The karoo biome: a preliminary synthesis
Part 2 – vegetation and history

R M Cowling and P W Roux (editors)

SOUTH AFRICAN NATIONAL SCIENTIFIC PROGRAMMES REPORT NO

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PREFACE

The karoo biome comprises the arid and semi-arid dwarf shrublands and open grasslands of South Africa. In comparison to other South African biomes, ecological patterns and processes in this biome are poorly understood, despite its size and economic importance. The Karoo Biome Project has been recently initiated to coordinate existing and stimulate new research in the region (Cowling 1986). One of the tasks of the Project is the synthesis of available information on the structure and functioning of karoo ecosystems. An earlier volume (Cowling et al 1986) synthesized available information on the physical environment of the karoo biome including chapters on geology, soils, climate, hydrology, geohydrology and soil erosion.

This volume synthesizes available data on vegetation and plant growth and provides an historical perspective essential for understanding present day patterns and processes. Not included is a chapter on vegetation patterns, typology and characterization. We refer readers to Acocks (1953) and Werger (1978); subsequent contributions in this field did not warrant a new synthesis to replace these overviews. Other chapters on vegetation expose the paucity of data on the demography, physiology and phylogenetic systematics of karoo plants as well as our poor understanding of the dynamics of karoo vegetation in ecological and evolutionary time. These data should provide the scientific basis for the development of sound management systems. The vertebrate fossil record of the Karoo is remarkable and plays a pivotal role in the study of the evolution of mammals. More palaeontological studies in the biome should be encouraged. A clearer picture is beginning to emerge of the ecology of the Khoi-San in the Karoo in precolonial times. However, there are still large gaps in our information.

It is clear that research progress in the karoo biome has been constrained by its remoteness to major research institutions (Cowling 1986). With the establishment of the Karoo Biome Project there has been a surge of interest among researchers from numerous universities and state institutions. Hopefully we are on the path towards a predictive understanding of the structure and functioning of karoo ecosystems. The value of this volume should not only lie in its use as a reference to published data, but also to raise problems and identify research gaps.

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ABSTRACT

This volume is the second in a series of syntheses of existing knowledge of the karoo biome. The first volume summarized what is currently known on the physical environment of the biome namely geology, soils, climate, hydrology, geohydrology and soil erosion. The focus of this volume is vegetation and its history. Included are chapters on vegetation physiognomy, plant growth, vegetation change, phytogeography, palaeo-ecology, palaeontology and archaeology.

SAMEVATTING

Hierdie volume is die tweede in 'n reeks van sinteses van huidige kennis van die karoobioom. Die eerste volume het 'n opsomming verskaf van huidige kennis van die fisiese omgewing van die bioom naamlik geologie, gronde, klimaat, hidrologie, geohidrologie en gronderosie. Hierdie volume fokus op plantegroei en plantegroeigeskiedenis, insluitende hoofstukke oor plantegroeifisiognomie, plantgroei, plantegroeiverandering, fitogeografie, paleo-ekologie, paleo-ontologie en argeologie.

ACKNOWLEDGEMENTS

The preparation of the second volume of this synthesis has been delayed due to a variety of factors, not least of which being several changes in editorial responsibilities. The long and tedious course, for both authors and editors, has been smoothed substantially by the assistance provided by Shirley Pierce, Lynette van Niekerk, Tisha Greyling and Lorraine Horn. Furthermore, the early support of D P J Opperman and continued support of B J Huntley is gratefully acknowledged.

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CHAPTER 1 PLANT PHYSIOGNOMY, PHENOLOGY AND DEMOGRAPHY

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INTRODUCTION

Arid and semi-arid ecosystems are characterized by a stochastically variable low annual rainfall (Noy-Meir 1973). High variation in the timing and amount of this water availability is a major selective force on the biotas of these regions and hence exerts a profound influence on ecosystem functioning. Physical and biological disturbances are also important selective agents and it is often difficult to separate anthropogenic (livestock grazing) and climatic determinants of vegetation structure and composition. Acocks' (1979) perceptive inferences from the accounts of 18th and 19th century travellers, farm names and vicariant plant populations indicate that the Karoo of today is a dramatically altered landscape. He asserts that most of the Karoo was once a grassland which has, in historical times, been replaced by a dwarf shrubland. Continuous selective grazing by domestic stock has reduced once productive parts of the Karoo to a desert pavement in places (Tidmarsh 1948; Acocks 1955; Roux 1980).

Most ecological research in the Karoo has concentrated on descriptive accounts of the vegetation (Acocks 1953; Werger 1978, 1986) and general changes in vegetation structure under different grazing regimes (Roux and Vorster 1983; Vorster and Roux 1983). A predictive knowledge of the phenological and demographic responses of species to climate and grazing is lacking. We know that a greater than normal summer rain in the eastern Karoo results in increased grass cover (Roux 1966). Little is known of the details of such a response. What is the sequence of climatic events which determines this? Is the increased grassiness a result of recruitment from soil stored seed or regrowth from existing but dormant tussocks, or both of these? How many seeds are produced and what proportion will germinate following autumn rains in the same year? The answers to these types of questions are fundamental to the development of a predictive understanding of karoo ecosystem functioning and a meaningful management policy.

In this chapter we describe the above- and belowground physiognomy of karoo plants and review available data on their phenological and demographic responses to different climatic and disturbance (chiefly grazing) regimes. In the light of this review we discuss karoo ecosystem functioning and comment on range management policies.

RAINFALL VARIABILITY: THE DRIVING ELEMENT

The Karoo incorporates a number of climatic types (Figure 1.1). In broad terms there is a decrease in the average annual rainfall and the average number of raindays from east to west (Anonymous 1957). Like other arid

and semi-arid regions (MacMahon and Wagner 1985; Orshan 1986) the variability in precipitation increases with decreasing annual total (Figure 1.2). Sites in the Succulent Karoo (winter rainfall) generally have a more reliable annual rainfall than the Nama Karoo (autumn/spring rainfall) (Figure 1.2). When only the Nama Karoo stations are considered, the relationship between annual average rainfall and coefficient of variation is highly significant ($r = 0,81$; $p < 0,001$).

The coefficient of variation of monthly rainfall for the winter months (May to July) in the Succulent Karoo is relatively low (Figure 1.3). This predictability of winter rain has profound influences on vegetation structure and functioning. Succulent dwarf shrubs are common and are unable to tolerate extended droughts (Von Willert et al 1985). A predictable moisture supply, albeit low, is probably necessary for their survival. Precipitation in the form of fog is important in the coastal regions of the Succulent Karoo (Acocks 1953; Schulze and McGee 1978; Werger 1978) and succulents are able to absorb moisture directly into their leaves (von Willert et al 1985). Mothes (1932 in Fahn 1964) found a good correlation between soil salinity and succulence. A complex relationship between a long summer drought, predictable winter rain and soil salinity may explain the exceptionally high cover and diversity of succulents in this region.

Over most of the Nama Karoo peak rainfall is recorded in autumn (Figure 1.3). There is no strictly summer rainfall (ie November to January) region in the Karoo and the whole region usually experiences summer drought. This has important implications for biological processes. Growth, flowering, germination and recruitment are closely tied to this relatively predictable autumn rain. However, like other arid and semi-arid regions, a single large-enough rainfall event or sequence of events at any time of the year can alter the composition of and processes within a community for years or even decades (Westoby 1980; Zedler 1981).

The amount of rain falling in any particular event also influences community processes. The greatest probability of a significant rainfall event (greater than 10 mm) occurring in the Succulent Karoo is in the winter months, and in spring and autumn in the Nama Karoo (Figure 1.4). Small rainfall events (less than five millimetres) are frequent and are also ecologically significant in that they could influence nutrient cycling and other plant processes (Sala and Lauenroth 1982).

PHYSIOGNOMY

Growth forms and life forms

The tendency to use growth forms and life forms synonymously is misleading. Growth form refers to the morphological architecture and general habit of the plant while life form refers specifically to the adaptive morphology in terms of its ability to survive the unfavourable season (Barkman 1979). Table 1.1 outlines the dominant growth and life form classes in the Karoo.

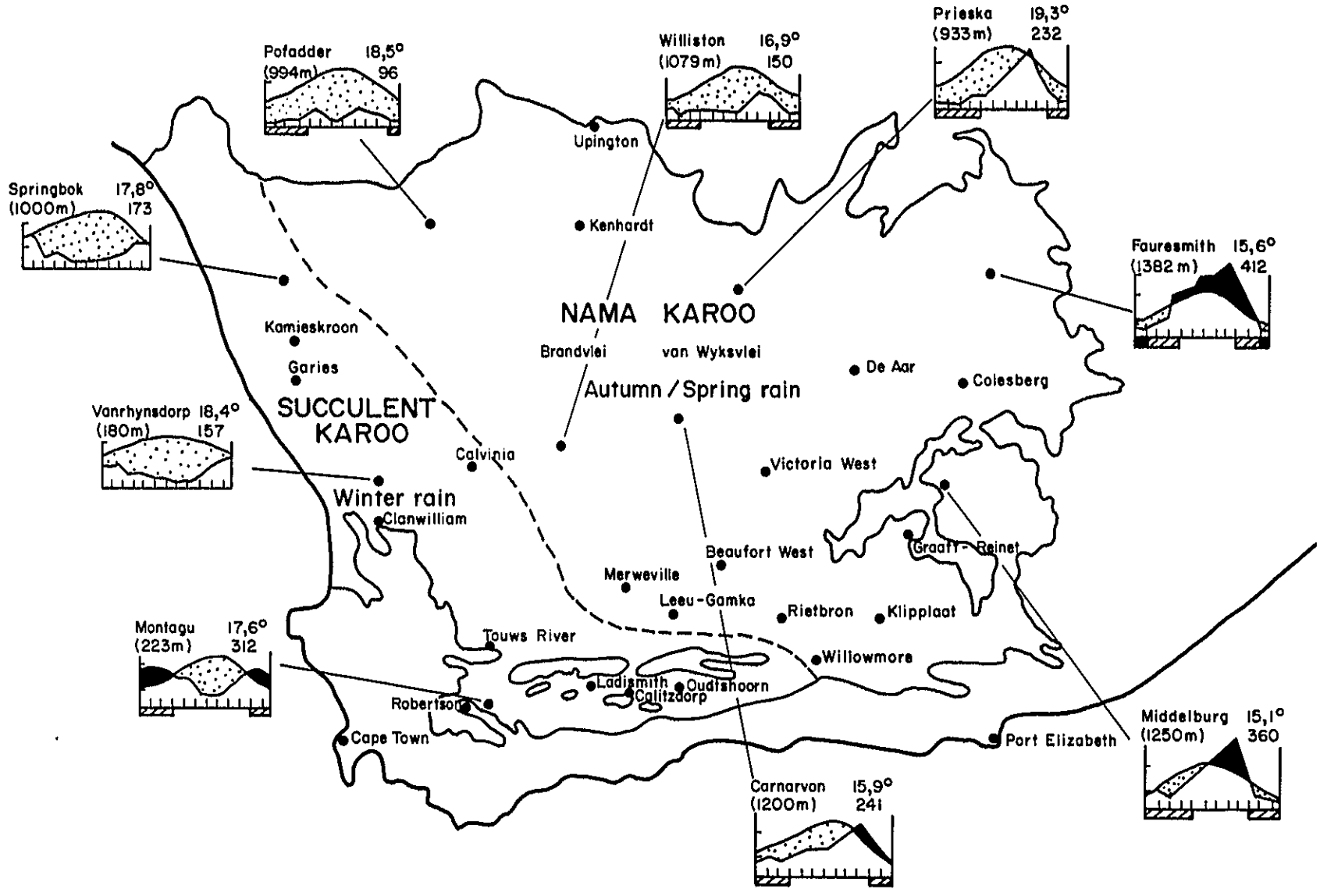

FIGURE 1.1. Climate regions and biomes (sensu Rutherford and Westfall 1986) of the Karoo.

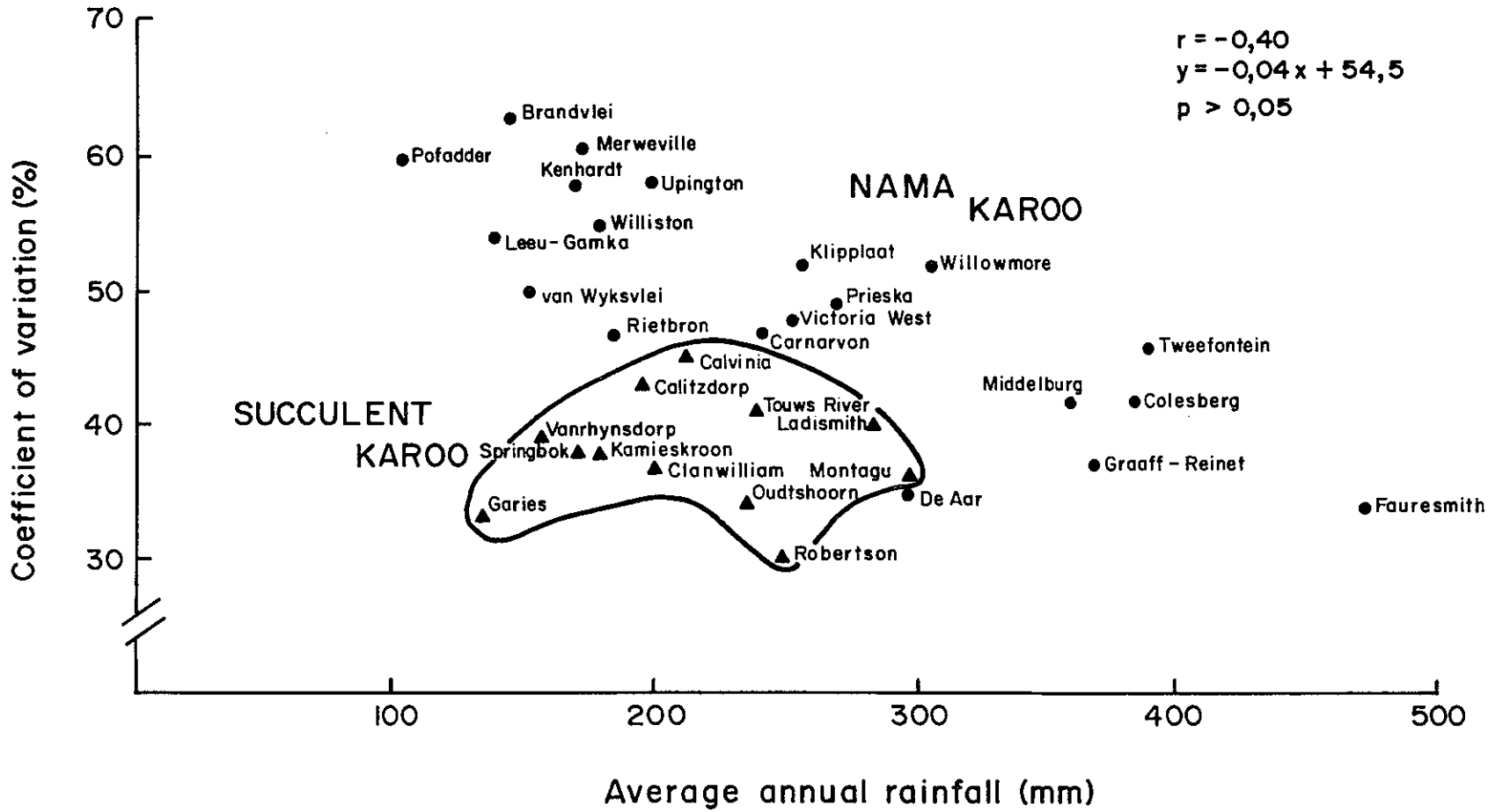

FIGURE 1.2. Linear regression of average annual rainfall with the coefficient of variation for 30 sites in the Karoo. Rainfall data are for 20 years (from Weather Bureau and Department of Agriculture).

TABLE 1.1. Dominant growth and life forms in the karoo biome (from Cowling 1986)

Growth form	Life form	Leaf consistency[1]	Dominant genera	Biogeographical affinity
Annuals	Therophytes	Orthophyll, succulent	Arctotis, Aristida, Cotula, Crassula, Dimorphotheca, Felicia, Heliophila, Hermannia, Grielum, Mesembryanthemum, Nemesia, Osteospermum, Senecio, Ursinea	Karoo-Namib, Cape
Geophytes	Cryptophytes	Orthophyll	Babiana, Bulbine, Ferraria, Homeria, Moraea, Lachenalia, Lapeirousia, Ornithogalum, Oxalis	Karoo-Namib, Cape
Grasses	Hemicryptophytes	Orthophyll	Aristida, Digitaria, Ehrharta, Enneapogon, Eragrostis, Oropetium, Sporobolus, Stipagrostis	Karoo-Namib, Sudano-Zambezian
Dwarf (0-0,25m) and low (0,25-1,0m) deciduous shrubs[2]	Chamaephytes	Orthophyll, fleshy	Didelta, Eriocephalus, Felicia, Galenia, Helichrysum, Hermannia, Indigofera, Lebeckia, Lightfootia, Lycium, Monechma, Rosenia Osteospermum, Pentzia, Plinthus, Pteronia, Rosenia, Selago, Sutera, Wahlenbergia, Walafrida	Karoo-Namib
Dwarf and low evergreen shrubs	Chamaephytes, Phanerophytes	Fleshy, sclerophyll	Barleria, Berkheya, Chrysocoma, Elytropappus, Eriocephalus, Euryops, Felicia, Guidia, Helichrysum, Hermannia, Pteronia, Relhania, Selago	Karoo-Namib, Cape
Dwarf and low succulent shrubs	Chamaephytes	Succulent	Aloe, Anacampseros, Androniscus, Conophytum, Cotyledon, Crassula, Drosanthemum, Eberlanzia, Euphorbia, Haworthia, Hoodia, Lampranthus, Malephora, Othonna, Psilocaulon, Ruschia, Sarcocaulon, Senecio, Sphalmanthus, Stapelia, Zygophyllum	Karoo-Namib
Mid-high (1-2m) and tall (>2m) deciduous shrubs[3]	Phanerophytes	Orthophyll	Acacia, Combretum, Commiphora, Ehretia, Grewia, Lycium, Rhigozum, Rhus	Sudano-Zambezian, Karoo-Namib
Mid-high and tall evergreen shrubs	Phanerophytes	Sclerophyll	Boscia, Carissa, Diospyros, Euclea, Heeria, Maytenus, Pappea, Rhus, Schotia	Tongaland-Pondoland Sudano-Zambezian
Mid-high and tall succulent shrubs	Phanerophytes	Succulent	Aloe, Cotyledon, Crassula, Euphorbia, Pachypodium, Portulacaria	Karoo-Namib, Tongaland-Pondoland

[1] Consistency classes according to Cowling and Campbell (1983)
[2] Deciduous shrubs include shoot, branch and leaf shedders (Orshan 1953)
[3] Deciduous shrubs include leaf shedders only.

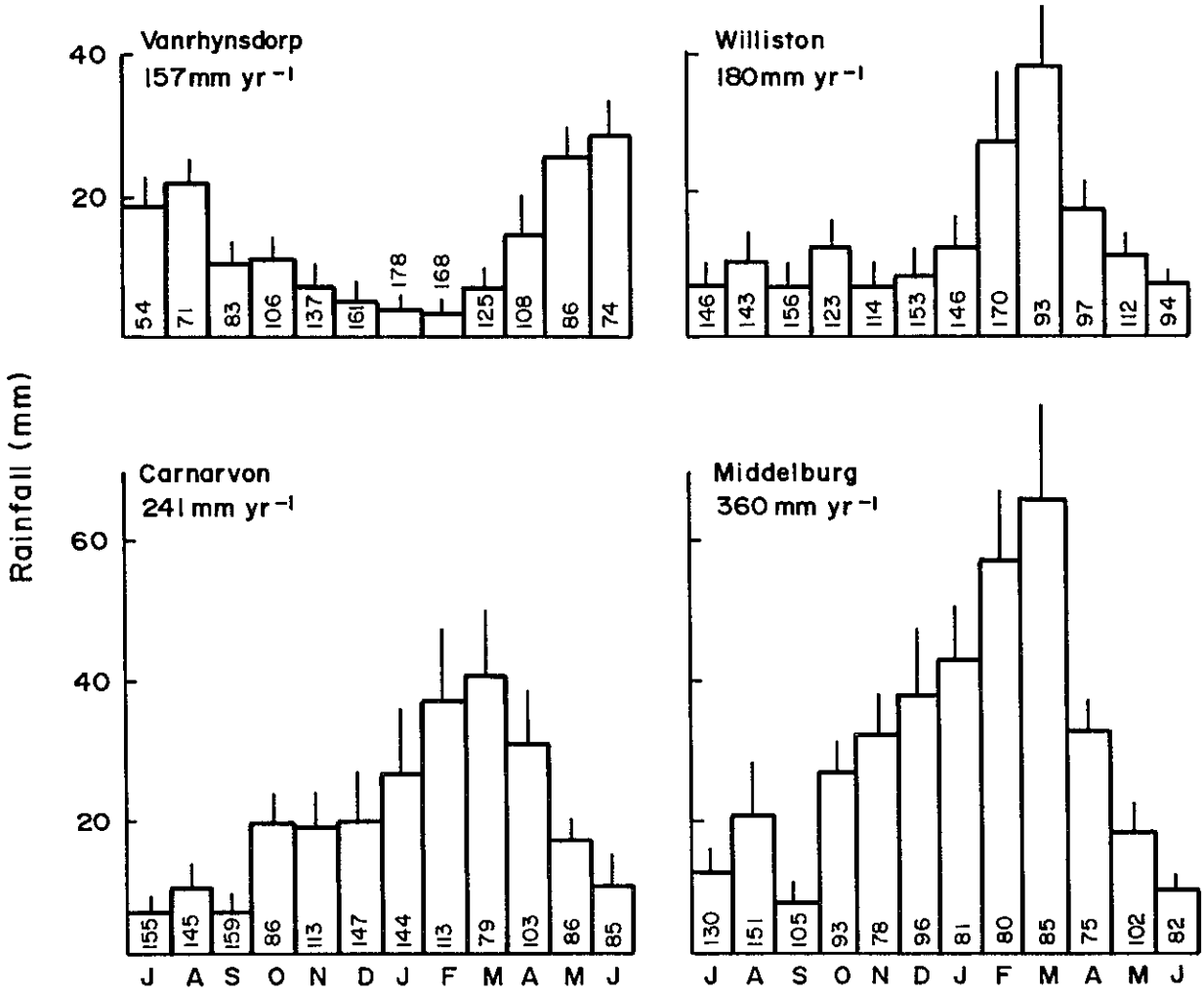

FIGURE 1.3. Average monthly rainfall and coefficient of variation of monthly rainfall for four sites in the Karoo. (Bars represent one standard error). Data for period 1966-1985 (from Weather Bureau and Department of Agriculture).

The popularity of Raunkiaer's (1934) life form classes has facilitated intercontinental comparisons of much descriptive value. Their functional significance, however, has been criticized (Cain 1950; Schulze 1982). The position of the perennating organ, which is seen as an adaptation for surviving the unfavourable season, forms the basis for life form classification. While this holds functional relevance for cold temperate climate plants it has little application in the Karoo. *Rosenia humilis*, *Barleria irritans* and *Euphorbia mauritanica* all have their perannating organ in roughly the same position and are all chamaephytes (Table 1.1). However, each species has a different functional response to the drought (M T Hoffman unpublished). Westoby (1980) points out that therophytes of semi-arid regions include a wide range of annuals with varied responses to different rainfall and disturbance regimes. The general term therophyte has no heuristic value in the prediction of such variation. Without negating the descriptive value of a growth form characterization of vegetation we suggest that the establishment of functional guilds, characterized in terms of physiologically significant

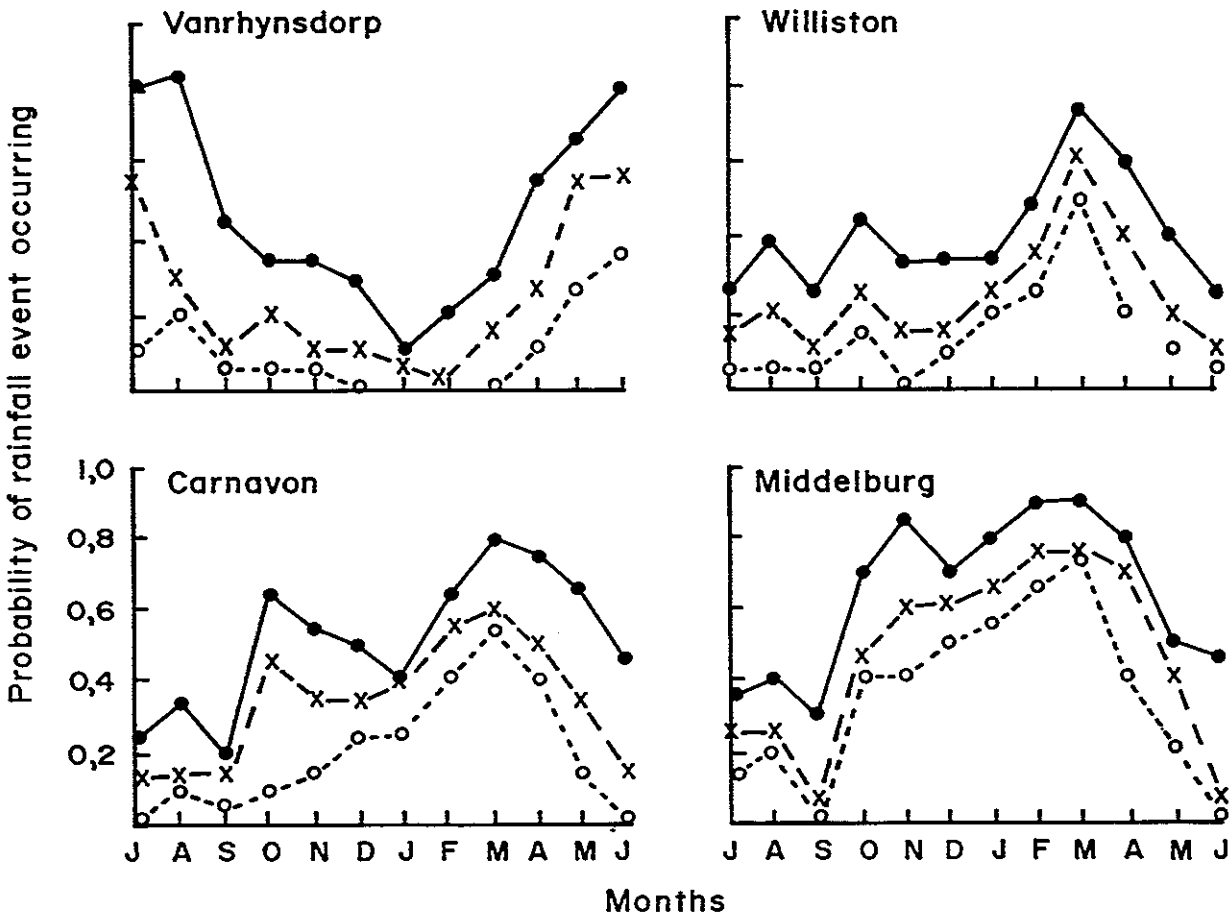

FIGURE 1.4. The probability of different size rainfall events occurring during the year at four karoo sites. ——, >10 mm; x--x, >20 mm; o·····o, >30 mm. Data for the period 1966-1985, from Weather Bureau and Department of Agriculture.

morphological traits as well as demographic responses to climatic and disturbance regimes, should receive urgent attention. There are virtually no data on these traits and processes for karoo species.

General climatic correlates of growth form distribution

Although broad trends in growth form distributions in the Karoo are apparent, differences at a landscape level also occur as a result of local variability in soil depth, soil texture, rock cover, slope and aspect. It is also possible that present-day growth form distributions have been determined by historical land-use practices.

Annuals. Westoby (1980) suggests that in desert and semidesert areas, a relatively predictable seasonal rainfall favours the development of an annual flora. The west coast forelands in the Succulent Karoo experience a relatively predictable winter rainfall regime (Figure 1.2). Dicotyledonous annuals, particularly in the Asteraceae and Brassicaceae (Leistner 1979) may dominate disturbed landscapes in spring. In the Nama Karoo dicotyledonous annuals are rare but annual graminoids (eg *Tragus racemosus*) may be locally abundant, often in disturbed habitats. The

alternating winter and summer annual floras, each with their own distinct germination cues, recorded in the arid regions of North America (Went 1949) and western Australia (Mott 1972) have not been recorded in the Karoo. Werger (1986), however, includes the southern Kalahari as part of the Karoo and reports on an annual summer flora with Sudano-Zambezian biogeographic affinities and an annual winter flora with Karoo-Namib biogeographic affinities for the region.

Geophytes. Like annuals, geophytes are most abundant, both in terms of species richness and cover, in the Succulent Karoo. Locally, however, and depending on climatic events and land-use practices, they may be quite conspicuous in the eastern Karoo. For example, *Moraea polystacha*, which is poisonous to stock, is common in severely overgrazed Steytlerville Karoo following good autumn rains.

Grasses. The overall increase in grass cover from west to east is correlated with an overall increase in rainfall and a declining proportion of winter rain (Acocks 1953; Werger 1978, 1986; Rutherford and Westfall 1986). Acocks (1964, 1979) maintains that low grass cover is a result of overgrazing and that grasses were important in the Succulent Karoo prior to European settlement. The generalized model of karoo vegetation changes in the last hundred years outlined by Roux and Vorster (1983) and modified by Hilton-Taylor and Moll (1986) supports this hypothesis and indicates that the loss of grass cover is the single most important change in karoo vegetation.

Dwarf and low evergreen and deciduous shrubs. A controversy exists as to whether nonsucculent karoo shrubs are evergreen or deciduous. Werger (1978, 1986) maintains that the Karoo is an evergreen shrubland while Cowling's (1986) list of dwarf and low deciduous shrubs (see Table 1.1) includes such dominant genera as *Pentzia*, *Rosenia*, *Eriocephalus*, *Felicia*, *Selago* and *Sutera* suggesting that nonsucculent karoo is a deciduous shrubland. More ecophysiological data are needed before environmental correlates of these growth form distributions can be made.

Dwarf and low succulent shrubs. This growth form includes leaf succulents (eg many Mesembryanthemaceae, *Senecio acutifolius*), stem succulents (eg *Euphorbia*, *Stapelia*, *Hoodia*) and stem and leaf succulents (eg *Crassula*, *Cotyledon*).

Dwarf and low leaf succulents dominate the Succulent Karoo. Stem succulents are common only on the eastern margins (ie in the Noorsveld) and on the northern fringes near the Orange River in the vicinity of Pofadder (Werger 1978). The incidence of succulence is correlated with a number of environmental variables. More critical experimental testing of these hypotheses is needed before cause and effect relationships are clarified. Werger (1986) suggests that succulents are rare in areas which have regular night frosts below minus four degrees centigrade, as frosts easily damage succulents. The reliance of succulents on a predictable, albeit low, annual rainfall as well as the correlation between soil salinity and the incidence of succulence has already been mentioned. In the eastern Karoo the incidence of stem succulence is positively correlated with levels of soil phosphorus, potassium, calcium and magnesium (M T Hoffman unpublished).

Mid-high and tall deciduous shrubs. Having distinct Sudano-Zambezian biogeographic affinities these elements (largely *Acacia* species) are

confined to the water courses and the northern subtropical fringes of the Karoo.

Mid-high and tall evergreen shrubs. The usually large-leaved, sclerophyllous, evergreen shrubs (eg *Rhus* species, *Carissa haematocarpa*, *Pappea capensis*, *Maytenus* species) are most common in the southern mesic parts of the Karoo where they occur on rocky hillsides, termitaria and heuweltjies. However, a number of species penetrate into the Great and Arid Karoo (Acocks 1979) usually along dolerite ridges. Werger (1986) suggests that moisture conditions are more favourable here than on the plains thus enabling the persistence of these drought-enduring growth forms.

Mid-high and tall succulent shrubs. The leaf and stem succulent *Portulacaria afra* (ie the Spekboomveld) dominates the steep, north-facing slopes of the southern fringes of the Nama Karoo. Most of this Spekboomveld has been destroyed by overgrazing in recent times. *Aloe* species are common along the south-eastern Karoo margins and in the northern areas of the Succulent Karoo (eg *Aloe dichotoma*). *Aloe ferox* often occurs along the ecotones between karroid and subtropical thicket vegetation in the south-eastern Karoo.

Root systems

High root:shoot ratios have been suggested as an adaptive mechanism for drought resistance in plants of arid regions (Walter 1963). However, this issue is not resolved and Barbour (1973) and Ludwig (1977) present data from North American deserts to suggest that xerophytic shrubs have lower root:shoot ratios than many mesophytic shrubs. Root:shoot ratios and rooting depths in the Karoo are likely to vary depending on soil depth, texture and water availability. Scott and van Breda (1938) measured roots of *Pentzia incana* to a depth of three metres in the deep Malmesbury shale-derived soils in the Worcester-Robertson Karoo. In the shallow Beaufort series soils of the eastern Karoo the roots of all shrubs seldom penetrate below 0,5 m (M T Hoffman unpublished). An individuals defoliation history is also likely to affect root:shoot ratios as researchers have reported root growth stoppage and even death after defoliation. (Troughton 1957; Muldoon and Pearson 1979; Richards 1984; Brown 1985).

Grasses. Grasses have shallow, fibrous root systems enabling them to respond rapidly to rainfall and to utilize small rainfall events which usually moisten only the top 10 mm of soil (Figure 1.5). Sheath layers prevent dessication and protect the roots from high temperatures (Troughton 1957).

Annual forbs. Our observations in the Central Lower Karoo indicate that annual forbs generally possess a thin, fibrous to fleshy, undivided tap root with a few short primary lateral roots evenly distributed along the length of the root. Root depths were normally in excess of 0,3 m. In order to ensure reproductive success and thus survive from one generation to the next, annuals must have access to a relatively permanent moisture supply. This is achieved by having a relatively deep tap root (Figure 1.5) which is probably produced at the expense of above-ground biomass. Werger (1986) reports that annuals in the Succulent Karoo possess shallow root systems. The predictable winter rains provide favourable water conditions enabling these annuals to maximize above-ground production without investing too many resources in below-ground parts.

Dwarf and low succulent shrubs. Most leaf and stem succulents possess a shallow lateral root system (Werger 1978) which may extend horizontally to a distance of over 2,5 m (Scott and van Breda 1939). They do not usually possess a tap root but there are exceptions (see Weiss and Yapp 1906; Cannon 1911). Shallow roots enable succulents to respond rapidly to small rainfall events (Jordan and Nobel 1984). The roots of succulents have to survive pronounced fluctuations in both temperature and soil water potential. Jordan and Nobel (1984) suggest that with the onset of drought, rapid dehydration of new roots and hydrated cortical tissue of old roots physically withdraws the root from contact with the soil. As a result of these changes in root hydraulic conductance, water stored in the leaves and stems of succulents is prevented from being lost to a drying soil.

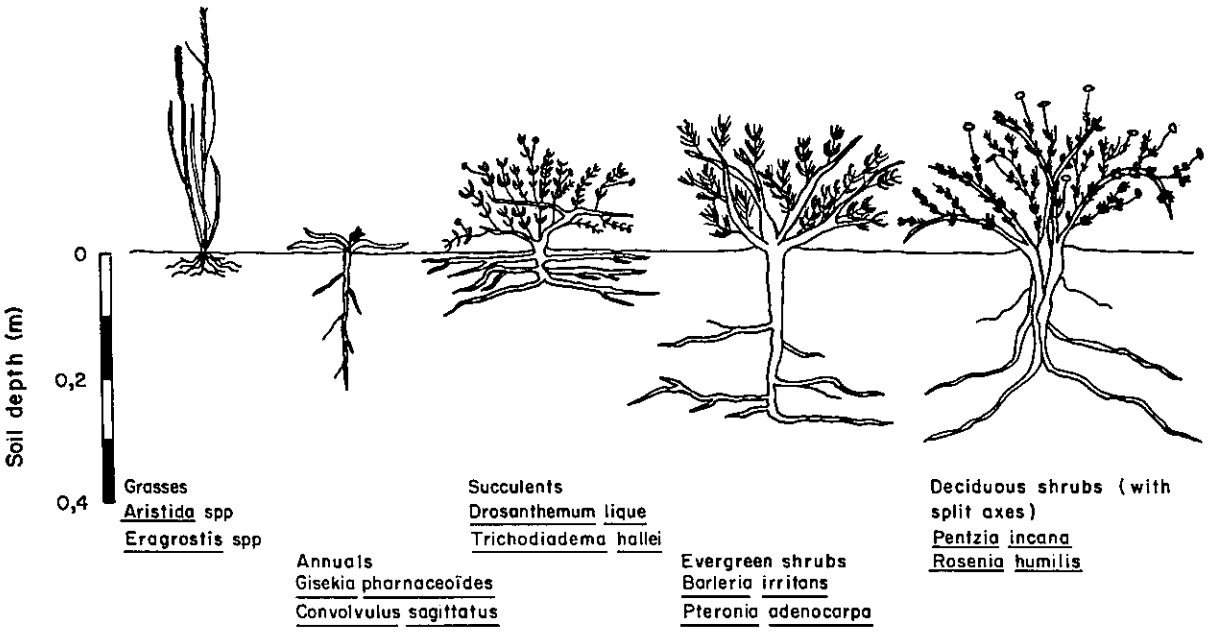

FIGURE 1.5. Major root systems in a central lower karoo community (M T Hoffman unpublished).

Dwarf and low nonsucculent shrubs. Karoo shrubs have a generalized type of root system with an extensive horizontal and vertical distribution in the soil profile (Figure 1.5). This enables shrubs to colonize a wide variety of habitats and to exploit areas in the soil profile which are not occupied by other growth forms. There is no single representative root system for karoo shrubs and there are often large differences between individuals of the same species. Evergreen shrubs (eg *Barleria irritans*) usually have a thick, fibrous, undivided tap root extending some way into the soil before dividing into an extensive lateral root system (Figure 1.5). In the deciduous shrubs (eg *Rosenia humilis*) the tap root usually splits at the soil surface giving rise to as many as

eight or more axes extending into the soil and branching in all directions. Plants with split axes are common in arid and semi-arid regions (Ginzburg 1963; Jones 1984). In the Karoo this trait is commonly found in the Asteraceae but also in other families (eg Aizoaceae, Selaginaceae). Besides being a possible means of vegetative propagation (Theron et al 1968), Jones (1984) has measured significant differences in xylem pressure potentials of different branches of large unwatered shrubs with split axes. Jones (1984) suggests that because of the spatial variation in the soil water distribution, one axis may have access to soil moisture not available to other axes and may thus survive extreme drought conditions.

The accepted notion of the structure of arid plant communities is that each growth form occupies a distinctive position in the soil profile (Yeaton and Cody 1976) and each exploits different moisture reserves at different times of the year (Went 1949; Noy-Meir 1973; Beatley 1974). Greig-Smith (1961) and Harper (1977), however, suggest that the competitive interactions of a species' belowground parts as well as their dispersal mechanisms determines the pattern evident in arid plant communities. These interactions are difficult to test and Barbour (1973) warns of the uncritical acceptance of pattern analysis dogma as it relates to arid and semi-arid areas (see Ismail and Babikir 1986). More detailed studies on rooting patterns and belowground competitive interactions as well as dispersal mechanisms and germination requirements need to be made before karoo community structure and pattern can be explained.

PHENOLOGY

Phenological patterns

Phenological responses of karoo plants are largely controlled by temperature and the timing and amount of rainfall. Endogenous rhythms probably do exist for some species (Henrici 1940), particularly the dwarf and low evergreen shrub component (eg *Helichrysum pentzioides*, *Barleria irritans*) (M T Hoffman unpublished). The predictable winter rainfall season exerts considerable control over phenology in the Succulent Karoo. The probability of additional rain after the first autumn rains is good. These conditions favour annuals (Westoby 1980) which are very conspicuous in this region. In all growth forms, growth starts in autumn, is depressed by the cold winter temperatures and resumes again in spring (van Rooyen et al 1979a). Flowering and seed set phenophases are generally predictable and occur in spring (August-October) (van Rooyen et al 1979a). Annuals complete their phenophases before the shrubs, and geophytes and succulents are the last to do so (van Rooyen et al 1979a).

In the Nama Karoo, where rainfall is less seasonal, phenological activity may be initiated at any time of the year (eg in *Sarcocaulon vanderietae*, *Sutera halimifolia* (Hobson et al 1970)) in response to precipitation "pulses" (Noy-Meir 1973, 1974). Different growth forms will have different phenophases because of the differences in germination and growth requirements and because of their particular distributions in the soil profile. Generally, the period of greatest biological activity is in autumn and spring (Roux 1966). The cold winter temperatures of this region may inhibit growth while high midsummer temperatures can likewise cause a decrease in growth of both the grass and shrub component (Vorster and Roux 1983).

Spatial variability in rainfall plays an important role in phenological patchiness at a landscape level. Because the Nama Karoo receives much of its rain in the form of localized thundershowers, two adjacent areas in an otherwise homogeneous landscape might differ significantly in the amount of rain and the period since the last rainfall. A mosaic of patches with different floristic and structural composition results (cf Wiens 1985).

Effects of defoliation on phenology

An understanding of the effects of the intensity, frequency and timing of defoliation on the phenology of individual or key species is fundamental to the development of sound management principles. All studies on Karoo species have focused on the effects of defoliation (clipping) on dry matter yields (usually aboveground) (Venter 1962b; Opperman et al 1969; du Preez 1972; Hobson and Sykes 1980). Du Preez (1972) compared the effect of defoliation during different months and with varying rest periods for a number of irrigated and nonirrigated shrubs in the Upper Karoo (Figure 1.6).

Du Preez (1972) completely defoliated five new individuals of each species each month (monthly dry matter yields) and those same individuals two months later. He clipped them again one year later. His results showed that:

1) The dry matter yields of karoo shrubs is water-limited and controlled by a complex relationship between water-availability and temperature. Low winter temperatures clearly depressed growth. The unpredictable and erratic rainfall pattern characteristic of arid and semi-arid areas fragments the growing season which is characterized by "pulses" of growth activity (Noy-Meir 1973). Recovery rates following defoliation may therefore be retarded (Brown 1985). Henrici (1951) and Walker et al (1986) stress the overriding influence that the timing and amount of rainfall has on community dynamics. Inter-specific competitive effects including grazing-modified competitive abilities were found to be insignificant in comparison with rainfall events in a "sourish-mixed veld" system (Walker et al 1986).

2) Defoliation suppresses and produces a lag response in dry matter yields. Sixty days after defoliation dry matter yields were lower than for nondefoliated control plants. Maximum growth occurred in February or March in nondefoliated plants and in April in defoliated plants. Severe and even moderate (50% defoliation) levels of defoliation suppress growth in most species examined (Jameson 1963; Opperman et al 1969; Tainton et al 1970; Leigh and Mulham 1971; Buwai and Trlica 1977; Hobson and Sykes 1980; Brown 1985). Garrison (1953) suggests that lighter defoliation treatments may enhance growth by removing apical dominance in some species. The consequent increase in twig production from lateral buds could increase the number of floral primordia and seed yield. Other researchers report on the advantages of light grazing (Booysen 1966; Hobson and Sykes 1980). Coughenour (1985) suggests that limited grazing may stimulate biomass production in grasses. The increased levels and frequencies of defoliation following European settlement, however, could be responsible for the large-scale vegetation changes in semi-arid rangelands (Brown 1985).

3) Defoliation greatly decreases dry matter yields when undertaken during or immediately after a growth period. These conclusions support those of other researchers (Tainton 1958; Opperman et al 1969; Tainton et al 1970; Buwai and Trlica 1977).

   The lack of data on the sources of translocated assimilates and their subsequent mobilization and utilization after defoliation limits our understanding of the effects of defoliation on regrowth (May 1960; Wallace et al 1977).

The patterns of photosynthate translocation and storage at different phenological stages (see Menke and Trlica 1981) are unknown for karoo plants and poorly described generally. Controversy exists as to whether carbohydrate root reserves are important determinants of plant regrowth. Some researchers (Muldoon and Pearson 1979; Brown 1985; Richards and Caldwell 1985) find little evidence to support this and suggest that root and shoot activity are in equilibrium (Brown 1985). Defoliating the above ground parts causes the death or immediate reduction in growth of some roots (Jameson 1963; Richards 1984; Brown 1985) because of the deprivation of respiratory substrates (Brown 1985). When growing, the above-ground parts supply the roots with enough assimilate, enabling them to supply the leaves and stems with the required water and nutrients. Other researchers, (Perry and Chapman 1976; Buwai and Trlica 1977) suggest that the declining levels of nonstructural carbohydrates in the roots following regrowth is evidence of translocation and the depletion of carbohydrate root reserves.

The literature is replete with examples from both schools of thought (Brown 1985) and patterns of photosynthate translocation and assimilation appear to be species specific and often dependent on morphological traits (Wiemann 1940; Opperman et al 1969; Tainton et al 1970; Trlica et al 1977; Brown 1985; Coughenour 1985; Walker et al 1986). Wallace et al (1977) found little storage of carbohydrates in the roots of a deciduous northern Mojave desert shrub *Ambrosia dumosa*, while Dahlman (1968) and Singh and Coleman (1977) found high values in some North American grasses. Richards (1984) reports that for two *Agropyron* grasses in a North American rangeland, root growth after defoliation used carbohydrates produced by photosynthesis during regrowth rather than by carbohydrate reserves synthesized prior to defoliation. The partioning of photosynthate among the various plant parts (roots, buds, flowers, stems, fruits etc) is dependent on the phenological state of the plant (see Wallace et al 1977; Menke and Trlica 1977; Fick and Sosebee 1981; Walker et al 1986).

The effects of the timing of defoliation on the mortality of mature plants is also important. Venter (1962b) showed in the eastern Karoo that 100% defoliation in the active growing season led to an increased mortality in three of the five karoo shrub species examined. Mortality of defoliated seedlings (less than one year old) is high and is a function of seedling age rather than season of defoliation (Parker 1985). Silcock (1977) reports that over 90% of seedlings of species in an Australian arid rangeland die without ever flowering. Flowering and seed set are vital for replenishment of seed banks and for the recruitment of new individuals. In the North American and Australian deserts defoliation has been shown to suppress flowering (Garrison 1953; Buwai and Trlica 1977; Brown 1985) and reduce seed production (Rausher and Feeny 1980; Parker 1985). Tainton et al (1970), however, report that defoliation increased

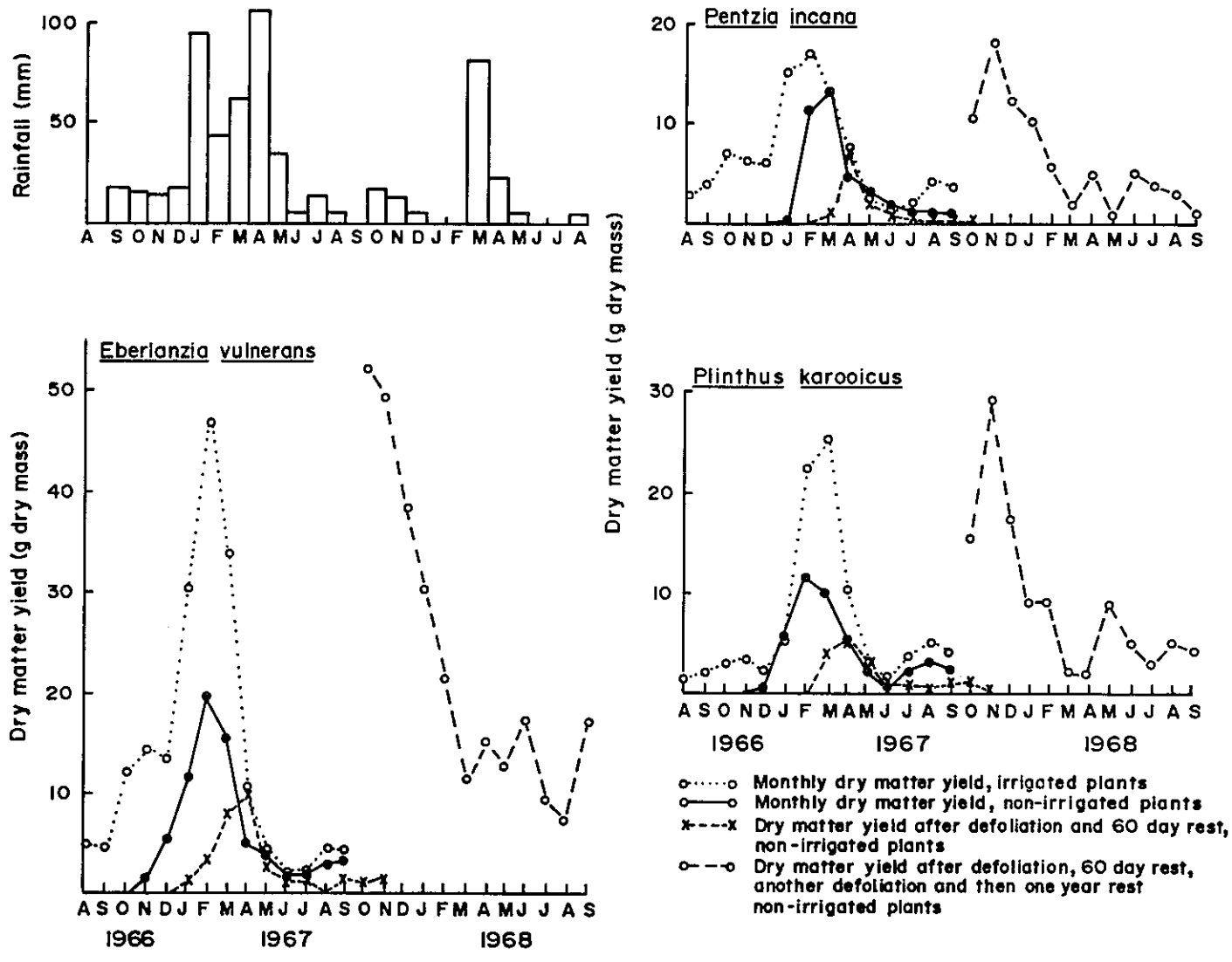

FIGURE 1.6. The dry matter yield of two deciduous shrubs and a leaf succulent (*Eberlanzia vulnerans*) at Carnarvon under different moisture and defoliation regimes (n=5). (Data from du Preez 1972).

flowering activity of a number of grasses examined. As far as we know there are not quantitative data on the effects of defoliation on the reproductive output of karoo species.

DEMOGRAPHY

Germination

Temperature, light and moisture are the most common environmental controls of seed germination (Koller 1969). Because of the variability and relative complexity of the relationships between these variables in arid and semi-arid areas, within- and among-cohort heterogeneity of germination cues has adaptive significance (Koller 1972). Noy-Meir (1973) suggests that the optimum strategy for germination in arid regions is one of "cautious opportunism". This ensures that only part of the seed bank will be lost if post-germination conditions are unfavourable for seedling survival. Seed polymorphisms, common in Asteraceae, Poaceae, Chenopodiaceae and Brassicaceae (Harper 1977), and in species of disturbed and semi-arid environments (Harper 1977; Weiss 1980) exemplifies this bet-hedging strategy. Polymorphic seeds with different germination cues (Brown and Mitchell 1983; Venable and Levin 1985), dispersabilities (Venable and Levin 1985) and competitive performances (Weiss 1980) may be adaptive in these variable environments (Harper 1977).

Germination studies in the Karoo have not explored the adaptive significance of traits and syndromes. The overwhelming variability in seed viability, longevity and responses to temperature (Henrici 1935a, 1939) is one of the few consistent generalizations. For most karoo species light has little or no effect on germination (Henrici 1939; Theron 1964) (Figure 1.7).

Studies to date show that the optimum constant temperature for germination of karoo plants is between 18 and 25°C (Henrici 1935a; Theron 1964; Venter 1962a) (Figure 1.8).

Henrici (1939) found that alternating the optimum temperature with a cold treatment generally delayed germination and gave different results for different species (see also Theron 1964; Venter 1962a). Some arid and semi-arid zone annual and perennial seeds respond favourably to a period of heat pretreatment (Capon and von Asdall 1967; Keeley and Meyers 1985). The hot summer months in the Karoo could promote seed maturation. The limited data on the effects of seed heat pretreatment suggest that different species have different responses. Some respond favourably (eg *Eragrostis lehmaniana*), others negatively (eg *Themeda triandra*) or not at all (eg *Sporobolus fimbriatus*) (Venter 1962a). However, only the first-mentioned species is widespread in the Karoo.

Since conditions optimal for germination might not occur for several years, seeds should be long-lived. This would ensure that if the climatic or grazing regime should result in no replenishment of the seed bank for a number of years, then at least local extinction would be prevented. There is a high degree of variability in seed longevity. Even seeds harvested from the same area at the same time show large variation in their after-ripening periods (Henrici 1935a). Polymorphic seed production may contribute to this variability (Harper 1977; Venable and Levin 1985). The

viability of karoo seeds was not depressed appreciably after twenty months storage (Figure 1.9) (Henrici 1939; Theron 1964).

In the Nama Karoo autumn is probably the optimum period for germination (Hobson et al 1970). Temperatures are not limiting and there is a high probability of repeated wetting and drying cycles over several days - conditions which enhance germination (Henrici 1935a). Seedlings, established in autumn, remain dormant in winter and benefit from spring rains enabling them to grow to a stage where they can withstand summer drought.

Dispersal

Vegetative propagation. Vegetative propagation is important in karoo communities. The dominance of species which propagate vegetatively (eg *Pentzia incana*) may be attributed to the selective advantage of vegetative propagation under continuous selective grazing. Vegetative propagation includes the development of adventitous roots from aerial stems which touch the ground (eg *Pentzia incana*, *Trichodiadema hallei*, *Portulacaria afra*), stolons (eg *Cynodon incompletus*), suckers (eg *Lycium cinereum*, *Rhigozum trichotomum*) bulbs (eg *Oxalis punctata*, *Moraea polystacha*) and the development of split axes (eg *Rosenia humilis*, *Plinthus karooicus*) (Theron et al 1968).

Fruit types and seed dispersal. We consider the dominant fruit types and dispersal mechanisms in a Central Lower Karoo community (Acocks 1953) and discuss their role in karoo plant community dynamics. Figure 1.10 shows that most plants from this community produce seed enclosed in a capsule, pod or follicle possibly providing some protection from predation (Ellner and Shmida 1981). Cues for dehiscence and seed release are either linked to drying and death of the inflorescence (eg *Indigofera sessilifolia*, *Hermannia linearifolia*) or to changes in moisture and relative humidity (eg Mesembryanthemaceae (Ihlenfeldt 1975), Acanthaceae (Gutterman et al 1967), Euphorbiaceae (White et al 1941)). Dry, indehiscent fruits are found predominantly in Asteraceae and Poaceae and are nearly all wind dispersed. Fleshy fruits are uncommon and are usually associated with species that are able to propagate themselves vegetatively (eg *Lycium cinereum*, *Protasparagus* speceies); restricted to rocky hillsides, termitaria and heweltjies (eg *Pappea capensis*, *Carissa haematocarpa*, *Rhus* species); parasites (eg *Viscum* species, *Thesium* species).

There is a wide range of dispersal mechanisms and often two or more are combined. Nearly 50% of the species are wind dispersed (Figure 1.10). In the Hester Malan Nature Reserve (Succulent Karoo) this figure rises to more than 66% (Rosch 1977). A variety of structures enhancing their dispersal efficiency have evolved. These include the development of a pappus (most Asteraceae), winged seeds (eg *Rhigozum obovatum*), comose seeds (most Asclepiadaceae) and tumbleweeds (eg *Brunsvigia* species). Small seed size also enhances long-distance dispersal (eg Crassulaceae, *Sutera atropurperea*) (Marloth 1894; Pijl 1972). In some cases the seed is scattered by the shaking of the dry capsule in the wind ("censer mechanism" (Pijl 1972)) (eg *Albuca* species, *Hermannia linearifolia*). In the dwarf, open shrublands of the Karoo, wind dispersal is clearly an effective dispersal strategy.

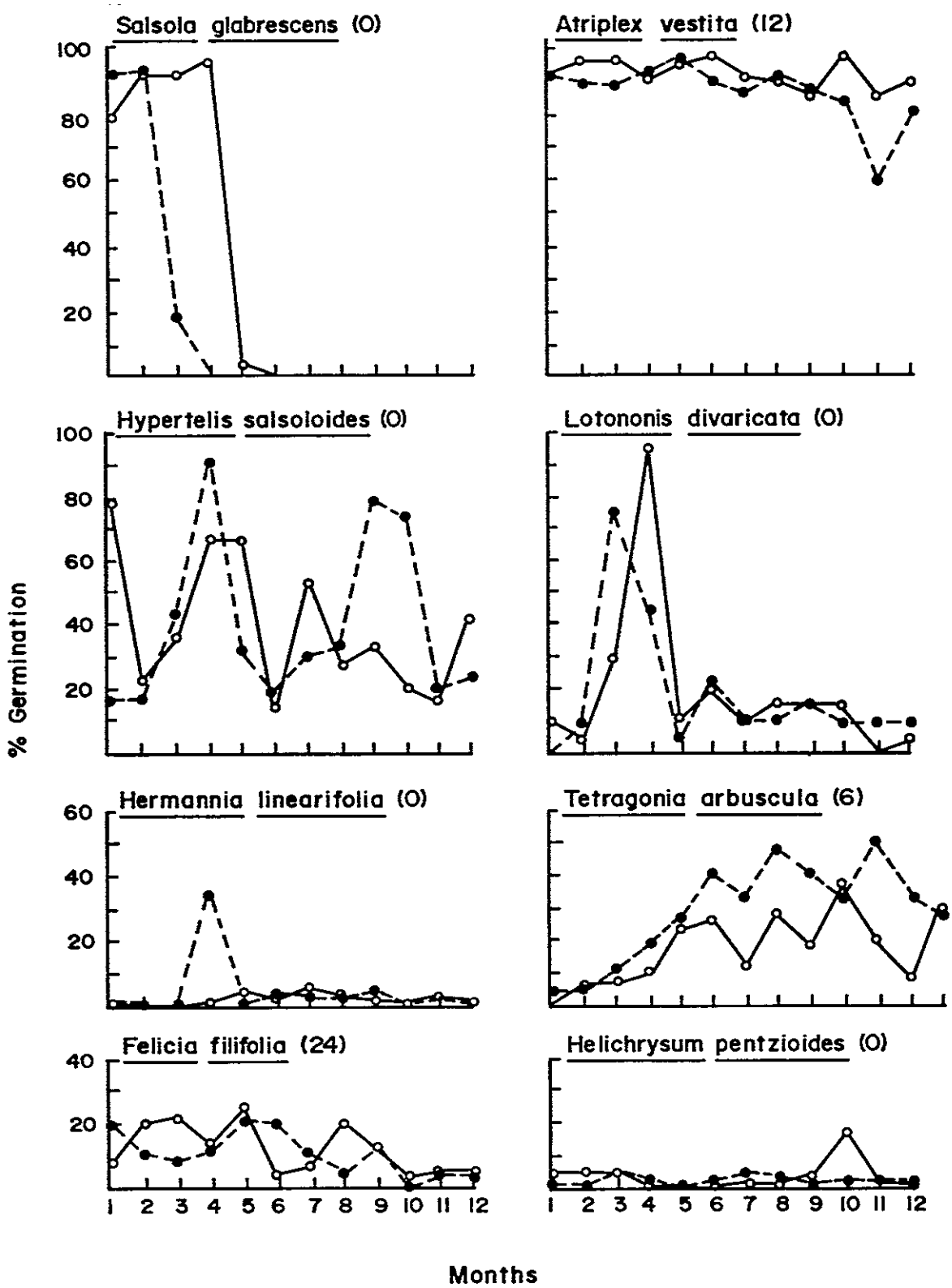

FIGURE 1.7. The effect of light and darkness at 20°C on germintion of successive plantings of karoo shrub seeds from the same initial harvest. A hundred seeds were planted each month. The number in brackets refers to the age (in months) of seed at first planting. Light = O——O, dark = •------•. Data from Henrici (1939).

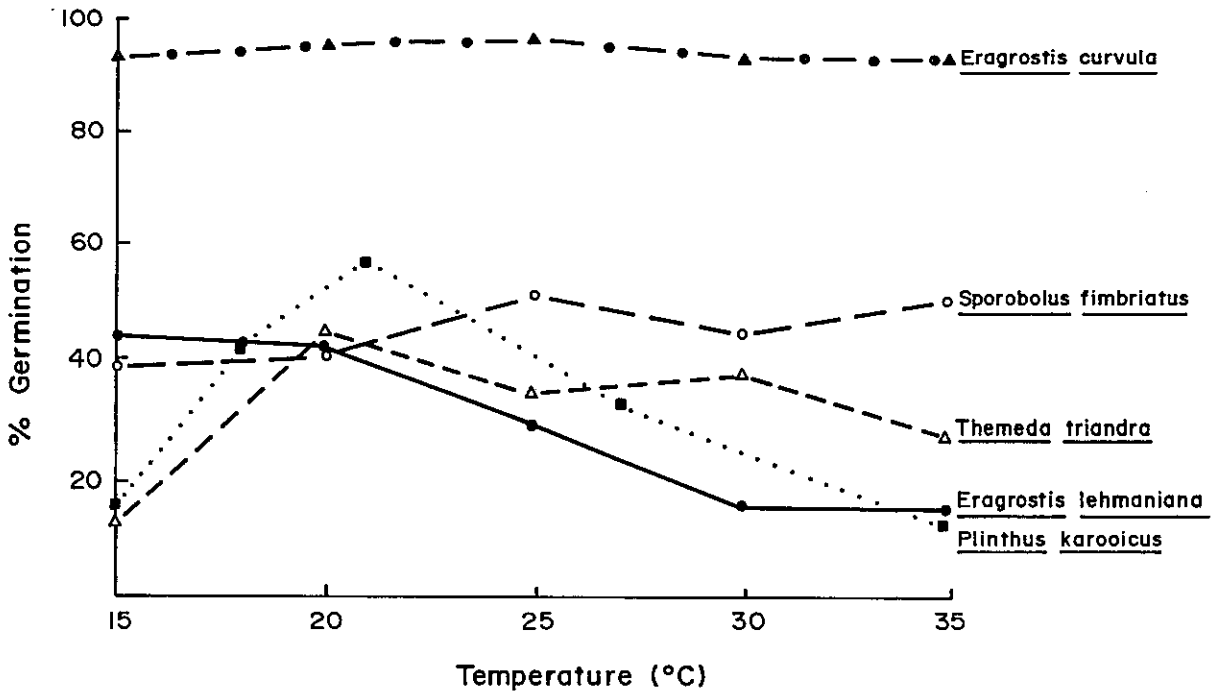

FIGURE 1.8. The effect of temperature on the germination of karoo species. Data from Theron (1964) and Venter (1962a).

Active self dispersal may be explosive (eg *Euphorbia ferox* (White et al 1941)) or by hygrochastic mechanisms (eg *Blepharis* species (Gutterman et al 1967), Mesembryanthemaceae (Ihlendfeldt 1975)). Many seeds are passively dispersed (eg *Leucas capensis*, *Limeum aethiopicum* (M T Hoffman personal observation)). Zoochory appears to be uncommon in karoo plants and most endozoochorous species have fleshy fruits. The role that ants, other insects and small mammals play in the seed dispersal of karoo plants in unknown. Species with seed structures enhancing epizoochory (eg *Aristida congesta* subspecies *congesta*, *Tragus racemosus*, *Tribulis terrestris*) are often the first to colonize disturbed sites.

Atelochory and antitelochory. The absence of dispersal-enhancing characters (atelochory) and the development of mechanisms which hinder dispersal (antitelochory) are a common occurrence in arid ecosystems (Zohary 1962; Pijl 1972; Ellner and Shmida 1981). Ellner and Shmida (1981) have recently challenged Zohary's (1937) generally accepted "mother-site theory" explanation for atelochory and antitelochory. Zohary (1937) suggested that the parent plant keeps most seed close to the site where it is able to successfully reproduce. Ellner and Shmida (1981) argue that rather than being a mechanism for reclaiming the mother site, atelochory has evolved as a response to the low benefit of long range dispersal mechanisms. They suggest that antitelochory is important in the

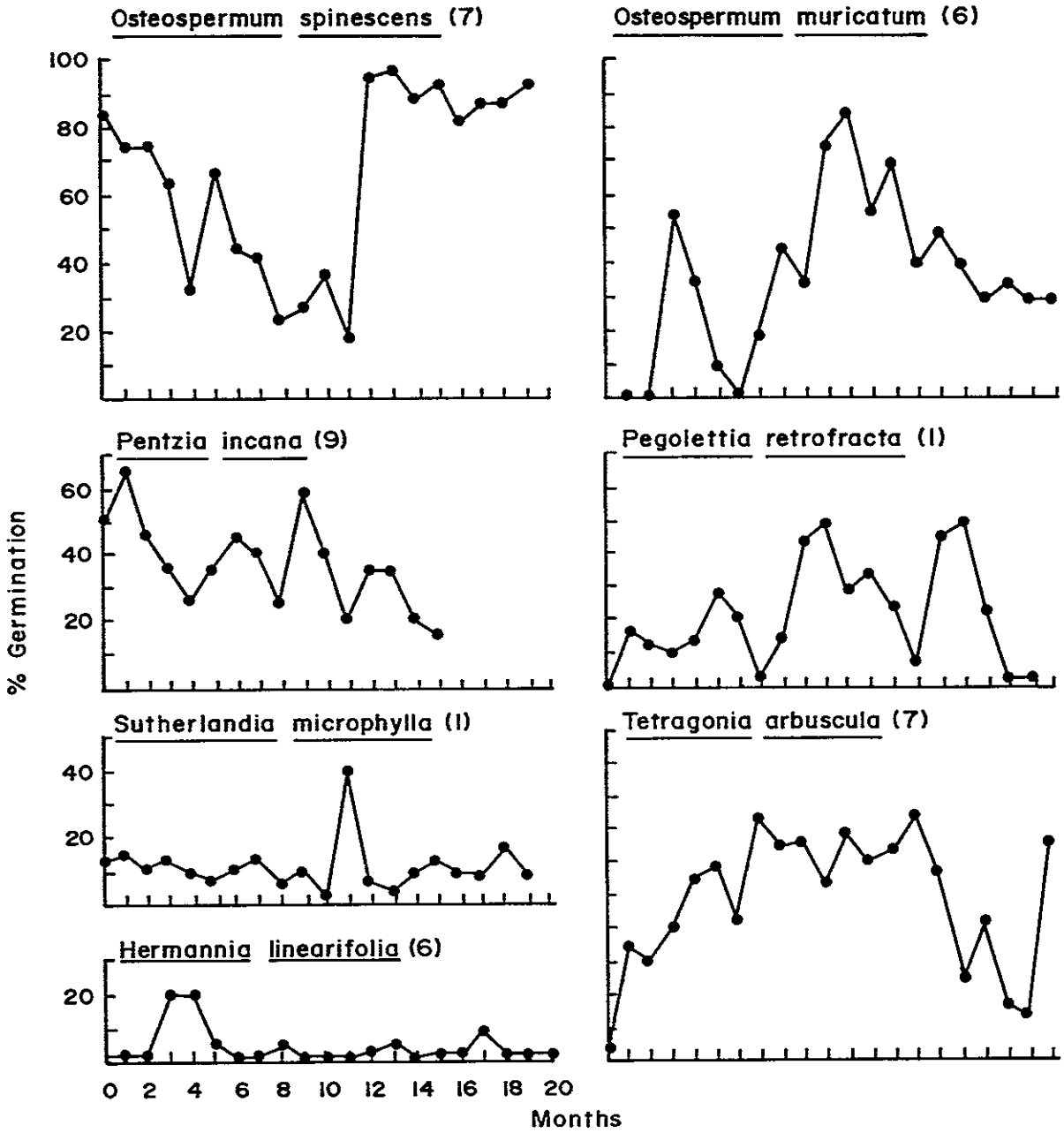

FIGURE 1.9. Germination of successive plantings of karoo shrub seeds from the same initial harvest. A hundred seeds were planted each month. The number in brackets shows the age (in months) of seed at first sowing. Data from Henrici (1939).

timing of seed dispersal and germination rather than having any benefit arising from limited seed dispersal per se. With the exception of studies by Stopp (1958) and Ihlenfeldt (1975), little is known about the incidence of atelochory and antitelochory in karoo communities. Atelochory is correlated largely with passive dispersal and only 13% of the plants in the Central Lower Karoo community studied were passively dispersed. Antitelochory in karoo plants takes a number of forms. Intact capsules which fall off the parent plant have limited dispersal potential (eg *Hermannia* species (M T Hoffman personal observation)) as do the seeds in the hygrochastic capsules of some Mesembryanthemaceae (Ihlenfeldt 1975). The sticky seeds and intertwining pappus of *Pteronia adenocarpa* also limits dispersal and the entire infructescence may be released (M T Hoffman personal observation). Serotiny, the canopy storage of seeds for greater than one reproductive cycle, as seen in *Rosenia humilis* (Bremer 1976) and numerous Mesembryanthemaceae (Ihlenfeldt 1975) is another form of antitelochory. In *R humilis* seeds are held in a capitulum for many years and are eventually released simultaneously, possibly after good rains (Bremer 1976). Interestingly enough, seeds of this asteraceous shrub lack a pappus. In the serotinous Mesembryanthemaceae, seed release occurs after the hygrochastic opening of the capsules (Ihlenfeldt 1975). Significant seed release is therefore cued to post rainfall conditions which are suitable for germination and recruitment. It is possible that between 10 to 20% of the species in the Nama Karoo possess antitelochoric mechanisms. In the Succulent Karoo, where Mesembryanthemaceae dominate, this figure will be considerably higher (see Rosch 1977; Werger 1986). We concur with Ellner and Shmida's (1981) suggestion that atelochory and antitelochory have an important function in the timing of seed dispersal. We do not view them as specific adaptations for reclaiming the "mother site".

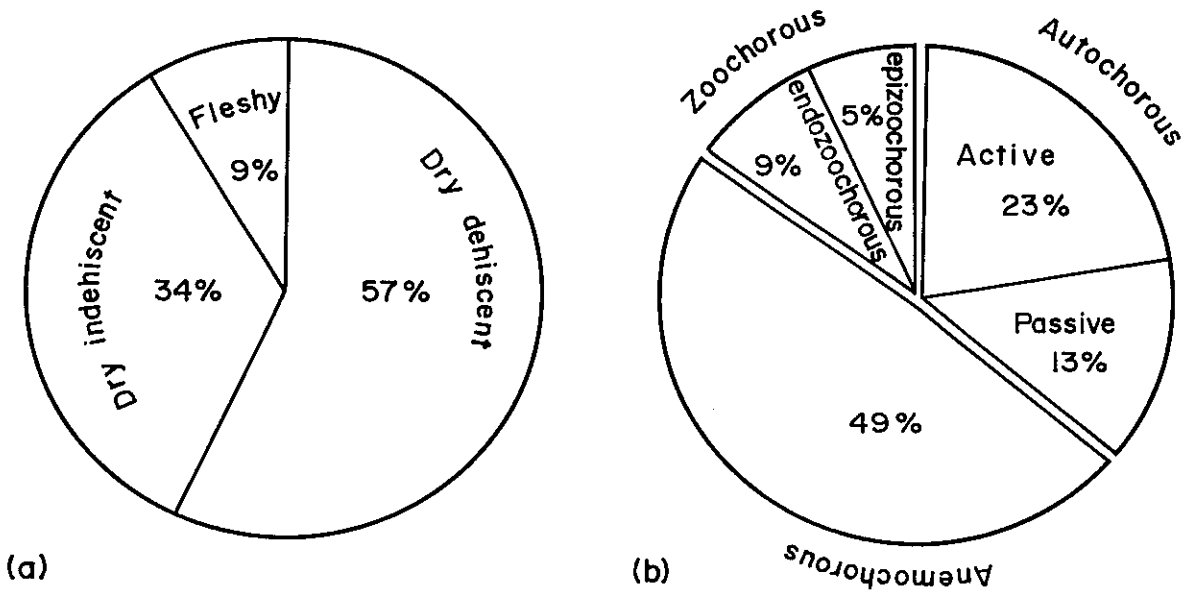

FIGURE 1.10. (a) Fruit types and (b) dispersal mechanisms in a Central Lower Karoo community (n=70).

Recruitment, establishment and mortality

We define recruitment as the stage in a plant's life history from seed germination to seedling and establishment as the survival to reproductive maturity. No single demographic response characterizes the karoo flora. A number of life histories have evolved in response to an unpredictable environment where drought, grazing and seasonal variability all combine to influence demographic processes. We anticipate that general demographic principles as reviewed by Cook (1979) will apply to karoo communities. These are:

1) Juvenile plants suffer the greatest mortality and there exists an inverse relation between the size of an individual in a cohort and mortality. There are no data for karoo perennials but data from Australian (Crisp 1978) and Sonoran semi-arid regions (Steenbergh and Lowe 1969; Turner et al 1969) support this. Survival rates of Namaqualand annual populations are highly variable within and between species at different sites (van Rooyen et al 1979b). Seedling mortality is highest within the first few weeks (van Rooyen and Grobbelaar 1982). The average survival rate of 64% for the Namaqualand annual flora (ie survival to "maturity") was generally higher than for annuals from the North American semi-arid regions (van Rooyen et al 1979b).

2) The two greatest sources of mortality are grazing and drought stress. Parker (1985) found heavy mortality of seedlings of a Sonoran desert shrub following insect herbivory. Grazing and trampling by mammalian herbivores is also a source of much mortality (Crisp 1978; McAuliffe 1986). The effects of drought stress are more difficult to discern. The "nurse plant" phenomenon, whereby seedlings readily establish beneath the canopy of certain plants (Shreve 1931), is common in most arid and semi-arid areas, including the Karoo. The microsites afforded by nurse plants protects seedlings from temperature fluctuations, exposure and grazing (Parker 1982); survival rates are thus high (McAuliffe 1984). These recruitment patterns often confer a distinct pattern on the whole community. Wind-blown seeds readily accumulate under these plants resulting in the cooccurrence of different growth form guilds in distinct "islands" of vegetation. The soil volume is partitioned and the component species often have different phenophases (P W Roux personal communication).

3) Disturbance usually precedes recruitment. The most important disturbance factors affecting plant demographic processes in the Karoo are drought and defoliation. Prolonged drought is often followed by substantial rains and good recruitment such as occurred in *Euphorbia coerulescens* after copious rains in November 1985 after a lengthy drought (M T Hoffman and R M Cowling personal observation). The drought- or grazing-induced death of mature individuals creates space in an environment where competition for water is great and allelophathic interference may occur (Beals 1968; Fonteyn and Mahall 1978; Phillips and MacMahon 1981). Soil disruption by browsing and burrowing animals may also stimulate recruitment. Van Rooyen and Grobbelaar (1982) reported a large increase in the number of Namaqualand annuals in periodically mixed soil. Fire is important in the eastern karoo mountains only (Roux and Vorster 1983). In karoo vegetation the interactions between the disturbance regime (ie nature,

magnitude, frequency) and the biologies of the species (ie life history, physiology) probably determines community composition (Denslow 1985). This composition is continually changing in response to singular extreme events (Westoby 1980) and sequences of extreme events (Zedler 1981).

There are no life history or fecundity schedule data for any karoo plants. There is some information on long-term compositional dynamics (Roux 1966) but changes in species importance were measured in terms of basal cover and not at a population level. How long do karoo shrubs and grasses live and under what conditions does recruitment occur? What are the responses of mature plants and seedlings to grazing and how does this effect reproductive output and establishment? When should grazing pressures be intensified or reduced in order to facilitate an important demographic process? There is an urgent need for answers to these questions if we are to provide a rational basis for the management of karoo veld.

IMPLICATIONS FOR COMMUNITY DYNAMICS AND RANGE MANAGEMENT POLICY

We have stressed the immense variability which exists in the phenological and demographic responses of karoo plants to stochastic rainfall and disturbance events. Booysen (1966) called for a physiological rather than an empirical approach to range management research, while Walker et al (1986) have stressed the importance of an event-orientated (rainfall) approach to grazing system management. Current karoo rangeland policy has evolved from the results of large integrative grazing trials (McNaughton 1967; Roux 1968; van der Walt 1971; Skinner 1976; Roux and Vorster 1983) and ignores the responses of individual species to this variability. Data on the physiology of shoot growth, phtosynthate storage and translocation and photosynthetic efficiency of individual species is lacking. The basis of the rangeland policy as encapsulated in the rotational grazing system programme (Roux 1968), assumes that karoo ecosystem dynamics are consistent with Clementsian succession theory, defined as a predictable change in species composition over time (Drury and Nisbet 1973). North American rangeland policy, which makes the same fundamental assumption, has recently been criticized (Westoby 1980; Sousa 1984). The Clementsian view in the rangeland context holds that grazing animals retard a predictable community replacement sequence. The final community would be in equilibrium with the prevailing environment (Westoby 1980). The correct stocking rate, which is correlated with the long-term average annual rainfall (van den Berg 1983), maintains the vegetation in an optimum state for grazers. Excessive stocking rate reverses the succession trend or alters its path (disclimax) and very low grazing pressure promotes the successional development towards the climax (Acocks 1955, 1964; Vorster 1982).

The concept of "area-selection" (Roux 1968), where grazers concentrate on particular areas of preferred forage resources, suggests that rangeland research distinguishes between edaphic climaxes, physiographic climaxes and disturbance climaxes. The vast vocabulary of polyclimax succession theory is therefore invoked to explain the anomalies. There is, however, probably no predictable change in species composition over time in semi-arid rangeland communites but rather a gradual or dramatic shift in population boundaries (Zedler 1981).

Moreover, the overwhelming influence that European vegetation management has had on community composition should be recognized. Westoby (1974, 1978) argues that large herbivores have nutrient constraints and optimize the nutrient content of their diet by selecting from a wide variety of plant species. Henrici (1935b) provides supporting evidence for the Karoo. This selectivity changes from individual to individual and from day to day among herbivores (Arnold and Hill 1972; Botha 1979) and is dependent on the physiological and phenological status of the plant (Henrici 1940; Botha 1979) as well as on the site (Henrici 1935b). If the amount of plant material consumed is independent of the relative abundance of the species then those plants which are relatively rare in a community and which provide a necessary nutritional component are going to decline in abundance (Westoby 1974; Louw 1969). It is this selectivity which influences specific population boundaries and thereby community composition. This process is not the same as altering a predetermined species replacement sequence.

There are other problems associated with the application of succession theory to karoo vegetation, arising largely from the assumption of directional succession towards a climax community (Zedler 1981). Most researchers envisage a climax Karoo dominated by palatable perennial grasses (Acocks 1953, 1955, 1964, 1979; Vorster 1982; Roux and Vorster 1983). Less palatable grasses and shrubs occur lower down a successional sequence which begins with annual grasses, widespread weeds ("opslag") and invader species (Blom 1981). Vorster (1982) has developed the Ecological Index Method of veld assessment which is based on the relative proportions of species as they occur in a generalized successional sequence. We view this slightly differently. The introduction of large numbers of nonindigenous herbivores, together with the elevated levels and frequencies of defoliation have been the major cause of community change in the Karoo. Clementsian succession theory and climax vegetation concepts cannot realistically explain these changes. Plant species (eg large perennial grasses) which were adapted to the sporadic but heavy nonselective grazing regime imposed by migratory herds have not been able to survive at these increased defoliation frequencies (Acocks 1971, 1979). Other plants, however, which possessed incidentally beneficial traits (exaptations) (Coughenour 1985) in the light of this increased alien grazing pressure have consequently increased (eg *Pentzia incana*, *Eriocephalus ericoides*, *Chrysocoma tenuifolia*, *Eberlanzia ferox*, *Aristida congesta* subspecies *congesta*). The following traits, either in isolation or in combination with others could be viewed as exaptations: plant size (eg Coughenour (1985) suggested that short grasses with a greater density of smaller tillers had an adaptive advantage over taller grasses under increased grazing pressure (see Acocks 1971)); chemical defenses (eg Louw et al (1967) found a good relationship between palatability and low per cent ether extract, Henrici (1935b) found some correlation between the chemical composition of karoo plants and their palatability and Cooper and Owen-Smith (1985) showed that high condensed tannin levels deter feeding by browsers); vegetative propagation (eg Coughenour (1985) suggests that grasses that are able to propagate vegetatively are adapted to compete for space in disturbed sites. The ability of *Pentzia incana* to propagate itself vegetatively may be an important adaptation under conditions of increased grazing pressure). Other traits could include demographic and physiological characteristics of species (see Crisp 1978).

Succession theory has little value in the development of rangeland policy because it is theoretically unsound and has limited heuristic and predictive value. A theory for the dynamics of semi-arid rangeland must account for the stochastic variability which characterizes the community dynamics of these regions (Westoby 1980). It is a suite of morpholocial, physiological and demographic traits which characterizes species responses to defoliation and climatic events and consequent community composition, rather than their position in a generalized succession sequence.

A flexible policy based on detailed knowledge of the physiological and demographic responses of karoo plants to climatic events and defoliation regimes is essential. At present there are so few data that even the construction of conceptual models is difficult. Some processes which should be studied are outlined in Figure 1.11.

CONCLUSIONS

Karoo ecosystems, like those of other arid and semi-arid areas are characterized by a variably low and unpredictable rainfall regime. The life histories and physiology of the biota have evolved in response to stochastic inputs of soil moisture and defoliation events. Succulent Karoo, with a relatively predictable winter rainfall can be distinguished from the less predictable autumn-spring rainfall of the Nama Karoo. Research on the Karoo has stalled in the descriptive stage and very little is known about its dynamics. This lack of data presents an important constraint in the development of a predictive management policy as does the continued adherence to Clementsian succession theory as a model for karoo community dynamics. The initiation of a long-term research programme which would enable researchers to describe and understand the effects of stochastic climatic events and sequences of such events on community structure and processes is vital.

ACKNOWLEDGEMENTS

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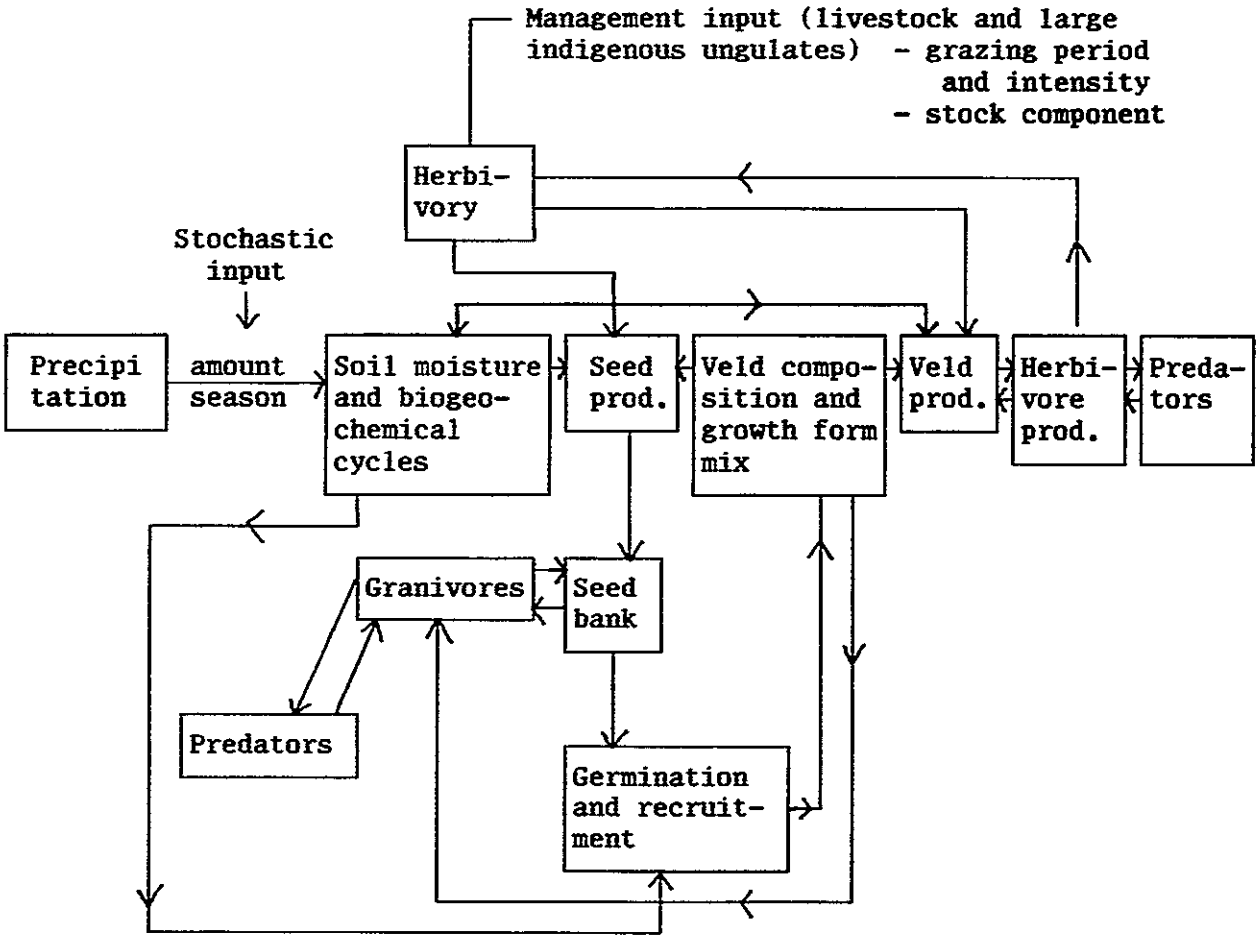

FIGURE 1.11. Schematic outline of some processes which should be studied for the development of karoo veld management models (from Cowling 1986).

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CHAPTER 2 PLANT GROWTH AND UTILIZATION PROCESSES

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INTRODUCTION

Grazing industries are complex ecosystems in which the main components are soils, vegetation, animals and man. In the context of stability and survival, the vegetation is the most important part of the karoo ecosystem as it provides forage for all herbivores, vertebrates and invertebrates. Directly and indirectly (through consumers) it also provides the detritus on which decomposers depend for organic matter production and nutrient recycling which are necessary for the maintenance of the physical condition and chemical fertility of the soil. Vegetation further provides a physical barrier to the overland flow of water, thus increasing infiltration and decreasing water erosion (and consequent nutrient loss).

By far the most important functions of vegetation are those which affect the stability of the ecosystem through protection of the soil resource. In these protective functions it is the biomass of the plant material remaining on the landscape and its spatial distribution which have the greatest effect. Floristic composition is important in determining the spatial distribution of plant material, palatability and the nature of the protection of the soil (eg grasses are more effective against erosion than are shrubs).

Conservation of these dynamic resources requires that management be aimed at maintaining the basic resources (soil and vegetation) in a productive state. Management aimed at maintaining or improving their status automatically ensures the continuity of the ecosystems and consequently animal production. The future of vegetation in the Karoo is bound up with the development of management principles for maintaining vegetation rather than stock. The development of management principles requires sound scientific knowledge of the processes involved in a grazing ecosystem, including:

- the production of the plant species in relation to climatic and soil variables;
- ecological and physiological responses of plants and plant communities to grazing; and
- principles underlying wind and water erosion, the effects of erosion on future viability of the system and the protective role of vegetation.

Below, a review is given of the existing knowledge available for understanding and describing the plant growth and utilization processes in the karoo biome.

The main processes with regard to climate, vegetation production and the plant:animal interaction are illustrated in Figure 2.1.

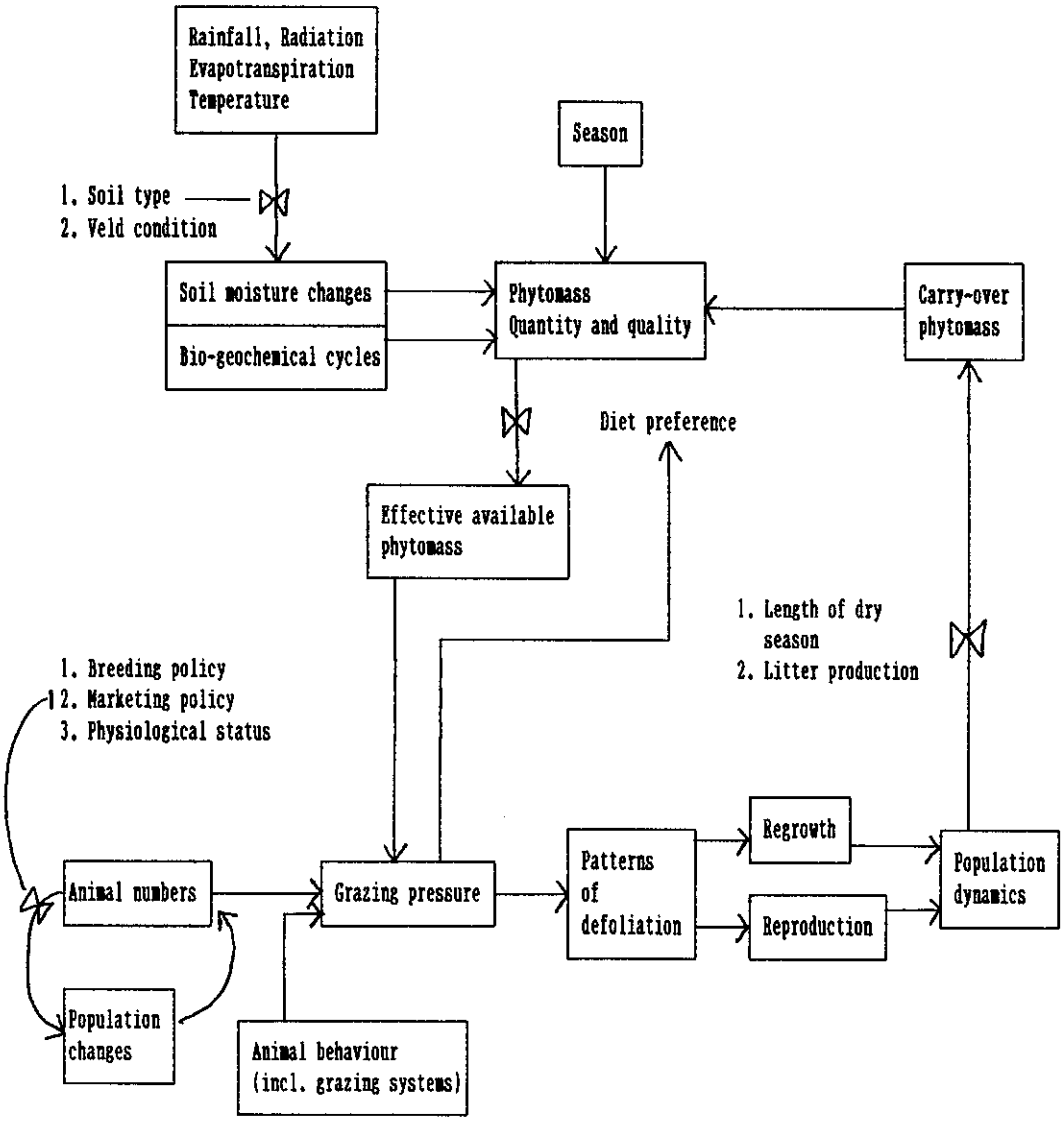
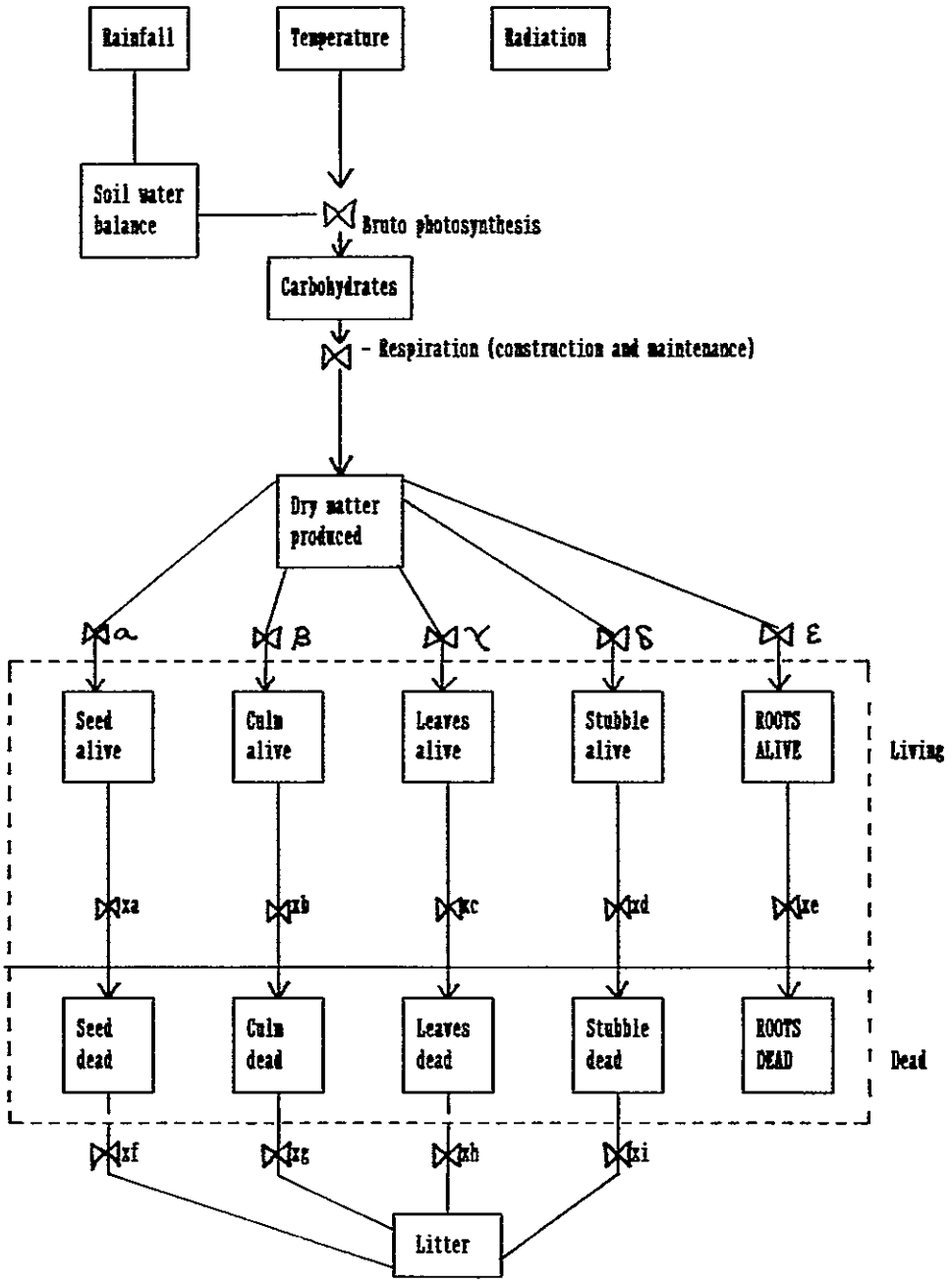


FIGURE 2.1. Diagrammatic representation of moisture, plant growth and utilization processes.

CLIMATE, WATER BALANCE AND PLANT GROWTH PROCESSES

Available data on production of karoo species are limited to growth curves for relatively few species over short periods of time (Venter 1962a; Du Preez 1972). At present an extensive study is being undertaken in eleven veld types in the Karoo (Botha 1978). Phytomass change over the long term is being determined for 103 perennial plant species as well as for a number of ephemerals and annuals. In addition, Joubert (1982) is studying the production of karoo plants under grazing conditions in the Central Upper Karoo for the purpose of devising grazing capacity norms.

Booysen (1982) developed a water balance:plant productivity model for a grass climax vegetation in the Karoo. The model consists of two submodels, a water balance model and a plant production simulation (Figure 2.2).



$\alpha, \beta, \gamma, \delta, \varepsilon$ = partitioning factors
xa - xi = carry-over factors

FIGURE 2.2. Diagramatic representation of energy and mass flow in a water balance:plant productivity model for the Karoo (after Booysen 1982).

The aim of the water balance model is to use rainfall, temperature, radiation and evapotranspiration in calculating the soil moisture potential. Evapotranspiration is corrected for changes in basal cover (density) and size of plants in order to determine the water balance for vegetation in different condition classes and under different defoliation regimes. The

retention curves of soils, effective root depth and bulk density of the soils are used to extrapolate the water balance submodel to different soils in the Karoo.

In the main simulation of plant productivity the calculated soil moisture, temperature and radiation are used to determine the efficiency of the photosynthetic process (Figure 2.2). Actual photosynthesis is taken as a function of the maximal photosynthetic efficiency multiplied by the prevailing soil moisture, temperature and radiation conditions. The grams of CO_2 photosynthesized per day, simulated under these conditions, are converted to grams carbohydrate per day. The amount of carbohydrate simulated in this way is taken as the amount of plant material produced by the process of photosynthesis. To determine dry matter gain for a specific day, maintenance and construction respiration are determined and subtracted from the gross photosynthesis.

A valuable part of the model is the partitioning of the simulated dry matter production into the different phenological stadia (Figure 2.2) as determined by various environmental triggers.

The factors determining the phenological partitionings were based on observations and general knowledge, as no quantitative data for describing and modelling of the phenological processes in the Karoo are available, except for limited data on the germination of the seeds of a few karoo species (Venter 1962b; Theron 1964; Roux 1968). The values of partitioning and transferring are determined by the phenological growth stage of the plant. The main triggers for the change-over to different phenological stages are illustrated in Figure 2.3.

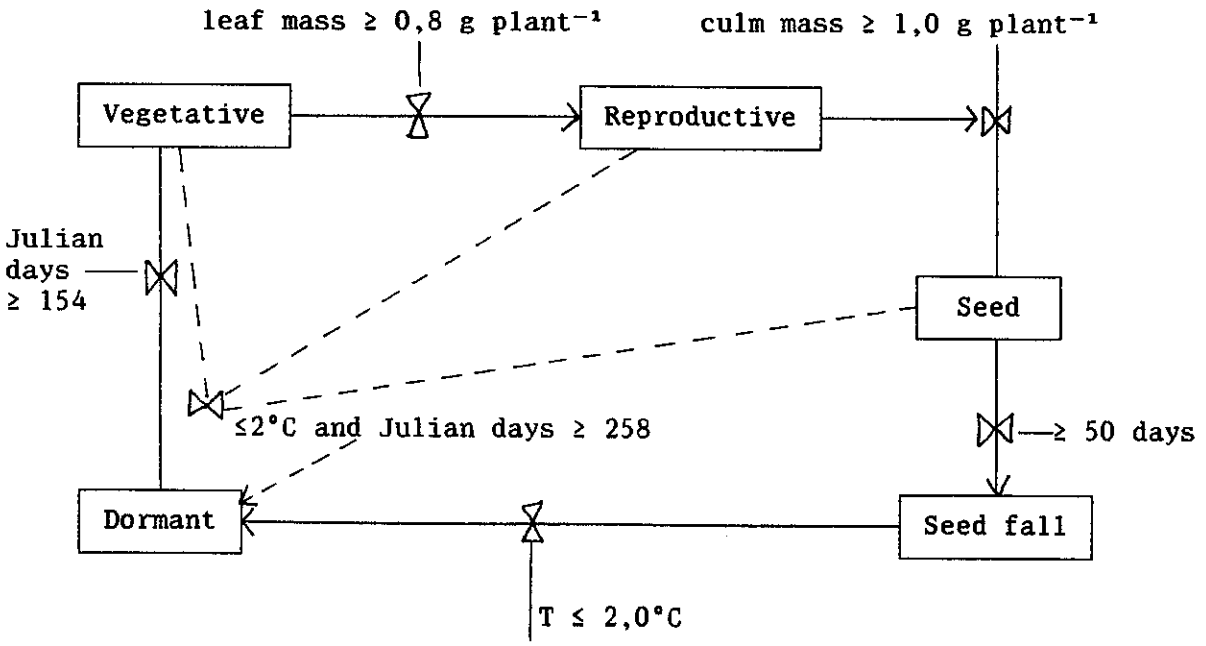


FIGURE 2.3. Phenological development of a climax karoo grass illustrating the main triggers used in the model for the change-over to different phenological stages (after Booysen 1982).

A defoliation factor is also incorporated in the model, taking the plant

back to the vegetative stage whenever defoliated. Success of regrowth and reseeding depend on environmental conditions such as availability of soil moisture and the temperature during the period following the defoliation.

UTILIZATION PROCESSES

Growth cycles in the larger part of the karoo biome are of relatively short duration. During these cycles the plants go through an initial period of rapid growth, whereafter the amount of green material steadily declines due to a lack of follow-up rain and rapid soil moisture depletion rates. The persistence and continued productivity of plant populations depend on how successful the plants are in completing their life cycles during each of their growth cycles. The survival of individual plants and completion of fruiting and seeding processes will mainly be determined by the time of defoliation and frequency and intensity at which they are defoliated during the growth cycle, whether by herbivores or insects (including periodic outbreaks of karoo caterpillar or locusts).

Below is a review of the existing knowledge on plant:animal interactions in the karoo biome. The components and main processes referred to are indicated in Figure 2.1.

Availability of phytomass

Not all phytomass produced is effectively available to the animal, mainly due to differences in the palatability of plant species and selective grazing patterns of the various consumer components in the Karoo (Figure 2.1). Whether phytomass will be utilized is also determined by the morphological features of the plants. Du Preez (1970) determined that plants with spines are only selected if their phytomass is processed and offered to the animals in another form (eg pellets). He further found in an experiment with ten karoo bush species that the highest preference was given to *Felicia muricata* and *Plinthus karooicus*, followed by *Eriocephalus spinescens*, *Pentzia incana* and *Salsola glabrescens*. Species such as *Phymaspermum parvifolium*, *Ruschia vulnerans* and *Eriocephalus glaber* were less palatable, while *Chyrsocoma tenuifolia* was the least preferred. Louw et al (1967) found the last metioned species to have a high ether extract content, which probably explains its unpalatability.

Roux (1968) found *Tetrachne dregei* to be highly palatable in comparison with other perennial grasses in its surroundings. Selective over-grazing on *T dregei* therefore occurs easily, in which case it is substituted with the unpalatable species *Merxmuellera disticha*.

The palatability of plants varies between different areas and seasons. *Chrysocoma tenuifolia* is seldomly grazed in the Fauresmith district, while in the Luckhoff district it forms an important part of the animal diet during spring (Henrici 1935). This author also found that *Salsola* species are well utilized in mixed veld, but in a monoculture, utilization is very poor. Both the Bushmangrass species *Stipagrostis obtusa* and *S ciliata* are well utilized during their active growth stage, but after seed formation, become completely unpalatable (Skinner 1964). When the grass tufts become semidecayed ("bloudak"), animals again concentrate heavily on these species.

Animals prefer grasses such as *Asthenatherum glaucum* and *Eragrostis lehmanniana* in Bushmangrass veld (Skinner 1964). Where these species have a high occurrence, the Bushmangrasses will be grazed much later in the growth season, often only after the first occurrence of frost.

Differences in the palatability of plants are a major factor contributing to selective grazing. This results in certain plants being overgrazed, while others are left untouched. In experiments in the False Upper Karoo, Botha et al (1983) found different selection patterns during the four main seasons and with different livestock types (Figure 2.4).

The selection pattern of different livestock types varied markedly. Cattle concentrated mainly on the grass component as a source of food throughout the study period. All animals showed a preference for the palatable karoo bush component during autumn and winter and for the unpalatable component during spring (ie mainly during their active growing periods). The grass component was selected mainly during the summer by the small stock. The ephemeral component of the karoo vegetation plays an important role as a food resource. Botha (1981) found this component to be present in the diet of the animals whenever available.

From the above it is clear that the phytomass that is effectively available (preferred) to the animals varies throughout the year and would therefore be an important factor in the modelling of phytomass change in karoo ecosystems. The factors to be considered in defining selection patterns and therefore modelling of the availability of phytomass to the animals, are summarized by Botha (1981) as follows:

- palatability of plants as determined by chemical composition, phenological stage, environmental conditions and morphology;
- associated species;
- climate, soil and topography;
- type of animal; and
- physiological status of the consumers.

Quality of phytomass

Various researchers have investigated the feeding value of karoo plants. An intensive study of the quality of veld in South Africa, including the Karoo, has been carried out by Du Toit et al (1940). Plants were analysed for crude protein, phosphorus, calcium, magnesium, potassium, sodium, chlorine and crude fibre. Variations in the different components were mapped to indicate the feeding value and shortages of veld in different areas.

Louw et al (1968a,b,c) analysed the important species in the Arid-, False Arid-, False Succulent-, Central Upper- and Western Mountain Karoo as well as the Noorsveld for ether extract, crude protein, crude fibre, nitrogen-free extract and various minerals. This investigation has shown that the quality of *Stipagrostis* species is extremely low when the tufts are dry. *Salsola tuberculata* is low in phosphorous throughout the year and has a very unfavourable calcium/phosphorous ratio (Louw et al 1968c).

Botha (1939) and Henrici (1945) studied the digestibility and feeding value of various karoo plants, and compared their results with the quality of lucerne. The digestibility and feeding value of *Tetragonia arbuscula*

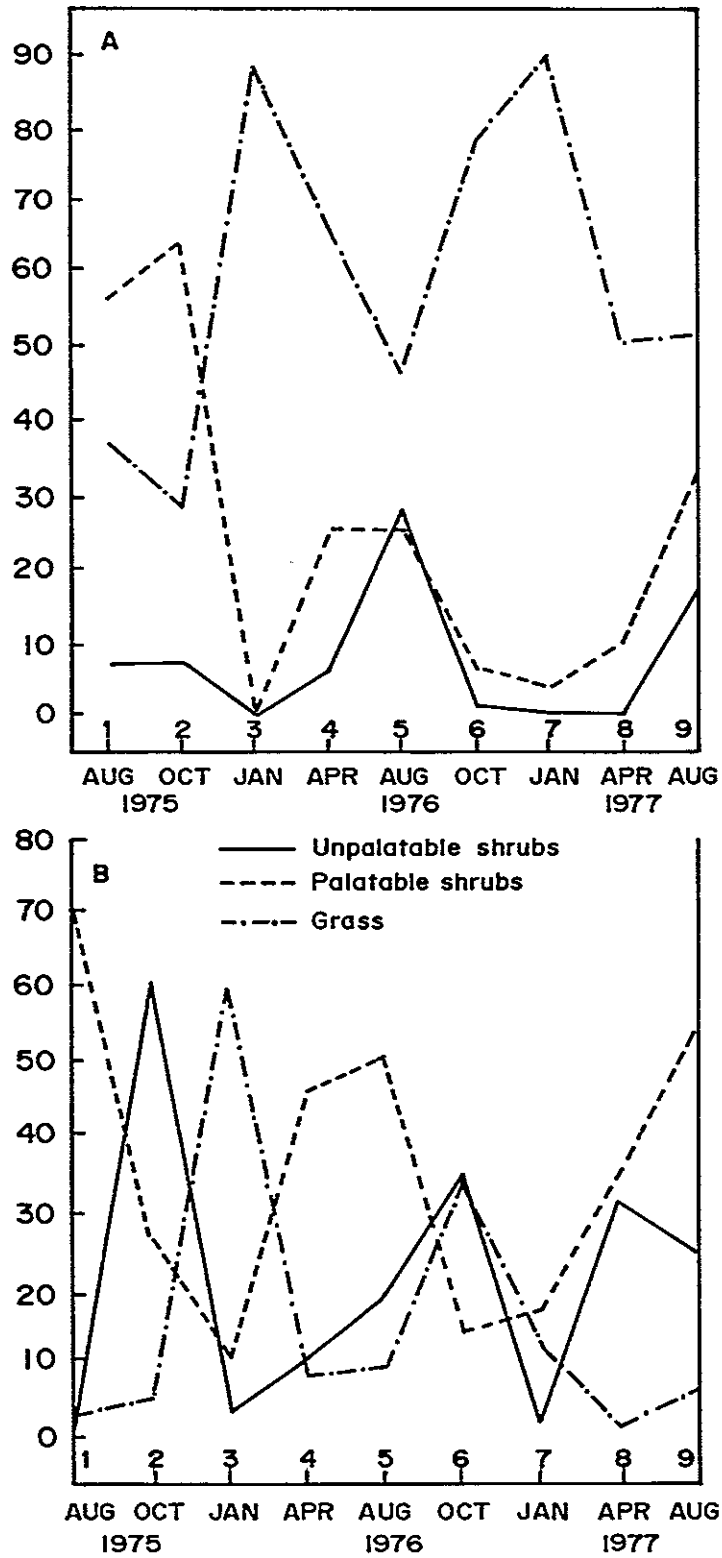


FIGURE 2.4 Composition of the diet of A) Afrikaner heifers and B) Dorper ewes during the period 1075 to 1977 (Botha 1981).

compared favourably with that of lucerne, while *Osteospermum leptolobum* and *Pentzia incana* had a higher feeding value than lucerne. *Pentzia sphaerocephala* contains a high percentage of digestible carbohydrates, while the feeding values of *Phymaspermum parvifolium* and *Sutera albiflora* were extremely low.

Grazing pressure

The amount of effective available phytomass, the number and physiological status of the animals and the system of grazing are the main determinants of grazing pressure (Figure 2.1). In the case of livestock the veld manager determines the number and composition of the consumer component on a farm, as well as the time and period of grazing on a specific piece of vegetation (camp). Bosch (1979) constructed a model in which the weekly population changes on a farm were calculated with regard to physiological status and numbers. Factors affecting the population were used for these calculations and include aspects such as expected mortalities, marketing policy, animal weights and breeding policy. The digestible energy, dry matter and crude protein requirements of the changing population were calculated using feeding requirement functions for maintenance and production.

Other consumer components which will affect the grazing pressure on the available phytomass are not controlled by man, eg game and periodic outbreaks of insect plagues. No quantitative information exists on the factors influencing the behaviour, migration and grazing of game populations on farms in the Karoo. However, several research projects are at present being carried out in the Mountain Zebra National Park on herbivore distribution, population structure and habitat selection (Hall-Martin 1976), small predators (Du Toit 1979) and the feeding habits of the Cape Mountain Zebra (Grobler 1979).

Data on insect herbivory are limited to a detailed study of the factors causing periodic outbreaks of karoo caterpillar (Möhr 1982).

Frequency and intensity of defoliation

Grazing pressure is one of the main factors determining the patterns of defoliation in that frequency and intensity of defoliation increase with increasing animal numbers. However, the grazing pressure on a specific species or physiognomic component in one grazing camp is not homogeneously spread over the entire area and defoliation patterns on one species are also influenced by factors such as the position of watering points, size of camps and the presence and spatial distribution of other palatable species (Bosch and Dudzinski 1984).

No information is available on the effect of grazing pressure on the frequency and intensity of defoliation by animals. Studies on the utilization of karoo vegetation include investigations of the effects of frequency and intensity of defoliation on selected species, and the long-term effects of grazing on plant communities as a whole (Tidmarsh and Hugo 1951; Roux 1966; van der Walt 1971; Hobson and Sykes 1980; van der Westhuizen 1980).

Defoliation studies on selected plant species

The sensitivity of the various species grazing is to a considerable extent related to the season and the growth stage. The degree of damage or the quantity of material removed from a plant, bears a direct relationship to the volume of edible material, stocking rate, plant morphological features and the natural resistance of the plants to grazing.

One of the earliest reports of a defoliation study in the karoo biome is that of Henrici (1951) on the effect of cutting and grazing on *Pentzia incana* under different systems of veld management. The study was carried out under drought conditions and illustrated in general, a negative effect of grazing on the productivity of the plants. Hobson and Sykes (1980) investigated the effects of defoliation frequency of three key karoo bush species, *Felicia muricata*, *Pentzia incana* and *Eriocephalus ericoides*. Increased production was found with decreasing frequencies of defoliation. It was further illustrated that species differ highly in their recovery potential. At low frequencies of defoliation *E ericoides* had the highest total production, indicating that this species was able to utilize the longer rest period better than the other two. Root studies have also shown that defoliation frequencies of more than six times per year reduced the root mass and consequent vigour and recovery of the plants.

Van der Westhuizen (1980) studied the influence of pruning on the growth habit, dry matter production, photosynthesis, carbohydrate and nitrogen content of a winter growing grass (*Ehrharta calycina*) and a karoo bush (*Osteospermum sinautum*). The results of the pruning treatment showed that dry matter production, nitrogen and carbohydrate content, was in each case related to the effect of pruning on the photosynthetic capacity of the plants.

Various qualitative studies on the effect of defoliation on the reproductive behaviour of three karoo bush species were carried out at the Agriculture Research Institute of the Karoo Agricultural Region. Although the plants were irrigated monthly, more than three defoliations during the year resulted in a significant decrease in the production of flowers (Figure 2.5).

Under natural rainfall conditions it can be assumed that this effect will become more apparent at even less frequent defoliations. As previously mentioned, growth cycles in arid areas are relatively short and when defoliated, plants seldom have time to regrow and reproduce before soil moisture becomes limiting.

Long-term effects of utilization of karoo vegetation

The first long-term grazing experiment in the karoo biome was initiated in 1934 in False Upper Karoo veld (Tidmarsh and Hugo 1951). One of the objectives of this experiment was to determine the effect of grazing during different seasons of the year on the composition of plant communities on different topographical units (Roux 1966). Valuable information was obtained on vegetation change due to differential effects of physical damage on various components in different seasons of the year. Communities grazed during the active growing periods of grass and dominated by it, were rapidly converted to shrub-dominated vegetation, whereas when shrubs

were grazed during periods of active growth, the grass component increased. Roux (1966) has shown that winter grazing in the long term caused a significant increase in the grass cover (Figure 2.6). However, when rainfall conditions became less favourable in the late 1950's and early 1960's the cover of both the grass and karoo bush components deteriorated and appeared unstable.

Similar studies of Bushmangrass veld have shown that summer grazing (November to January) depressed the basal cover of *Stipagrostis ciliata* as well as that of *Stripagrostis obtusa*, whilst the effect of winter grazing (May to July) was to increase the cover of *S ciliata* (van der Walt 1971).

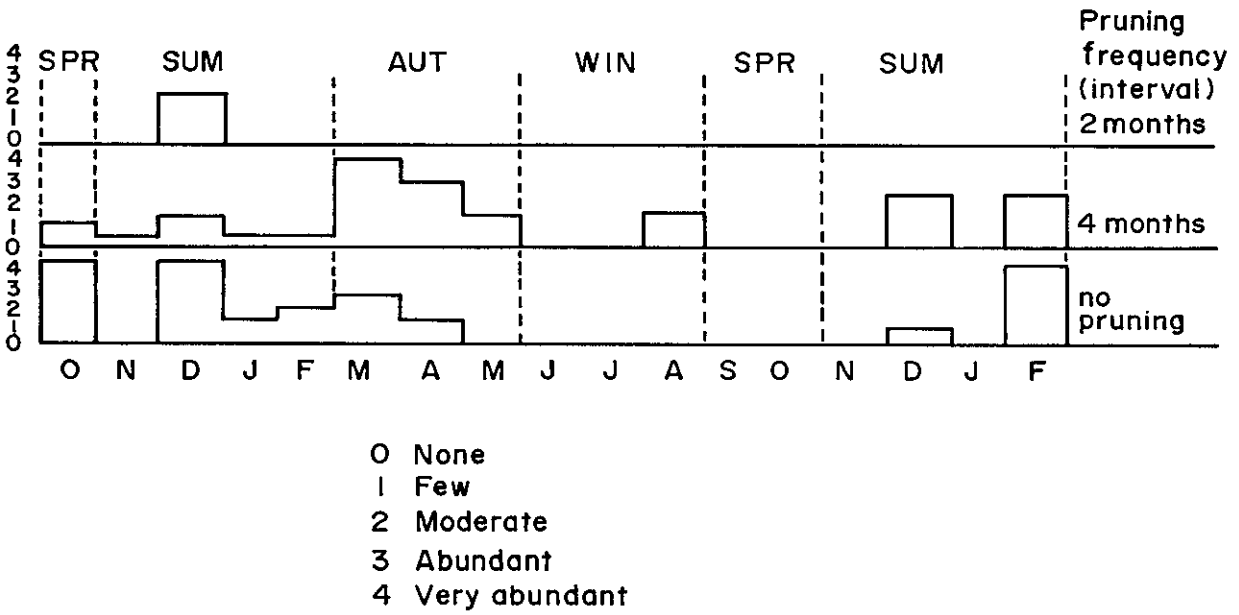


FIGURE 2.5. Production of flowers of *Pentzia incana* plants pruned at different frequencies (after Hobson and Sykes 1980).

The stocking densities in all these grazing experiments were kept constant and no information is available on the effect of different grazing pressures or the rates of changes in species composition.

Various ecological studies have been carried out in karoo vegetation, describing retrogression and succession under different grazing conditions (Tidmarsh 1947, 1948; Skinner 1964; Roux 1966, 1967, 1968; van den Berg 1971; van der Walt 1972; Vorster 1980; Roux and Blom unpublished).

The main seral stages of plant retrogression in the semi-arid False Upper Karoo have been described as a change from the *Themeda triandra* stage to the *Eragrostis lehmanniana*, *E curvula* and *Sporobolus fimbriatus*-stage and eventually to communities in which *Aristida* species, *Tragus koeleroides* and *Eragrostis bicolor* become the dominant grasses. The intermediate and pioneer stages are also accompanied by

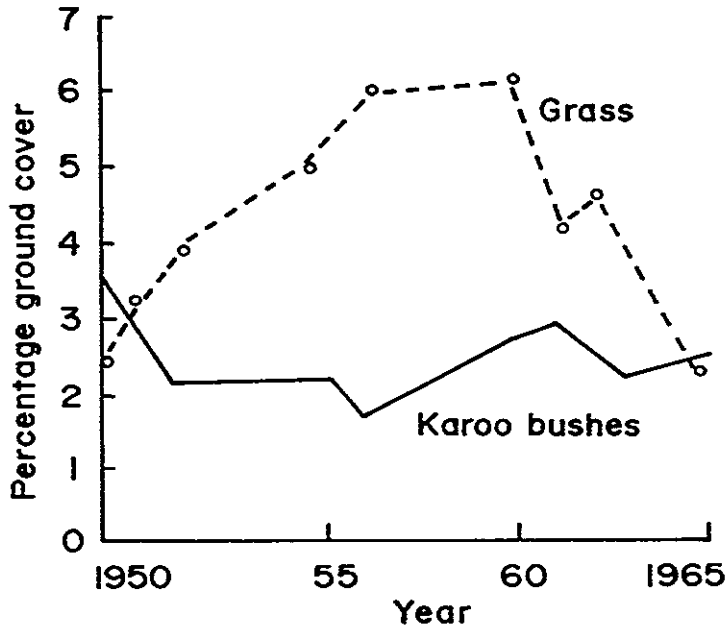


FIGURE 2.6. The long-term effect of winter grazing on the physiognomic composition of karoo veld during the period 1949 to 1965 (data from Roux 1966).

invasion of karoo shrubs such as *Pentzia* species and *Chrysocoma tenuifolia*. The invasion of karoo bushes in the collapse of communities dominated by grass, becomes increasingly important towards the western lower rainfall areas of the False Upper Karoo and Central Karoo.

In the arid karoo areas *Stipagrostis ciliata* and *S obtusa* are the dominant grasses of both the climax and pioneer stages (Skinner 1964). Degradation is accompanied by a reduction in the cover of these grasses, proliferation of a complex of ephemerals and subsequently the invasion of undesirable karoo bushes such as *Pentzia spinescens*, *Zygophyllum flexuosum*, *Galenia africana* and *Rhigozum trichotomum* (Acocks 1953; Bosch 1978).

SYNTHESIS AND FUTURE RESEARCH PRIORITIES

A valuable source of information on plant growth and utilization processes has been built up over approximately 50 years of research in various parts of the karoo biome. However, most of the more detailed studies and modelling of plant growth and utilization processes are limited to the eastern and less arid False Upper Karoo. Care should therefore be taken in extrapolating basic ecological principles from this area to the more arid central and western parts of the Karoo where deficiencies in the knowledge and understanding of grazing ecosystems clearly exist. The more extreme the environment, the greater the need for careful management and flexibility in management systems.

Understanding how grazing ecosystems are functioning warrants a detailed knowledge of the basic principles involved in the growth and utilization processes. Information on the interactions between animals, soil, climate and plants and especially the physiological and morphological reaction of plants to utilization are prerequisites for explaining vegetation change and devising management strategies for karoo vegetation.

The key questions related to plant growth and utilization processes that are revealed as deficiencies in the present knowledge of karoo ecosystems, can be summarized as follows:

- Growth rhythms and productivity of various species and physiognomic components in relation to climate, soil, topography and utilization.

- Efficient water use and the effect of drought on ecological processes and populations.

- Quantitative description and modelling of diet preference and the factors influencing the selection patterns of different animal types and animals in different physiological states, and inclusion of these processes in plant productivity models to determine effective available phytomass and grazing pressure.

- The effects of grazing pressure and other associated factors on the frequency and intensity of defoliation.

- The role of nondomesticated animals and insect populations in grazing ecosystems, including quantification of the factors controlling their behaviour and densities.

- Quantitative data on the effects of utilization on reproduction of the plants, including determinations of the minimum requirements of seed production for maintenance or improvement of desired populations in the long term.

- Determining safe utilization levels to ensure maximum continual productivity and to ensure that the minimum seed production requirements are obtained during each period of grazing.

- Demographic studies of plant population dynamics in an attempt to quantify the flux of numbers that occur in natural populations and how the processes of population dynamics (eg birth rates, mortality rates, life cycle patterns) are affected by grazing and other factors.

- Quantitative description of biogeochemical cycles in karoo ecosystems.

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CHAPTER 3 VEGETATION CHANGE IN THE KAROO BIOME

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INTRODUCTION

It is an indisputable fact that vegetation in the karoo biome has changed significantly since the colonization of the Cape of Good Hope in 1652. A comparison of vegetation descriptions by Thunberg (1793), Barrow (1801, 1804), Burchell (1822), Lichtenstein (1812, 1815), Campbell (1822), and Thompson (1827) with present day conditions indicate the extent of these changes. However, these early descriptions are usually not only vague but also largely confined to well travelled routes. Furthermore, most of the early travellers were from European countries and their descriptions were often biased by subjectivity and overreaction (Kokot 1948). It is nonetheless possible to glean from these accounts descriptions adequate to form a general concept of the vegetation in earlier times.

This account describes vegetation change in the karoo biome over the past few centuries. The extent of change has been gleaned largely from historical accounts and descriptions of contemporary vegetation. The causes for, and nature of vegetation change are discussed and suggestions for future research are made.

VEGETATION CHANGE IN RECENT CENTURIES

Acocks (1975) presented hypothetical changes in gross vegetation patterns over the last 500 years as a series of maps. He delineated the present extent of karoo occurrence (Figures 3.1 and 3.2). The major changes identified by Acocks (1975, 1979) were:

- The striking spread of the Karoo at the expense of sweet grassveld.

- This spread eastwards into the sweet grassveld of the north-eastern Cape and southern Orange Free State has amounted to 250 km in parts and it is still proceeding (Jarman and Bosch 1973). The vegetation of the Great Karoo, including the Central Lower Karoo (the wide basin between the Swartberg and the Great Escarpment) was thought to have been strongly grassy (Acocks 1964). Today it is dominated by dwarf shrubs and scattered shrubs.

- In the Little Karoo sweet grassveld of the valley floors, dominated by *Themeda triandra*, *Pennisetum macrourum*, *Panicum stapfianum*, *Hemarthria fasciculata*, and *Arundinella nepalensis*, has been replaced by shrubs such as *Acacia karroo*, *Buddleia salicifolia*, and *Rhus* species (Acocks 1964). The mountain grassveld fringing the Little Karoo and dominated by *Themeda triandra*, *Ehrharta* species, *Merxmuellera* species and *Pentaschistis* species has been largely replaced by *Elytropappus rhinocerotis* (Acocks 1975,

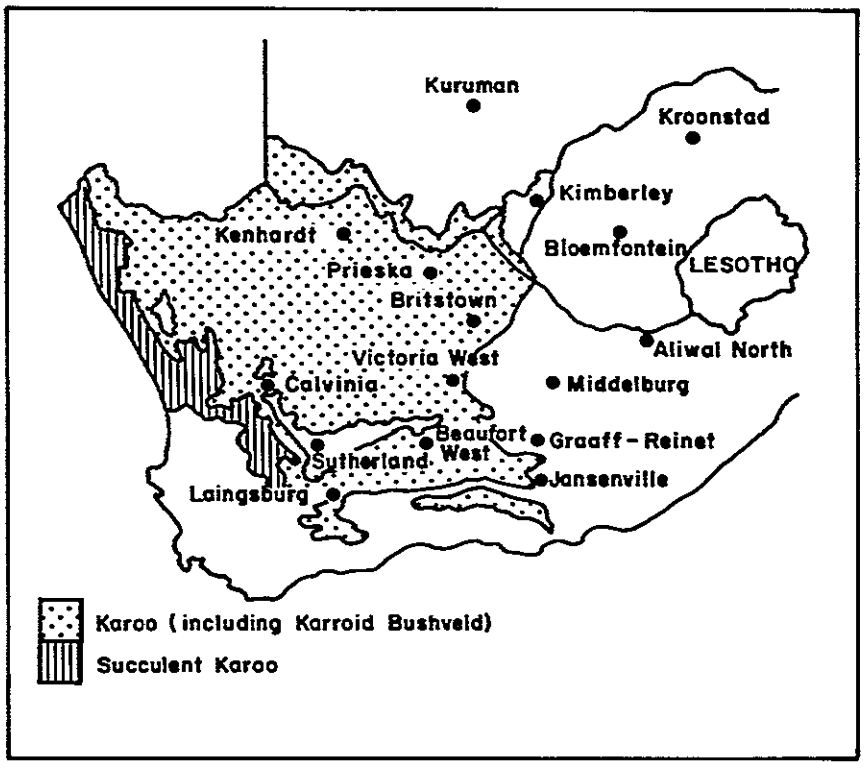


FIGURE 3.1. The hypothetical distribution of the Succulent Karoo and (Nama) Karoo (including Karroid Bushveld) at 1400 AD (Acocks 1975).

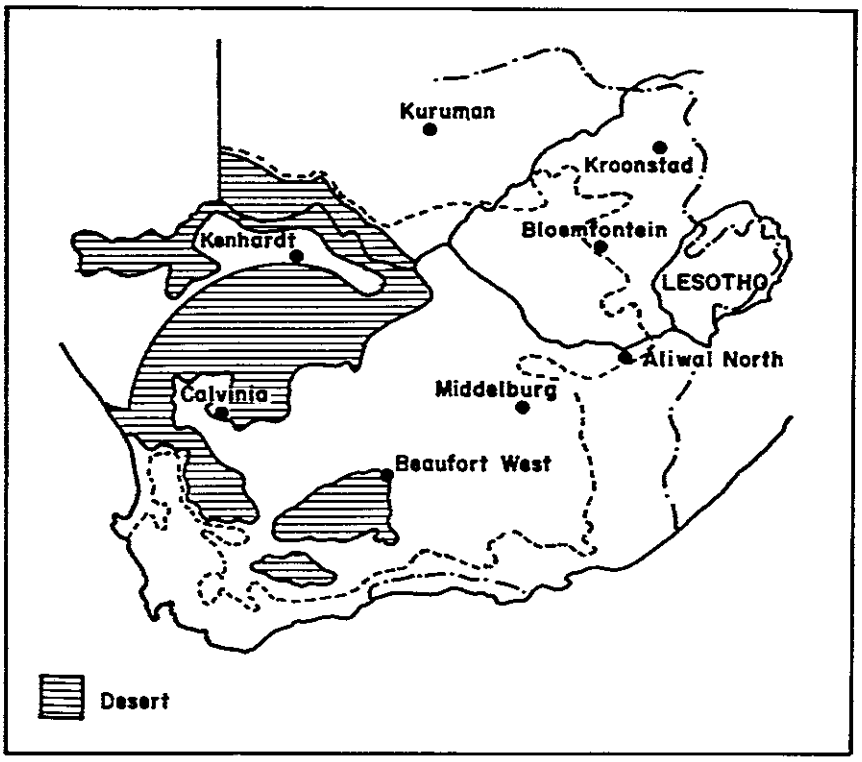


FIGURE 3.2. The occurrence of desert, extent of karoo (-----) and extreme limit of karoo patches (—·—·—) at 1950 AD (Acocks 1975).

1979). Acocks suggests that the drier (130 to 250 mm yr^{-1}) central parts of this area were formerly dominated by grasses such as *Sporobolus iocladus*, *Digitaria argyrograpta* and *Eragrostis bergiana* in the valleys, and *Stipagrostis ciliata* var *capensis* and *S obtusa*, on the hills. *Panicum maximum*, *Stipa dregeana* var *elongata*, *Ehrharta erecta* and *Cenchrus ciliaris* were common beneath larger shrubs. The grass component has all but disappeared, while the unpalatable *Pteronia pallens* is dominant over vast areas. Weedy *Mesembryanthemum* species have also proliferated.

- The invasion of Arid Karoo into Central Upper Karoo.

  The Bushman grassveld (*Stipagrostis* species) of the Upper Karoo (1 000 to 1 300 m) is becoming replaced on shallow rocky soils by Arid Karoo species such as *Euphorbia mauritanica*, *Galenia africana* and *Rhigozum trichotomum*.

- The invasion of Succulent Karoo into the Arid Karoo and Western Mountain Karoo.

  The Succulent Karoo occupies the coastal plain between the Orange and Olifants Rivers and also the basins between the Cape Fold Mountains and the Escarpment (eg Tanqua Karoo) in the south-western part of the biome. Unpalatable succulents are replacing non-succulent palatable shrubs in an upwards (Western Mountain Karoo) and eastwards (Arid Karoo) direction (Acocks 1975).

- The invasion of Karoo down the Fish and Sundays River valleys and adjacent basins.

  This has been discussed for the Fish River by Acocks (1975). Hoffmann and Cowling (in preparation) provide quantitative evidence for the replacement of subtropical thicket (Noorsveld) by *Pentzia incana* karoo in the Sundays River valley.

- Desertification

  In the arid western regions, very extensive near deserts have developed.

In the karoo biome, vegetation change is always associated with the invasion into, or replacement of, mesic types by arid types (Acocks 1975). As indicated earlier, the most dramatic change has been the replacement of sweet grassveld by an open karroid shrubland. De Klerk (1947) indicated a rapid spread of karoo over the last 100 years into sweet grassveld in the southern Orange Free State (Figure 3.3). Tidmarsh (1948) also suggested a massive eastwards expansion of the Karoo at the expense of sweet grassveld (Figure 3.4).

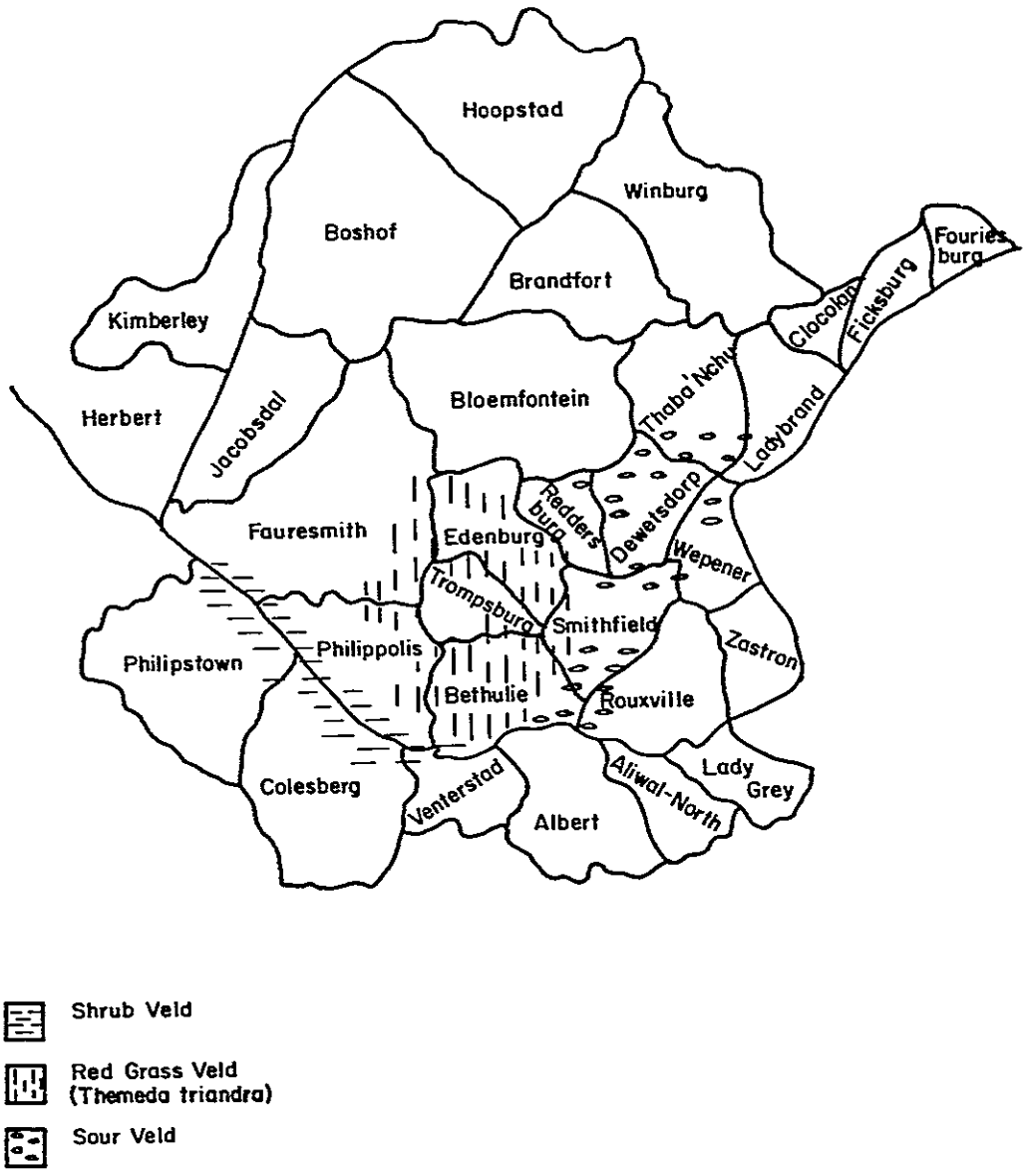


FIGURE 3.3 (a) Map of the Orange Free State showing the limits of shrubland (karoo) in 1847 (De Klerk 1947).

Roux (1981), and Roux and Vorster (1983) describe vegetation change in the Karoo as taking place in five overlapping phases (Figure 3.5). They regard these phases as serial stages in the desertification process. The phases are: primary degradation (Phase 1); denudation (Phase 2); revegetation (Phase 3); secondary degradation (Phase 4); and desertification (Phase 5). The present occurrence of these phases in the biome range roughly from west to east in the order of Phase 5 to 1. Phases 1, 2 and 5 roughly coincide with Acocks (1975) maps 1, 2 and 3.

The major changes in the biome appear to be primarily embodied in the replacement of the originally grass-dominated vegetation by shrubby karoo vegetation; the gradual disappearance of thinning-out of perennial grass; the spreading and thickening of so-called undesirable dwarf shrubs and taller woody shrubs; the increase in pioneer species. All these large

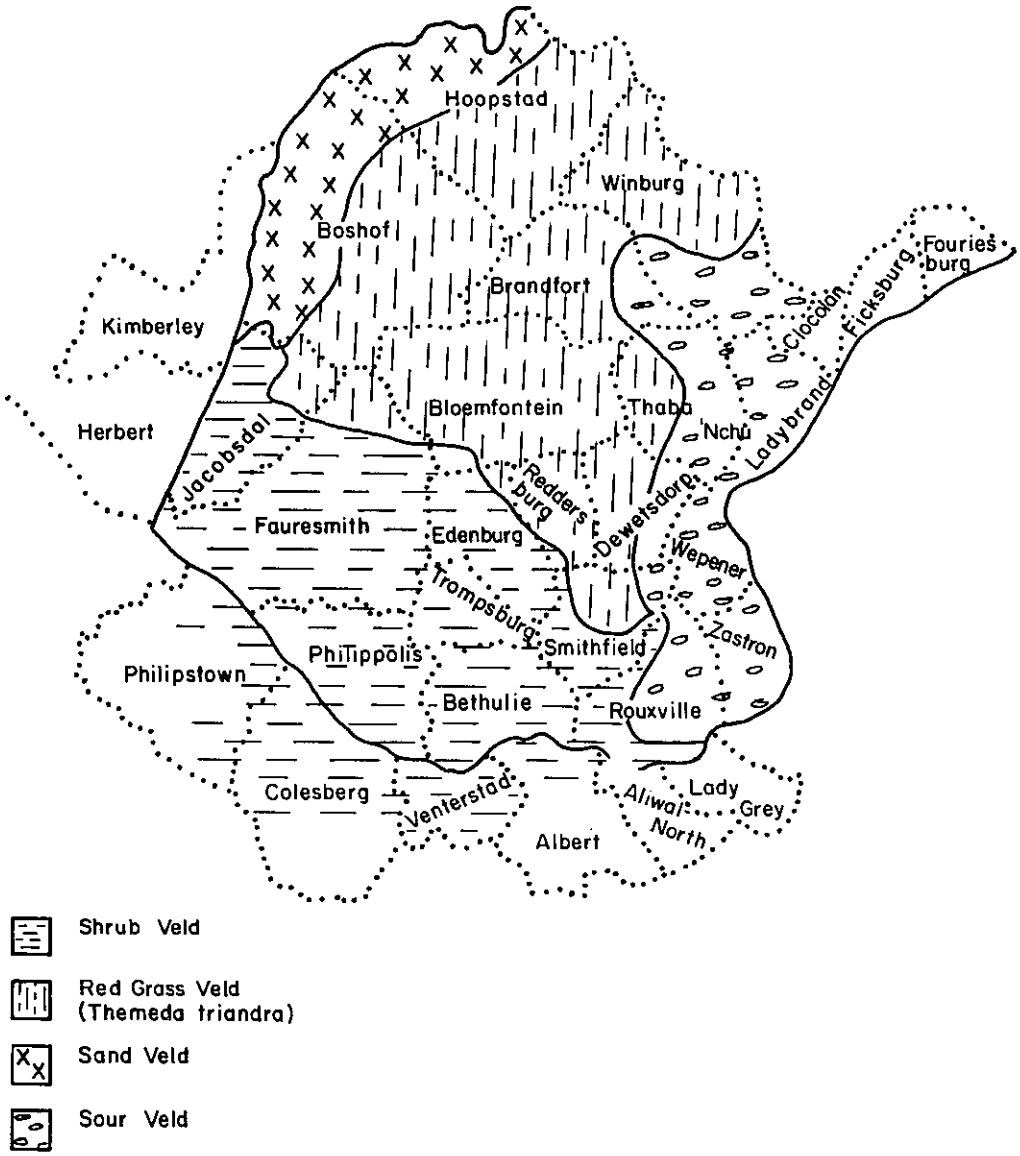
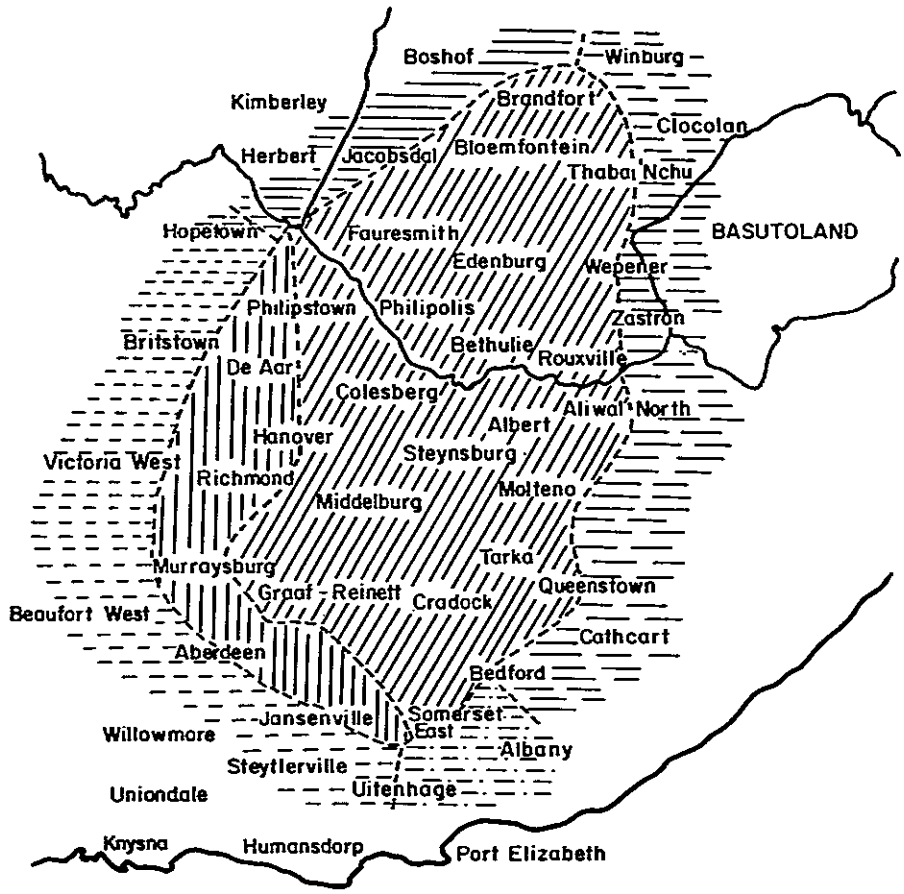


FIGURE 3.3 (b) Map of the Orange Free State showing the limits of shrubveld (karoo) in 1947 (De Klerk 1947).

scale changes can ultimately be equated with desertification, desertization and aridization processes (Roux and Vorster 1983). The process of aridization is enhanced by sparser vegetation which leads to increased runoff, higher soil temperatures, increased soil moisture evoporation and accelerated soil erosion. The general result is a decrease in the effectivity of the rainfall, decreased soil moisture status, and a harshening of the micro-climate. Aridization is generally accompanied by an increase in short-lived and xerophytic species.

Several investigations have been launched to assess the deterioration of natural vegetation in South Africa. The more important of these were by The Drought Investigation Commission (Anonymous 1923), The Desert Encroachment Committee (Anonymous 1951), the Commission of Investigation into Agriculture (Anonymous 1968) and the Departmental Committee for Veld Deterioration (unpublished data). A general conclusion is that the



Marginal Grassveld Region

Eastern Mixed Karoo

Semi-arid Grassveld

Arid Karoo

Higher rainfall Grassveld

Coastal Grass Scrub & Savannah

FIGURE 3.4 (a) Invasion of Eastern Mixed Karoo (karoo) into Marginal Grassveld (sweet grassveld) at the eastern margin of the karoo biome in 1848 (Tidmarsh 1948).

grazing capacity of the Karoo has decreased between 30 and 50% as a result of vegetation deterioration (see Anonymous 1923; Anonymous 1972; Vorster and Meyer 1983).

CAUSES OF VEGETATION CHANGE

Vegetation change in the karoo biome has been attributed to the effects of grazing, cultivation, fire, insect herbivory, climatic deterioration as well as interactions between these processes. These are discussed in more detail below.

Marginal Grassveld Region

Eastern Mixed Karoo

Semi-arid Grassveld

Arid Karoo

Higher rainfall Grassveld

Coastal Grass Scrub & Savannah

FIGURE 3.4 (b) Invasion of Eastern Mixed Karoo (karoo) into Marginal Grassveld (sweet grassveld) at the eastern margin of the karoo biome in 1948 (Tidmarsh 1948).

Grazing

Introduction of domestic stock. Indisputably, the main cause of vegetation change in the biome is the impact of extensive small stock farming. The vast herds of largely migratory ungulates indigenous to the biome (Skead 1982) have been almost completely replaced by domestic stock (sheep and goats) enclosed within farm boundaries. These animals, with distinct grazing habits and selective preferences (Botha 1981) were introduced into a heterogeneous vegetation which was formerly utilized exclusively by a wide spectrum of feral grazers (Roux 1968a). This radical change in grazing regime inevitably evoked major changes in the vegetation especially in respect of species composition and phytomass.

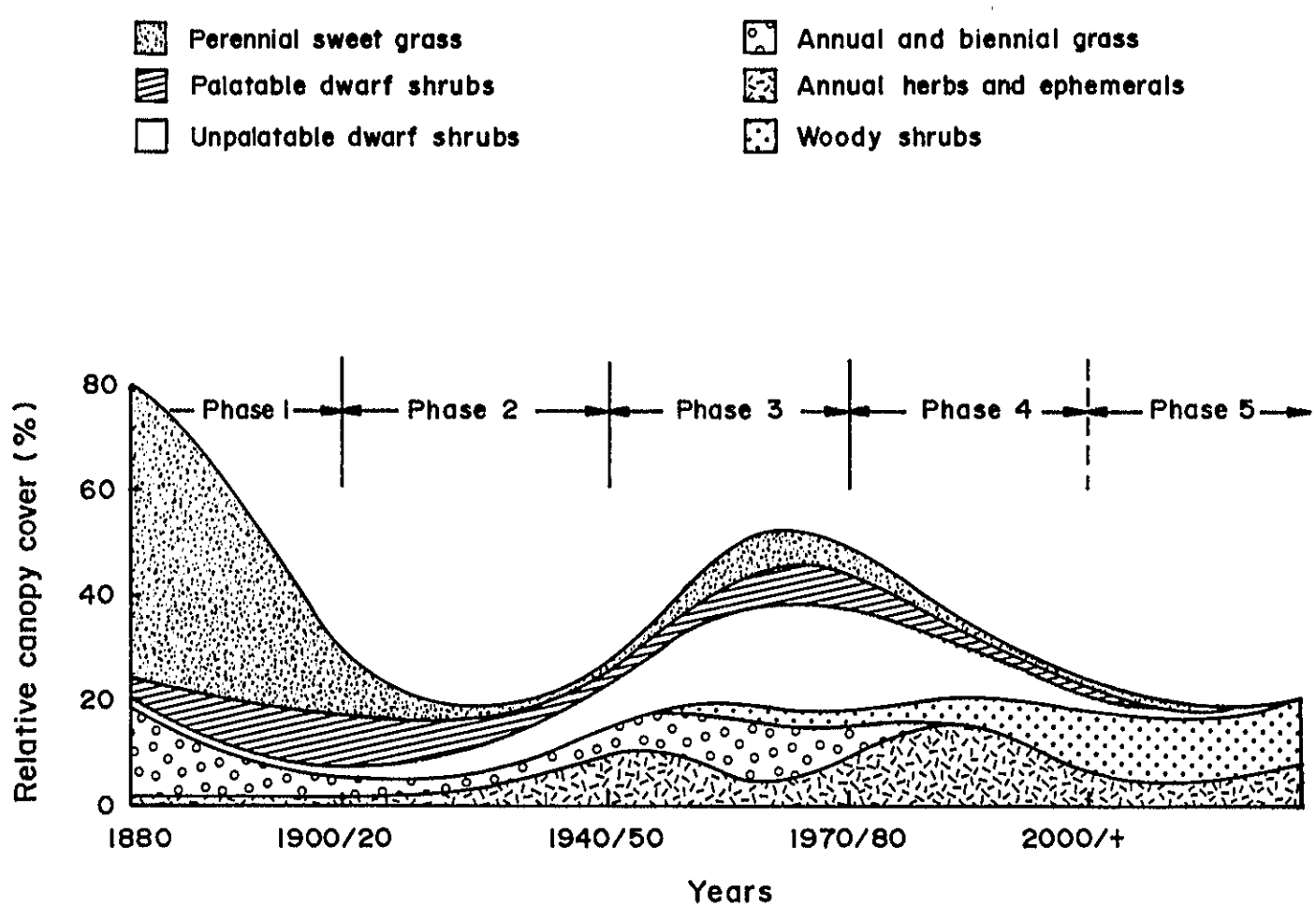


FIGURE 3.5. Five phases of change in cover of the main components of vegetation in the Upper Karoo (Roux and Vorster 1983).

Vegetation change brought about by domestic stock completely eclipses natural change; it is therefore very difficult to determine the rate of natural change. However, vegetation change is evident in plots protected from grazing over the long term (see Figure 2.6 this volume). These changes appear cyclical and are most probably governed by short-term trends in the rainfall (Roux 1966).

The direct and indirect physical impact of fenced-in and permanently settled domestic stock on the environment, such as the disturbance of the ground surface, trampling of plant material, pulverization of soil and organic material, and the stimulation of erosion and runoff, can be regarded as a very significant factor adversely affecting vegetation (Roux and Opperman 1986).

Overgrazing. The impact of grazing by domestic animals is aggravated where stock numbers are excessive and the rate of the removal of vegetation exceeds the rate of recovery. Even if stock numbers are within limits but utilization practices are out of phase with the natural requirements for growth, reproduction and physiological processes essential to the maintenance of the stability of the vegetation, grazing can still be very destructive (Roux unpublished).

Where stock numbers are kept in check and ecologically based grazing systems (Roux 1968b) are applied, high grass and palatable shrub cover is maintained and promoted (Tidmarsh 1947, 1951; van der Walt 1961; Bedford and Roberts 1975; Lund 1975a,b; Jordaan 1976a,b; van Zijl 1980; Roux 1983). Severely eroded and denuded land surfaces have recovered partially within 40 years after reducing stock numbers drastically and applying special grazing treatments (Roux and Opperman 1986). However, in most cases economic factors pressurize entrepreneurs to overexploit the natural resources.

Grazing and drought. Grazing during and immediately after drought periods is a major cause of detrimental change. It appears that the drought of 1948 to 1950, coupled with heavy continuous grazing, was ultimately responsible for the death of large numbers of palatable plants. This, together with sustained grazing during the establishment phase following good rains, resulted in the recruitment of unpalatable species only (Tidmarsh 1951). This effect, which was experimentally demonstrated, possibly explains why karoo vegetation, subjected to continuous grazing over the long term, rapidly declines in terms of sustaining sheep conditions at an acceptable level (Roux unpublished).

Drought may cause high mortality of some species which, in the absence of continuous grazing, would re-establish after good rains. However, under current grazing practices, local extinction of species after drought is not uncommon, resulting in possibly irreversable changes in vegetation structure and composition.

Cultivation

In the moister parts of the karoo biome (eg western Orange Free State), extensive dry-land cropping has resulted in the complete replacement of the vegetation. Such practices in an arid biome are particularly harmful and a main cause of desertification (Dregne 1983). Where cultivation has been discontinued, it requires many years before abandoned lands become

revegetated. During this interim period wind and water erosion are particularly severe. The frequent occurrence of severe dust storms and the formation of sand dunes and other aeolian deposits are ample proof of the detrimental effects of agrarian activities in the marginal cropping areas.

Fire

Fire has probably never been a significant factor in the Karoo (Edwards 1984). However, it is possible that after a series of high rainfall years, sufficient fuel would accumulate to support extensive fires, particularly in *Stipagrostis* species dominated veld and the grassy Karoo of the eastern mountains. Limited local fires caused by lightning may occur from time to time (Roux and Smart unpublished). Such fires, despite their infrequency, probably have a great influence on the structure of karoo communities (Huntley 1984).

Insect herbivory

Insect herbivory also contributes to vegetation change, although this has been little studied. The combined effects of livestock grazing, drought and insect herbivory may be particularly harmful. Insects of significance are the karoo caterpillar, harvester termite, and locusts (Tidmarsh 1951). Studies on plant-insect interactions in the Karoo are an urgent priority.

Climatic effects

The macroclimate. That macroclimatic patterns have changed during the Pleistocene and even the Holocene, is an indisputable fact (Tyson 1986). Van Zinderen Bakker (this volume) presents models of vegetation change in the Karoo between 50 000 to 12 000 BP. The indications are that the Karoo expanded eastward during warm and dry periods (interglacials) whereas during the cooler and wetter periods (glacials) temperate grasslands predominated. Palynological studies currently in progress will provide a more precise insight into the changes.

There have been several attempts to link contemporary vegetation change to climatic deterioration. Tidmarsh (1948) argued that the destruction of vegetation in the western part of the karoo biome adversely affected the climate in the east. A greater soil exposure in the arid west would have led to higher temperatures and an increased desiccatory effect of the predominant westerly winds. This could affect the climate in the biome eastwards and consequently cause vegetation change.

Kokot (1948) conducted an investigation into the evidence bearing on climatic changes over southern Africa. His main conclusions were that during the Holocene the rainfall records for South Africa did not disclose a long-term decline and that there was no evidence that the deteriorating vegetation in the Karoo has resulted from decreased rainfall. Furthermore, he found ample evidence that the desiccatory effect of vegetation denudation occurring in many parts of South Africa had caused an increase in dust storms, possible increase in temperature, increased wind speed and a greater overall evaporative demand.

It is unlikely that climatic change has played a significant role in

affecting vegetation change in the biome over the last three centuries.

The microclimate. Microclimatic conditions play an important role in the germination and establishment of seedlings of karoo plants. Plant-induced changes in the microclimate increase with increasing plant size and density (Geiger 1957). The decrease in plant cover, which has occurred in most of the karoo biome, has resulted in a greater microclimatic temperature extremes, increased surface wind movement and an alteration in plant and soil water-relationships.

Practically no information exists on the rate and magnitude of change in karoo biome microclimates. However, it is reasonable to assume that exposed soils which are both droughty and prone to capping, are unsuitable substrata for the establishment of mesophytic species. These conditions would favour an increase in hardy, xerophytic species, many of which are both unproductive and unpalatable to sheep.

Productive and palatable species such as *Tetrachne dregei* (Roux 1968a) and *Plinthus karooicus* (Theron 1964) require relatively high soil moisture conditions for growth and establishment. The hardier, less palatable and encroaching species such as *Chrysocoma tenuifolia*, *Eriocephalus glaber*, *E spinescens*, *Lycium arenicolum*, *Pteronia glauca*, *P sordida* and *P tricephala* have lower transpiration rates than the more palatable species such as *Phymaspermum parvifolium* (du Preez 1964). The replacement of the more productive and palatable species by hardy unpalatable shrubs can be regarded as a major facet in vegetation change in the biome.

VARIABILITY AND RESILIENCE OF KAROO BIOME VEGETATION

Variability

The two main floristic components of karoo vegetation, the shrub and grass floras generally respond optimally and differentially to rainfall and temperature conditions prevailing during specific seasons. The shrubs, as well as most of succulents and winter (C_3) grasses respond optimally to rainfall during the cooler months (March to September), whereas summer (C_4) grasses react optimally to summer rainfall (October to March) (Roux 1966, 1968a). Many of the pioneer and invasive shrub species (*Chrysocoma tenuifolia*, *Felicia muricata*, *Lycium* species, *Pentzia globosa*, *P incana*, *P spinescens)* respond favourably to rainfall irrespective of seasonal occurrence (possibly excluding mid winter). Most of the Karoo is a vast tension zone located between the summer rainfall grasslands and the winter rainfall succulent shrublands.

As a result of long- and short-term rainfall variability, both in terms of seasonality and amount, certain species or floral elements are promoted selectively over others (Roux 1966). Such specific reaction may lead to marked temporary changes in the physiognomy of the vegetation. This is especially noticeable in the broad ecotones between shrubland and grassveld in the eastern Karoo. In this region exceptional grass growth was recorded between 1952 and 1958, whereas shrub cover increased between 1947 and 1950 (see Figure 2.6 this volume).

From a graziers point of view karoo plants can be classified according to

relative palatability to domestic stock (Blom unpublished). Usually the less palatable species are best adapted to survive and reproduce successfully under harsh environmental conditions and thus replace the more palatable species as a result of drought or overgrazing. An understanding of the phenological responses of karoo plants to variations in climatic and grazing regimes forms the basis for predicting changes in species composition of vegetation grazed by stock during different seasons (Figure 3.6).

Resilience

The resilience concepts used are those of Caughley and Walker (1983) and Pimm (1984).

It is often asserted that arid ecosystems are fragile, unstable, delicate and sensitive (UNCOD 1977). However, such a description does not unconditionally apply to the karoo biome as much of the vegetation is relatively stable and resilient. Marked changes in the composition of karoo vegetation, even under continuous overgrazing, may take decades. Furthermore, compositional change is not always accompanied by a change in structure and physiognomy. The rate of compositional change depends on the type of vegetation. Terms such as fragile are possibly only applicable where vegetation is in a pioneer stage after complete destruction.

A typical patch of central karoo vegetation comprises three major components.

Primary matrix. This is a relatively stable matrix composed of a variety of dwarf and low karoo shrubs and, more rarely, perennial grasses. This matrix forms the primary vegetational structure and is usually characterized by one or two dominant species. It is considerably resistant to change, has stable populations and a moderate to low resilience. Variable rainfall patterns result in variations in the phenological dominance of different species in different years. This gives rise to the impression that the vegetation has changed or is changing.

This matrix is the result of the destruction by selective grazing, of the original and largely stable vegetation consisting of a mixture of perennial grasses, dwarf and low shrubs. Destruction was followed by a stage of unstable equilibrium before the vegetation stabilized in the present shrub matrix. With mismanagement, primarily overgrazing by sheep, this matrix gradually thins out and a change in the dominant species occurs. A secondary component becomes established and may completely replace this primary matrix.

Some of the main species occurring in this matrix are *Atriplex vestita*, *Eberlanzia spinosa*, *Eriocephalus ericoides*, *E spinescens*, *Euphorbia coerulescens*, *Drosanthemum lique*, *D tuberosum*, *Galenia africana*, *Limeum aethiopicum*, *Lycim arenicolum*, *L oxycladum*, *Nenax microphylla*, *Osteospermum spinescens*, *Pentzia incana*, *P spinescens*, *Plinthus karooicus*, *Pteronia glauca*, *P glomerata*, *P sordida*, *P pallens*, *P tricephala*, *Rhigozum trichotomum*, *Rosenea humilis*, *Salsola nigrescens*, *S tuberculata*, *Zygophyllum microphyllum*, *Z suffruticosum*, and many more including

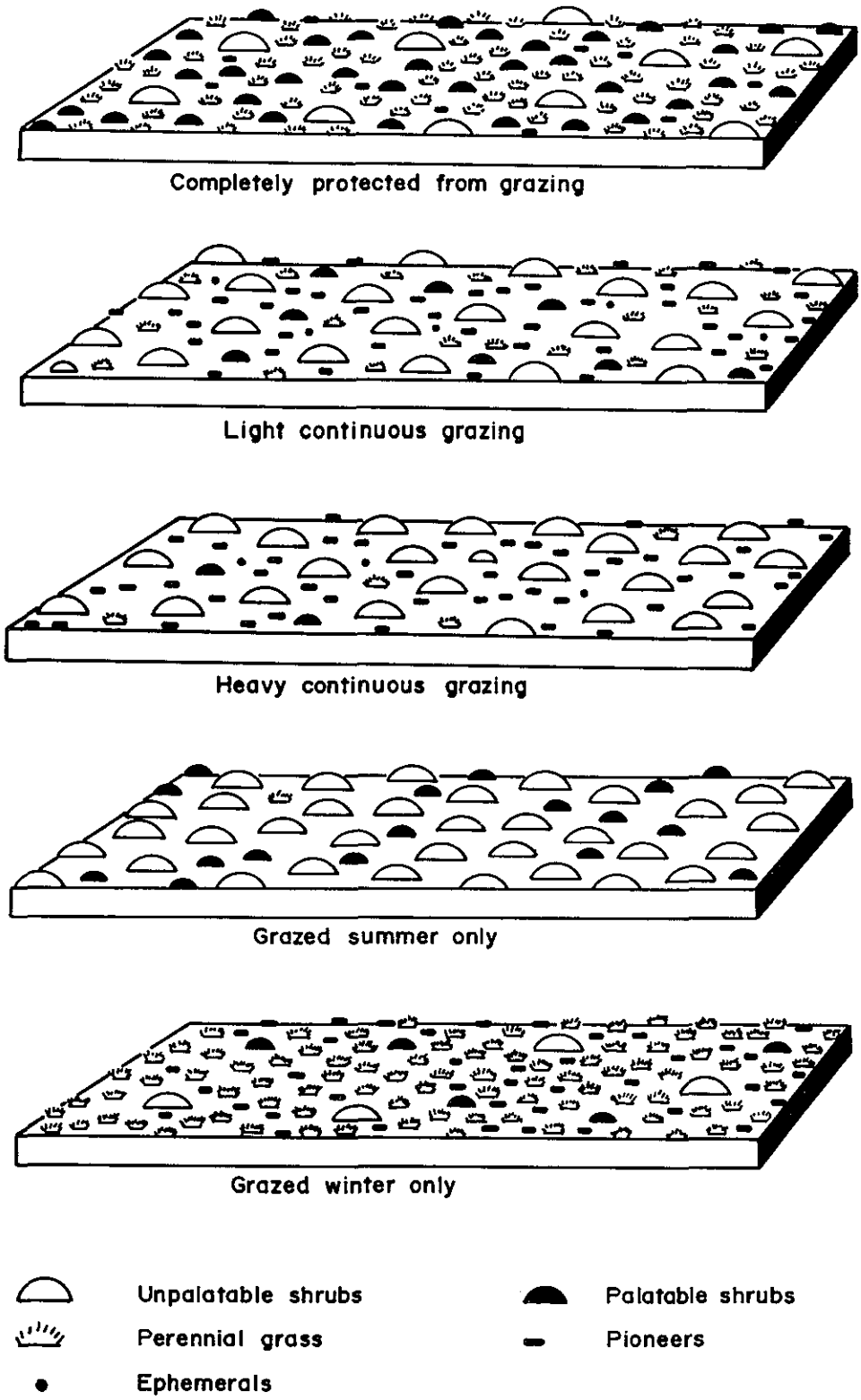


FIGURE 3.6. Diagramatic representation of the effects of experimental grazing treatments, over the long term, on karoo veld situated on a basal pediment. The figures are based on quantitative survey data.

numerous Mesembryanthemaceae. Grasses in this matrix are *Aristida brevifolia*, *A diffusa*, *Stipagrostis ciliata*, *S obtusa*, *S uniplumis*, *Themeda triandra*, *Tetrachne dregei* and a few more. These grasses are less resilient to grazing pressure than the shrubs.

Secondary component. The primary matrix is interspersed with an unstable but highly resilient secondary component. It consists of a variety of grasses (perennial and biennial) and pioneer karoo shrubs. At any particular time usually one or two species are dominant. This secondary component is particularly affected by seasonal rainfall. After good summer rains short-lived grasses may dominate the landscape. With good management grasses may persist for a number of years, but under grazing stress, the grass species are replaced by pioneer karoo shrubs.

Some of the more important species in this category are: *Arthrosolen polycephalus*, *Chrysocoma tenuifolia*, *Euphorbia mauritanica*, *Felicia muricata*, *F ovata*, *Othonna pallens*, *Pentzia globosa*, *Psilocaulon absimile*, *Walafrida geniculata* and *W saxatilis*. The more common grass species are *Aristida diffusa*, *Cenchrus ciliaris*, *Cynodon incompletus*, *Digitaria argyrograpta*, *Eragrostis bicolor*, *E curvula*, *E lehmanniana*, *E obtusa*, *Heteropogon contortus*, *Panicum coloratum*, *P stapfianum*, *Sporobolus fimbriatus* and *Tragus koelerioides*.

Ephemeral component. A third component consists largely of pioneer grasses and annuals. Populations of this ephemeral and largely weedy flora are highly unstable. This component is interspersed in the primary matrix and secondary component, or may cover exposed areas of soil when favourable moisture conditions prevail. In the arid western areas of the karoo biome, where large tracts of veld densely populated by annuals (Rösch 1977), this component is an important source of stock feed.

THE MANNER OF VEGETATIONAL CHANGE

Changes in karoo vegetation take place in situ; centrifugally (spreading outward in all directions); by convergence (the occupation of an area by vegetation or species surrounding vegetation of a different status or composition); frontally or directionally (change from west to east with shifting ecotones or frontal zones); and by migration (the spreading of specific species or associates into other areas). Migration or spreading could also be linear such as along river banks and road enclosures.

Change occurs over the long term, medium term, short term or temporally. Large scale permanent change is usually over the long term (half-a-century or longer). Permanent or reversible change can take place over the medium term, whereas temporal changes are over the short and very short term.

Long-term permanent changes

Widespread invasion of karoo into adjacent vegetation types, as described by de Klerk (1947); Tidmarsh (1948) and Acocks (1975) can be regarded as irreversable.

Medium-term change

The most noticeable changes in the karoo biome are over the medium term. This has been demonstrated by quantitative surveys in veld management experiments (Tidmarsh 1951; Roux unpublished; Figure 2.6 this volume). These changes are primarily reflected in the considerable fluctuations in species' populations (Roux unpublished). Furthermore, the magnitude of change is governed by the seasonal rainfall and grazing treatment (Tidmarsh 1951; Roux 1966). Medium-term change may be of a temporary or permanent nature. This appears to depend on the duration of the maintenance of a specific grazing treatment and the resultant loss of soil (Roux and Opperman 1986). Where significant soil loss has taken place, change is often irreversible. The longer the vegetation is subjected to disturbance, the greater the chance that change is irreversible.

Short-term change

These temporary changes occur over the short term and are chiefly embodied in phenological change, effects of drought, seasonal change in rainfall and short-term grazing. Seasonal growth rythms account for temporary change in above-ground phytomass and digestible organic matter (Vorster and Roux 1983).

Temporal change

Temporal changes resulting from the appearance of ephemeral species, are of particular importance. Hitherto this aspect has not received sufficient attention. Rösch (1977) has studied the monthly changes in the species composition and phenology of Namaqualand vegetation in the Hester Malan Nature Reserve near Springbok. From this study it is clear that the main vegetative cycles of most species are concentrated in the months March to October whereas the main flowering periods are from August to October. A few species showed two flowering periods per year.

Considerable research is still to be done on annual and short-lived (opslag) plants. This component of the vegetation is not only valuable in providing grazing but may also play an important role in vegetation development.

CHANGES IN SPECIES DISTRIBUTION AND DENSITY

Vegetation change is often accompanied by gross changes in the distribution and density of species. The presence or absence of certain species may indicate change or be harbingers of future changes. Some valuable species which have become thinned out within their distributional boundaries over the last 50 years include *Euphorbia coerulescens* (van der Walt 1965) and *Portulacaria afra* (Acocks 1975). Others include large shrubs and trees which are now almost relictual in the Karoo (eg *Acacia erioloba*, *Aloe dichotoma*, *Boscia* species, *Nymania capensis*, *Pappea capensis*, *Pachypodium namaquanum*, *Rhus lancea* and *Schotia afra*). Karoo shrubs which have become reduced in number are *Limeum aethiopicum*, *Mestoklema tuberosa*, *Nenax microphylla*, *Plinthus karooicus* (Theron 1964), *Polygala asbestina*, *Salsola nigrescens*, *Tetragonia arbuscula* and *Zygophyllum microphyllum*. Shrubs which are likely to become extinct include *Euryops empetrifolius*, *Felicia ovata*,

Indigofera stipulacea, *Phymaspermum schroeteri*, *Pentzia quinquefida*, *Pteronia membranacea* and *P oblanceolata* (J P H Acocks personal communication). Many of the rare succulents (*Euphorbia* species, *Haworthia* species, *Mesembryanthemaceae*, *Stapelia* species) are also endangered (Hall and Veldhuis 1985).

Perennial grasses which were once common but have now become relatively inconspicuous include *Digitaria argyrograpta*, *Fingerhuthia sesleriaeformis*, *Helictotrichon capense*, *Panicum* species, *Setaria neglecta*, *Tetrachne dregei*, *Themeda triandra* and few others. A classic relict is *Secale africanum* which occurs only in two isolated refugia in the Roggeveld.

Numerous species, mostly those which are generally classed as undesirable, have become denser or increased in number within their distributional areas. Trees and tall shrubs include *Acacia karroo*, *A mellifera* var *detinens*, *Euclea undulata*, *Rhus erosa*, *Rhigozum trichotomum*, *R obovatum*, *Lycium* species and *Eriocephalus aspalathoides*. Some dwarf and low shrubs which have become dominants include *Augea capensis*, *Chrysocoma tenuifolia*, *Eriocephalus spinescens*, *Eberlanzia spinosa*, *Euphorbia mauritanica*, *Galenia africana*, *G fruticosa*, *Hertia pallens*, *Monechma desertorum*, *Pentzia globosa*, *P incana*, *Protoasparagus* species, *Pteronia glauca*, *P incana*, *P pallens*, *P tricephala*, *Rosenea opositifolia* and *Zygophyllum suffruticosum*. It is not possible at present to state with accuracy whether these species are in the process of expanding their geographical ranges. However, it is certain that some species are increasing their ranges as a result of ecological mismanagement. These include *Eberlanzia ferox*, *Acacia mellifera* var *detinens*, *A karroo*, *Rhigozum trichotomum*, *Protoasparagus* species and *Aloe* striata. Grasses which have spread into adjacent regions and extended their distributional areas are *Stipagrostis obtusa*, *S ciliata*, *S uniplumis*, *Cenchrus ciliaris* and *Merxmuellera disticha* (from the mountains). In the case of *Stipagrostis* species the main body has become thinned out and spread into new habitats eastward, especially on newly formed aeolian deposits.

Invasive alien species which are spreading within the karoo biome or from adjacent biomes, are *Opuntia aurantiaca*, *O rosea*, *O imbricata*, *Cereus peruviana*, *Prosopis* species, *Alhagi camelorum* and *Nicotiana glauca*. *Opuntia megacantha* which was formerly a national pest (late 1800 up to about 1940) has been almost completely controlled by the introduction of Cochenille. At present it appears that this species is again becoming a major pest in the south-eastern sector of the biome.

FUTURE CHANGE AND RESEARCH

It is clear that extensive vegetation changes have occurred and are still in progress in the karoo biome. Today there are several extensive tension zones or ecotones where change is taking place faster than elsewhere. It is expected that such changes will accelerate in the near future. The role of the present widespread and disasterous drought cannot be overlooked in this respect and it can be expected that it will contribute significantly in promoting change.

The zones in which the most rapid change appears to be taking place are in

the transitional tension zones between karoo and various grassveld types (see Acocks 1975, Map 2). The monitoring of vegetation change over the short and long term in these transitional zones can be regarded as a high priority. Other areas of high priority which need to be monitored are Bushmanland (desert grassland) and its transitions to surrounding types of vegetation and the transitional zones between winter and summer rainfall karoo. Monitoring will require the use of exclosures, quantitative vegetational surveys, soil surveys, climatic data and aerial photography.

Autecological studies are required on key species which are indicative of vegetation change. Some of these include *Augea capensis*, *Chrysocoma tenuifolia*, *Eberlanzia ferox*, *Eriocephalus ericoides*, *Felicia filifolia*, *F muricata*, *Galenia africana*, *Hertia pallens*, *Lycium* species, *Pentzia globosa*, *P spinescens*, *Protasparagus* species, *Pteronia pallens*, *P incana*, *Rhigozum tricotomum*, *Rosenea humilis*, *R oppositifolia* and *Walafrida saxatilis*. Population and ecophysiological studies on these species would undoubtedly contribute significantly to a predictive understanding of processes and mechanisms involved in vegetation change and desertification (see Theron 1964). Grasses in need of study include *Antephora pubescens*, *Cenchrus ciliaris*, *Merxmuellera disticha*, *Schmidtia kalahariensis*, *Setaria neglecta*, *Stipagrostis brevifolia* and *S umplumis*. Grasses which have already received attention are *Tetrachne dregei* (Roux 1968), *S ciliata* and *S obtusa* (Skinner 1964).

Ephemeral species are of particular importance in the biome, especially in Namaqualand and the western parts of the Karoo. Until recently (Rösch 1977), studies on these species have been neglected. Research on the population dynamics of this ephemeral flora will be of great interest.

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CHAPTER 4 PHYTOGEOGRAPHY AND ORIGINS OF THE KAROO FLORA

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INTRODUCTION

In recent years much attention has been given to biogeographic patterns in the Southern Hemisphere. The nucleus of the biota of southern Africa was generally considered to be of Gondwanan origin (van Zindern Bakker 1976). Increasing knowledge about taxa and their phylogenetic relationships has indicated that the modern biotas of southern Australia and southern South America are more closely related to each other than either is to that of southern Africa (Keast 1973).

Distribution patterns, both modern and historical, are difficult to evaluate against the background of the controversies in historical biogeography, particularly those regarding the relative importance of dispersalism and vicariance as causal mechanisms for distributions (Poynton 1983). This dispute is further compounded by the argument between proponents of phylogenetic and evolutionary systematics, over punctuated and gradual modes of evolution (Vrbra 1985).

In this review it will become evident that both vicariance and dispersalism have played a role in the evolution of the karoo flora. Similarly, both punctuated equilibria and phyletic gradualism hypotheses can be used to explain speciation in the karoo.

In this chapter I review the phytogeography of the karoo flora and examine critically hypotheses on its origins.

FLORISTIC COMPOSITION

At present it is impossible to give an accurate account of the floristic composition of the karoo. This is largely due to the paucity of herbarium collections (Gibbs Russel et al 1984) and more importantly the numerous taxonomic problems. Many common karoo families, particularly the Mesembryanthemaceae, Aizoaceae, Asteraceae and Euphorbiaceae, are in taxonomic disarray. The Mesembryanthemaceae, for example, has on average 3,7 names per taxon. At present 2 684 taxa in this family are recognized (Gibbs Russell and Staff of the National Herbarium 1984) but critical revision will probably reduce the number of accepted taxa to about 1 200 (Gibbs Russell and Glen 1984). Another example illustrating these taxonomic problems is the genus *Asparagus* which is widely distributed in the Karoo. A recent revision (Obermeyer 1984, 1985) has split the genus of 44 species into two genera and 79 species.

The problems outlined above have made it extremely difficult to estimate the size of the flora. Estimates on the size of the karoo flora range from 3 500 species (White 1983) to 7 000 taxa (calculated from Gibbs Russell (in press) Le Roux unpublished and my own work). Similarly, endemism estimates range between 35% and 50% (Werger 1978a; White 1983).

Below is a brief analysis of the floristic composition of the Karoo, based on data in Werger (1978a), Goldblatt (1978) and White (1983).

Excluding Welwitschiaceae, there is no endemic family in the Karoo-Namib Region (sensu Werger 1978a), but there are a number of characteristic families with many endemic genera and species. These include Asclepiadaceae particularly the Tribe Stapelieae (six endemic genera, c 160 endemic species); Aizoaceae/Mesembryanthemaceae (c 95 endemic genera, c 1500 endemic species); Poaceae particularly the Tribe Stipeae; Liliaceae sensu lato; Iridaceae; Scrophulariaceae and Asteraceae. There are approximately 60 additional endemic genera including *Adenolobus*, *Arthraerua*, *Augea*, *Calicorema*, *Ceraria*, *Didelta*, *Ectadium*, *Grielum*, *Hypertelis*, *Kaokochloa*, *Leucophrys*, *Leucosphaera*, *Microloma*, *Monelytrum*, *Nymania*, *Phymaspermum*, *Plinthus*, *Sisyndite* and *Xerocladia*.

Many genera have important concentrations of endemic species in the Karoo, including *Aloe*, *Anacampseros*, *Babiana*, *Chrysocoma*, *Cotyledon*, *Crassula*, *Eriocephalus*, *Euphorbia*, *Gasteria*, *Haemanthus*, *Haworthia*, *Hermannia*, *Pelargorium*, *Pentzia*, *Pterona*, *Relhania*, *Sarcocalon*, *Stipagrostis*, *Tetragonia* and *Zygophyllum*. Some of these genera, eg *Pteronia*, are almost confined to the Karoo while others, eg *Euphorbia*, are cosmopolitan.

For detailed descriptions of the vegetation of the Karoo see Acocks (1975), Werger (1978a) and White (1983).

PHYTOGEOGRAPHY

Regional characterization and domains

The phytogeography of southern Africa has been extensively discussed by Werger (1978b). This review is therefore confined to a brief description of the various subdivisions proposed which affect the status of the Karoo-Namib Region.

In the early phytogeographical subdivisions of southern Africa (eg Grisebach 1872), the Karoo-Namib Region was not recognized as a distinct phytochorion. However, Bolus (1875, 1905) and subsequent authors have recognized the Karoo as a phytogeographical unit, distinct from the Kalahari and Sudan Regions (Werger 1978b). Subsequent authors have been mainly concerned with the separation of the Cape Floristic Kingdom (sensu Good 1974; Goldblatt and Bond 1984) from the neighbouring phytochoria (Weimarck 1941). Most of these classifications were based on physiognomic criteria rather than taxon distributions. In 1947, Lebrun published a phytogeographical map of Africa which has, with some changes, formed the basis of contemporary phytochorological concepts (Werger 1978b). However, Lebrun was very doubtful as to the hierarchical status of the Karoo-Namib Region and reluctantly included it as a separate domain in his Sudano-Zambezian Region. Since Monod's (1957) review of African chorology, the Karoo-Namib has been regarded as a distinct region within the African part of the Palaeotropic Kingdom.

Monod (1957) subdivided the Karoo-Namib into three domains: the Karoo Domain, the Namaqualand Domain and the Namib Domain. Subsequent authors (Troupin 1966; Aubréville 1975), have adjusted the boundaries of these

domains. Troupin's (1966) map is not considered an improvement because some boundaries cut across floristically and ecologically homogeneous areas while some clear chorological boundaries were not recognized (Werger 1978a). Werger (1978a) argues that domains should be clearly characterized both chorologically and ecologically. He subdivided the Karoo-Namib Region into four domains: Namib, Namaland, Western Cape Karoo, and one subdomain: the southern Kalahari (Figure 4.1).

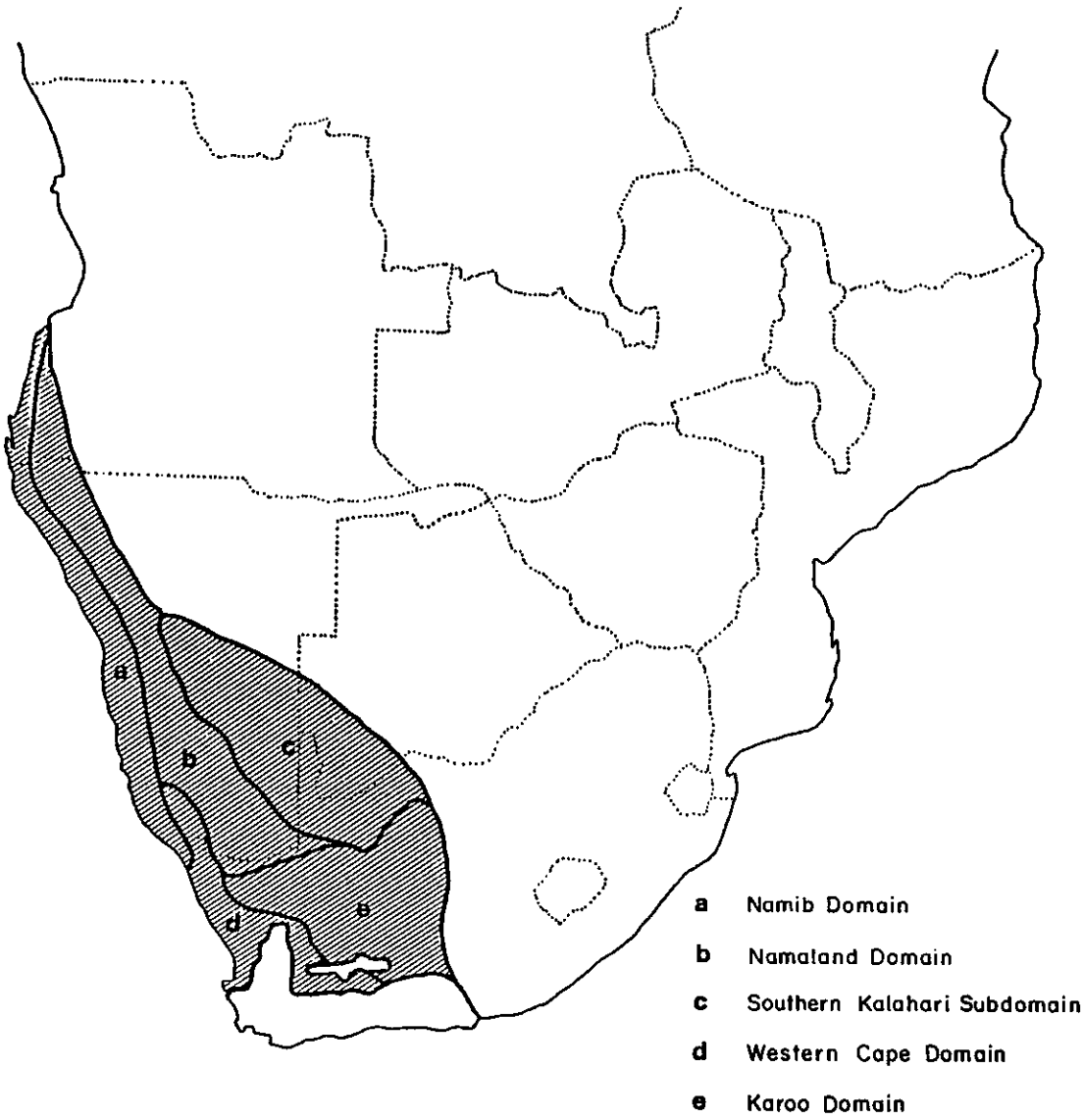

FIGURE 4.1 Domains in the Karoo-Namib Region (from Werger 1978a).

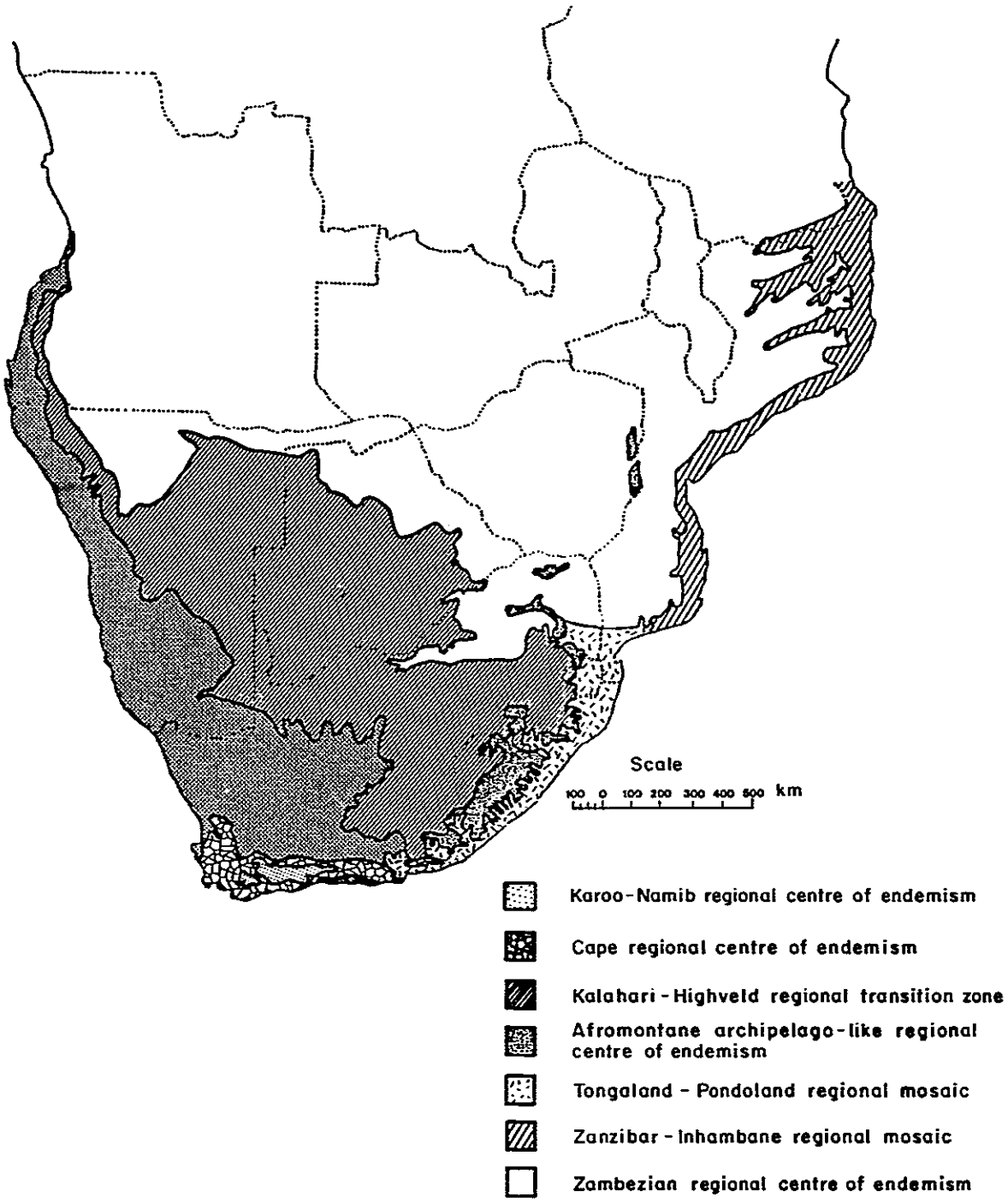

FIGURE 4.2 Phytochorological subdivision of southern Africa (from White 1983).

Recently, White (1983) presented a new phytochorological map of Africa (Figure 5.2) which comprised nonhierarchical units defined in terms of endemism. This was done by using four major categories of equal rank. These categories are Regional Centres of Endemism, Archipelago-like Centres of Endemism, Archipelago Centres of Extreme Floristic Impoverishment, and Regional Transition Zones and Mosaics. The centres of

endemism are defined as areas where at least 1 000 plant species are endemic and that these constitute at least 50% of the total number of species in the centre.

White's map, though maintaining the salient structures of other phytochorological maps, has wide or narrow transition zones separating the clearly characterized centres of endemism. These correspond mainly to regions or domains in other classifications. White's map differs from that of Werger's in that it:

- excludes the Kalahari Sub-Domain from the Karoo-Namib Region. Despite the arguments of Werger (1973a) most researchers in the area agree with this (A Gubb personal communication);
- recognizes that enclaves of the Karoo-Namib Region exist within the boundaries of the Cape Region; and
- does not subdivide the Region into smaller units, ie the Karoo-Namib is viewed as being one regional centre of endemism.

However, both White's (1983) treatment (Figure 4.2) and Werger's (1978b) more formal hierarchical approach (Figure 4.1) result in maps with a high degree of congruence.

Centres of Endemism

The Karoo-Namib Region may be divided below the domain level (Figure 4.1) into centres of endemism. These are relatively small areas with concentrations of endemics or of closely-related species (Nordenstam 1969) and must not be confused with White's (1983) centres of endemism. Similarly, other areas are notable for their lack of endemism and/or relative paucity of species.

A preliminary map showing some of these areas in the western, south-western and southern parts of the Karoo-Namib Region is presented in Figure 4.3. Source material for this map comes from Weimarck (1941), Croizat (1952, 1962), Acocks (1953, 1975); Nordenstam (1969), Werger (1978a), Oliver et al (1983), B Bayer (personal communication), and A Le Roux (personal communication).

The centres are preliminary and in most cases subjectively determined. This map must be regarded as a working hypothesis which is currently being tested by the application of multivariate techniques to a large floristic data set. A detailed description of the areas defined on the map and of the nomenclature used is not discussed here as it will be presented elsewhere (Hilton-Taylor in preparation). Five centres are recognized, viz the Gariep Centre, Karas Centre, Vanrhyndorp Centre, Little Karoo Centre and Sneeuberg Centre (the latter is not strictly part of the Karoo). The remaining areas have not been assigned any phytochorial status at present. It should also be noted that the centres within the Cape Region (fynbos biome) (cf Weimarck 1941; Taylor 1980; Oliver et al 1983) have not been shown although the outliers in the Karoo are mapped.

ORIGINS OF THE FLORA

The present day diversity of biota in southern Africa, their phylogenetic relationships and adaptations to different environments are manifestations

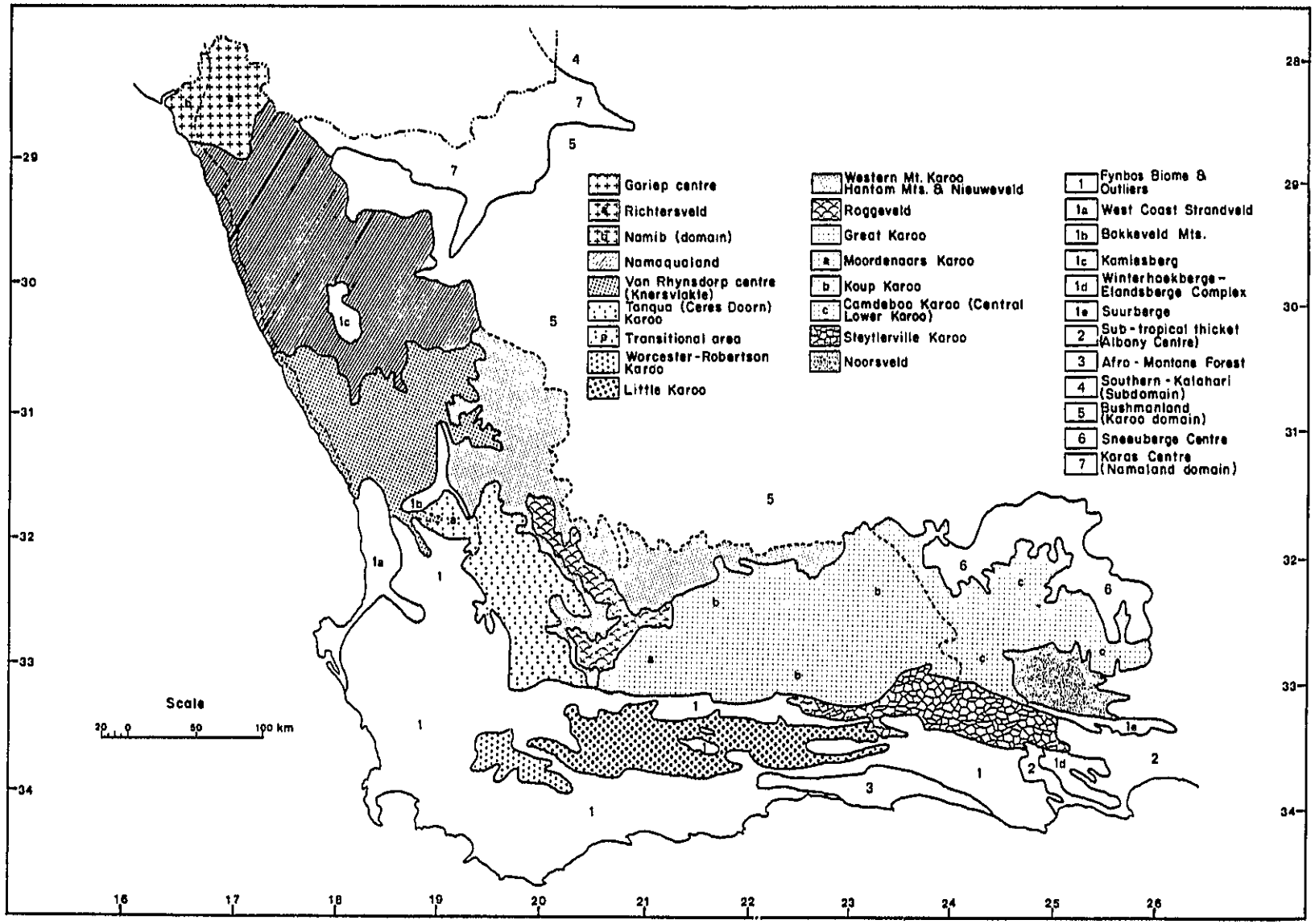

FIGURE 4.3 Preliminary phytogeographical centres of the Western Cape Domain and adjacent areas.

of important palaeogeographic events since the separation of Africa from Gondwanaland between the mid-Jurassic and mid-Cretaceous times (Raven and Axelrod 1974). During the rafting of Africa to its present position it not only experienced the long-term development of the post-Gondwana physiographic features (du Toit 1966; Haughton 1969; King 1967, 1978; Truswell 1970, 1977) but also the major Tertiary palaeoceanographic events of the southern ocean which profoundly affected global climates (Deacon 1983a,b) and hence the speciation and distribution of biota. These climates were further greatly modified by the waxing and waning of the Pleistocene glaciations.

The Tertiary and Quaternary periods comprise the last 65 My of earth history (the Cenozoic era). This era is noteworthy as the period important in the evolution and progressive modernization of the angiosperms. An understanding of the climatic changes during this period has relevance to the discussion of the origin of the karoo flora. As these climatic changes are fully reviewed by Deacon (1983a,b), they will only be mentioned briefly here.

General hypotheses

Bews (1921, 1922, 1925) considered the karoo flora to be a product of specialization of the tropical flora bordering it to the north and east, in response to the onset of arid conditions. Bews (1925) further suggested that in the east, karoo was derived from the bushveld (now termed the Subtropical Thicket) via the Fish River Scrub. Acocks (1953) agreed that this hypothesis applied to areas like the Great Karoo and Little Karoo where most of the large shrubs and trees are thicket species. Cowling (1985), however, argues that data from the contemporary thicket flora indicate that Subtropical Thicket has become established only recently in the southern and south-western Cape. He hypothesizes that the thicket flora has replaced karroid shrubland since the onset of Holocene warming. He also presents evidence that suggests the karroid succulent flora has had a lengthy history in the area. The large trees and shrubs in the Little and Great Karoo, eg *Euclea undulata*, *Schotia afra* and *Maytenus* species are indicative of the replacement. This has resulted in the savanna-type structure of vegetation in parts of the Little and Worcester-Robertson Karoo, with a karroid dwarf succulent shrub understorey and a subtropical tree overstorey.

Levyns (1964) though recognizing links between the karoo and fynbos floras, also considered the Karoo to have a northern tropical origin, she suggested two separate migration waves and regarded the karoo flora as being younger than the fynbos flora. Levyns (1964) postulated that the plants in the first migration consisted mainly of low succulent bushes and geophytes which concentrated in the west, whereas the later migration was of larger plants which spread over the entire area. Levyns (1964) does not indicate when or by what process these migrations took place.

Compton (1929) argued that two overriding selective forces in the Karoo were aridity and grazing. In order to survive the pressures of these two forces, karoo plants exhibit a number of features or primary adaptations which distinguish them from plants of adjacent regions. These features are:

Leaf succulence	- Crassulaceae and Mesembryanthemaceae
Stem succulence	- Euphorbiaceae and Asclepiadaceae
Geophily (monocots)	- Iridaceae and Liliaceae sensu lato
Geophily (dicots)	- Geraniaceae and Oxalidaceae
Unpalatibility	- Shrubby Asteraceae
Resurrectionism	- The ability to revive after rain, particularly in the Asteraceae

These features are present in the floras to the north and south of the Karoo. Hence Compton (1929) argued that from these floristic elements there "occurred an inward converging march from all sides to populate the arid central Karoo. But those families like Proteaceae and Ericaceae, showing none or insufficient of the necessary features, were left behind on the margins of the arid Karoo".

Compton never considered the possibility of speciation in the Karoo and outward movement into surrounding areas. Neither did he consider that the same adaptational features could have evolved independently to the same or even different selective forces.

Acocks (1953) also considered the karoo flora to be derived from both the Cape the tropical floras, but with a stronger influence of the Cape Flora, particularly in the western portions of the Karoo (see also Axelrod and Raven 1978). Acocks (1953) argued that the succulent habit, which is so characteristic of the southern and western Karoo, is not peculiar to any one vegetation type, but is rather a response to low moisture conditions. Succulents are present in all vegetation types of South Africa. Karoo succulents could therefore be derived from both the Cape and tropical floras (Acocks 1953). According to Raven (1983), the evolution of such extreme drought-adapted vegetation in the Southern Hemisphere started about 16 My. This was during the formation of the East Antarctic Ice Sheet, the formation of which reached a maximum approximately 13 My.

Goldblatt (1978) and Werger (1978a) argue that the karoo flora, because of its highly endemic and specialized nature, evolved in southern Africa over a very long period. Quoting Axelrod (1972), Goldblatt (1978) maintains tht there has always been a zone of reduced precipitation between tropical and temperate regions and that even in mesic landscapes there will always be edaphically dry habitats where drought adapted plants existed. Thus the karoo flora would be derived in part from an ancient xeric stock in which evolution and radiation were promoted from the Neogene as the climate became progressively drier. If this were the case, then one would expect to find a great number of endemic genera and a number of endemic families. However, high levels of endemism are confined to the species level. Furthermore many succulent taxa appear to be still undergoing extensive speciation (species limits cannot be clearly defined for *Haworthia* and a number of taxa in the family Mesembryanthemaceae (B Bayer and H Hartmann personal communication).

A possible explanation for the above contradiction may be found in an argument presented by Stebbins (1952). He hypothesized that dry and changing environments promote rapid evolution. The anomaly in this argument is that mesophytic communities are generally richer in species that are xeric ones. Stebbins (1952) argued that this was because the comparison of rich, mesic and poor, xeric communities was based on observations made at only one point in geological time, ie the present.

Though a xeric community may only support a few species at present or at any given time, it may have supported as many or more species than a mesic community over a longer period because of a greater turnover in species composition. What Stebbins has suggested is that in arid areas species turnover is faster than in mesic areas. Mesic communities on the other hand, because of their stability, may be rich due to the fact that they have accumulated species over a relatively long period. If species turnover is slow, very old and young (phyletically) species may coexist.

Observations from Mesic Mountain Fynbos (sensu Moll et al 1984a) and Karoo support Stebbins's (1952) argument. Mesic Mountain Fynbos communities have an extremely high number of species which include many old "Gondwanan" elements, whereas karoo communities generally have a lower number of species (recent evidence indicates that parts of the Karoo have high gama and possibly delta diversity) with many neoendemics. However, it is difficult to test the rate of species turnover in arid areas using fossil and palynological data since these areas do not generally accumulate suitably fossiliferous deposits. One can only test by inference from fossil sites bordering the arid areas or by phylogenetic analysis of present-day taxa. In testing such a hypothesis one also has to consider the palaeoclimatic changes, particularly the development of aridity in the Karoo.

Stebbins (1952) argued that there were three reasons why evolution could be expected to be relatively rapid in arid or semi-arid regions. These are all pertinent to the Karoo. Firstly, in areas where moisture is limited, local diversity in topography, soil, etc has a greater effect on the character and composition of the vegetation than in more mesic regions. The western portion of the Karoo, where species richness is the greatest, is extremely diverse environmentally. Secondly, semi-arid climates with regional diversity promote the division of large or medium sized populations into smaller units which although isolated from each other, may still interchange genes through occasional "migration", and establish populations that may give rise to new taxa. The presence of numerous taxonomic clines in karoo taxa, eg in *Haworthia* (B Bayer personal communication) supports this. Thirdly, in arid regions many different specialized structures (eg reduced leaf size, specialized leaf coverings, deciduous habit, swollen stems, geophily, etc) can evolve which may enable plants to withstand periods of severe drought. Such adaptational diversity (which many karoo plants exhibit) within a species would be particularly favourable for further divergent evolution.

Axelrod (1967, 1972) gave further evidence in support of Stebbins (1952) and extended the hypothesis by pointing out that it was not restricted to climatically arid regions, but also to dry edaphic sites which can occur in more mesic regions. Axelrod (1972) argued that these dry edaphic sites may have acted as local refugia for unique taxa adapted to drought, during periods of climatic amelioration. This formed the basis for Goldblatt's (1978) argument presented above.

Apart from in situ evolution, many karoo taxa have their origins elsewhere. The next two sections expand on the migrational origins of the karoo flora.

The arid disjunction: a possible explanation for the origin of certain karoo taxa

The recognition of distinct disjunct distribution patterns in certain taxa

(or closely related taxa) occurring in the Karoo-Namib Region and again in the arid areas of north-eastern Africa (Somalia, Ethiopia and Kenya) has provided insights into origins of the karoo flora. These disjunctions have received considerable attention in recent years and detailed surveys of the plant taxa involved have been presented by Verdcourt (1969), Monod (1971) and De Winter (1971). The subject has also been reviewed by Goldblatt (1978) and Werger (1978b).

De Winter (1971) recognized six categories of disjunctions which included families; genera and species limited to the southern and northern arid areas of Africa; species with vicariant subspecies or varieties in the southern and northern areas; and vicariant, closely related species with one confined to the northern and the other to the southern arid areas. Apart from these disjunctions there are also a number of taxa which show a contiguous distribution, but which are particularly strongly represented in both arid areas (Werger 1978a).

Initially, long-distance dispersal was used to explain these disjunctions. However, it has since been discovered that many species of arid regions are poorly dispersed (eg Ihlenfeldt 1971). A more likely explanation is that the present disjunctions are a relict situation of formerly continuous distributions (Balinsky 1962; Volk 1964; De Winter 1966, 1971; Monod 1971; Werger 1973b, 1980). It is postulated that in the past the two arid zones were connected on one or more occasions by an arid corridor stretching across Africa from Somalia via Kenya, Tanzania and Zambia to Botswana, Namibia and South Africa. Cooke's (1964) hypothetical vegetation map of Africa at 50 to 60% of the present rainfall, suggested such a possible corridor. Balinsky (1962) has shown that the north-eastern and south-western parts of Africa are at present still connected by a relatively arid tract in which the rainfall is less than 10 mm per month on average during at least three consecutive months per year. This arid tract coincides with the suggested arid corridor.

Opinions differ on how long ago the arid areas were continuous. Volk (1964) and Burtt (1971) suggested that it operated during the Tertiary. Other authors (eg Verdcourt 1969) suggest that it was more recent. The palaeoecological evidence indicates that the corridor probably existed many times with its most recent existence being during the last glacial maximum some 18 000 years BP (van Zinderen Bakker 1975, 1982).

Although it is now generally agreed that the disjunct pattern is a result of vicariance, dispersalism cannot be ruled out. Such an arid corridor could well have allowed the dispersal of northern tropical arid species southwards into the Karoo (or vice versa). These dispersal events could be the "waves of migration" referred to by Levyns (1964). The significance of the contribution of the arid disjunction to the karoo flora cannot be determined until a comprehensive taxonomic and evolutionary study of the karoo flora is done.

Karoo flora derived from fynbos

The relationships between the Cape (fynbos) and karoo floras have often been discussed and most authors (eg Levyns 1950, 1964) argue that the two floras do not merge to any extent. Acocks (1953), on the other hand, argued that the widespread and common nonsucculent shrub or "karoo bush" taxa are derived from the Cape rather than the tropical flora. Many common karoo genera (eg *Chrysocoma*, *Eriocephalus*, *Euryops*, *Hermannia*,

Lightfootia, *Pentzia*, *Phymaspermum*, *Pteronia*, *Selago* and *Walafrida)* are all well represented in the Cape Floristic Region and in fynbos in particular (Acocks 1953). Furthermore, many karoo species in the families Asteraceae, Scrophulariaceae and Selaginaceae have close fynbos relatives (Goldblatt 1978). Other taxa such as *Oxalis*, *Babiana*, *Gladiolus*, *Crassula* and *Pelargonium* all have marked centres of distribution within the winter rainfall region, straddling both the Karoo-Namib and Cape Regions.

It is generally accepted today that the climatic fluctuations of the Pleistocene resulted in the expansion and contraction of the limits of fynbos vegetation with concomittant contractions and expansions of the Karoo. This temporal and spatial interdigitation of the two floras would have promoted speciation within each of the floras and possibly given rise to new taxa in the reciprocal area. This hypothesis can only be tested by rigorous phylogenetic analysis. The results of which will clearly illustrate relationships, but causal factors will remain speculative. Evidence to date indicates that only a few Cape taxa (eg *Lobostemon glaucophyllus* and *Ferraria antherosa)* have their origins in the Karoo (Taylor 1978), whereas there are a number of studies indicating that many karoo taxa are derived from fynbos taxa. In the Poaceae, the genus *Ehrharta* is centred in the Cape Region, but a few species have spread into other phytochoria, particularly karoo phytochoria, where they have given rise to new species (Gibbs Russell and Robinson 1983). Primitive species of *Euryops* were widespread montane taxa (probably of a southern origin). Subsequent evolution gave rise to ecological types capable of inhabiting lower lying areas of fynbos and Karoo (Nordenstam 1969). In the Calendulae (Norlindh 1946) the primitive forms of *Dimorphotheca* in the Cape Region gave rise to the genera *Gibbaria*, *Castalis*, *Osteospermum* and derived *Dimorphotheca* species. The last-mentioned three groups are now widespread in the winter rainfall area of the Karoo. After rigorous phylogenetic analysis, Bremer (1978) adopts a combined vicariance and dispersal explanation for the distribution of *Leysera*. According to his model the ancestral species was widespread in the Cape and Karoo. The distribution of the putative ancestor was fragmented giving rise to the primitive *L langipes*, now confined to mountain fynbos in the south-western Cape, and a homogeneous perennial group. This group subsequently split to give rise to a perennial Cape renosterveld (more arid than fynbos) species and an annual karoo species which dispersed to North Africa via the arid corridor. The latter subsequently split into two sister species.

Unfortunately very few plant taxonomic studies have been based on phylogenetic systematics. This is largely because the initial construction of phylogenetic trees was based on unsound principles and shaky evidence (Bremer 1976). Today, however, the procedure is based on a firm theoretical ground which cannot be dismissed as phylogenetic speculation.

From the above examples it is relatively easy to infer adaptive advantages in sclerophyllous taxa, especially for both arid and infertile environments. Small (1973) has hypothesized that there should be a degree of overlap in the ecological amptitude of plants adapted to arid and infertile environments. In the context of Cape and karoo floras this hypothesis implies that certain fynbos taxa growing on nutrient deficient soils and which exhibit xeromorphic characters, could have given rise to karoo taxa. Cowling and Campbell (1983) rejected Small's (1973)

hypothesis for the Gamtoos region in the south-eastern Cape as there were no species common to both the xeric nonfynbos coenocline and fynbos ceonocline. Despite its tautological reasoning Small's (1973) hypothesis is still worth considering.

The fynbos islands on the tops of karoo mountains and the renosterveld shrublands on top of the escarpment, are generally used as evidence for the expansions and contractions of the Cape and karoo floras (Axelrod and Raven 1978; Werger 1983). These islands are considered to be relics which indicate the former extent of fynbos vegetation during colder and wetter periods. The evidence that these islands are relics is extremely tenuous and could just as easily be interpreted as expanding noda (R M Cowling personal communication). Similarly Brenan (1983) commenting on Werger's (1983) paper said that we are not always correct in using islands of vegetation outside their normal distribution areas as evidence of past climatic changes. Brenan (1983) argued that these islands could be features of an advancing vegetation type or alternatively they are indicators of an ecotone boundary.

A scenario of expanding sclerophyllous shrubland (due to climatic changes) and subsequent speciation in succulent shrubland is presented by Werger (1983). Werger argues that expanding sclerophyllous vegetation resulted in the isolation of succulent shrubs to a few favourable sites. Here, selection pressures on the small gene pools resulted in the parapatric evolution of distinct species in each or several of these islands. With the amelioration of the climates, the area suitable for these succulents increased and hence the distribution areas expanded. This scenario could explain the patchy and localized distribution patterns of closely-related, yet distinct, species of succulents in the Vanrhynsdorp and Little Karoo centres today (Hilton-Taylor personal observation).

A similar argument for speciation in eastern karoo succulents is proposed by Cowling (1985). Here it was postulated that variability in intensity and frequency of frost during the glacials resulted in the fragmentation of previously continuous populations. Because of short dispersal distances of most succulent taxa, vicariant speciation occurred.

It would seem therefore, that the karoo flora, particularly that of the western portions and higher lying areas, has a strong affinity to the Cape flora. Although this could be regarded as purely a winter rainfall adaptation, such affinities must be taken into consideration when examining the phytogeography of the region.

Evidence from palaeontological studies

In formulating biogeographical hypotheses on karoo vegetation history one needs to analyse the distribution, phylogeny and ecology (including ecophysiology) of the components of karoo contemporary vegetation. These hypotheses must then be tested, using independently derived geomorphological, climatic, palaeontological and palynological data (Cowling 1985). The fossil record may in fact be regarded as the "final arbiter" in these tests (Cowling 1985). Unfortunately the fossil record for the karoo since the late Tertiary is very poor. Hence it is necessary to draw on palaeontological evidence from a wider area to supplement the fossil record from the region.

Coetzee et al (1983) have thoroughly reviewed palynological studies and vegetation history of the fynbos. Much of the evidence presented can be used to extrapolate climatic conditions and vegetation history in the karoo. The section that follows summarizes the major fossil findings since the start of the Tertiary and the various interpretations of this evidence.

The beginning of the Tertiary was marked by widespread extinction of older Cretaceous elements and a modernization of floras on a world-wide scale (Coetzee 1983). The Paleogene, the first half of the Tertiary, saw the start of a trend towards cooler and drier climates (Deacon 1983a). Palynological evidence for the Paleogene is available from sedimentary infillings of Kimberlite pipes, particularly from the Arnot pipe at Banke in southern Bushmanland (Coetzee et al 1983; Scholtz 1985). Today this is an elevated plateau area lying between the winter rainfall region and the arid Kalahari.

The Arnot microflora appears to represent a dry "subtropical" forest flora. An interesting feature of the deposits is the presence of a number of fynbos elements, including Proteaceae, Ericaceae and Restionaceae (Scholtz 1985). These taxa may have formed an understorey in the forest. Axelrod and Raven (1978) interpret the evidence from this site as indicating that the temperate forest was depleted in the late Eocene and had an admixture of more xeric elements ancestral to those found in present fynbos communities. Tankard and Rogers (1978) have suggested a relatively dry climate and summer rainfall for this site some 40 My. However, Deacon (1983b) argues that it is premature to interpret the microflora in specific terms of past climatic and vegetation patterns without a more complete investigation.

The dry forests can be assumed to have persisted into the Miocene, at least along river courses, progressively giving way to more open woodland (Coetzee et al 1983). The early and mid-Miocene fauna in the Namib and along the Orange River indicate a woodland mosaic but with more open habitats developing (Corvinus and Hendey 1978; Deacon 1983b). The western interior of southern Africa has a long history of relative dryness, indicated not only in the Arnot microflora but also in the late Creataceous deposits in Botswana (Lancaster 1979). Axelrod and Raven (1978) have argued that the drier interior margins of the present-day fynbos region, would have been an important area for the distribution of sclerophyllous taxa, preadapted under seasonal climates and available to occupy the fynbos region when summer dry climates developed.

There are details of the Axelrod and Raven (1978) model, particularly the timing of events and the proposed large-scale displacement of vegetation, that can be questioned. There is little direct information on the vegetation of the present-day arid areas comprising the Karoo-Namib during the Miocene and Pliocene periods, thus making dating of events extremely difficult. Taylor (1978) commented that a vegetation category like fynbos which is associated with particular substrata, cannot be considered to migrate as a unit and that the response to climatic changes is towards adjustment in the range of some individual taxa and not mass migration (the term migration is generally used to describe the dispersal of a taxon following the disappearance of an ecological or physical barrier, not long-distance dispersal across barriers (Vrbra 1985)). An additional problem is that Axelrod and Raven (1978) equate the term fynbos with a

broader category of sclerophyllous vegetation than is currently used among local researchers (Deacon 1983b). The Arnot evidence, however, can be interpreted as supporting their general thesis of an early association of some taxa now prominent in the fynbos, with the drier karoo vegetation types. It is also possible that similar drier vegetation associations existed from an equally early time in, for example, areas affected by rain shadows within the present fynbos region. These may have persisted and today could constitute the elements found in the Little Karoo and Worcester-Robertson Karoo areas.

A major change in the vegetation is indicated from the end of the Miocene when the palynological evidence from sites in the fynbos area (Saldanha, Cape Flats and Wilderness) shows progressive impoverishment of the rain-forest vegetation and significant increases in pollen of typical Cape taxa (Coetzee et al 1983). The dating suggests that this evidence relates to the fragmentation of the distribution of rainforest and the spread of fynbos in response to changes towards cooler and summer-dry climates at the end of the Tertiary and in the Pleistocene. The Plio-Pleistocene period is poorly documented in the fossil record of the Karoo, but Tankard and Rogers (1978) assume progressive dessication with more xerophyllous vegetation replacing grassland (which had probably replaced the woodland by the early Pliocene) from the Pliocene into the Pleistocene.

The composition of the karoo shrubland communities was affected by the climatic pulses of the Plio-Pleistocene. However, their present status is a result not only of the effects of the climatic changes, but also of natural or man-made fires and other human activities, particularly the increase in agricultural utilization of the karoo. Today, because of the low productivity of karoo vegetation, the accumulation of combustible fuel is insufficient to support a fire. In high rainfall seasons productivity may exceed utilization and fires might occur. This is in fact what happened in 1975 when widespread fires were experienced in False Karoo areas where grass production had been high following several good rain seasons (Huntley 1984). These fires despite their infrequency today, were probably more frequent in the past and would undoubtedly have influenced the dynamics of karoo vegetation.

Acocks (1953) presented a model which documented and predicted recent and future changes in South African vegetation. One of his maps depicts the vegetation as he hypothesized it to have been at approximately 1400 AD. The differences between this map and the present veld types map illustrates the changes that have taken place with the introduction of agriculture and permanent settlement (see Roux and Theron this volume, for a description of the phases of desertification in the karoo as a result of overutilization and mismanagement). There is a long history of man's presence in the Karoo, unfortunately his effects on the environment have not been researched to the same extent as for the fynbos region (see Deacon 1983d). This is possibly due to the difficulty of finding archaeological traces because of the ephemeral nature of early settlements (Webley 1982). A recent paper by Sampson (1986), however, documents extensive settlement by early pastoralists (pretrekboer) of the Upper Sea-Cow Valley in the north-eastern Cape. The effects of these San camps are clearly visible in the landscape today as the archaeological residues of the camps are associated with vegetation patches characteristic of disturbed sites. One can only speculate as to what effect these settlements may have had on the karoo flora.

The late Pleistocene and Holocene cave sequences, excavated in the course of archaeological investigations, form the basis for our present knowledge on climatic and vegetation changes over the period coeval with the last interglacial, glacial and present interglacial. The arguments on the climatic changes and their effects are well documented in van Zinderen Bakker (1976, 1978, 1982, 1983); Deacon (1983a,b,c); Partridge (1985) and Vogel (1985). It was during this period that modern plant communities evolved.

The analysis of charcoals from a dated series of stratified hearths in the Boomplaas Cave (Deacon et al 1983) gives an indication of the succession of woody components in the vegetation of the Cango Valley over some 40 000 years. This to some extent is representative of changes in the vegetation on the margins of the Little Karoo. From the evidence obtained it was hypothesized that conditions during the last glacial maximum, in the Cape coastal region at least, were cold and dry (Deacon 1983c). There is a growing body of evidence in favour of this hypothesis (Deacon 1983a; Cowling 1985).

In contradiction to data from the southern Cape, a recent paper on freshwater shell deposits in the north-western Karoo, provides evidence for a widepsread cold, wet phase during the late Pleistocene (Kent and Gribnitz 1985). In their discussion on the causes, these authors accept the hypothesis of a northerly movement of the South Atlantic anticyclonic cell and possibly stronger westerlies. This hypothesis is the cause of much debate (Deacon 1983c; van Zinderen Bakker 1982). Unfortunately many fossil deposits have alternative interpretations which result in a great variety of palaeoclimatic reconstructions for southern Africa during the Quaternary.

From all these studies it is evident that it is not possible to generalize, not even about the late Pleistocene, because environmental oscillations were relatively rapid and conditions were more severe at some times than at others. The impact of these oscillations is not fully reflected in the palaeoecological record. What is certain though, is that the fossil evidence underscores the point that vegetation communities are not fixed but are dynamic associations of taxa changing through time. The consequence of which is that the distribution and composition of some modern communities was only established at the end of the Pleistocene and are in effect still transient.

OVERVIEW

The hypotheses concerning the origins of the karoo flora and the evidence obtained from palynological studies have highlighted the need to review the phytogeographic status of both the Cape Floristic Kingdom and Karoo-Namib Region, particularly that part receiving winter rainfall.

Bayer (1984) has argued convincingly that the Fynbos Biome (which is equated with the Cape Floristic Kingdom/Region) is not a valid biogeographical unit, and that a winter rainfall biome, incorporating karoo and fynbos communities, is more realistic. It is clear that there is a high degree of affinity between the karroid shrublands of the Western Cape Domain and the shrublands of the Cape Floristic Kingdom, particularly Renosterveld and Strandveld (Boucher and Moll 1981; Moll et al 1984a,b).

It is postulated that these shrublands have evolved from both Cape and Palaeotropical elements in response to the onset of summer drought and as such, are as much part of the Cape Floristic Kingdom as are the fynbos heathlands (Moll et al 1984c).

Some phylogenetic evidence was presented earlier in this review that certain karoo taxa are derived from fynbos taxa. It was also stated that many taxa have a marked winter rainfall distribution in both the Karoo-Namib and Cape Region. Similarly some taxa are clearly Karoo-Namib endemics while others are Cape endemics. Some of these distribution patterns are illustrated in Figure 4.4 to 4.9.

Sarcocaulon (Figure 4.4) is clearly a Karoo-Namib genus with its centre of diversity in the Richtersveld or Gariep Centre (Moffett 1978, 1979). *Muraltia* (Figure 4.5) is a Cape genus restricted to fynbos and with its centre of diversity in the Caledon area (Oliver et al 1983). Figure 4.6 shows the distribution of *Pelargonium* a fairly widespread genus but with 80% of the c 200 taxa restricted to the winter rainfall region, the area to the west of the 40% winter rainfall isohyet (stippled line). The main centre of diversity is in the Worcester area (van der Walt and Vorster 1983). Looking at the distribution of the subfamilies of the Poaceae (Figure 4.7) it is apparent that the Arundinoideae and Pooideae are almost entirely restricted to the winter rainfall region (see Gibbs Russell 1986 for a full explanation of this map). Figures 4.8 and 4.9 (from Nordenstam 1969) illustrate to some extent the dichotomy between Cape flora versus winter rainfall flora. Figure 4.8 shows that the genus *Aspalathus* is restricted to the Cape Region, with only a few species occurring outside the area of the map. The centre of diversity as with most pure fynbos taxa is in the south-west, in the Caledon area. *Eurypos*, however, is well represented within and without the Cape Region and is essentially a winter rainfall genus, extending well north of the area shown on the map (Figure 4.9). There are a number of centres of diversity, viz Worcester, Laingsburg area, Nieuweveld Mountains and the Sneeuberge. This is characteristic of many winter rainfall genera.

The analysis of floristic data from the region is still in a preliminary stage, hence no conclusions can yet be made regarding the validity of a winter rainfall region. It is interesting to note, though, that in the recent categorization of southern African biomes (Rutherford and Westfall 1986), the Karoo Biome (sensu Huntley 1984) is divided into two separate biomes. These are the Nama-Karoo Biome and the Succulent Karoo Biome. The latter biome is restricted to the "even winter and strong winter rainfall areas with greatest summer aridity in southern Africa" (Rutherford and Westfall 1986) ie the winter rainfall biome of Bayer (1984) excluding the fynbos.

To date, phytochorological units have not corresponded to biome units largely because phytochoria have been subjectively derived. Rutherford and Westfall (1986) argue that if phytochoria were classified according to rigorous phytosociological methodology with adequate sampling, then correspondence to biomes would be better. Preliminary indications from my analysis of floristic data confirms their argument.

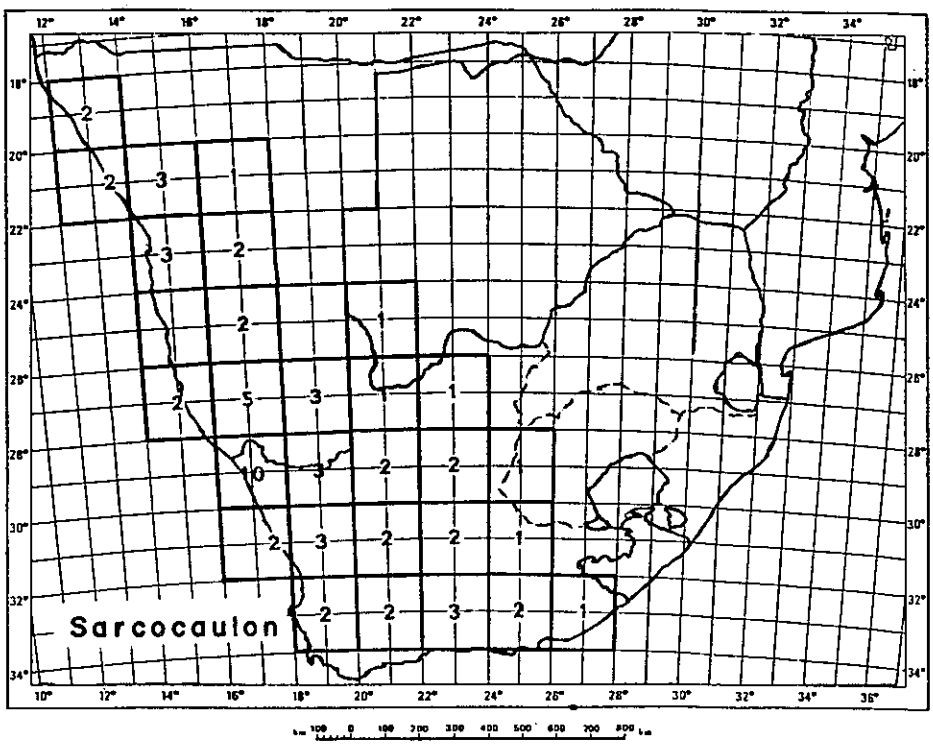

FIGURE 4.4 Distribution of *Sarcocaulon* with the number of species per two degree grid (from Moffett 1978).

FIGURE 4.5 Distribution of *Muraltia* with the number of species per quarter degree grid (from Oliver et al 1983).

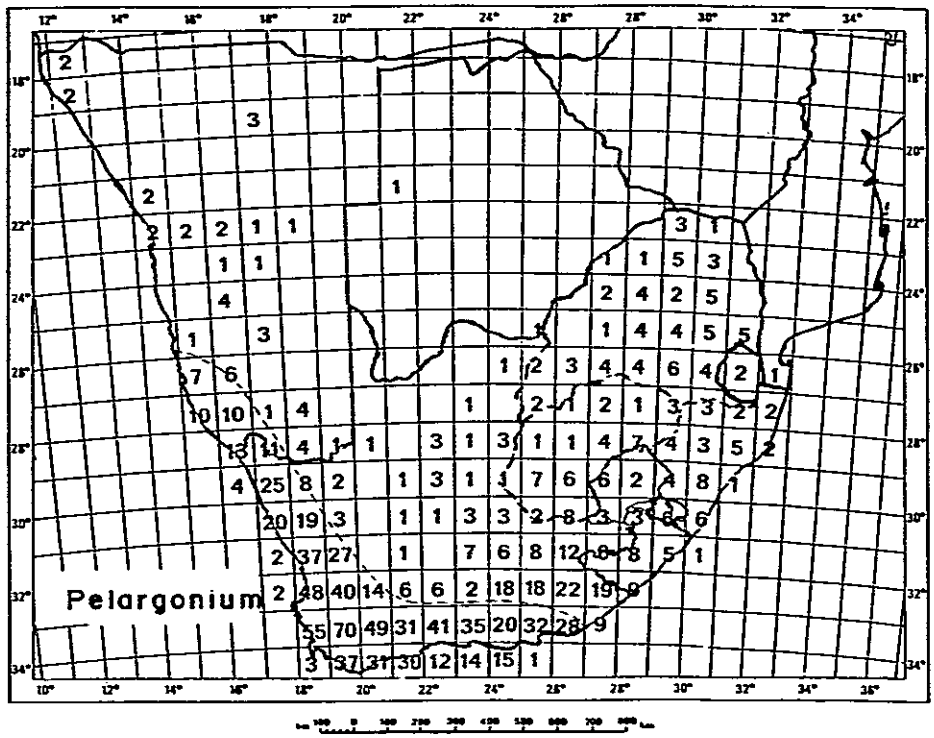

FIGURE 4.6 Distribution of *Pelargorium* with the number of species per degree grid (from van der Walt and Vorster 1983).

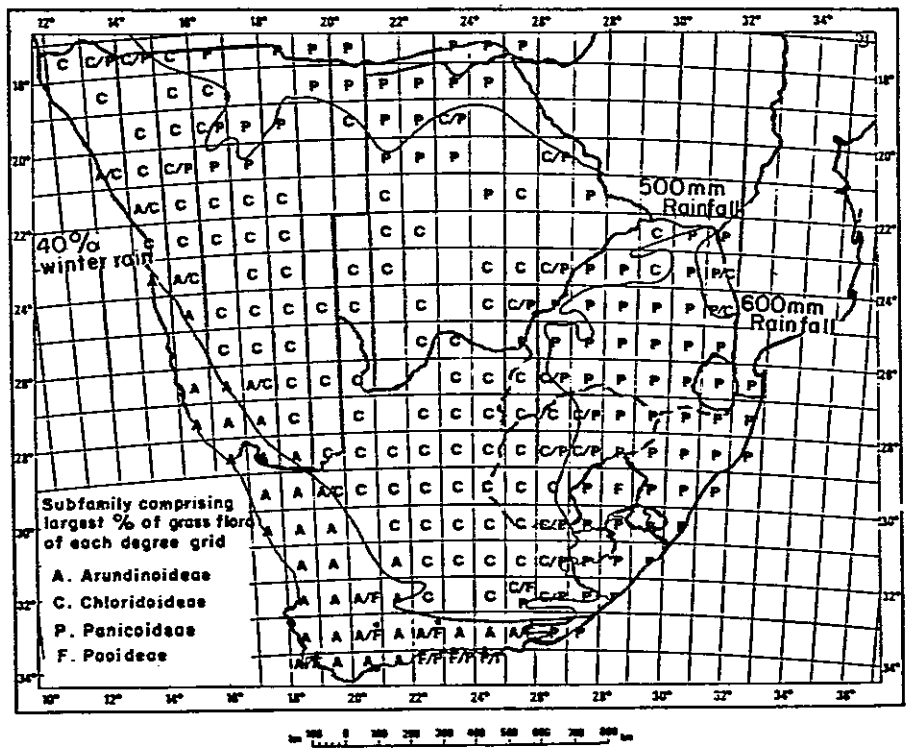

FIGURE 4.7 Distribution of Poaceae subfamilies, with the subfamily comprising the largest percentage of the grass flora of each degree grid indicated (from Gibbs Russell 1986).

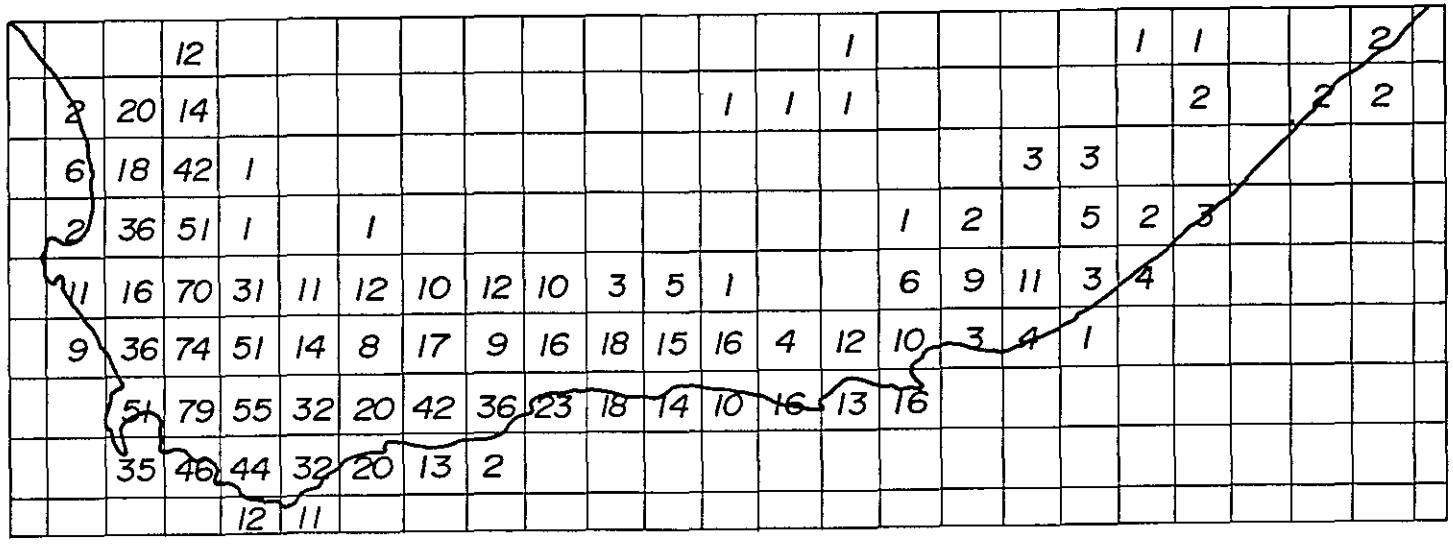

FIGURE 4.8 Distribution of *Aspalathus* with the number of species per quarter degree grid (from Nordenstam 1969).

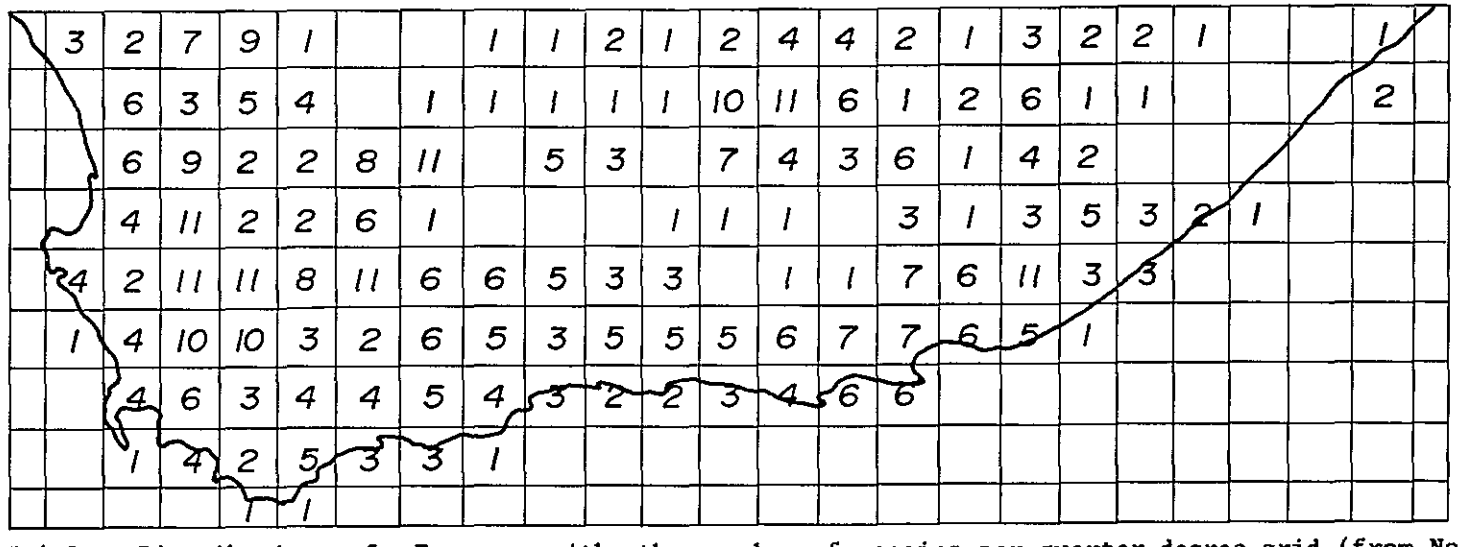

FIGURE 4.9 Distribution of *Euryops* with the number of species per quarter degree grid (from Nordenstam 1969).

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CHAPTER 5 LATE CENOZOIC PALAEOECOLOGY

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INTRODUCTION

Palaeoecological studies provide an insight into past environmental change and as such provide the background for present day changes in environments and vegetation. An understanding of late Cenozoic palaeoecology in the Karoo is especially significant since it should resolve the controversy regarding recent vegetation changes in the area.

THE TERTIARY

Very little is known about the Cenozoic environmental history of the Karoo. Nevertheless this region has experienced important changes since during the Late Tertiary when it was about 15° further north than at present (Smith et al 1981). At this time northern Africa was strongly influenced by the warm Tethys Sea and was covered with tropical rainforest while southern Africa received much moisture from the southern westerlies and was clothed by subtropical rainforest (Axelrod and Raven 1978). The karoo region gradually became more isolated as a consequence of epeirogenic uplifts of the subcontinent in Cenozoic times. The consequence of this process was that the climate of the Karoo gradually became more continental with warmer summers, colder winters and less precipitation. The Cape folded mountains along the southern boundary and the escarpment along the eastern side, shield the basin effectively from the influence of the equable maritime climate. At present, cyclonic winter rain cannot enter the basin to any great extent, while summer rain only penetrates so far south on rare occasions (Schulze 1965). The mean annual temperature ranges from 12 to 16°C (Schulze and McGee 1978), while the temperature can drop below zero on 90 to 150 days per annum (Schulze 1965).

Another very important factor affecting the palaeoenvironment of the Karoo was the gradual decrease in global temperature during late Cenozoic times, which has been illustrated by the oxygen isotope curve of the Southern Ocean (Shackleton and Kennett 1975a).

A reconstruction of the vegetation and palaeoenvironments of the late Cretaceous and early Tertiary has been made on the basis of a palynoflora from kimberlite pipes in the north-western karoo (Coetzee et al 1983; Scholze 1985). Here it has been suggested (Scholze 1985) that the angiosperm palynomorphs are indicative of a climate somewhat drier and probably cooler than tropical rainforest regions to the north and that this shift in climatic conditions took place early in the Palaeocene. An open-canopied drier type of largely deciduous forest existed in the region, probably with an understorey of Proteaceae, Restionaceae and Ericaceae - the precursors of the present-day fynbos flora.

Aridification continued in the Karoo through Oligocene-Miocene times and the dry woodland opened up to be replaced by thorn scrub and savanna woodland, with some sclerophyll vegetation still present (Axelrod and

Raven 1978). In the southern coastal region subtropical rainforest gave way to subtropical laurel forest. A considerable drop in global temperature in Oligocene times would have accelerated this aridification.

In the late Miocene-early Pliocene, conditions were aggravated further as the Antarctic ice sheet reached its maximum volume (Shackleton and Kennett 1975b) and the Benguela current and its upwelling lowered the temperature along the west coast (Siesser 1978). The South Atlantic anticyclone strengthened, and aridity spread further inland from the west. This was the time that the mediterranean type of climate was evolving at the south-western Cape, and the sclerophyll fynbos vegetation replaced the last tropical-subtropical forest elements in the coastal region (Coetzee 1978, 1980).

The karoo vegetation must have evolved from the preceding vegetation of scrub and savanna-woodlands, while many elements indicate a relationship with the fynbos (Hilton-Taylor this volume). The adaptation to dry conditions has been a long process which, according to Axelrod and Raven (1978), goes back to early Miocene times.

THE LATE QUATERNARY

In late Pleistocene times, glacial-interglacial cycles intensified selection for adaptations to aridity and enhanced speciation as the glacial periods were increasingly more arid. During the last glacial maximum, the atmospheric circulation was accelerated by some 17% (Newell et al 1981). This in turn caused a more energetic oceanic circulation with the result that along the west coast the Benguela current and its accompanying upwelling lowered the temperature of the ocean water two to five degrees centigrade (Morley and Hays 1979). The Agulhas current was also colder and a negative temperature anomaly of more than four degrees centigrade occurred along the south coast (CLIMAP members 1976). Periglacial phenomena in the high Drakensberg and on screes and in caves along the south coast indicate decreases in temperature of at least five degrees centigrade during the last glacial maximum. With recent isotopic palaeotemperture determinations of underground water, and a stalagmite by Vogel (1983), the decrease in temperature has been assessed to have been in the order of five to 5,5°C.

Pollen analysis

As a consequence of climatic variations which occurred in late Quaternary times, the area covered by karoo vegetation types must have changed. The dating of these events is important for our understanding of the evolution of karroid environments. Pollen analysis can perhaps give a clue to these changes. In semi-arid regions like the Karoo it is very difficult to find pollen-bearing deposits and dateable material, as pollen is destroyed by oxidation in sediments which are exposed to long dry periods. Some information is available along the northern margin of the present Karoo region where fossil pollen has been preserved under fairly humid conditions around some old thermal mound springs and in ancient lake basins and caves.

Around the thermal springs of Florisbad (28°42'S), 45 km north-west of Bloemfontein, alternating layers of clay, loam and sand which contain

countable numbers of pollen grains, have been accumulated. Four "peaty" horizons consist of carbonaceous clay and sand, rich in organic matter. Former palynological studies of these deposits (van Zinderen Bakker 1957) resulted in a palaeoclimatic interpretation which is no longer valid. Recent pollen analytical results indicate considerable changes in humidity. Lack of aboslute dating of this sequence of some 200 000 years old has so far delayed the publication of the modified interpretation.

It can be postulated that during the last glacial maximum there was greater humidity as a consequence of lower evaporation, and some invasion of winter rain encouraged the spread of grassveld so that the region of the karoo diminished. Processes of this nature have been observed at Aliwal North (30°39'S) where peaty deposits with a depth of 10,5 m occur around hot water medicinal springs. The cores studied by Coetzee (1967) have been dated with six radiocarbon determinations and range in age from 12 600 ±110 BP (GrN 4011) to 9 650 ±150 BP (GrN 4012). Aliwal North is at present situated in a summer rainfall area near the vegetational ecotone between grassveld to the north and east of it and semi-arid karoo to the south and west. The pollen analysis results from this site were compared with surveys of atmospheric pollen carried out at Bloemfontein situated in the dry Cymbopogon Themeda veld north-west of Aliwal North, and at Middelburg in the False Upper Karoo south-west of the site.

The pollen spectra of these plant communities can be well distinguished. They consist of nonarboreal pollen in which Poaceae, Chenopodiaceae and Asteraceae dominated. As these springs are not classified as saline, fossil pollen of Chenopodiaceae can be considered to indicate dry climatic conditions rather than the brackish conditions of the swamp round the springs. From values of this pollen exceeding 10%, combined with high percentages of Asteraceae, very dry and warm karroid conditions at Aliwal North can be inferred. High peaks of the Poaceae pollen curve indicate more humid grassveld conditions. Using these criteria, several north-eastward advances and south-westward retreats of the Karoo region could be indentified within the time span of 12 600 to 9 650 BP. Near 12 600 ±110 BP, pollen spectra represent grassveld and cooler conditions, which are especially indicated by the presence of nine per cent pollen of *Stoebe plumosa*, a plant which belongs to the lower part of the Austro-Afro-alpine Belt. The pollen spectra of the upper levels of the deposits are representative of a very dry and warm climate and have an age of 9 650 ±150 BP.

The climatic data inferred from the pollen evidence from Aliwal North can be extended by comparing the final pollen zone with the results of the valuable study by Deacon (1974). She compared the distribution in time and space of 223 dated archaeological sites, covering the Wilton and Smithfield cultures. The results of this investigation show that no dates exist for occupation sites from the inland plateau for the period between 9 500 and 4 600 BP, while sites along the coast and in the lower mountainous areas were occupied for long periods of time without this hiatus. Deacon (1974) suggests that the aridity could have made the inland plateau less attractive for hunter-gatherers. The mountain and coastal sites offered a much wider environmental variety especially when they were occupied seasonally. The Aliwal pollen diagrams (Coetzee 1967) indicate that at about 9 650 BP dry grassveld which surrounded the spring was replaced by dry karroid vegetation. It is interesting to note that Meadows and Hall (unpublished) found stratigraphical evidence in a variety

of vlei sediments in southern Africa for drier conditions from about 8 000 to 4 000 BP.

More pollen evidence is available from the Orange Free State, north of the present Karoo. In the Kalahari Thornveld of the Alexandersfontein basin (28°52'S), Scott (1975) found proof for karroid vegetation sometime during the second half of the Holocene. The evaluation of pollen spectra at such sites is difficult, however, as Chenopodiaceae here could testify to halophytic vegetation, while the Compositae pollen found is not of the usual type for the area and is poorly represented.

At the Voightspost site between Bloemfontein and Kimberley (29°10'S), Horowitz et al (1978) showed that Smithfield people lived in a dry climate with karroid vegetation around 1 220 BP. The occurrence of sand of aeolian origin supports the pollen evidence based on a spectrum of only 100 sporomorpha. The vegetation was later replaced by the present grassveld.

These data show that not much is known about the environmental changes which occurred in Holocene times. The Karoo must have expanded and retreated on many occasions. Much more research is needed especially along the borders of the Karoo to unravel the vicissitudes of climate and vegetation of this region.

CONCLUSIONS AND RECOMMENDATIONS FOR FURTHER RESEARCH

- It is of great importance for our understanding of the evolution of climate and vegetation of the Karoo that new sites for pollen studies are found. In this generally dry region the best results can be expected from: deposits round old springs; deposits in caves; old deposits of manure (eg from hyrax); sites on high mountains. In this respect pollen analysis of vlei sediments in the Winterberg Mountains is already underway (Meadows and Meadows 1985).

- Future analyses and dating of the Florisbad sequence may elucidate the climatic history along the northern boundary of the Karoo.

- The assessment of the present pollen deposition in different parts of the Karoo will be essential for the explanation of fossil pollen spectra.

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CHAPTER 6 PALAEONTOLOGY

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INTRODUCTION

The rocks occurring in the karoo biome contain a wealth of fossils ranging in age from Mid-Precambrian to Holocene. Although the Precambrian record is incomplete and fragmentary, it is fortunate that the Cape and Karoo beds, which jointly account for the greatest surface area of the biome, provide an almost continuous record of sedimentation and evolution of life from the Ordovician to the Triassic.

Space constraints prevent us from referring to the unfossiliferous rocks as well as the major breaks in the sedimentary and fossil record. The fossil record of the biome is summarized in Figure 7.1 (see back cover) which includes a list of the major geological events which helped to shape southern Africa.

This chapter should be read in conjunction with the geological description of the karoo biome (Visser 1986).

SODIUM GROUP

Precambrian rocks are usually devoid of fossils. However, blue-green algae living in favourable sedimentological environments left traces in the form of easily recognizable hemispherical bodies in cherty limestones. These so-called "stromatolites" were formed by the trapping of fine sediments by sticky algal mats.

The upper beds of the Sodium Group exposed in the T'Kuip Hills north of Britstown, contain stromatolite-bearing limestones interbedded with coarse clastics and lavas (Grobler and Emslie 1976). Different types of stromatolites formed in small isolated basins in a shallow environment. Variations in type of stromatolite indicate a response to shifting environments.

At times a sudden influx of clastic sediments caused burial and extinction of the algae which subsequently reinvaded the area as soon as conditions became more stable and favourable again.

GRIQUALAND WEST SEQUENCE

Rocks deposited in the south-western portion of a once vast epeiric sea, occur in the Prieska-Griquatown area. Dolomite, limestone, chert and shale of the Ghaap Plateau Dolomite Formation accumulated on the platform portion of the basin. The climate was arid to semi-arid with a low percentage of oxygen in the atmosphere (Tankard et al 1982). A large and varied assemblage of stromatolites, together with other sedimentological

features, indicate deposition in a tidal and subtidal marine environment (Truswell and Eriksson 1973). Although the blue-green algae inhabited all the shallow marine ecological niches, the different types of stromatolites are nevertheless restricted to well-defined sedimentary environments which, through time, shifted in response to tectonic activity.

NAMA GROUP

The Nama beds deposited in a shallow epicontinental basin, provide the first evidence from southern Africa for the sudden expansion of metazoans during the Late Precambrian. Rocks from just beyond the north-western limit of the area contain impressions of invertebrate animals related to the rare but world-wide Ediacara Fauna (Germs 1972) of Late Precambrian age. North of Vanrhynsdorp the uppermost unit of the group, the Fish River Subgroup, contains a sparser fauna. *Phycodes pedum*, an Early Cambrian trace fossil (Germs 1974), as well as indistinct trails, left by as yet unidentified invertebrates, have been found. The upper Nama beds thus span the palaeontologically important Precambrian-Phanerozoic boundary.

CAPE SUPERGROUP

During the Early Palaeozoic, continuous sedimentation took place over a long geological time span in the relatively stable area of Gondwana which today comprises all the southern continents plus India. As can be expected, similar stratigraphic successions containing similar fossil assemblages are now found in South Africa, South America, the Falkland Islands and Antarctica; all fragments of the old supercontinent. Sedimentary environments, ranging from continental to near-shore and shallow marine, shifted in space and time and the resulting assemblages of body and trace fossils reflect the varying environmental and climatic conditions.

Table Mountain Group

When compared with the overlying Bokkeveld and Witteberg Groups, the thick succession of mainly sandstones deposited on a stable shelf is relatively unfossiliferous.

In the Graafwater area, tidal deposits near the base of the group (Tankard et al 1982) contain a trace fossil assemblage indicative of shallow water and even subaerial conditions. Invertebrate burrows and trackways left by trilobites and other arthropods have been identified (Rust 1967; Anderson 1975).

Localities yielding marine fossils occur just outside the geographical area of the karoo biome but they are briefly described here because of their scientific importance. A restricted benthonic assemblage contains: bryozoa; inarticulate and articulate brachiopods and crinoids; all attached epifaunal filter-feeders. One mobile scavenger, a homalonotid trilobite, and a few chinitozoans have also been identified (Cocks et al 1969; Cramer et al 1974).

The clean sandstones constituting the bulk of the Table Mountain Group

were deposited in an intertidal to shallow subtidal environment and are, as can be expected, almost barren except for an occasional *Skolithos* burrow, a trace fossil of an invertebrate filter-feeder.

Bokkeveld Group

The mudstones, shales and sandstones of the Bokkeveld Group represent deltaic to marine sedimentation on a tectonically unstable shelf (Theron 1972; Tankard et al 1982). The continuous landward and seaward shifting of the coastline resulted in a stacking of sediments deposited in environments ranging from shoreline to shallow and even deeper marine. Moreover, owing to continuous regression during Bokkeveld times, the marine beds at the base of the group grade upwards into deltaic and continental beds.

The marine fossils from the lower beds indicate that the geographical area of deposition of the Bokkeveld was part of the Austral or Malvinokaffric Faunal Province which included South America, the Falkland Islands and Antarctica during the Emsian Age of the Early Devonian Period (House 1971; Johnson and Boucot 1973). Whereas the Early Silurian Malvinokaffric fauna of the Table Mountain Group was very restricted both geographically and in diversity, the Emsian faunal assemblage of the Bokkeveld was larger and more widely distributed. Brachiopods and pelecypods are common, with trilobites, gastropods, echinoderms, cephalopods and coelenterates also present.

The fairly large number of invertebrates recorded (Du Toit 1954; Theron 1972) tends to mask the true nature of the assemblage, but a comparison with the Old World Provinces proved that the Bokkeveld Malvinokaffric assemblage is a cold water one with low diversity, especially amongst the brachiopods and trilobites. This restricted nature is also shown by the notable rarity of corals, cephalopods and bryozoans (House 1971; Johnson and Boucot 1973).

Although a study of the palaeoecology of the Bokkeveld has been neglected, it is possible to broadly reconstruct faunal communities. A near-shore benthonic community was dominated by scavenging trilobites and infaunal filter-feeders such as pelecypods and inarticulate brachiopods. Towards deeper water the assemblage changed, with epifaunal filter-feeders becoming dominant. Trace fossils in the form of burrows and tracks are more apparent in the sandy and silty rocks deposited closer to the palaeoshoreline. Burrows inhabited by infaunal filter-feeders occur in the sandstones while finer sediments deposited in deeper water contain a wide assemblage of tracks left by sediment-feeders and scavengers.

Isolated spines of primitive fishes found in the basal unit of the group at the Gamka Dam mark the first appearance of vertebrates in the fossil record of southern Africa. Of more importance are fossils discovered in upper Bokkeveld beds near Barrydale. This remarkable fish-and-plant assemblage indicates fresh water conditions probably in a deltaic environment. The arthrodire placoderms, acanthodian spines and lycopods described by Chaloner et al (1980) have affinities with similar assemblages from Antarctica, Australia and Europe.

The western shallow water deposits of the Bokkeveld contain lycopod stems. Psilopsids are of minor importance.

Witteberg Group

The Witteberg sequence represents a transition from shallow marine to shoreline to continental beds deposited on a stable shelf during the Late Devonian and Early Carboniferous Periods.

The lower predominantly argillaceous units with interbedded sandstones contain a wealth of trace fossils ranging from *Skolithos* tubes in the sandstones to various types of traces left by infaunal and epifaunal sediment-feeders and a few filter-feeders. The most common trace fossil is *Spirophyton* found in shallow offshore environments. Outcrops in the Touws River-Ladismith area have yielded rare examples of inarticulate and articulate brachiopods and also pelecypods (Hiller and Dunlevey 1978). The inarticulate brachiopod *Lingula* and stunted articulate brachiopods, indicate a near-shore environment with below normal salinity.

Rare fragments of a eurypterid and a few valves of *Palaeestheria* were found in black shales in the eastern outcrop areas (Rennie 1934).

Stems and other fragments of lycopods, sphenopsids and psilopsids also occur (Plumstead 1969). The resistant quartzite beds from the middle division as seen on the southern and western borders of the Karoo contain scattered lycopod stems.

The upper formations mark the transition of freshwater terrestrial environments with a typical fish-and-plant assemblage. Large numbers of a few fossil species comprising lycopods, sphenopsids and other as yet unidentified plants are found together with fishes in concretions and channel deposits. Several palaeoniscid fishes have been identified (Gardiner 1969; Jubb and Gardiner 1975). Acanthodian spines are common in some beds. The latest find is a giant eurypterid.

These fossiliferous beds of the upper Witteberg which have been dated as of Viséan Age (Early Carboniferous), present the highest stratigraphic unit for which a reasonably accurate geological age could be determined.

The Cape-Karoo contact represents a gap in the geological record. This gap in the fossil record is magnified by the overlying unfossiliferous tillite beds which were deposited under harsh glacial conditions.

KAROO SEQUENCE

Dwyka Formation

Through the Mid and Late Carboniferous, Gondwana drifted into the polar region and a period of glaciation followed. A considerable hiatus, represented by a paraconformity between the glacial sediments (tillites and diamictites) and the underlying Witteberg, probably spans much of the Carboniferous (Dunlevey and Hiller 1979). The period of glaciation naturally influenced the biota of western and central Gondwana extensively with the result that the Dwyka sediments are almost devoid of fossils of this period. Sparse plant remains within the tillite (Plumstead 1969) and miospores and cuticular material from interglacial shales (McLachlan and Anderson 1973), however, indicate that the basin and surrounding highlands were not uniformly glaciated. Unglaciated areas supported vegetation.

An exciting aspect of the palaeontology of the Dwyka Formation is the discovery of a fossil fauna of Cambrian age in light grey limestone erratics. The fauna consists mostly of archaeocyathids which show a remarkable similarity at the species level with forms of Antarctica (Oosthuizen 1981). Trilobites, oncolytes and stromatolites are also present. Although these equatorial forms have no bearing on the palaeoecological reconstruction of the Dwyka, they are of extreme importance as it is the only material known to date that was derived from another continent. The distribution of the fossiliferous erratics may hold the key to locating the point of entrance of the glaciers that transported the material onto the African continent. Such information may prove invaluable in fitting the Gondwana continents. A detailed study of the distribution of the fossiliferous erratics should therefore be undertaken. To date, their distribution has been documented from north of Gamka Dam to Leeukloof in the Willowmore district in the east (Oosthuizen 1981).

As the proto-Karoo area drifted out of polar latitudes a general northward retreat of the ice followed. In the wake of the retreating ice a marine transgression ensued, and with it came a marine fauna that colonized the generally shallow epicontinental embayments. The depression of the crust below sea level was caused partly by ice loading, but an orogenesis migrating towards the Karoo basin from the south and south-east probably added to the effect of the ice by downwarping the crust in front of it.

Fossils of this cold water fauna are found in the mudstones that overlie the tillites in the western, southern and eastern parts of the basin. The presence of this marine "Eurydesma fauna" (consisting of various molluscs, brachiopods, radiolarians, echinoids, asteroids, crinoids, crustaceans and foraminifers) has long been known from the Kalahari-Karoo basin and southern Namibia. This marine horizon has now, however, been traced all over the Kalahari-Karoo basin and was recently also discovered in Natal by E van Dyk (personal communication).

The horizon in Natal, in line with the diachronous tillite-Prince Albert contact, lies in the uppermost tillite itself in contrast to its position above the tillite in the south and west. The position of the marine fauna in the Dwyka formation in Namibia likewise reflects the diachronosity of the tillite-Prince Albert contact.

In the southern and eastern Karoo the fossiliferous horizon lies a few centimetres above the tillite in nodules of radiolarian tests. These nodules yielded abundant driftwood fragments, coprolites of which some are spiral, fish scales and possible placoderm head shields.

In the radiolarian nodules a three-dimensionally preserved shark neurocranium was found by R D F Oosthuizen on his farm Zwartskraal in the district of Prince Albert. The skull is unusual in that it has the nasal capsules preserved in toto (Zangerl 1981).

It is of interest to note that a similar fossiliferous marine horizon is known from the Paraná basin in Uruguay in a similar stratigraphic position in relation to the tillites (Beltan 1978).

Ecca Group

Water depth in the Karoo basin which underlies the karoo biome was greater than that in the Namibian or Paraná basins. Whereas deep water continental shelf-type phosphatic sediments accumulated towards the south-east, shallow water sediments were deposited elsewhere as the Nossob and Aub sandstones in the Kalahari-Karoo basin and as the Palermo Formation in the Paraná basin. These sandstone formations are highly bioturbated, and abundant trace fossils of the shallow water, tidal flat ichnofacies occur in them.

The downwarping in the southern and western part of the Great Karoo basin did not influence the Paraná or more northerly basins in the Kalahari and Namibia. Sedimentologically the central Paraná basin and Kalahari basin therefore resemble each other more closely than they resemble the Great Karoo basin in the west and south.

When the Prince Albert Formation was deposited, the climate ameliorated to such an extent that heavily forested areas developed in the coastal regions that fringed the embayments. Evidence of such aforestation is presented by the abundance of silicified tree trunks in the near coastal sediments eg the Douglas-Blaauwkrantz area near Kimberley.

Overlying the Prince Albert Shale Formation is a thin but widespread, white weathering black shale, the "White Band" or Whitehill Formation. The black shales of this formation accumulated in shallow marine embayments and it is postulated that the Whitehill and the almost identical Iraty Formation of the Paraná basin were deposited in shallow contemporaneous embayments of a central sea arm that occupied a position between the continents of Africa and South America. The water bodies were stratified with anoxic, toxic bottom brines that prevented the establishment of a benthonic fauna. A study of the biozonation of the formation has shown it to be an isochronous unit (Oelofsen 1981), perhaps the only one in the Karoo basin (Visser 1982). The biostratigraphy of the Iraty and Whitehill formations shows a remarkable correspondence, stressing the fact that the two formations are contemporaneous. The problem arises that, whereas the Whitehill was traditionally regarded as being of Early Permian age, palynological data and datings on insect wings from the Iraty indicate a Mid Late Permian (Kazanian) age for the latter formation.

Because of the poor conditions of the bottom waters in the Whitehill and Iraty embayments only pelagic forms populated the waters. In the Whitehill at least two genera of the free swimming, filter-feeding, anapsid reptile family, the Mesosauridae occur. On osteological evidence the mesosaurids from the Whitehill and the Iraty seem to be identical at species level. Several species of paleoniscid fish (of which only one has been described by Broom, *Palaeoniscus capensis);* at least two species of crustaceans *Notocaris tapscotti* Broom and a form that resembles the South American *Clarckekaris* (Oelofsen and Araujo 1983); insect wings; a fossil cephalochordate; and rare fragments of plant material are known from the shales.

The outlier of Whitehill near Worcester and south of the Worcester fault scarp, which is identical in biozonation to the rest of the basin, is proof of this. The fauna that populated the basin could migrate unhindered at least as far south as this outlier.

Shortly after deposition of the Whitehill Formation the southern shores of the basin were elevated, and main sediment transport directions that were mainly from the north and north-west since the Eocambrian, changed to south and south-east. The elevation (orogeny) probably finally severed the contact the basin had with the world oceans.

From the elevated areas towards the south, rivers drained northwards into the inland basin and eventually built the deltas of the Waterford Formation, creating dry land habitable for a terrestrial fauna. The uppermost unit of the Waterford Formation in the west has been interpreted as a low sinuosity fluvial channel facies (Turner 1978). In overbank times *Shizoneura* was found in growth positions and glossopteris leaf fragments are preserved. In the Worcester outlier, glossopteris fragments appear lower down in the stratigraphy in a position probably comparable to the Pietermaritzburg Formation of Natal. The large leaves indicate a temperate climate (E Kovács-Endrödy personal communication) and apart from perhaps severe winters, very little of the harsh climate of the Dwyka glaciation remained.

Dry land on the deltas and suitable climate paved the way for the first wave of terrestrial reptiles that migrated into the basin. Fossils of these first terrestrial inhabitants in the Waterford Formation have been reported from near Zeekoegat (Rubidge and Oelofsen 1981). The Ecca reptile fauna occurs almost 800 m below the first purple mudstones of the traditional *Tapinocephalus* zone (Dinocephalian/*Pristerognathus-Diicitodon* assemblage zone of Keyser and Smith 1978). This fauna is consequently much older than the *Tapinocephalus* fauna and may help to bridge the gap between the latter fauna and older faunas elsewhere (eg the Russian zone I and II faunas).

The Ecca reptile fauna is characterized by the small herbivorous *Eodicynodon*. *Eodicynodon*, although being a dicynodont (Barry 1970), has some very primitive features. In some respects it differs from all other later dicynodonts. Recently a large dinocephalian and some small forms tentatively identified as primitive Therocephalians by J A van den Heever were discovered by Rubidge. Whereas the Ecca has for a long time been regarded as unfossiliferous it now seems to contain a complete pre-*Tapinocephalus* zone fauna which will require thorough study in years to come.

In contrast to the relatively strong orogenetic source area that was active to the south and south-east of the basin, the northern shores were fringed by what is today a buried palaeolandscape that lay between the highland area of Precambrian rocks in the north and a low undulating plain to the south. This southern shelf according to Tankard et al (1982) provided the relatively stable, but gently subsiding platform for prograding delta systems which eventually covered the glacial outwash fans, peat bogs and periglacial lakes of the deglaciated basin margin. Apart from trace fossils like *Arenicolites*, *Rhizocorallium* and *Diplocraterion* and an abundance of plant and insect remains, the northernly Ecca has yielded no fossils.

Beaufort Group

The boundary of the Beaufort Group with the underlying Ecca is arbitrary and diachronous and according to Tankard et al (1982), most logically

taken at the base of the lowermost regressive sandstone which corresponds more or less to the base of the Waterford Formation. Another criterion which has been used, the presence of abundant reptilian remains (*Tapinocephalus* zone fauna), has also become redundant by the discovery of the Waterford fauna. The Ecca-Beaufort contact is at best difficult to define for it represents a gradual change from delta top distributionary channel system or prodelta slope to a meandering river pattern with flanking flood plains (Keyser and Smith 1978).

In 1854 Bain first drew attention to the reptilian fauna that inhabited the basin. The fossils of the Beaufort Group today represent one of the most complete and best preserved assemblages of terrestrial fossil vertebrates known (Keyser and Smith 1978). The fauna is of prime importance in understanding the evolutionary transition from reptile to mammal.

Early efforts to make stratigraphic sense out of the Beaufort sequence resulted in what became known as the Lower, Middle and Upper Beaufort stages which were based on lithological and palaeontological criteria. In recent years lithostratigraphic and biostratigraphic divisions were separated and efforts have been made to establish more precisely delineated biozones. Keyser and Smith (1978) give an historic review of the development of the Beaufort biostratigraphy and add their own detailed system. Although being the most modern, the zonation of the latter authors is not universally preferred (cf van den Heever and Hopson 1982). The six-fold zonation of Broom (1909) and its modification by Kitching (1977) led to the widely used *Tapinocephalus*, *Cistecephalus*, *Daptocephalus* and *Lystrosaurus*, *and Cynognathus* zones still in use (Cluver 1979). Tankard et al (1982) give a synoptic overview of the way in which the old and new (Keyser and Smith 1978) systems integrate, but it is clear that the last word on the biozonation of the Karoo has not been written. The mere discovery of the Ecca fauna in the Waterford Formation calls for a reconsideration of the present system.

Bio- and chronostratigraphic units differ basically, and nowhere is this better illustrated than in the Beaufort Group where it is not possible to eliminate the effect of preference the reptiles had for particular environments that shifted and migrated with time, more or less independently of sedimentological controls.

Through the work of various researchers over the years (Keyser 1966; Turner 1978, 1979; Smith 1978, 1979), a picture of the palaeoenvironment in lower Beaufort times has emerged. Close scrutiny of aerial photographs has revealed exhumed palaeolandscapes with sinuous channels, point bars with accretionary scroll bars, flood plains and crevasse splays. The different subenvironments each contain their own characteristic suite of vertebrate remains. Levée deposits for example, are distinguished by interlaminated mud and siltstones with desiccation cracks, raindrop marks, leaf remains and calcareous nodules from palaeocalcrete horizons. The presence of desert rose pseudomorphs and evidence of seasonal flash floods indicate semi-arid to arid conditions. Stunted vegetation confined to the banks of the main channels provided a habitat for most terrestrial forms while the probably perennial streams and pools housed aquatic and amphibious forms.

From an important study by Smith (1978, 1979), it became clear that skulls

and mandibles are concentrated in levée deposits and represent the lag from which the postcranial elements were stripped and removed by overbank flooding. Ephemeral lakes on the flood plains were fed by these periodic sediment-laden floods. Abundant evidence of the effect of wind on shallow waterbodies in these lakes and pools is preserved in the form of falling water-level marks, flat topped, ladderback and double crested ripples. Further features of shallowing, emergence and desiccation are the presence of algal mats, casts of gypsum crystals and fossil traces of arthropod and vertebrate trails in places traversing algal mats.

On the flood plains, Smith (1978, 1979) recognizes proximal and distal facies. Proximal facies are taphonomically characterized by "skull only" assemblages whereas the distal facies contains the odd disarticulated vertebra and occasionally complete skeletons of pareiasaurs. This is interpreted as reflecting a low periodicity of inundation in an area of ephemeral pools and more permanent lakes of the central flood basins. Pareiasaurs (and fish) were almost the only forms that frequented the lakes of the central flood basins whereas other terrestrial forms kept to the vegetated channel banks.

Mammal-like reptiles formed a major component of the reptile fauna supported by the vegetation on the channel banks. In some of the more permanent ponds, fish (usually *Atherstonia)* flourished. The arid conditions probably caused the vegetation to be sparse and the plants to be stunted as shown by the overall paucity of plant remains (Kitching 1977) and the apparent dwarfism displayed by glossopteris leaves of the lower Beaufort (E Kovács-Endrödy personal communication to Smith 1978).

The "head only" beds (proximal flood plains) in the *Tapinocephalus* and *Endothiodon* zones were attributed to carnivores with a preference for postcranial parts (Hotton 1967). Carnivores with dentition capable of crushing bone are unknown from the lower Beaufort. Crushing of bones would moreover not have been cost effective as bones with marrow cavities are unknown from the lower Beaufort. According to Smith (1978), carnivores such as pristerognathids and gorgonopsians may, however, have been instrumental in accelerating the deterioration process of carcasses of small herbivorous dicynodonts by the opening up of the body cavity and also by attacking the neck and disarticulating the skull and postcranium. The mere piercing and rupturing of a tough skin may in itself have speeded up the process.

Of the numerous reptiles present in the Karoo sequence, initially only two groups were represented. The first, the Pareiasauria are specialized herbivorous cotylosaurs. The pareiasaurs were abundant in early Karoo times and the large semi-aquatic herbivore inhabitants of the ephemeral ponds and lakes of the distal facies of the flood basins belonged to this group.

The phylogenetically more important mammal-like reptiles (Therapsida) dominated the fauna, and even in the Ecca and lower Beaufort show a strong radiation. Largest were the Dinocephalia of which both large herbivores (eg *Tapinocephalus* and *Moschops*) and large carnivores (eg *Anteosaurus*) are present. The herbivorous dinocephalians exhibit an extreme thickening of the bones, especially the skull roof which may have served in protecting the brain in a headbanging ritual.

The bulk of the herbivorous forms were made up of the Dicynodontia which started off as relatively small forms of the lower Beaufort community. It is possible that the Dicynodontia of the *Tapinocephalus* zone are descendants of the dicynodonts of the earlier Waterford (Ecca) fauna. The dicynodonts, because of their herbivorous nature, extraordinary jaw mechanism and the replacement of teeth by a horny beak in most forms, exhibit major alterations in skull structure. Some dicynodonts were probably gregarious.

Together with the carnivorous dinocephalia, the herbivores were preyed upon by the Gorgonopsia and Therocephalia and later in the Triassic, also by the cynodonts which probably evolved from the Therocephalia. The Gorgonopsia became extinct at the end of the Permian, their extinction coinciding with the appearance of the Cynodontia and competition from these more advanced forms may have been a factor in the extinction of the Gorgonopsia. Even before the extinction of the Gorgonopsia, the dicynodonts disappeared towards the top of the *Tapinocephalus* zone while the numbers of the Therocephalia were reduced.

The Therocephalia became highly specialized eg the Waitsiidae and Scaloposauridae, and it is thought that the rodent-like Bauriamorphs with their battery of flat grinding teeth, probably for the grinding of seeds, are descendants of the scaloposaurs. The extremely advanced mammal-like *Bauria* is thought to have had cheek pouches and a chewing action of a type that today is known only in mammals.

By the end of the Permian the climate in the Karoo basin became wetter and much more water was available. A profound change in the faunal assemblage also took place. Not only had the dicynodonts replaced the gorgonopsians as the prominent carnivores, but similarly, the pareiasaurs, and a plethora of dicynodont genera of the previous drier period had been replaced by a single dicynodont genus, *Lystrosaurus*. This semi-aquatic, dwarf hippopotamus-like animal is thought to have populated the marshy landscape of that time.

Advanced cynodonts like *Trinaxodon* preyed upon lystrosaurs and it is thought that this carnivore exhibited many of the physiological adaptations of true mammals, and from the cynodonts, mammals probably evolved.

During deposition of the *Cynognathus* zone the climate became more arid and hotter again, and the lystrosaurs, which were adapted to a wetter climate, disappeared. The only dicynodont to survive into this period is the large *Kanneymyeria*. Apart from the development of mammal-like chewing mechanisms by carnivorous cynodonts, herbivorous forms such as *Trirachodon* also developed a masticatory apparatus, an indication of a high rate of metabolism.

In addition to the synapsid mammal-like reptiles and anapsid cotylosaurs (eg the pareiasaurs and procolophonids), all early diapsid forms are found as fossils in the karoo region. *Youngina* for example, may be on the lineage that gave rise to lizards and snakes, and forms like *Mesosuchus* are closely related to *Sphenodon*, the only living representative of the Rhyncocephalia.

The earliest known archosaurs are also found in the Karoo beds in forms like the crocodile-like *Chasmatosaurus (Protosuchus)* and the semibipedal *Euparkeria*. From the primitive archosaurs the early dinosaurs evolved during the Triassic and Jurassic Periods.

Throughout the karoo episode a varied amphibian population flourished alongside the reptiles.

Several genera of karoo reptiles are also found as fossils in other Gondwana continents. *Lystrosaurus* for example is also known from Antarctica, India and China, and members of the pareiasauria and procolophonids were recently discovered in Rio Grande do Sul, Brazil (Araújo 1982). The *Glossopteris* flora typical of the Ecca and Beaufort was replaced by a *Dicroidium* flora in the Stormberg during which period the climate became progressively more arid.

CRETACEOUS, TERTIARY AND QUATERNARY BEDS

Within the karoo biome lies part of the Algoa basin and the Oudtshoorn basin, both of Jurassic-Cretaceous age. These fault-bounded basins are attributed to half graben-type subsidence and sediments accumulated during an arid to semi-arid climate. The aridity in the Oudtshoorn basin led to the development of playa lake conditions and the formation of gypsum and limestone lenses. Fossils include leaf imprints, wood and dinosaur teeth (Tankard et al 1982).

The Algoa basin falls largely outside the karoo biome but mention can be made of the abundance of fossil plant material, mostly wood (conifer and cycad) and ferns. A dinosaur *Algoasaurus* and freshwater bivalves (eg *Unio)* are known from the sedimentary beds. Towards the east the sediments transgress into a marine facies which, however, falls outside the karoo biome. Sedimentary rocks deposited since the Jurassic are unknown from the central karoo and therefore no substantial fossil record is available apart from small localized deposits in kimberlite calderas. Some of the beds contain dinosaur bones and from others, like the Banke pipe, spores and pollen of Tertiary age were recovered. This pipe also yielded scores of *Eoxeno poides* fossils together with fragments of crocodile and turtle postcrania. A systematic collection of fossils in these occurrences is long overdue and will provide information on late Cretaceous and Tertiary environments in the central part of the country.

On the northern fringes of the karoo biome in the Vaal and Orange River drainage basins, late Pliocene to Early Pleistocene "high level" gravels contain mammalian fossils, the most diagnostic being the Pliocene elephant *Mammuthus subplanifrons* (Tankard et al 1982).

Younger Pleistocene age gravels contain rare fossils and artifacts.

CONCLUSIONS

A study of the palaeontology of the karoo biome shows that fossil assemblages were restricted to clearly defined physical environments. During a period of stability or when the environment changed gradually, the nature and composition of an assemblage changed slowly as organisms

evolved. On the other hand when rapid changes took place, the assemblages were drastically affected.

The fauna and flora of the modern (Holocene) karoo biome are not the direct descendants of forms of life which had inhabited the region since the Precambrian but are derived from a Tertiary assemblage. It is therefore imperative that the Tertiary and Quaternary histories of the biome should be investigated.

The physiography of the present-day karoo is the end product of the processes of weathering and erosion acting on the surface of the continent from the Mid-Jurassic onwards and especially during post-Miocene (post-Mid-Tertiary) times. The final processes are still active today.

A palaeontologist entrusted with the task of constructing a full and complete history of events of the last 25 million years, is forced to look at small isolated outcrops of Tertiary and Quaternary beds unevenly scattered over the biome.

A fully integrated study of the geology, palaeontology, geomorphology and climatology of the Tertiary and especially the Quaternary periods in the biome should provide us with facts which can be used in predicting the affects of future changes in the environment on the fauna and flora.

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CHAPTER 7 ARCHAEOLOGY

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INTRODUCTION

The karoo biome, as indicated in Figure 7.1, represents a substantial part of South Africa. It is unfortunately true, however, that the amount of archaeological research that has been undertaken in the Karoo is in no way proportional to its importance in terms of area in South Africa. There are several reasons for this. In the formative years of South African archaeology, systematic attention was focused on the Australopithecine sites in the Transvaal and northern Cape, on the Vaal River gravels sequence on the northern fringe of the Karoo and at various cave sites in the southern Cape. Much surface collecting was nevertheless undertaken throughout the country and here the Karoo was as well represented as any other area, but modern approaches in archaeology have shown that stone artefacts divorced from their original context are uninformative, apart from the obvious fact that they demonstrate the past existence of man in the area. The growth of modern archaeology in South Africa has been centred in the larger museums which began employing archaeologists in the early 1960's, and in some universities. Research, initiated from museums particularly, tended, for reasons of policy and logistics, to be limited to the areas "served" by those institutions. Because the Karoo does not support any museums large enough to employ archaeologists, it has tended to fall behind in the development of knowledge of the prehistory of the country. What little is known about the archaeology of the Karoo can only be inferred on the basis of systematic research that has been undertaken around the periphery of the region. (Figure 7.1 shows some of the sites that are of importance in this regard). Some caution is, however, necessary as these sites, situated as they are on the edges of the Karoo, adjacent to very different environments, must of necessity reflect patterns different from those to be expected in the central areas of the Karoo. A notable exception to the situation just described is in the work undertaken in the Middle Orange River area in conjunction with the Orange River Scheme by Sampson (1968) and ongoing research in the Zeekoe Valley (Sampson 1985). These projects have and will make an important contribution to the archaeology of the Karoo, but they are confined to very restricted areas.

There is as yet no general agreement on the cultural-stratigraphic terminology to be used in archaeology in South Africa and there is therefore some ambiguity attached to the terms that appear in the literature. The problem stems from the fact that earlier research was concerned with defining major technological stages in terms of essentially static hierarchical models, whereas most current research is focused on the study of dynamic cultural systems within much smaller time-space frameworks. The cultural-stratigraphic terms used in this discussion may be defined as follows:

Industry - a group of assemblages of artefacts from sites or defined horizons within multilayered sites which share a large number of technical

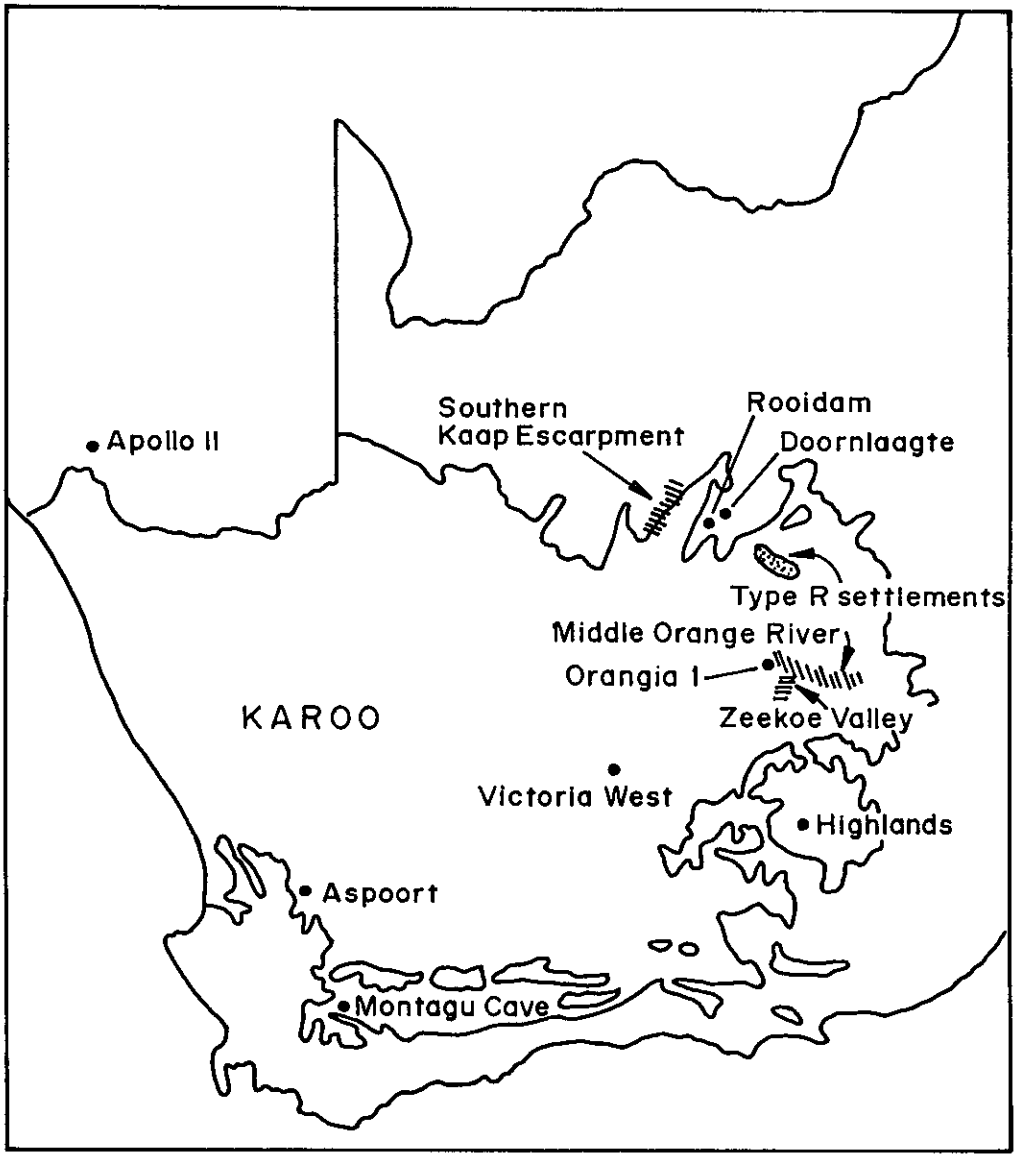

FIGURE 7.1 Approximate locations of sites mentioned in the text. Southern Kaap Escarpement includes Limerock 1 and 2, Dikbosch 1 and 2, and Burchell's Shelter. Middle Orange River includes Blydefontein, Zaayfontein, Riversmead and Glen Elliott.

and typological features.

Industrial Complex (or "Culture" in older literature) - a group of industries regarded as belonging to a common cultural tradition.

Early Stone Age, Middle Stone Age and Later Stone Age - informal stages which group Industrial Complexes that show a broad technological similarity.

As any cultural-stratigraphic hierarchy refers to cultural norms which

need not necessarily change at the same rate or pass through the same stages, it cannot be assumed to have any fixed chronological base. Dating of the various Industries or Industrial Complexes may therefore have only very localized significance and in the case of a less well-studied region such as the Karoo, even less precision can be expected. In order to overcome this difficulty, the archaeology of the Karoo, in this discussion, is described within a broad geostratigraphic framework.

THE MIDDLE PLEISTOCENE

The middle Pleistocene lasted from about 700 000 to 130 000 BP (years Before Present) and it is during the latter part of this period that the first traces of man can be detected in the Karoo. Archaeological remains dating to this period are recognized on the basis of a series of distinctive stone artefacts, most notably bifacially worked handaxes and cleavers, which are generally assigned to the Acheulean Industrial Complex or the Early Stone Age (Figure 7.2). Although handaxes and cleavers have been reported at various localities in the Karoo, well-documented occurrences are limited to a few sites around its periphery (Clark 1967). Most important among the excavated sites are Doornlaagte (Mason 1966) and Rooidam (Fock 1968) in the northern Cape and Montagu Cave (Keller 1973) in the south-western Cape; the Middle Orange River and Zeekoe Valley Projects have also produced a few surface sites that have been systematically sampled (Sampson 1985). It is consequently true to say that little is known about the Acheulean in the Karoo proper. Uranium-series dating of the Rooidam site suggests a minimum age of about 200 000 BP for the terminal Acheulean (Szabo and Butzer 1979). The earliest human occupation of the Karoo in all probability dates to well before this time. A much earlier date can be suggested on the basis of the occurrence of the so-called "Victoria West Industry". The "industry" which was first described by Jansen (1926) was recognized by what was thought to be a distinctive prepared core stone flaking technique resulting in "hoenderbek" (chicken beak) and "horse-hoof" shaped cores. Subsequent research, however, showed that this technique was not peculiar to the central Karoo, but occurred widely in the Acheulean at a specific stage in its earlier development. The occurrence of these distinctive cores in the central Karoo can therefore be taken as evidence of human occupation well before 200 000 BP, although more precise estimates of age are impossible of this stage.

Little is known in South Africa of the demography of human populations during the Acheulean (Deacon 1975). It is clear that both cave and open sites were occupied, but the factors controlling such occupation are at present unknown. Detailed mapping of Acheulean sites relative to a range of environmental factors may give some leads, but site visibility in this remote period is a very real problem. Until such time as large-scale systematic research on the Acheulean in the Karoo is undertaken, archaeologists will be able to say little more than that man was present either intermittently or continuously during this period.

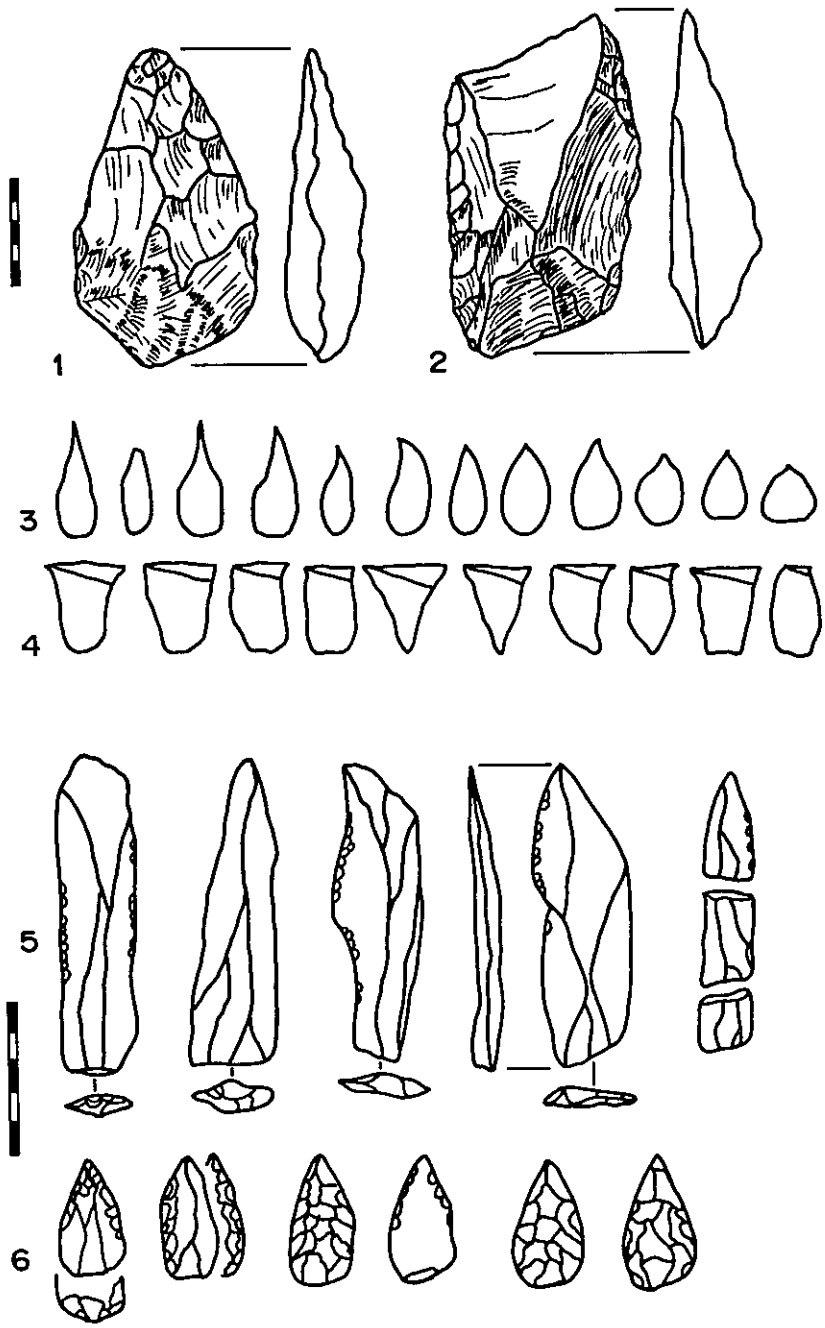

FIGURE 7.2 1. typical handaxe and 2. cleaver from the Acheulean Industrial Complex of the Early Stone Age (after Keller 1973). 3. a selection of handaxes and 4. cleaver shapes to give an indication of variability; size is also highly variable (after Kleindienst 1962). 5. a selection to typical Middle Stone Age points showing variable amounts of retouch (after Sampson 1972). All the above artefact types are associated with a wide range of other tools, utilized and waste pieces. In most cases, although characteristic, the above illustrated artefacts constitute a very small proportion of any assemblage. Scales in centimetres.

THE LATE PLEISTOCENE

The late Pleistocene, which lasted from approximately 130 000 to 40 000 BP, brackets a series of industrial complexes known collectively as the Middle Stone Age. Assemblages of Middle Stone Age artefacts differ from Early Stone Age in that handaxes and cleavers have disappeared and have been replaced by a variety of characteristic flake tools. "Typical" Middle Stone Age assemblages contain long, narrow, blade-like flakes, pointed flakes (some retouched bifacially) and denticulated pieces, as well as evidence of distinctive flaking techniques (Figure 7.2).

Studies of the Middle Stone Age in southern Africa have a long history and have resulted in the recognition of a large number of industrial complexes and industries (many of which have still to be given precise definition), which relate to each other through time and space. This variety of names is a reflection, in the first place, of what must have been a far more complex cultural response on the part of Middle Stone Age people to the spatially and temporally varying environments in which they found themselves. It is also, however, a reflection of the archaeological problems of insecure dating in this time range and limited understanding of the variability that is to be expected within, as well as between, different industries.

Middle Stone Age artefacts have been recognized widely in the Karoo (Clark 1967) but in most cases, being undated surface occurrences, they have provided limited information about demographic patterns during the late Pleistocene. What is perhaps the most important evidence relating to the Middle Stone Age of the north-eastern Karoo has come from the Middle Orange River area. Excavations at the site of Orangia I, near Petrusville, revealed a series of seven semicircular structures composed of large blocks and cobbles (Sampson 1968). These have been interpreted as the bases of windbreaks that were built out of thorn bushes or branches. The inner part of the "skerms" (shelters) appeared to have been hollowed out, perhaps for sleeping. It has been estimated that the site would have been occupied by a group of about 12 individuals. Discrete groupings of different artefact types were found among the stone structures and these patterns may be interpreted in terms of activity areas once more comparative data are available.

Orangia I has been linked typologically to a series of other sites in the Middle Orange River project area to form part of a suggested sequence for the central interior (Sampson 1968). This sequence, though undated, does reveal some shifts in artefact parameters which are paralleled in other parts of South Africa. The Middle Stone Age of the Karoo must therefore be seen in the broader context of the Middle Stone Age of South Africa, but at this stage of research, population shifts and exploitation patterns specific to the Karoo have not been identified.

THE TERMINAL PLEISTOCENE AND HOLOCENE

The terminal Pleistocene and Holocene lasted from about 40 000 BP to the present, and it is during this period that industries, referrable to the Later Stone Age, appeared. The transition from Middle Stone Age to Later Stone Age in South Africa in general is difficult to pinpoint because many sites show a hiatus in occupation after the occurrence of "typical" Middle

Stone Age assemblages and before the appearance of artefacts which would generally be accepted as Later Stone Age. The reasons for this hiatus are at present unknown but they are almost certainly bound up with the major demographic and cultural changes which are reflected in the strongly contrasting artefact assemblages produced before and after the break. The transition is, however, regarded as lying between about 40 000 and 30 000 BP.

The Later Stone Age is better known than any other stage in the prehistory of South Africa. This is the result, not only of intensive research that has been undertaken in the eastern, southern and western Cape, but also of relatively good preservation of faunal and botanical food waste in addition to the usual stone artefacts. The Later Stone Age of the Karoo is poorly documented. An overview of this period for the area can only be given with reference to the better studied eastern Cape sequence.

In the eastern Cape, the period from the transition to the Later Stone Age, perhaps 30 000 BP to about 20 000 BP, is represented by a series of assemblages which have yet to be analysed and described in detail (Klein 1974; Deacon 1978). The period after about 20 000 BP saw the existence of three relatively stable tool-making episodes or what have been termed "homeostatic plateaux" (Deacon 1976) known as the Robberg Industry (18 000 to 12 000 BP), the Albany Industry (12 000 to 8 000 BP) and the Wilton Industry (from 8 000 BP onwards). Each of these industries was distinguished by a series of characteristic artefacts: the Robberg was characterized by microlithic bladelets and small scrapers; the Albany by large scrapers and relatively few retouched pieces; and the Wilton by a large variety of retouched pieces including scrapers, borers, adzes and backed artefacts (Figure 7.3).

The pattern established in the eastern Cape appears to have parallels in the southern and western Cape (Deacon 1978; Schweitzer and Wilson 1982), and the various industries may ultimately be seen as parts of a more widespread series of industrial complexes. If this sequence is taken as a norm against which to compare the Karoo Later Stone Age, some interesting facts emerge.

Although Later Stone Age artefacts have been recognized in surface scatters throughout the Karoo, systematic research has only been undertaken in two areas on the northern periphery of the region - the southern part of the Kaap Escarpement (Humphreys 1979) and the Middle Orange River area (Sampson 1972), and at two other sites on the east and south-west edges of the Karoo - Highlands (Deacon 1976) and Aspoort (Smith and Ripp 1978). In a major synthesis derived from his work on the Middle Orange River, Sampson (1974) recognizes the existence of three industries in the Karoo which have been related to more widespread industrial complexes. The earliest of these industries is known as Lockshoek and is characterized by large scrapers. This industry was originally called Smithfield A (Goodwin and Van Riet Lowe 1929) and has clear parallels with the Albany Industry of the eastern Cape; both the Lockshoek and Albany Industries have, in fact, been assigned to the Oakhurst Industrial Complex (Sampson 1974; Deacon 1980). Although the Lockshoek Industry and the Oakhurst Industrial Complex as a whole are at present not clearly understood, these assemblages represent the earliest recognized Later Stone Age artefacts in the Karoo. This means that at present there is no evidence in the region for an equivalent of the earlier terminal Pleistocene

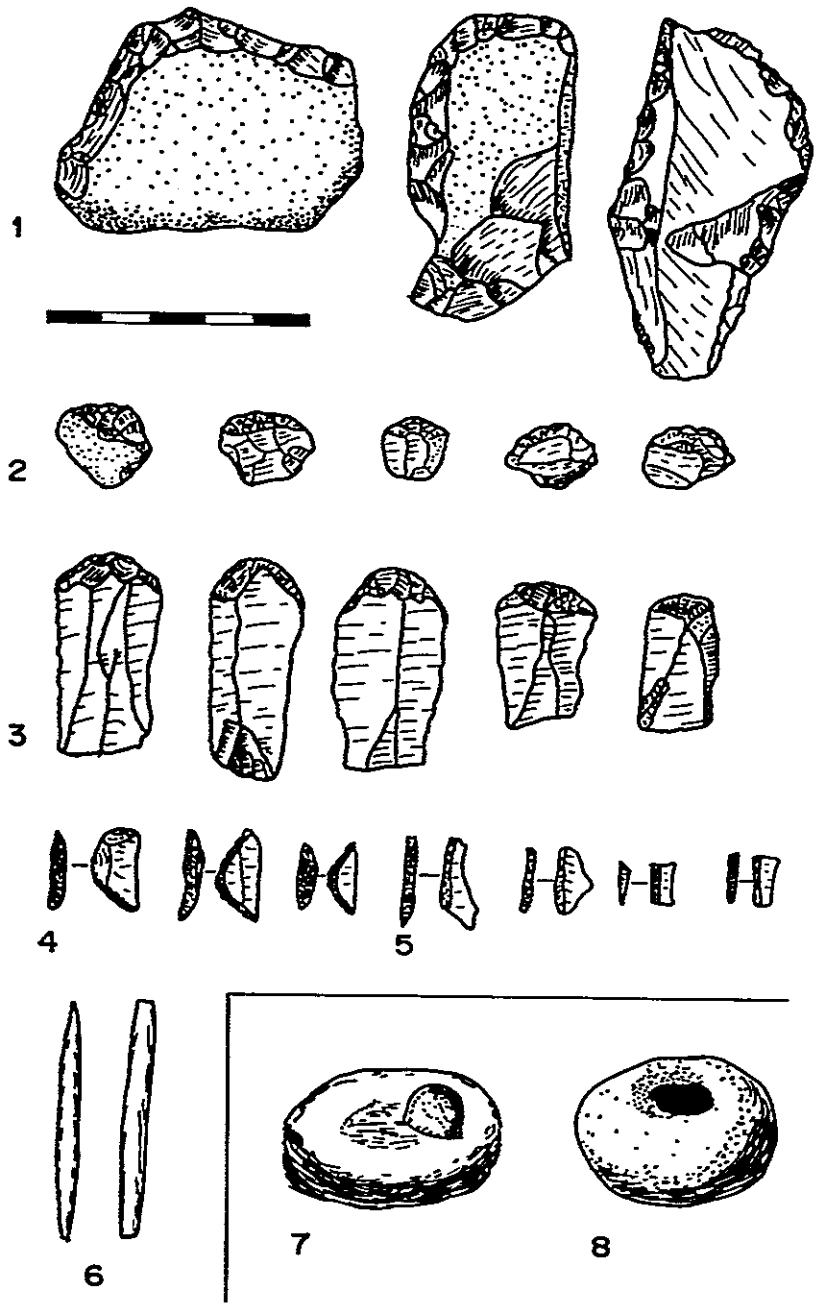

FIGURE 7.3 A selection of Later Stone Age artefacts (after Sampson 1967a,b). 1. scrapers typical of the Lockshoek Industry (Oakhurst Industrial Complex). 2. small convex scrapers typical of the Wilton Industrial Complex. 3. large end scrapers from the Smithfield or terminal part of the Wilton of the interior of South Africa. 4. crescents and 5. backed blades typical of the Wilton. 6. bone point and linkshaft for use on arrows. 7. upper and lower grindstones (not to scale). 8. bored stone for weighting a digging-stick (not to scale). Scale in centimetres.

assemblages recognized in the eastern Cape.

The Wilton Industrial Complex is clearly represented in the central interior of South Africa, and the Karoo and eastern Cape manifestations of these industries have much in common. It is a curious fact, however, that to date, none of the Karoo sites which have produced Wilton assemblages has yielded dates in excess of about 4 500 BP. Chronologically and also technologically therefore, only the later half of the Wilton Industrial Complex appears to be represented in the Karoo. Sampson (1974) assumes that the earlier part of the Wilton in the Karoo has yet to be discovered but other researchers (Humphreys 1972a; Deacon 1974) have suggested that this apparent hiatus is real and that the central interior was devoid of population from about 9 500 to 4 500 BP. Dating and raw material trends in the Middle Orange River area suggest in that area at least, the terminal Later Stone Age people moved in only after about 4 000 BP (Humphreys 1972a).

The third industrial complex recognized in the Karoo by Sampson is the Smithfield. This complex is characterized by long end scrapers which appear to be absent in the eastern and western Cape areas, and so Sampson has suggested that the Smithfield was a purely local development in the central interior. Other researchers (Humphreys 1979) have, however, preferred to see the assemblages assigned to the Smithfield as being merely a late development within the Wilton Industrial Complex as a result of the use of a specific type of raw material (known variously as lydianite, indurated shale or hornfels) available throughout roughly the northern half of the Karoo. This problem which was demographic and cultural rather than simply terminological implications, is one that has yet to be resolved.

If the Karoo Later Stone Age sequence as a whole is compared with that of the eastern Cape, it is immediately clear that a series of distinct breaks seems to have occurred in the Karoo over the last 30 000 to 40 000 years. While this may be a function of the limited amount of research undertaken, it may equally be related to changing demographic patterns in the past. The pattern occurring in the Karoo may be summarized as follows: the earliest recognized Later Stone Age occupation of the Karoo must have taken place between about 12 000 to 9 000 years ago (assuming a rough equivalence in age between the Lockhoek of the Karoo and the Albany of the eastern Cape); thereafter there was an apparent depopulation of the area until about 4 000 to 4 500 years ago when the area was reoccupied until historical times.

In seeking an explanation for these breaks in the sequence it is necessary to note some aspects of the ways in which hunter-gatherers exploit their environments and this is relevant, of course, because all the archaeological traces described so far are referrable to hunter-gatherer populations. It has now been recognized ethnographically and archaeologically that all hunter-gatherer groups adopt a mobile existence closely coordinated with the seasonal variations and fluctuations in the food resources available in their environments. While variations in the availability of animals may influence seasonal movements, it can be shown that the faunal remains from archaeological sites generally tend to reflect the animals available in the vicinity of the site rather than specialization on any specific species (Table 7.1). Plant foods are much more sensitive to seasonal variations, and ethnographic observations show

that it is primarily these food resources that control the seasonal migration patterns. Archaeological studies, particularly in the western Cape (Parkington 1977), have been able to document the seasonal rounds of hunter-gatherer groups occupying the area during the last few thousand years. Information is available there and in other areas on the staples of the various diets and the seasonal shifts that took place in response to annual fluctuations in their availability. If this insight into prehistoric hunter-gatherer strategies is applied in the Karoo some ideas may be put forward to explain the apparent breaks in occupation. Much work has yet to be undertaken in the Karoo to establish the actual or potential subsistence ecology from the point of view of prehistoric hunter-gatherers, but it may be assumed that certain plants would have formed the staples for these groups. It may prove to be the case that the available staples were not adaptable to environmental change on the scale of that which took place in the Karoo during the terminal Pleistocene and Holocene (Van Zinderen Bakker 1976). Hunter-gatherers may therefore have been left with no alternative but to withdraw to the peripheral, better endowed areas. The Karoo may, in the past, have been a marginal area which was only occupied during favourable environmental circumstances and when population pressures in the peripheral areas forced expansion or "over-flow" into the Karoo. Clearly much more research is required, but the available palaeoenvironmental and archaeological evidence suggests that such occupation took place in the terminal Pleistocene and Holocene only between about 12 000 and 9 000 BP and from about 4 500 BP to the present. Such breaks in occupation may also have been a feature of the Early Stone Age and Middle Stone Age but, as already indicated, not enough data are available for any clear patterns of occupation to have emerged.

Another aspect of the Holocene archaeology of the Karoo that is of interest is the rock art which occurs in the form of both engravings and paintings. Rock engravings appear to be limited to the interior of South Africa and are substantially represented in the Karoo. Rock paintings, occurring as they do in caves and shelters, have a much more limited distribution in the Karoo, but they are nevertheless present at various places (Rudner and Rudner 1968). Dated examples of rock art from sites around the periphery of the Karoo show that this art form has a history going back at least 25 000 years (Deacon et al 1976; Wendt 1976; Thackeray et al 1981). The rock art of the Karoo itself is undated but it would be of interest to discover whether different "phases" in the rock art (if such exist) can be correlated with the various periods of occupation of the region as evidenced in the stone artefacts. Despite these possibilities, however, the rock engravings provide a valuable source of information on the past occurrence of wild animals (eg Fock 1966).

At around 2 000 BP a significant change took place in the archaeological record along the western and southern coastal regions of South Africa. This change took the form of the appearance of pottery and the bones of domestic sheep and/or goats and possibly also cattle. These new elements in the archaeological record are taken as representing the advent of pastoralism in South Africa. To date the archaeological evidence indicates that pastoralism arrived in South Africa via the west coast and there is no evidence of the herders who settled in the south-western and southern Cape having moved far into the Karoo at an early date. The historian Elphick (1977) has, however, pointed to the availability of better pasturage in the central interior than occurs along the west coast and has suggested that the herders may in fact have entered South Africa

TABLE 7.1 The minimum numbers of individuals of larger mammals represented in selected late Holocene archaeological sites in the karoo biome. Data adapted from Klein (1979, Table 6), Deacon 1976, Table 49) and Thackeray 1979, Table 3a). In the case of Apollo 11 only the "LSA Wilton" and "LSA with pottery" levels have been included. "Cf" indicates a possible/probable indentification

	Limerock 1	Limerock 2	Dikbosch 1	Dikbosch 2	Burchell's Shelter	Blydefontein	Zaayfontein	Riversmead	Glen Elliott	Highlands	Apollo 11
Lepus cf *capensis*, Cape hare	-	-	-	-	-	-	-	-	-	9	-
Pronolagus cf *rupestris*, Smith's red hare	-	-	-	-	-	-	-	-	-	10	-
Leporidae gen et sp indet, hare(s)	4	8	5	2	1	11	2	12	11	-	10
Hystrix africae-australis, porcupine	-	-	-	2	1	-	-	6	2	8	-
Pedetes capensis, springhare	3	3	-	-	-	-	-	6	5	-	-
Manis temmincki, pangolin	-	-	-	-	-	-	-	1	-	-	-
Papio ursinus, chacma baboon	-	?1	-	1	-	2	-	2	1	-	1
Canis sp, jackal	-	-	-	-	1	-	-	3	6	-	-
Vulpes chama, silver fox	-	-	?	1	-	-	1cf	-	2	1	-
? *Proteles cristatus*, aardwolf	-	-	-	-	-	-	-	-	-	2	-
Herpestes ichneumon, Egyptian mongoose	-	-	-	-	-	-	-	1cf	-	-	-
Cynictus penicillata, yellow mongoose	2cf	1	1	1cf	-	4	-	2	6	-	-
Felis libyca, wildcat	-	1	-	-	-	2	-	4	-	-	1
Felis caracal or *F serval*, caracal or serval	-	-	1	-	-	1	-	-	4	-	-
Panthera pardus, leopard	-	-	-	-	-	1	-	1	-	-	-
Orycteropus afer, aardvark	-	-	-	-	-	-	-	5	3	-	-
Procavia capensis, rock hyrax	2	4	4	2	1	17	-	12	5	44	34
Equus quagga/E burchelli, quagga/zebra	2	7	6	?1	1	7	-	3	5	4	-
Equus zebra cf *hartmannae*, mountain zebra	-	-	-	-	-	-	-	-	-	-	4
Rhinocerotidae gen et sp indet, rhinoceros	-	-	3	-	-	-	-	1	-	-	-

TABLE 7.1 (continued)

	Limerock 1	Limerock 2	Dikbosch 1	Dikbosch 2	Burchell's Shelter	Blydefontein	Zaayfontein	Riversmead	Glen Elliott	Highlands	Apollo 11
Hippopotamus amphibius, hippopotamus	-	-	1	-	-	-	-	-	-	-	-
Phacochoerus aethiopicus, warthog	1	1	1cf	1	-	-	-	5	7	6	1
Tragelaphus strepsiceros, greater kudu	1	-	-	-	1	-	-	-	-	-	-
Taurotragus oryx, eland	-	-	3	-	-	-	-	-	3	-	-
Redunca fulvorufula, mountain reedbuck	-	-	3	-	1	8	-	6	-	6	-
Hippotragus sp(p), roan/sable antelope	-	?1	-	-	1	-	-	-	-	-	-
Oryx gazella, gemsbok	-	-	-	-	-	-	-	-	-	-	?1
Pelea capreolus, vaalribbok	-	-	-	-	-	10	-	3	-	-	-
Connochaetes gnou/Alcelaphus buselaphus, black wildebeest/red hartebeest	-	2	6	-	3	7	?1	6	12	3	-
Antidorcas marsupialis, springbok	-	-	3	-	1	-	1	-	24	26	1
Sylvicapra grimmia, grey duiker	-	1	-	-	-	-	-	-	-	-	-
Cephalophus monticola, blue duiker	-	-	-	-	-	-	-	-	-	?3	-
Oreotragus oreotragus, klipspringer	-	-	1	-	-	3	-	-	-	1	5
Raphicerus campestris, steenbok	4	9	5	2	2	3	4	3	6	33	-
Syncerus caffer/Bos taurus, Cape buffalo/cattle	1	-	-	?2	-	2	1	1	-	-	-
Ovis aries/Capra hircus, sheep/goat	1	-	1	1	-	-	-	-	-	-	-

via the Vaal and Hart Rivers and through the central Karoo to the southern Cape. Unfortunately, despite the attractiveness of this hypothesis, apart from some insecure dates on isolated sheep teeth from the northern Cape (Humphreys 1974; Beaumont 1980), there is no direct evidence for a route via the Karoo for the advent of pastoralism. Current research by Sampson in the Zeekoe Valley (on the route postulated by Elphick) has not yet yielded evidence of early pastoralism (C G Sampson personal communication). The question of the origins of pastoralism in the Karoo has yet to be resolved, and it is probably safest at this stage to accept the advance of the Khoi-Khoi (Hottentot) groups from the Cape during the late 1700's and 1800's as being the first extensive herder occupation of the Karoo, excepting, of course, for the extreme western strip along which pastoralism appears to have entered South Africa.

There is one major phase in the archaeology of South Africa that is totally unrepresented in the Karoo. This is the Iron Age which is the archaeological reflection of the early Bantu-speaking farmers who occupied parts of the Transvaal, Natal and Transkei from about AD 200. The reason that Bantu-speakers did not advance into the Karoo would appear to be environmental. The southern limits of Iron Age settlement coincide very closely with the 400 mm isohyet and it likely that areas receiving less than this amount of precipitation were too dry for crop production using traditional techniques (Humphreys 1976; Maggs 1976). Interaction clearly took place between Iron Age communities and hunter-gatherer groups in the fringe areas of the Karoo. The Type R settlements of the Riet River areas in the south-western Orange Free State appear to indicate an independent advance to pastoralism on the part of hunter-gatherers in contact with other stock-owning communities (Humphreys 1972b). Studies in this and other contact zones on the outer edges of the Karoo offer good prospects for archaeological research.

The prehistory of the Karoo can be said to have ended with the advance of the trekboers of the 1700's and with the historical records left by the early missionaries and explorers who penetrated the central interior of South Africa. The records left by these travellers throw valuable light not only on the peoples whom they met but also give insights into the origins of the patterns of change which the arrival of the new life-style set in motion; these changes were not only of a social nature but also had an impact on virtually all other aspects of the karoo biome.

CONCLUSIONS

It is clear from this discussion that extensive and intensive research is required to bring our knowledge of the archaeology of the Karoo up to the level achieved in some other parts of South Africa. While some ongoing research such as that in the Zeekoe Valley can be expected to make a significant contribution to archaeology it is nevertheless confined to a restricted area. A high priority should therefore be placed on investigating some of those vast expanses of the Karoo that are still untouched archaeologically. A first requirement is the establishment of a more complete cultural sequence for the region. The cultural sequence itself will have to be seen in the context of the environmental conditions prevailing during its development. It has already emerged that the Karoo was probably a marginal environment that set severe limitations on the range of resources exploitable by hunting and gathering groups, but the actual

impact of the environment on man needs much clearer definition. On the other hand, very little is known about the impact of man on the karoo environment. It appears that, in the southern Cape, prehistoric hunter-gatherers were directly involved in the extinction of several large mammals at the beginning of the Holocene (Klein 1980). Man-animal relationships may have been at least as dramatic, if not more so, in a marginal environment like the Karoo. Moreover, hunting and gathering groups were seen in historical times to have set fire to the vegetation in order to attract game to the new growth that would result (Burchell 1822). The impact of this and other hunting strategies on the flora of the area will only emerge once a clearer understanding of the ecology of the prehistoric hunter-gatherers of the Karoo has been gained.

Clearly, the Karoo is an area of immense challenge and opportunity for archaeological research.

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GEOLOGICAL AGE	RADIOMETRIC AGE ma	STRATIGRAPHIC COLUMN	OCCURRENCE OF FOSSILS	HISTORY OF LIFE	MAJOR GEOLOGICAL EVENTS IN THE HISTORY OF THE KAROO BIOME
QUATERNARY	1,8	Quaternary Successions	Mammals Pelecypods	Rapid evolution of hominids Many mammals become extinct	Erosion and partial destruction of Tertiary land surfaces. Younger plains are formed.
TERTIARY	65	Tertiary Successions	Pelecypods Mammals Angiospermophyta	Grasslands develop Ungulates spread First primates	Climate gets warmer. Fluctuations in sea level. Colder climate sets in. Uplift. Rivers incise.
CRETACEOUS	141	Uitenhage Group	Dinosaurs Tracheophyta	Radiation of mammals Reptiles decline First mammals Angiospermophyts spread rapidly	Extensive plains of the interior form. Intrusion of Kimberlites. Cape fold ranges emerge.
JURASSIC	195	UPPER UNITS OF THE KAROO SEQUENCE NOT EXPOSED IN THE KAROO BIOME		First birds Rise of the dinosaurs	Gondwana drifts apart. Coastline forms. Uplift of interior. Erosion starts. River systems develop. Drakensberg volcanism. Intrusion of dolerites.
TRIASSIC	230	KAROO SUPERGROUP: Beaufort Group	Glossopteris Sphenopsids; Reptiles Amphibians; Fishes		Folding of Cape and Karoo beds in the south.
PERMIAN	280	KAROO SUPERGROUP: Ecca Group	Fishes, Pelecypods Mesosaurids, Palaeoniscids, Arthropods, Fishes, Radiolarians	"Gymnosperms" radiate Tracheophyta decline Reptiles spread	Coalfields form.
CARBONIFEROUS	345	KAROO SUPERGROUP: Dwyka Formation			Beginning of true continental deposition Glacial period in Gondwana.
DEVONIAN	395	CAPE SUPERGROUP: Witteberg Group; Bokkeveld Group	Fishes; Lycopods; Trace Fossils; Brachiopods pelecypods; Trilobites and other invertebrates	First reptiles First amphibians Tracheophyta evolve and radiate	End of deposition in shelf seas. Existence of Malvinokaffric Faunal Province
SILURIAN	435	CAPE SUPERGROUP: Table Mountain Group	Trace Fossils	First fishes	Short glacial period Marine Transgression begins
ORDOVICIAN	500				Period of erosion
CAMBRIAN	570	NAMA GROUP: Fish River Sub Group	Trace Fossils		Deposition in shelf seas and on continent
PRECAMBRIAN	2300	Griqualand West Sequence	Stromatolites	Ediacara Fauna Evolution and spread of Invertebrates	Evolution of the atmosphere Existence of intracontinental sea
	2310	Sodium Group	Stromatolites	Blue-green algae and bacteria	Crustal instability and volcanism

Figure 7.1 The stratigraphic occurrence of fossils in the karoo biome