instance, absence of grasses as a particular functional guild in areas of the Karoo may indicate that past grazing practices resulted in the loss of topsoil which formed the basis of a particular available niche.

Future research should perhaps concentrate on refining the ideas proposed in this thesis and by other workers, and investigate the validity of resource partitioning as a real mechanism in the ecology of all arid regions of southern Africa.

5.1 REFERENCES

Hoffman, M.T. and Cowling, R.M., 1987. Plant physiognomy, phenology and demography. Ch. 1 in : Cowling, R.M. and Roux, P.W. (eds.). 1987. The karoo biome - a preliminary synthesis part 2 - vegetation and history. S.A. Nat. Sci. Progr: no. 142, C.S.I.R., Pretoria.

Kemp, P.R., 1983. Phenological patterns of Chihuahuan desert plants in relation to the timing of water availability. J. Ecol. 71 : 427-436.

Mooney, H.A., 1974. Plant forms in relation to environment. Ch. 7 in : Strain, B.R. and Billings, W.D., (eds.), 1974. Vegetation and environment. Dr. W. Junk, The Hague.

Noy-Meir, I., 1973. Desert Ecosystems : Environment and producers. Ann. Rev. Ecol. Syst. 4 : 25-51.

Noy-Meir, I., 1981. Spatial effects in modelling of arid ecosystems. Ch. 16 in : Goodall, D.W. and Perry, R.A. (eds.), 1981. Arid-land ecosystems : structure, functioning and management. Vol 2. Cambridge University Press, Cambridge.

Orians, G.H. and Solbrig, O.T., 1977. A cost-income model of leaves and roots with special reference to arid and semi-arid areas. Am. Nat. 111 (980) : 677-690.

Sammis, T.W. and Gay, L.W., 1979. Evapotranspiration from an arid zone plant community. J. Arid Env. 2 : 313-321.

Solbrig, O.T., Barbour, M.A., Cross, J., Goldstein, G., Lowe, C.H., Morello, J. and Yang, T.W., 1977. The strategies and community patterns of desert plants. Ch. 4 in : Orians, G.H. and Solbrig, O.T. (eds.). 1977. Convergent evolution in warm deserts. Dowden, Hutchinson and Ross, NY.

Solbrig, O.T., 1986. Evolution of life-forms in desert plants. Ch. 4 in Polunin, N. (ed.). 1986. Ecosystem theory and application. John Wiley and Sons, New York.

Westoby, M., 1980. Elements of a theory of vegetation dynamics in arid rangelands. Isr. J. Bot. 28 : 169-194.