CAPE ELEMENTS ON HIGH-ALTITUDE CORRIDORS AND EDAPHIC ISLANDS

by

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PREFACE

The experimental work described in this thesis was carried out in the School of Botany and Zoology, University of Natal, Pietermaritzburg, from January 1998 to December 2003, under the supervision of Professor Trevor Edwards and co-supervision of Professor Richard Beckett. Fieldwork was conducted in numerous Ezemvelo KZN Wildlife reserves, particularly the uKhahlamba-Drakensberg Park, and was coordinated by Mr. C. R. Scott-Shaw.

These studies represent original work by the author and have not otherwise been submitted in any form for any degree or diploma to any University. Where use has been made of the work of others it is duly acknowledged in the text.

Signed: .... (Clinton Carbutt)

Pietermaritzburg (December 2003)

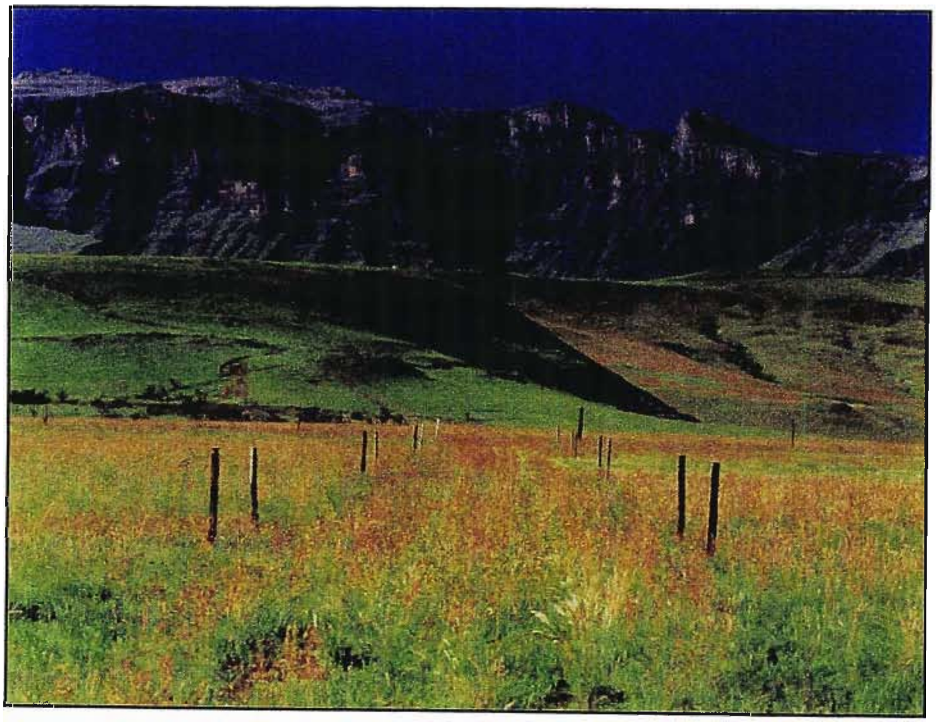
Supervisor: .... (Prof. T. J. Edwards)

Co-supervisor: .... (Prof. R. P. Beckett)

FRONTISPIECE

"As for man, his days are like grass, he flourishes like a flower in the field; the wind blows over it and it is gone, and its place remembers it no more. But from everlasting to everlasting the Lord's love is with those who fear Him, and His righteousness with their children's children - with those who keep His covenant and remember to obey His precepts. The Lord has established His throne forever, and His kingdom rules over all" (Psalms 103: 15 - 19).

In loving memory of Leonora (Leonie) Mary Prozesky, who dearly loved the mountains



MLAMBONJA WILDERNESS AREA, NORTHERN KWAZULU-NATAL DRAKENSBERG

PUBLICATIONS

The following publications have arisen from this course of study:

CARBUTT, C. & EDWARDS, T. J. 2001. Cape elements on high-altitude corridors and edaphic islands: historical aspects and preliminary phytogeography. *Systematics and Geography of Plants* 71: 1033-1061.

CARBUTT, C. & EDWARDS, T. J. 2004. The flora of the Drakensberg Alpine Centre. *Edinburgh Journal of Botany* 60(3): 581-607.

FORMAT

All chapters with the exception of Chapters 1 and 5 ('Introduction' and 'Conclusion') have or are being prepared for journal submission. The format of this thesis therefore is that of a number of free-standing chapters. Slight repetition in the introductory sections of each chapter is therefore inevitable. References follow after each chapter.

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Finally, to Hilary and Nathi, my beloved family, I love you both very much!

ABSTRACT

Common to the temperate floras throughout sub-Saharan Africa is a group of taxa with strong ties to the Cape Floristic Region (CFR) (≈ Cape elements). Their distribution is limited to the eastern escarpment of Africa (e.g. the Drakensberg Alpine Centre - DAC), on nutrient-rich humic soils, as well as on isolated sandstone outcrops of low elevation, on nutrient-poor soils (e.g. the Pondoland Centre - PC), suggesting that intrinsic soil fertility is not the primary determinant of their distribution. The principal aim of this study was to determine which aspect of the edaphic environment of the DAC is most influenced by temperature, that may indirectly render it nutrient-poor and therefore provide suitable niches for Cape elements, as in the PC. A multidisciplinary approach involving aspects of plant biogeography, plant ecology, plant ecophysiology and soil chemistry was therefore adopted. The study regions were the DAC, PC and the KwaZulu-Natal Midlands. The flora of the DAC was resurveyed for this study, and is richer than previously thought: 2818 native taxa, most of which (2520) are angiosperms. The phytogeography of the DAC and PC is discussed, and comparisons are made with the floras of KwaZulu-Natal and the CFR. Their climatic environments, as well as those for the CFR and Sneeuberge, were compared using rainfall and temperature data from a range of sources. These climatic regimes were correlated with the floristic patterns of Cape elements for the high-altitude regions of South Africa and Lesotho. Altitude and rainfall increased, and temperature decreased, as the number of Cape elements increased towards the DAC. This study provided a contemporary inventory of the Cape elements of the DAC and PC. A total of 89 genera are recognised as Cape elements, of which 60 (c. 67%) are shared between the two regions. The highest number of Cape elements recorded for the eastern escarpment was the DAC (72 genera), with the highest number from all sites analysed being the PC (77 genera). The most Cape elements are contributed by the Asteraceae, Scrophulariaceae, Iridaceae, Fabaceae, Orchidaceae and Restionaceae, partly due to the success of annual aerial parts and their geophytic growth forms, which are convergent in these families. Further compartmentalisation into life and growth forms shows that most Cape elements of the DAC and PC are either ericoid (and sclerophyllous) or mesic herbs and shrubs. The ecological and ecophysiological aspects of this study involved the use of reciprocal pot experiments established along a gradient of altitude from coastal hinterland to mountain, that investigated the interactions between altitude, temperature and substrate on plant productivity in sites known either to support or to exclude Cape elements. Three soils were used at each site, representative of the DAC, PC and KwaZulu-Natal Midlands. The interactions between 'soil' and 'site' (≈ the climatic environment) were quantified using a temperate test taxon (*Diascia*) that has a strong Cape-centred distribution. Plant characters relating to morphology and nutrient content, and soil characters relating to fertility, were used as the basis for comparing treatment effects (soil-site interactions). Soil nitrogen availability was assayed using pot experiments with *Eragrostis curvula* (Schrad.) Nees. Wheat pot experiments revealed no Al^{3+} toxicity in 'Drakensberg' soil. Non-metric multidimensional scaling (NMDS) and redundancy analysis (RDA) indicated that all soil-site interactions were significant contributors to biomass differences, and that the Cape taxon performed poorly in the nutrient-rich Drakensberg soil at low altitude. Soil samples indicated that Drakensberg soil was the most nutrient-rich, and Pondoland soil the most nutrient-poor. Although total nitrogen in Drakensberg soil was six times higher than Pondoland soil, both soils mineralised similar low levels of nitrogen at their respective spring temperatures. The result for Drakensberg soil (simulated so as to include the effect of altitude) meant that only 1.7% of its total nitrogen was mineralisable at 12°C (its mean spring temperature). These findings suggest that nitrogen mineralisation rate is a key growth-limiting factor in the DAC, exacerbated by a number of complex interactions with soil pH and organic matter. It is hypothesized that Cape elements are preadapted to high-altitude habitats. These habitats are nutrient-deprived due to low temperatures, which reduce metabolic rates and the movement of ions in cold soils. This constraint imposes nutrient-related stresses similar to those of the CFR and PC. Taxa that are adapted to the nutrient-poor soils of the CFR are preadapted to the temperature-induced 'nutrient-poor' soils of the DAC and vice versa. This 'compatibility' has allowed the reciprocal exchange of taxa between regions, as suggested by cladistic biogeographical analyses using *Cliffortia*, *Disa*, *Moraea* and *Pterygodium*. The strong overlap of Cape elements between the CFR and PC is a product of similar nutritional niches and ancient floristic continuity. The result therefore is a high number of Cape elements common to the DAC and PC.

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'I have an old belief that a good observer really means a good theorist.'

Darwin (1860)

CHAPTER 1

INTRODUCTION

1.1 FLORA OF SOUTHERN AFRICA

Southern Africa has the most species-rich temperate flora in the world, contributing some 10% (c. 30 000 species) of the world's vascular plants (Van Wyk & Smith, 2001). The tropical African flora, by comparison, is relatively species-poor (Brenan, 1978; Goldblatt, 1978). Much of southern Africa's phytodiversity is attributed to its diversity of climate, topography, geology and soils, which collectively generate ecological gradients and high species-packing (Cowling *et al.*, 1989; Cowling & Hilton-Taylor, 1997). The subcontinent supports five phytochoria (Werger, 1978; White, 1983), seven biomes (Rutherford & Westfall, 1994; Rutherford, 1997) and in South Africa, c. 70 major vegetation types (Acocks, 1988; Low & Rebelo, 1996).

In addition to high species richness and species density (Cowling *et al.*, 1989; Cowling & Hilton-Taylor, 1994), the flora of southern African (FSA) also has high levels of endemism (c. 60%, including 13 families and 560 genera) (Goldblatt, 1978; Taylor, 1978; Gibbs Russell, 1985; Cowling & Hilton-Taylor, 1997). The prominence of endemism at all taxonomic levels confirms the region's status as a distinct phytogeographical unit: the southern, temperate element of the African flora (Goldblatt, 1978; Cowling & Hilton-Taylor, 1997).

1.2 STUDY REGIONS AND STUDY SITES

The two floristic centres of diversity and endemism relevant to this study are the Drakensberg Alpine Centre (DAC) and Pondoland Centre (PC) (Van Wyk & Smith, 2001; Carbutt & Edwards, 2004). Study sites within the DAC were located at Cathedral Peak, Garden Castle and Sani Pass, which form part of the greater uKhahlamba-Drakensberg Park. Study sites within the PC were located at Oribi Gorge and Umtamvuna.

1.3 UNDERLYING PREMISE

Many taxa of the Cape Region (Goldblatt & Manning, 2002) have evolved on leached, nutrient-poor acidic soils subject to a Mediterranean climate (Cowling & Richardson, 1995). Cape taxa, however, also occur as communities along the eastern escarpment of sub-Saharan Africa and on sandstone outcrops of the eastern seaboard. Their occurrence on the nutrient-poor Msikaba Formation 'edaphic islands' in Pondoland (Abbott *et al.*, 2000) is a product of similar nutritional niches and ancient floristic continuity with the Cape Region (Van Wyk, 1990). More surprising is the prominence of Cape taxa on nutrient-rich substrates of the DAC, a mountainous region forming part of the eastern escarpment of southern Africa. The DAC and PC exhibit a remarkable overlap of Cape elements (Carbutt & Edwards, 2001) despite their horizontal separation of between 280 and 400 km, and despite their differences in altitude, precipitation, temperature and substrate. The primary aim of this study was to determine which ecological processes were most likely responsible for the sharing of Cape elements in two regions with different ecological constraints.

1.4 PHILOSOPHY OF APPROACH

The research presented in this thesis is essentially a multidisciplinary account involving aspects of plant biogeography (phytogeography), plant ecology, plant ecophysiology and soil chemistry. Environmentally correlated patterns often make sense only when a historical perspective has been adopted (Daubenmire, 1947; Cowling & Holmes, 1992; Linder *et al.*, 1992) because biogeographical patterns are the results of ecological and historical factors (Cowling, 1983).

A quantitative (mechanistic) perspective was adopted. This approach, often labelled 'reductionist' in execution, allows a theoretical understanding of how changes in ecological systems affect plant communities, supported by empirical testing of data generated from a wide range of sources (Schoener, 1986; Ricklefs, 1987). The application of mechanistic, predictive models is necessary for the sustainable management of dwindling natural resources (Tilman, 1990).

1.5 OVERVIEW OF METHODS

Biogeography is based largely on explanatory hypotheses that are supported by the known facts of distribution. The best biogeographical hypotheses are those that follow the hypothetico-deductive model (Ball, 1976), the principles of which are described in detail by Mentis (1988). The phytogeographical elements of this study incorporated a review of the Afroalpine and Afromontane regions; a resurvey of the DAC flora; the computation of taxa relevant to the questions posed (floristics); comparisons between the DAC and PC on the basis of their Cape elements and environmental gradients; transformed cladistics; and the use of a Geographical Information System (GIS) to determine the current temperature regimes experienced by the floras of the Cape Region, DAC and PC.

Ecological work was conducted in summer rainfall areas to evaluate plant performance in a range of soils at three sites along a gradient of altitude. Reciprocal pot experiments were established in the DAC, PC and KwaZulu-Natal Midlands (the latter occurring midway in between the former), in order to investigate the interactions between altitude, temperature and substrate on plant productivity in sites known either to support or to exclude Cape elements. These interactions were quantified using a temperate test taxon with a strong Cape-centred distribution. Plant characters relating to morphology and nutrient content, and soil characters relating to fertility, were used as the basis for comparing treatment effects (soil-site interactions). Experimental field studies are helpful in determining the primary constraints in a given environment, particularly their relative importance along major geographic gradients (Vitousek, 1982; Vitousek & Sanford, 1986). Determining these relationships enables the quantification of trade-offs and elimination of dubious hypotheses (Tilman, 1990).

1.6 RESEARCH BENEFITS

Paying attention to particular patterns of consistent occurrence is important. Such patterns suggest a relationship between the prevailing conditions and the physiological and genetic composition of their communities (Mason, 1946), because particular forms are repeatedly generated when favourable conditions represent stable states inherent in the processes involved (Pollard, 1988). Determining the factors responsible for shaping the distribution patterns in question will provide insights into (1) the phytogeographical and ecological relationships shared between the floras and vegetation of the Cape Region, DAC and PC; (2) the dynamics of nutrient-poor systems, the results of either substrate or temperature; and (3) the movement of temperate taxa along high-altitude corridors in response to climatic shifts; and in doing so, (4) promote further awareness of two species-rich centres of phytodiversity.

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'The flora of the Drakensberg .... has aroused the interest and curiosity of botanists for many years. A number of species are also common to the Cape and other mountain areas of Africa.'

Trauseld (1972)

'(The Cape flora) is so distinctive that it is possible to recognise as belonging to it plants or groups of plants which occur in stations quite outside its main area. They are chiefly on mountains along the east side of Africa, and are found as far as the Equator and in Abyssinia and Madagascar. It must be pointed out that these outliers of the Cape flora are floristic groups, and not usually outlying patches of the characteristic Cape vegetation.'

Adamson (1947)

CHAPTER 2[a]

HISTORICAL ASPECTS AND PHYTOGEOGRAPHY

2.1 INTRODUCTION

The flora of 'Capensis', referred to as the Cape Floristic Region (CFR) *sensu* Van Wyk & Smith (2001) and Goldblatt & Manning (2002), occupies the Mediterranean to semi-Mediterranean Cape Region of South Africa (31° 00′ - 35° 00′S; 18° 00′ - 27° 00′E) (Taylor, 1980; Linder *et al.*, 1993; Goldblatt & Manning, 2000). This temperate region was long considered to house the smallest of the world's six floral kingdoms, the others being the Holarctic (Boreal), Palaeotropic, Neotropic, Australasian and Antarctic Kingdoms (Takhtajan, 1986). However, the concept of a 'Cape Floral Kingdom' is not universally accepted (Goldblatt & Manning, 2000, 2002). Encompassing only 3.5% (c. 90 000 km^2) of southern Africa (0.04% of the world's land surface), this region houses 44% (c. 9030 species in 990 genera) of southern Africa's vascular flora, exceeding all size-comparable regions of the world (Goldblatt & Manning, 2000, 2002). Six families, c. 162 genera (16%) and c. 6200 species (69%) are considered endemic to the CFR (Cowling & Hilton-Taylor, 1997; Cowling & Heydenrych, 1999; Goldblatt & Manning, 2002).

High species-richness has resulted in communities with high alpha diversity (Taylor, 1972, 1980; Linder, 1985a) and high beta and gamma diversity for the region as a whole (Kruger, 1979; Taylor, 1980; Linder, 1985a; Cowling & Richardson, 1995). The CFR is therefore recognised as a global epicentre of biodiversity (Cowling *et al.*,

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[a] Based on: CARBUTT, C. & EDWARDS, T. J. 2001. Cape elements on high-altitude corridors and edaphic islands: historical aspects and preliminary phytogeography. *Systematics and Geography of Plants* **71**: 1033-1061.

1992; Cowling & Richardson, 1995) and is treated as a distinct phytogeographic unit, supported by White's (1978) recognition of the CFR as one of six major southern African floristic regions. The CFR is loosely equivalent to the Fynbos Biome[a] of Rutherford & Westfall (1994) and Low & Rebelo (1996), although the exact boundaries of the Fynbos Biome are often disputed (Moll *et al.*, 1984, cited in Moll & Bossi, 1984).

2.2 CAPE-LINKING ELEMENTS: DEFINITIONS

The phytogeographical literature relating to sub-Saharan Africa makes numerous reference(s) to Cape (≈ fynbos) elements in various regional floras (Weimarck, 1941; Levyns, 1958, 1964; Hedberg, 1961, 1965; Wild, 1964, 1968; Brenan, 1978; Hilliard, 1978; Killick, 1978a; Hilliard & Burtt, 1987). Widespread use of the term 'fynbos' (also referred to as 'macchia'), coined by Bews whilst describing the 'fynbosch' shrublands of South Africa (Bews, 1916: 137), has often led to confusion and debate (Moll & Jarman, 1984a). For example, Kruger (1979), Moll & Jarman (1984a) and Cowling & Richardson (1995) argued that the absence of a significant restioid element outside of the CFR disqualifies use of 'true' fynbos terminology elsewhere. Instead, these authors refer to 'grassy fynbos' of the Afromontane region to distinguish it from 'Cape' fynbos. Cowling (1984) and Moll & Jarman (1984a) refer to 'Cape fynbos' and 'Afromontane fynbos' for the CFR and high-altitude regions of southern Africa

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[a] The Fynbos Biome comprises fynbos and renosterveld vegetation; the CFR includes, in addition to the former, enclaves of succulent Karoo vegetation, Afromontane forest, and at its eastern limit, subtropical thicket (Goldblatt & Manning, 2000; Van Wyk & Smith, 2001).

respectively. Despite these subtle distinctions, the general consensus amongst botanists is that all evergreen, sclerophyllous vegetation in Africa may be categorised as fynbos (Moll & Jarman, 1984a). Preferably, application of 'fynbos' terminology to shrubland vegetation should only be applied if the vegetation in question is floristically characterised by species, genera or families that are of Cape affinity and physiognomically by the occurrence of either ericoid, proteoid and restioid elements (Moll & Jarman, 1984a). Fynbos is considered a unique form of heathland (Kruger, 1979; Specht, 1979; Boucher & Moll, 1981; Moll & Jarman, 1984b), a view which has raised objections (e.g. Cowling & Holmes, 1992).

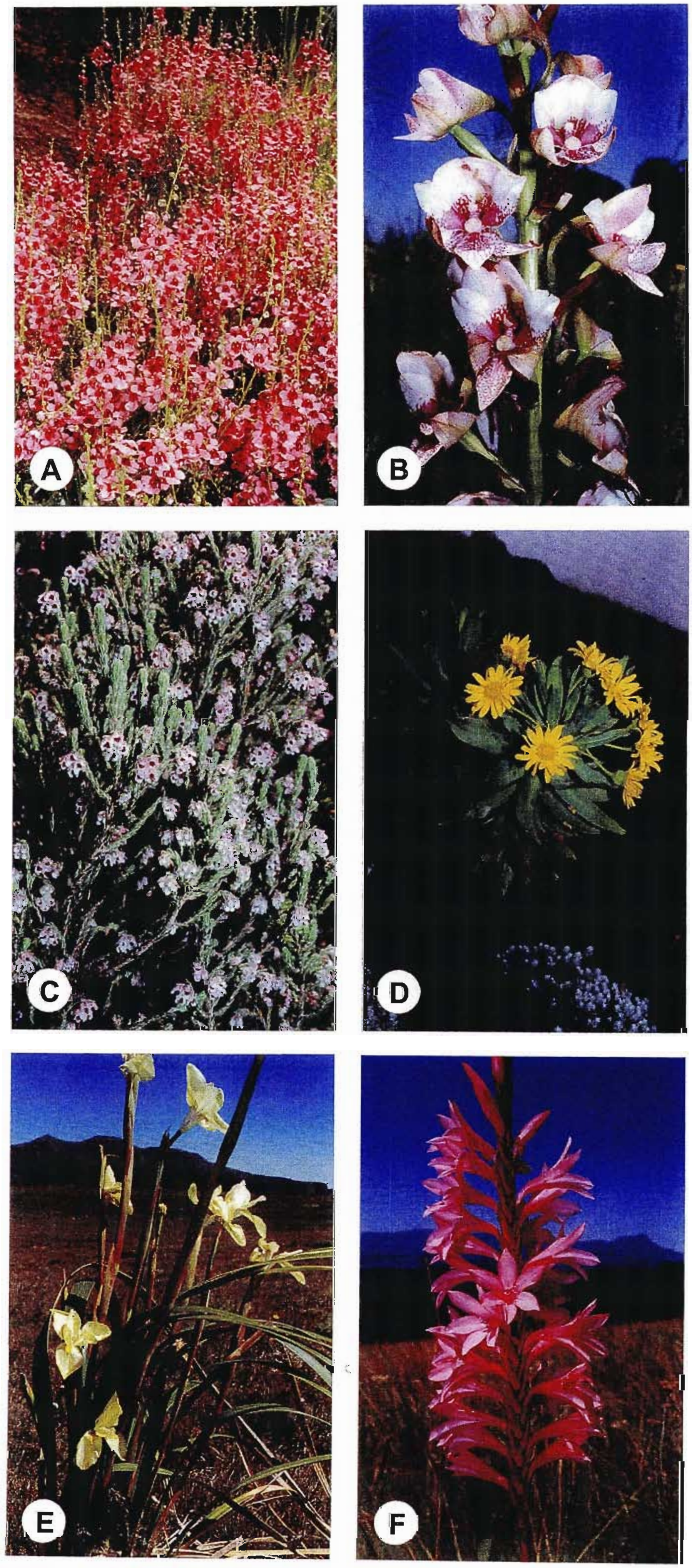
Definitions concerning the term 'Cape elements' are less prevalent. Cape elements are defined as taxa, usually genera, whose species are most heavily concentrated in the CFR (Fig. 2.1). Any reference to 'fynbos' or 'heathy shrublands' in the summer rainfall region of southern Africa is to describe this vegetation as one physiognomic component of a larger group of taxa known as 'Cape elements', without trying to jeopardise the distinction between floristics and physiognomy.

2.3 CAPE ELEMENTS ON HIGH-ALTITUDE CORRIDORS

2.3.1 OVERVIEW OF THE AFROMONTANE PHYTOCHORION

Remarkable continuity is a feature shared across the temperate floras of Africa, particularly with respect to their ecological relationships and phytogeographical patterns (White, 1981; Linder, 1990). Despite the distances between adjacent highlands (White, 1981), the homogeneity of physiognomy is produced by a suite of shrubby and herbaceous taxa that are common to most montane areas of Africa

Fig. 2.1. Examples of Cape elements from the Drakensberg Alpine Centre and Pondoland Centre. A. *Diascia* Link & Otto; B. *Disa* Berg.; C. *Erica* L.; D. *Euryops* Cass.; E. *Moraea* Mill.; F. *Watsonia* Mill.


A
B
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F

(Meadows & Linder, 1993). Much of the Afromontane vegetation (Fig. 2.2C & D), especially of the southern Afromontane region, is characterised by a mosaic of forest patches ('islands') in a 'sea' of grassland, with or without heathland elements (Meadows & Linder, 1989, 1993). Furthermore, the vegetation of the tropical African highlands is partitioned into a number of 'belts' that change with altitude: the alpine (Fig. 2.2A), ericaceous and forest (Fig. 2.2D) belts (Hedberg, 1955). Whether or not the alpine belt should be included within the boundaries of the Afromontane region, or whether or not the alpine belt should be lumped with the ericaceous belt to form the 'altimontane' belt (Grimshaw, 2001), are peripheral issues[a] (see also Section 2.3.5 for further details).

The Afromontane region of Africa (Fig. 2.3) is an archipelago-like regional centre of endemism with 3000 (75%) of its 4000 species considered endemic. Familial and generic endemism, however, is extremely low (White, 1983). Beentje *et al.* (1994) refer to the 'Afromontane Regional Centre of Endemism' which is considered the product of a complex evolutionary history and obscure origins (White, 1981). The delimitations of this phytochorion, completed by White (1978), and later fine-tuned (White, 1993, cited in Friis, 1998), are considered robust and testable, corroborated by numerical pattern analyses (Linder, 1998), large-scale spatial patterning of distributional data (Linder, 2001), and by avian zoochoria of forest elements in tropical Africa (Dowsett-Lemaire & Dowsett, 1998). A comprehensive

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[a] It appears that the Afroalpine and Afromontane regions are lumped together in the broader, phytogeographic context, while treated separately on a finer level to differentiate between the alpine vegetation of tropical Africa and the forest vegetation of lower elevations (cf. White, 1978; Hedberg, 1997).

Fig. 2.2. Vegetation of the highlands of north-east Africa. A. Afroalpine vegetation (Sanetti Plateau, Bale Highlands, Ethiopia); B. *Lobelia rhynchopetalum* Hemsl., endemic to the Afroalpine region of Ethiopia; C. *L. gibberoa* Hemsl., a forest-dwelling giant lobelia of the Afromontane region, restricted to tropical Africa; D. Afromontane vegetation (Harenna Forest, Bale Highlands, Ethiopia).

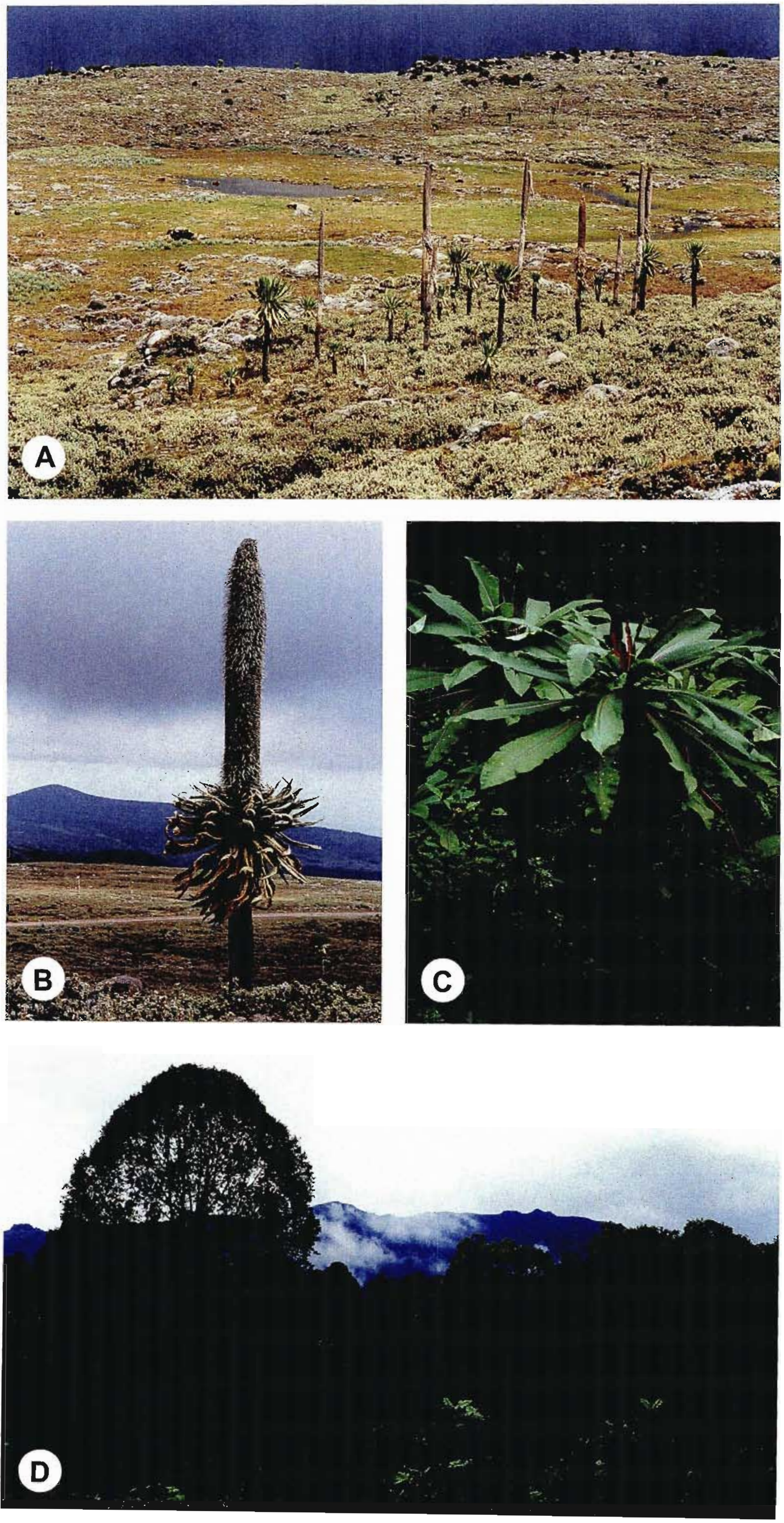
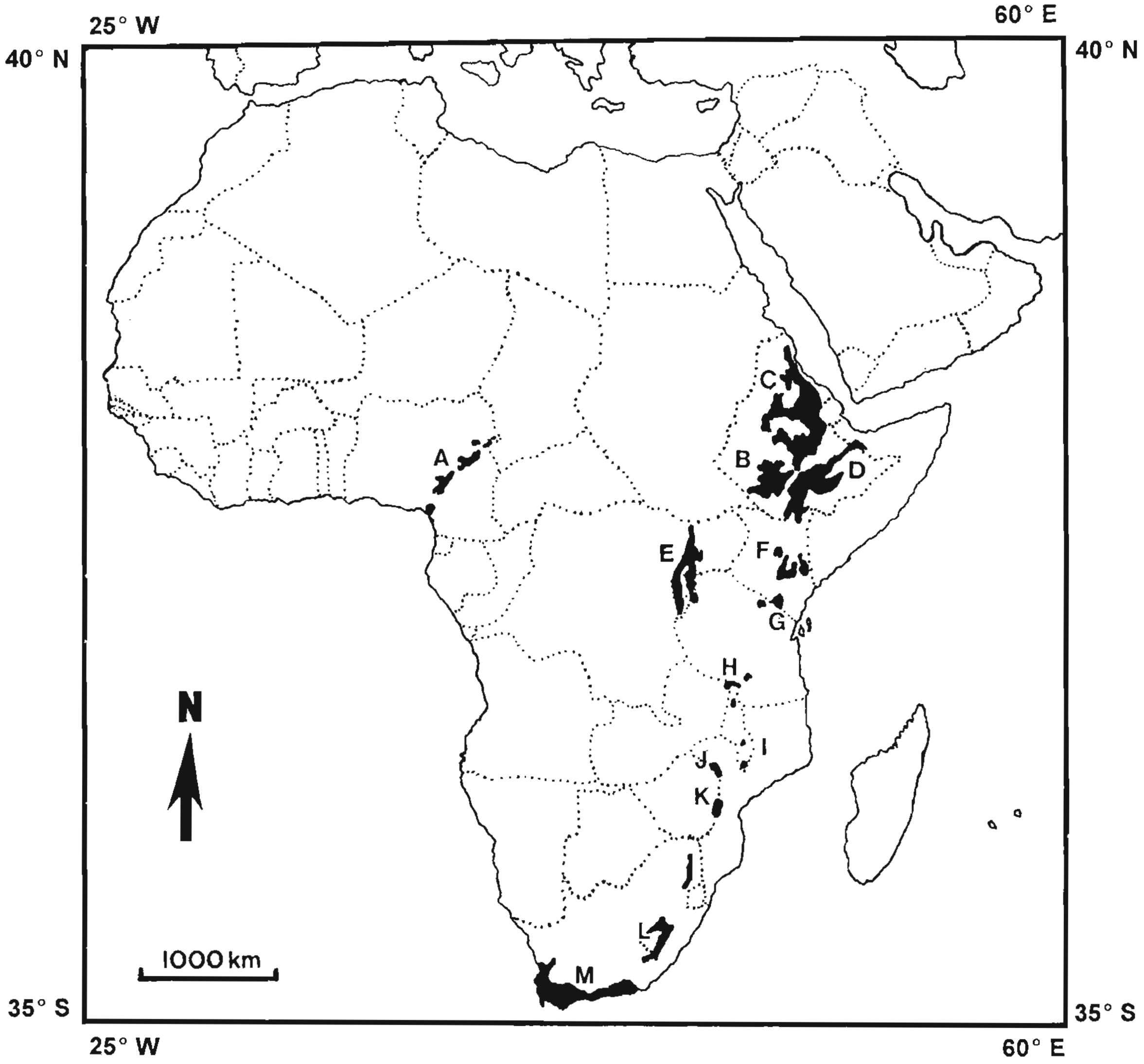

A
B
C
D

Fig. 2.3. The phytogeographical limits of the Afromontane region (A - L) according to White (1983), Linder (1990) and Hedberg (1994), and the Cape Floristic Region (M) according to Goldblatt & Manning (2000). A, Cameroun Mountains; B - D, Ethiopian Highlands (north-east Africa - Ethiopia); B, Coqe Mountains; C, Mangestu (4072 m)-Choke (4113 m)-Mt. Guna (4225 m)-Semien (4550 m)-Mt. Abuna Yosef (4190 m)-Mt. Abuye Meda (4012 m)-complex; D, Mt. Kaka (4190 m)-Mt. Bada (4036 m)-Bale Mountains (4321 m)-complex; E, Ruwenzori Mountains (Mt. Stanley - Uganda/Democratic Republic of Congo - 5109 m); F, Mt. Elgen-Aberdare-Mt. Kenya (Kenya - 5199 m)-complex; G, Mt. Kilimanjaro (Tanzania - 5890 m); H, Nyika Plateau (MalaŴi - 2607 m); I, Mt. Mulanje (MalaŴi - 3001 m); J, Nyanga Mountains (Mt. Nyangani, Zimbabwe - 2593 m); K, Chimanimani Mountains (Mt. Binga, Zimbabwe - 2440 m); L, Drakensberg Alpine Centre (Thabana Ntlenyana - 3482 m); M, Cape Floristic Region (CFR). Note: Stippled lines represent international boundaries. All phytogeographical domains are delimited by black shading. Maximum peak heights are listed for most peaks. Other significant mountainous areas not featured include Mt. Meru (Tanzania - 4566 m); Virunga Volcanoes, Karisimbi (Uganda/Rwanda/Democratic Republic of Congo - 4507 m); Mt. Elgon (Kenya/Uganda - 4315 m); Aberdare Mountains (Kenya - 3900 m); and Mt. Guge (Ethiopia - 4200 m) (adapted from Hedberg, 1994).


25° W
60° E
40° N
40° N
C
A
B
D
E
F
G
H
N
I
J
K
L
1000 km
M
35° S
35° S
25° W
60° E

account concerning the development of African chorology is presented by Friis (1998).

Chapman & White (1970) extended the Afromontane region to the Cape Region in South Africa. The series of Afromontane forest patches in South Africa, stretching from the Soutpansberg Centre in the north to the Outeniqua Mountains in the south, are included in the Drakensberg Afromontane Regional System (CPD site Af67) (Beentje *et al.*, 1994).

Linder (1990, 1994) proposed recognition for the 'Afrotemperate' region to combine sub-Saharan Africa's two temperate floras, the Cape flora and the Afromontane flora, because they are not clearly distinguishable on ecological and floristic grounds. Within this unified region, three localised centres of endemism are recognised: the CFR Centre, the Afromontane Centre, and the Drakensberg Centre. This phytogeographical classification of the temperate flora of Africa introduces a pan-African classification, thereby integrating phytogeographical and ecological concepts, and provides a framework for testing various hypotheses on its composition and origin(s) (Linder, 1990). This framework was adopted to explain the occurrence of Cape elements at high-altitude (using the Drakensberg Alpine Centre) and on edaphic islands at low altitude (using the Pondoland Centre).

2.3.2 THE AFROALPINE CONNECTION

The term 'Afroalpine' was first assigned to the species-poor flora characterised by giant life-forms (*Lobelia* and *Senecio* spp.) occurring on (mostly) volcanic mountains (> 3000 m) along the highlands of east and north-east tropical Africa (14° N - 6° S;

25° E - 40° E) (Hauman, 1933, 1956, cited in Hedberg, 1961) (Fig. 2.2A & B). This disjunct tropical high-altitude flora was first recognised as a regional centre of endemism by Hedberg (1961) (81% endemism and four endemic genera) and hence an independent Afroalpine region. Its flora comprises c. 300 - 350 vascular plant species (White, 1978). The major vegetation types of the Afroalpine region are moist *Dendrosenecio* woodland, *Helichrysum* and *Alchemilla* scrub, *Carex* bogs and tussock grasslands (Hedberg, 1994, 1997).

2.3.3 ALPINE VEGETATION IN SOUTHERN AFRICA?

The term 'alpine' has been used by chorologists, ecologists and palynologists in southern Africa to describe the vegetation of mountain summits in the Cape Region (Marloth, 1902; Schelpe, 1946), KwaZulu-Natal (West, 1949; Killick, 1963; Edwards, 1967; Acocks, 1988) and the Lesotho Malotis (Van Zinderen Bakker, 1955, 1981, 1983; Jacot Guillarmod, 1971; Herbst & Roberts, 1974; Acocks, 1988).

The occurrence of true alpine vegetation in southern Africa, and whether or not it should form part of the Afroalpine region, has often been questioned. Marloth (1902), on ascending selected high peaks of the Cape Region, noted an increasing incidence of alpine growth forms from c. 1800 m. However, the ubiquity of xerophytic taxa extending to lower elevations, and the absence of permanent snow deposits on peaks during winter, led Marloth (1902) to reject the possibility of a distinct alpine zone. Bews (1916), however, viewed the vegetation of the Cape mountain summits as 'alpine' because of their characteristic alpine growth forms (i.e. cushions, mat-forming dwarf shrublets, rosettes etc.). Botanical research of the Klein Swartberg (c.

2000 - 2100 m) in the central Cape Region (McDonald *et al.*, 1993) supported Marloth's (1902) viewpoint, and resulted in the application of 'sub-alpine' terminology to the high-altitude vegetation of the Cape Region (Linder *et al.*, 1993). The widespread occurrence of xerophytic traits amongst Cape taxa is probably an adaptation to summer drought and is preadaptive to the alpine environment. These factors may explain the lack of abrupt altitudinal zonation in the high-altitude vegetation of the Cape Fold Mountains, as noted by Marloth (1902), Linder *et al.* (1993) and McDonald *et al.* (1993).

The Drakensberg Alpine Centre, especially its north-eastern portion (≈ KwaZulu-Natal/Lesotho escarpment), does exhibit a degree of altitudinal zonation, albeit because the towering basalt cliffs of the escarpment clearly separate sub-alpine grasslands from diminutive alpine heathlands. This dramatic rise in altitude with associated steep changes in other environmental gradients is expected to form a sharp ecological boundary, inducing an associated change in growth form to 'alpine'. Killick's designation of 'alpine' terminology was used in the ecological sense to demarcate vegetation zones (Killick, 1963, 1978a, 1978b, 1994) and was based on climatic data (Killick, 1963, 1978b, 1978c), in similar fashion to Marloth (1902). These altitudinally-induced changes in vegetation, however, are not as abrupt as those documented for the East African Mountains (Hedberg, 1997) such as Mt. Elgon on the Kenya/Uganda border (Hamilton & Perrott, 1981), as well as Mt. Cameroun in West Africa (Richards, 1963) and MalaŴi (Chapman & White, 1970).

2.3.4 AFROALPINE CONNECTION WITH SOUTHERN AFRICA?

The Afroalpine flora, treated initially in isolation (e.g. Hedberg, 1955), was later investigated by Hedberg (1961, 1965, 1986 & 1994) and Linder (1990) for its phytogeographical affinities. Hedberg (1961, 1965) recorded some 25 Afroalpine species as having connections to the mountains of southern Africa (16 with South Africa), and concluded that the Afroalpine flora of tropical Africa comprises a 10% southern African element (Table 2.1). This low percentage has resulted in the Afroalpine and southern alpine regions being considered distinct (Edwards, 1967; Hilliard & Burtt, 1987). This view was supported by White (1983), who preferred the term 'altimontane' to differentiate vegetation above the tree-line in southern Africa (the term 'altimontane' was also adopted in a different context by Grimshaw as mentioned previously). Although Killick (1978a) initially regarded the southern alpine region as being Afroalpine, his subsequent views recognised it as the 'Drakensberg Alpine Region' (DAR) (Killick, 1994), because of its strong Cape ties and endemic element. This distinction is reiterated with the DAR being further recognised as an official centre of diversity and endemism, namely the 'Drakensberg Alpine Centre' (DAC) (Van Wyk & Smith, 2001). 'DAC' is synonymous with earlier names such as the 'Eastern Mountain Region' in a southern African context (Phillips, 1917) and the 'South-eastern Mountain Regional Mosaic' in an African context (Hilliard & Burtt, 1987). Sub-regions within the greater DAC should still be referred to as 'Drakensberg' and not 'DAC' (e.g. 'KwaZulu-Natal Drakensberg').

The ecological constraints of the northern and southern alpine regions also set them apart (Beentje *et al.*, 1994). The alpine climate of southern Africa is seasonal, experiencing low mean temperatures, wet summers and abundant snow during winter (Tyson *et al.*, 1976). The climate of the high-altitude tropics is characterised by significant daily temperature ranges repeated throughout the year (Hedberg, 1964; Sarmiento, 1986). Reflective of their environment are the 'giant' life forms of *Lobelia* and *Senecio* in East Africa (Hedberg, 1964; Mabberly, 1986) and the convergent *Espeletia* and *Puya* of the Andean Páramo (Meinzer & Goldstein, 1986). The strong possibility of nocturnal freezing necessitates pachycaulous leaf architecture. Large caulescent leaf rosettes insulate the developing shoot apex whilst thick bark and a marcescent collar of leaves insulate the stem (Hedberg, 1964; Mabberley, 1986; Meinzer & Goldstein, 1986). Warm daytime temperatures probably release adequate soil nutrients to sustain the large plants (Hedberg, 1964). The context of local environment therefore needs to be applied in the interpretation of adaptive syndromes.

Others, however, have regarded the two alpine regions as synonymous; the only differences relate to nomenclatural distinctions for a southern context. For example, the prefix 'austro' was coined by Coetzee (1967) to distinguish the southern Afroalpine element from the tropical Afroalpine element (cited in Hilliard & Burtt, 1987). Van Zinderen Bakker & Werger (1974) applied the term 'Austro-Afroalpine' to the bogs of Lesotho, while Werger (1978) suggested that chorologists term the southern African Afroalpine region the 'Austral Domain of the Afroalpine Region' and the tropical East African Afroalpine region the 'Central Domain of the Afroalpine Region'. This account considers the southern African alpine region as being distinct from the northern African ones, and follows the 'DAC' terminology of Van Wyk & Smith (2001).

Table 2.1. Breakdown of the phytogeographical elements highlighting the complex derivation of the Afroalpine flora of tropical East Africa (adapted from Hedberg, 1961, 1965, 1986, 1994). Note: *The Afroalpine and Afromontane elements are sometimes combined (e.g. Hedberg, 1997). **The southern African element comprises the South African and Cape elements.

Element	No. of taxa	Percentage of total (%)
Pantemperate (subcosmopolitan)	87	33
Afroalpine* (endemic)	52	20
Northern Hemisphere (Boreal)	34	13
Afromontane*	30	12
Southern African**	**25**	**10**
Mediterranean	18	7
Himalayan (Siwalik)	8	3
Southern Hemisphere	6	2
	$\sum$ = 260	**$\sum$ = 100%**

2.3.5 'AFROALPINE AND AFROMONTANE': ONE DELIMITATION OR TWO?

One must decide whether or not the Afroalpine and Afromontane regions are synonymous. Weimarck (1941), White (1978) and Hedberg (1997) viewed the Afroalpine and Afromontane regions as being only marginally different, resulting in their holistic treatment as a single phytogeographic unit, with distinctions being made only on ecological grounds. Others, however, have regarded them as separate. For example, the DAC above 1800 m was considered Afroalpine (Killick, 1978a), whilst that below was considered Afromontane (White, 1978). Hilliard & Burtt (1987) suggested that the entire DAC designated as 'Afroalpine' by Killick (1978a) be assigned to the Afromontane region. This study follows the views expressed in the footnote relating to Section 2.3.1.

2.3.6 CAPE ELEMENTS ON HIGH-ALTITUDE CORRIDORS

The Afromontane and Cape regions share similar ecological niches (Linder, 1990); it is therefore not surprising that many Cape elements occur in the Afromontane highlands, in cool environments where rainfall is high and soils are leached (Brenan, 1978; Killick, 1978a; Taylor, 1978, 1980; Meadows & Linder, 1989; Cowling & Richardson, 1995). For example, c. 45 of the 114 *Protea* species grow outside of the CFR (Beard, 1963, 1993; Rourke, 1980), predominantly as members of either *Protea* savannah (plateau woodland) or montane grasslands and high-altitude fynbos of the Afromontane highlands (Beard, 1959, 1963, 1993; Rourke, 1998). Similarly, although the CFR accounts for 657 species of *Erica* (Goldblatt & Manning, 2002), c. 115 species occupy the highlands of Africa and Madagascar (Oliver, 1989; 1991). The general prominence of Cape elements at high-altitude is noteworthy (Figs 2.4 & 2.5).

The notable exception to an Afromontane distribution is the occurrence of Cape elements on the Auas Mountains (c. 2400 m), part of a highlands complex south-east of Windhoek in Namibia (Rennie, 1936). This range comprises pre-Cambrian quartzites and is believed to have served as a western track of migration to the Huilla Plateau of the Angolan Highlands (Rennie, 1936; Adamson, 1947).

Cape elements occur on mountains in the dry regions immediately north of the CFR, especially on Kamiesberg in Namaqualand (Adamson, 1938; Kruger, 1979; Rourke, 1990) and on the quartzitic ridges and mountain summits of the Little Karoo (Levyns, 1964; Kruger, 1979). Cape elements in the summer rainfall region of South

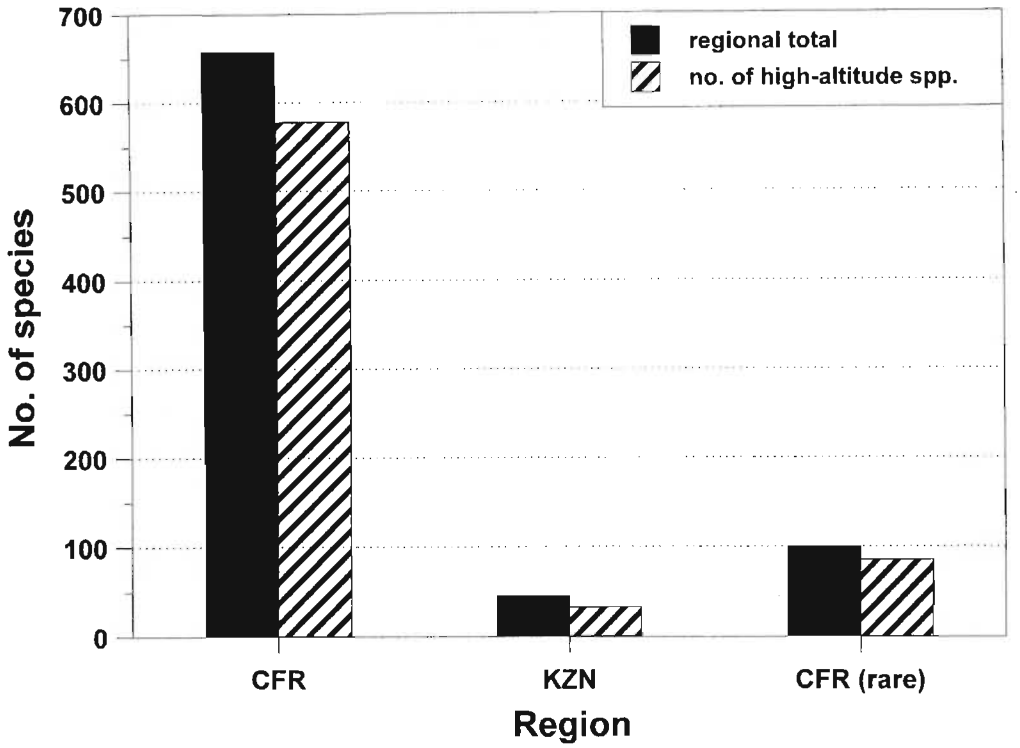


Fig. 2.4. Comparative account of the number of *Erica* species (Ericaceae) for the Cape Floristic Region (CFR) (after Goldblatt & Manning, 2002) and KwaZulu-Natal (KZN) (after Schumann & Kirsten, 1992), representing both total numbers and high-altitude specialists. High-altitude limits: CFR $\geq$ 800 m; KwaZulu-Natal Drakensberg $\geq$1800 m. CFR (rare) refers to the number of rare and threatened *Erica* spp.

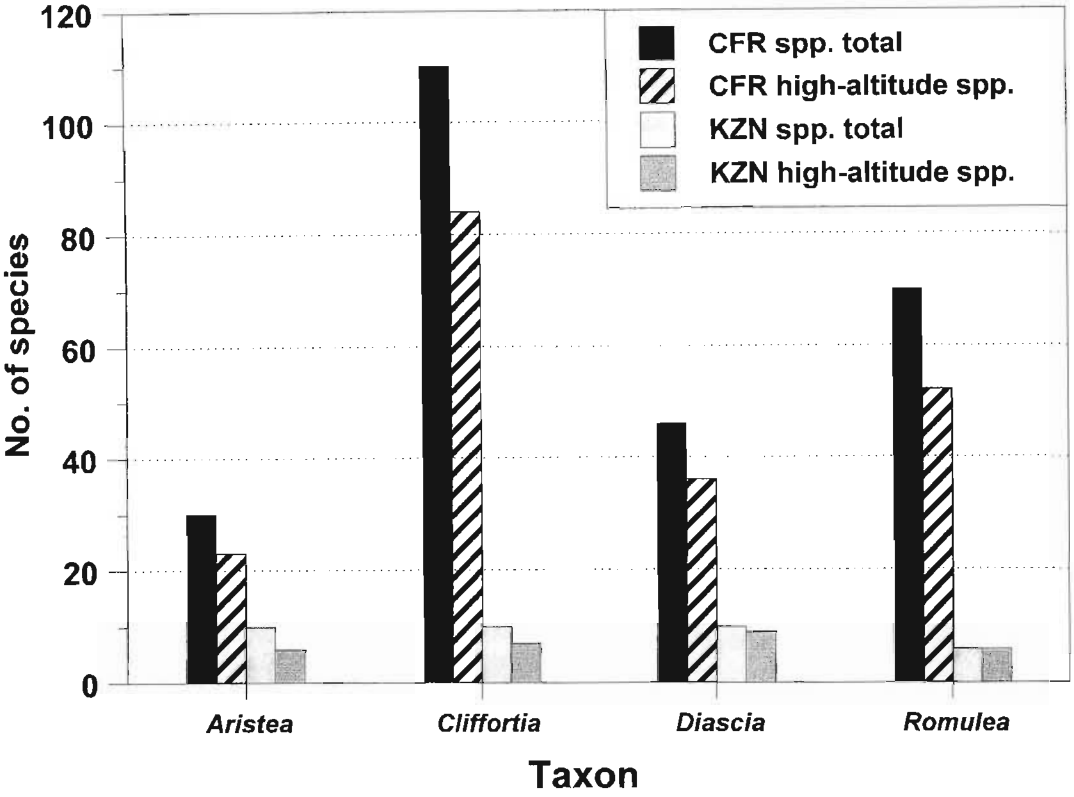


Fig. 2.5. Comparative account of four genera in the Cape Floristic Region (CFR) and KwaZulu-Natal (KZN), representing both total numbers and high-altitude specialists. High-altitude limits: CFR ≥ 800 m; KwaZulu-Natal Drakensberg ≥1800 m. Taxon numbers follow the authorities listed in Tables 2.13 - 2.15 and 2.17.

Africa are also associated with high-altitude habitats. The Amatole Mountains in the Eastern Cape (Story, 1952; Beard, 1958; Trollope, 1971; Phillipson, 1987); Thaba 'Nchu in the south-eastern Free State (Roberts, 1966; Du Preez & Bredenkamp, 1991); Korannaberg in the eastern Free State (Du Preez & Bredenkamp, 1991; Du Preez, 1992) and the Maloti Mountains of Lesotho[a] (Jacot Guillarmod, 1962; Killick, 1979; Schmitz-Ruch, 1984; Talukdar, 1994) all accommodate Cape elements.

Furthermore, Cape elements of the DAC contribute significantly to all three of its vegetation belts, and form part of two of three climax vegetation types. The 'heathy' Cape elements of the montane belt are referred to as 'montane heathlands' (Killick, 1979); the rank stands of sub-alpine vegetation (physiognomically similar to that of the Fynbos Biome) are referred to as 'subalpine heathlands' (Killick, 1979); and the diminutive shrubland communities of the summit area are referred to as 'alpine heathlands' (Killick, 1979, 1997; Moll & Jarman, 1984b). Montane heathlands in the DAC are often associated with Clarens Formation Sandstone, occurring as patches atop the sandstone cliffs of the 'Little 'Berg'. They were referred to as 'Cave Sandstone Scrub' (Killick, 1963), but have been updated as 'Clarens Heathlands' (Carbutt & Edwards, 2001). Although the application of heathland terminology to fynbos vegetation in South Africa has generally proved contentious (Cowling & Holmes, 1992), its application is in no way meant to invoke the northern hemisphere heathland concept in which ericaceous elements are dominant. Another contentious use of terminology is 'tundra'; it is generally considered spurious when referring to alpine environments (Körner, 2001), including those of southern Africa (Van Zinderen

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[a] The Maloti Mountains of Lesotho form part of the Drakensberg Alpine Centre

Bakker, 1981), but has been applied to the DAC summit (e.g. Killick, 1997).

Subalpine fynbos is more extensive in the northern KwaZulu-Natal Drakensberg than further south. These communities occur at Royal Natal National Park (especially along the ridges leading up to the Amphitheatre beyond the Tugela Valley and Vemvaan, Devil's Hoek and Dooley regions). The Tendele area of Royal Natal National Park supports climax fynbos on a steep, remote hillside in the Dooley-Tiger Falls area, at an altitude of c. 1800 m. This rank, sclerophyllous shrubland has not been burnt for 20 years (Ezemvelo KZN Wildlife, unpublished report) and includes numerous *Cliffortia* and *Erica* species. Similar taxa were noted at a *Widdringtonia* fynbos site at Giant's Castle, central KwaZulu-Natal Drakensberg. This expansive patch of fynbos has not been burnt in 40 years (Ezemvelo KZN Wildlife, unpublished report) and the absence of Afromontane forest elements indicates that this site is not seral to forest. Cathedral Peak (Mlambonja) Wilderness Area (Killick, 1963, 1978a, 1979; Edwards, 1967), especially the steep slopes of the Mlambonja-Xeni-Tseketseke continuum, the valley of the Delmhlwazini River, and further south, the upper region of Sani Pass of the Mkhomazana Valley (Killick, 1978b), all support subalpine fynbos communities.

In general, these fynbos patches occur from c. 1800 m (lower limit of Clarens Formation Sandstone) and extend into well-drained steep valleys and spurs, sometimes reaching the sub-alpine/alpine ecotone at c. 2800 m, usually adjacent to forest patches (at their lower limit) and/or rock bands which act as natural fire exclusion barriers. They contribute significant numbers of Cape elements in such habitats.

Cape elements have also been reported from the northern limit of the Drakensberg Range, particularly the Wolkberg Centre (Matthews *et al.*, 1993), Mariepskop (Van der Schijff & Schoonraad, 1971), the Sabie region (Deall & Backer, 1989) and Legalameeste Nature Reserve (Stalmans *et al.*, 1997).

Beyond the borders of South Africa, Cape elements have been reported from the Chimanimani and Nyanga Mountains (Wild, 1951, 1956, 1964, 1968; Phipps & Goodier, 1962), both of eastern Zimbabwe. The Chimanimani-Nyanga Centre (Van Wyk & Smith, 2001) is synonymous with the Inyangani Sub-centre of the CFR (Weimarck, 1941). Cape elements also occur on the solitary massif of Mt. Mulanje in south-eastern Malaŵi (Whyte, 1894; Chapman & White, 1970; Strugnell, 2002) and the high-altitude plateau of Nyika (2607 m) in northern Malaŵi (C. Willis *et al.*, unpublished data; Willis *et al.*, 2001). The north-eastern limit for Cape elements is the Ethiopian Highlands of tropical East Africa (Hedberg, 1961, 1965, 1986, 1994); their western limit are the mountains of Cameroun (Richards, 1963; Killick, 1979).

Beyond Africa, the distribution of Cape elements extends to the central highlands of Madagascar (Weimarck, 1941; Wild, 1964; Rourke, 1998; Lock, 2001) and to the Mascarene Islands of Mauritius, Rodrigues and Réunion (Weimarck, 1941; Cowling & Richardson, 1995). These Cape elements are mostly represented by species of *Aristea* and *Stoebe* and their closest relatives are taxa of the Drakensberg Range and the tropical African high-altitude regions (Weimarck, 1941).

2.4 STUDY REGION NO. 1: THE DRAKENSBERG ALPINE CENTRE[a]

2.4.1 GEOGRAPHY

White's (1978) classification of the Afromontane archipelago recognised seven regional mountain systems, of which the Drakensberg Range is the most southern. This range forms part of the Great Escarpment at the eastern periphery of the southern African plateau (Partridge & Maud, 1987), extending for almost 1000 km from Elliot in the south, to Tzaneen in north-eastern South Africa.

The DAC is a composite of the highest enclaves centred within the greater Drakensberg Range (Fig. 2.6). It straddles Lesotho and South Africa between 28°30' S - 31°20' S and 27°00' E - 29°40' E (Tyson *et al.*, 1976) and covers c. 40 000 km^2 (Killick, 1994). It includes the Eastern Cape Drakensberg and Witteberge, the KwaZulu-Natal Drakensberg, the Maloti Mountains of Lesotho and the eastern Free State (Fig. 2.7).

2.4.2 GEOLOGY AND CLIMATE

The geology of the DAC is relatively simple, consisting of horizontal strata of sedimentary and igneous deposits (Van Zinderen Bakker, 1981). The escarpment and plateau regions are dominated by igneous (≈ basalt) deposits of the Drakensberg Group. These early Jurassic basalts are remnants of lava flows that spread across most of Gondwana approximately 160 to 180 million years ago, during the initial Gondwana breakup (King, 1982; Whitmore *et al.*, 1999). They overly

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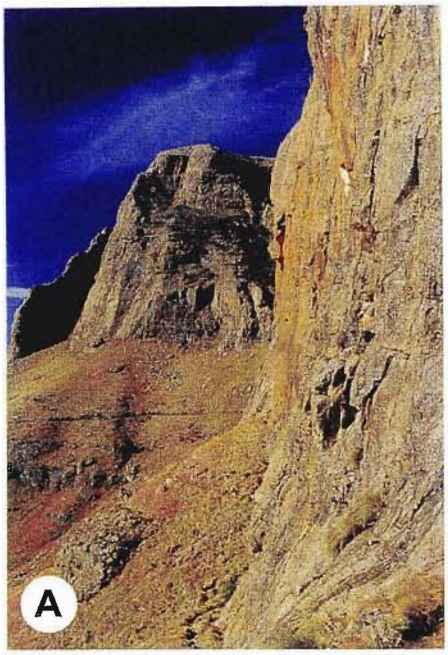
[a] FROM: CARBUTT, C. & EDWARDS, T. J. 2004. The flora of the Drakensberg Alpine Centre. *Edinburgh Journal of Botany* **60**: 581-607.

Fig. 2.6. High-altitude environments of the Drakensberg Alpine Centre. Seasons are indicated in parentheses. A. Sentinel Peak, Witsieshoek region (autumn); B. Bushman's Nek (winter); C. The Giant's Cup, Cobham (autumn); D. & E. The Twelve Apostles region, Sani Top (summer); F. Rhino Peak, Garden Castle (summer); G. Mlambonja Wilderness Area (summer); H. Amphitheatre summit, near Beacon Buttress (winter).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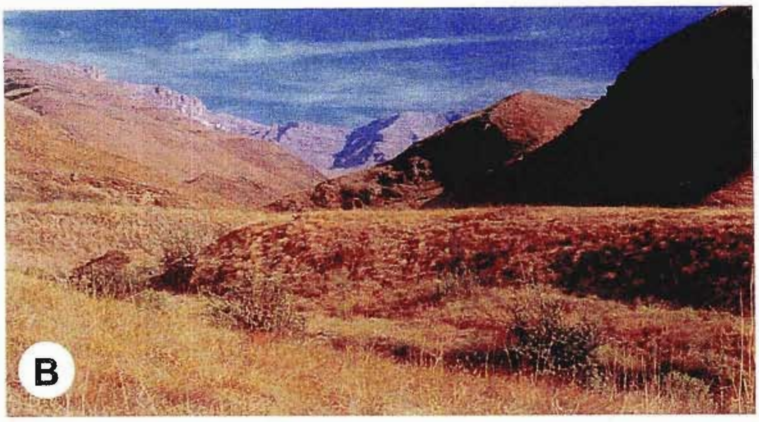
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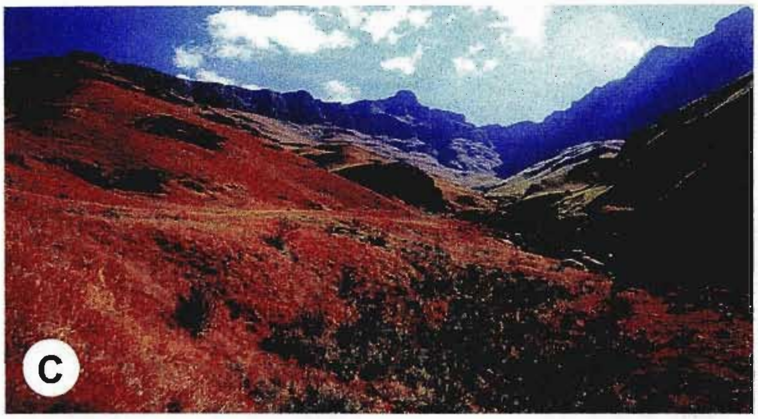
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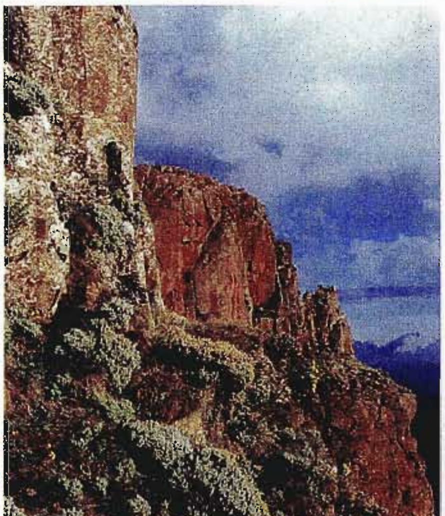
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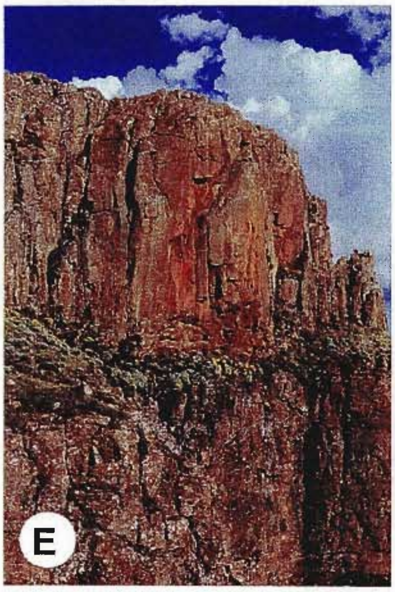
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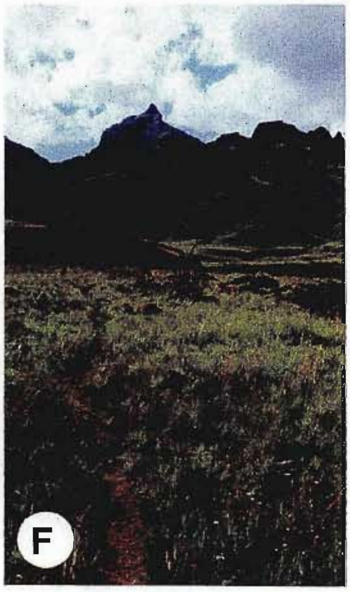
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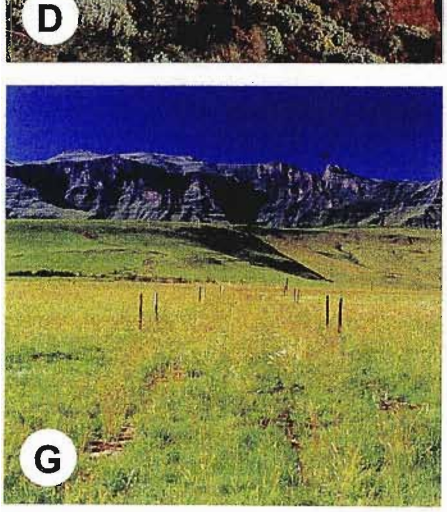
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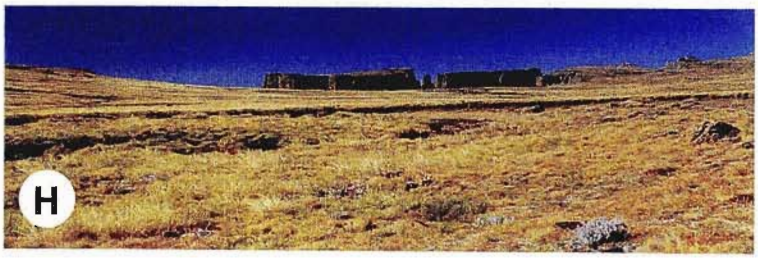
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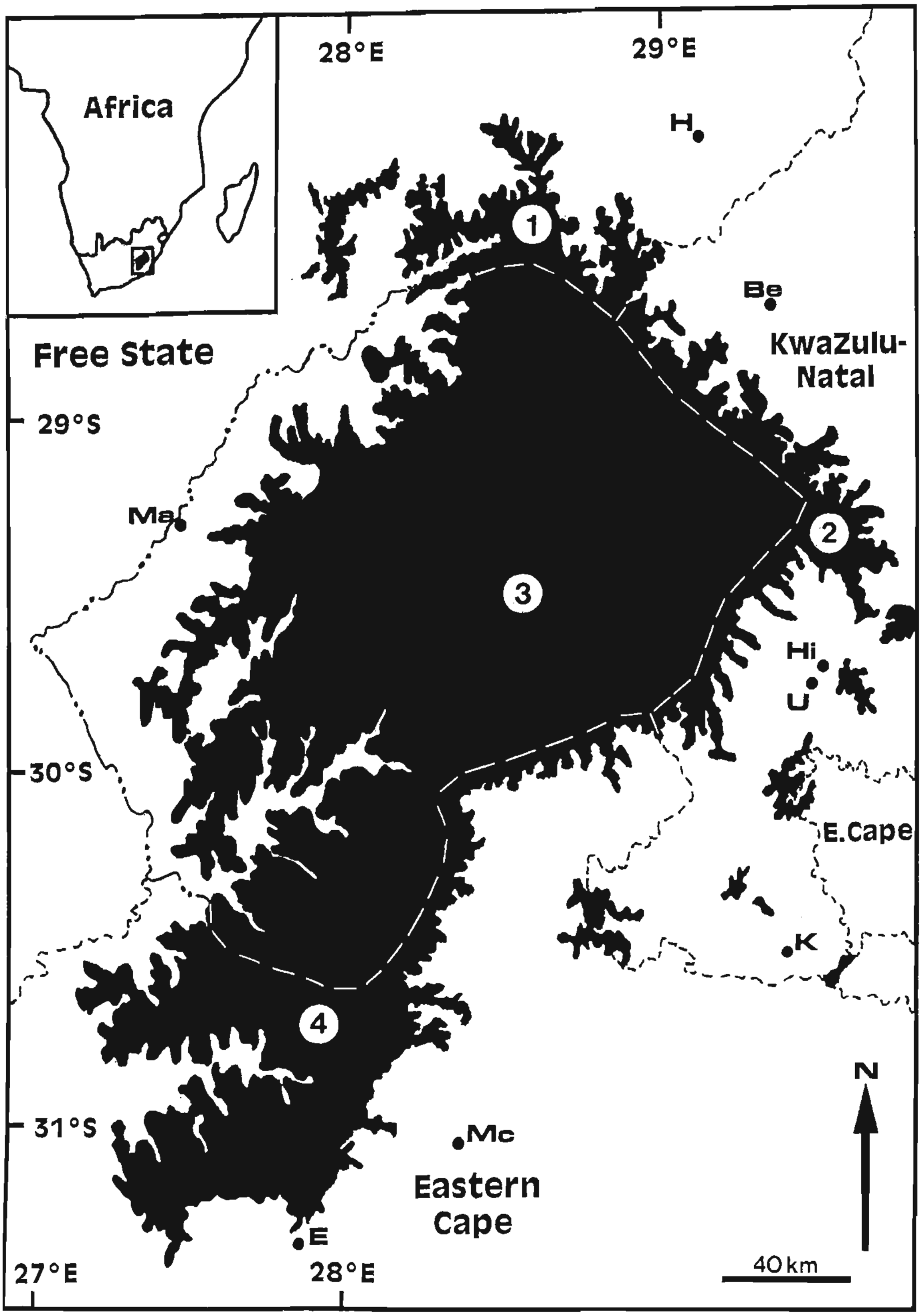
Fig. 2.7. The Drakensberg Alpine Centre (DAC) comprising (1) eastern Free State, (2) KwaZulu-Natal Drakensberg, (3) Lesotho Maloti Mountains, and (4) Eastern Cape Drakensberg and Witteberge. Adapted from Hilliard & Burtt (1987). Abbreviations for towns: Be, Bergville; E, Elliot; H, Harrismith; Hi, Himeville; K, Kokstad; Ma, Maseru; Mc, Maclear; U, Underberg.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sandstones of the Clarens Formation (previously Cave Sandstone). These aeolian sandstones were deposited during late Triassic desertification. Both igneous and sandstone deposits form part of the Karoo Supergroup (Whitmore *et al.*, 1999).

The climate is classified as temperate with summer rainfall. Mean annual rainfall varies from c. 640 mm to 1800 mm (Tyson *et al.*, 1976). The thin soils on the summit plateau are generally waterlogged during summer and are subjected to freeze-thaw processes during winter (Killick, 1994).

2.4.3 METHODOLOGY

The native and exotic floras of the DAC were compiled from several sources, using the flora accounts of Lesotho (Jacot Guillarmod, 1971; Kobisi & Kose, 2003), the southern KwaZulu-Natal Drakensberg (Hilliard & Burtt, 1987; Meter *et al.*, 2002) and the uKhahlamba-Drakensberg Park (Porter *et al.*, 1999), in conjunction with field guides to the trees (Pooley, 1993) and mountain flowers (Pooley, 2003) of the Eastern Region. The flora of the Eastern Cape Drakensberg is less well known and was further supplemented by inventories from quarter degree grid squares generated by PRECIS (National Herbarium, **Pre**toria **C**omputerised **I**nformation **S**ystem; Gibbs Russell, 1985). Species totals were further verified using Arnold & De Wet (1993), in combination with specific taxon treatments and with specimens lodged in the Natal University Herbarium (NU). Suspect records were omitted. The boundaries of the DAC follow the 1800 m contour limit used by Hilliard & Burtt (1987) and Van Wyk & Smith (2001), and include outlying enclaves such as Little Bamboo Mountain (2421 m), Kamberg (2095 m), Mahwaqa Mountain (2083 m) and the Ngele Range (2268 m).

Floristic ties between the southern KwaZulu-Natal Drakensberg and these outliers are strong (J. E. Granger, unpublished data), which further justifies their inclusion with the DAC. The 1800 m benchmark altitude was difficult to maintain, because the DAC's alpine regions spread to slightly lower elevations at its northern and southernmost limits (≥ 1700 m). The checklist arrangement conforms mostly to the Englerian system followed by Arnold & De Wet (1993), with Scrophulariaceae, Asparagaceae and Hyacinthaceae following Hilliard (1994, 1999), Fellingham & Meyer (1995) and Speta (1998) respectively. Lists of the native and exotic angiosperm floras of the DAC are presented as two appendices; both include infraspecific taxa and putative hybrids. All floristic analyses used only native taxa.

2.4.4 FLORA AND VEGETATION - HISTORICAL OVERVIEW

The DAC is regarded as being the only true alpine region in southern Africa (Linder, 1990), which, in conjunction with the CFR, constitutes the southern (Gondwanan) source of the temperate flora of Africa (Hilliard & Burtt, 1987; Linder, 1990, 1994). The flora of the DAC is an interesting repository for taxa of diverse origin, including both temperate and subtropical elements (Killick, 1963; Hilliard & Burtt, 1987). The DAC's close alliance with the CFR (Weimarck, 1941; Killick, 1978a; Hilliard & Burtt, 1987; Bainbridge *et al.,* 1991) is evident at the generic and tribal ranks, examples of the latter include the Orchidaceae - Disinae (Linder, 1983) and Scrophulariaceae - Manuleae (Hilliard, 1994). Studies on the floras of the Eastern Cape and KwaZulu-Natal Drakensberg have linked both to the CFR and Afromontane regions (Killick, 1963; Bester, 1998).

The DAC is recognised as one of southern Africa's eight 'hot-spots' of botanical diversity as indexed by species-richness and endemism (Cowling & Hilton-Taylor, 1994). PRECIS estimated the DAC flora at 2046 vascular plant species, with a subsequent total of 2153 vascular plant species (± 2000 angiosperms) given by Porter *et al.* (1999). No existing account has satisfactorily surveyed the entire DAC flora; previous accounts were either based on smaller regions occurring within the DAC or are outdated (e.g. Phillips, 1917) (Table 2.2). Determining the true size of its flora is very important in order to appraise its value as a centre of both diversity and endemism.

The plant diversity of the DAC may also be explained by its rich array of life and growth forms. The vegetation of the DAC is diverse because it includes both the mesic vegetation of the KwaZulu-Natal escarpment and the vegetation of the drier Eastern Cape Drakensberg and Lesotho interior. The rainfall gradient between the windward KwaZulu-Natal Drakensberg escarpment and the more leeward Lesotho and Eastern Cape interior (Carbutt & Edwards, 2001) appears to play a significant role in the distribution of taxa.

The DAC is located within the Grassland Biome (Rutherford & Westfall, 1994; Low & Rebelo, 1996), hence the high number of grass species and grassland forbs. Pockets of indigenous forest, however, are common, especially in the northern, warmer and wetter habitats of the DAC (Hilliard & Burtt, 1987), occupying south and south-east facing aspects, mostly on steep gradients in sheltered sites excluded from fire. The montane forests support ferns, mosses and other cryptogams, whilst hygrophilous, aquatic and lithophilic communities occupy the DAC's wetlands, tarns and rocky outcrops.

The phytodiversity of the DAC is accounted for by the altitudinal, climatic, topographic and edaphic gradients on a broad scale (Bainbridge *et al.*, 1991), and the multitude of micro-habitats (combinations of relief, aspect, exposure and slope angle) on a finer scale (Körner, 1999), which collectively present suitable ecological niches for prolific species coexistence.

Table 2.2. Summary of some regional angiosperm floras contributing to that of the Drakensberg Alpine Centre (DAC). The Eastern Mountain Region is loosely equivalent to the DAC. *Killick's (1963) study was centred in the Cathedral Peak Research Catchments, forming only a part of the Cathedral Peak Wilderness Area.

Study region	Families	Genera	Species
Eastern Mountain Region (Phillips, 1917)	91	466	1553
Cathedral Peak Wilderness Area* (Killick, 1963)	91	373	861
Lesotho (Jacot Guillarmod, 1971)	95	526	1537
Southern KwaZulu-Natal Drakensberg (Hilliard & Burtt, 1987)	91	404	1375
Eastern Cape Drakensberg (Bester, 1998)	116	506	1926
Drakensberg Alpine Centre (this survey)	**134**	**630**	**2520**

2.4.5 FLORISTIC ANALYSIS

The native flora of the DAC is richer than previously thought: 2818 taxa, most of which are angiosperms (c. 89%), with c. 7% bryophytes, c. 3% pteridophytes and 0.2% gymnosperms (Table 2.3). The native angiosperm taxa are listed in Appendix 2.1. The 2818 taxa are placed in 205 families and 781 genera ($\bar{x}$ = 3.6 species per genus) (Table 2.3). Dicotyledons constitute over half the families, genera and species (Table 2.3).

Species/genus indices are highest in the angiosperms, especially in the

Table 2.3. Synopsis of the native flora of the Drakensberg Alpine Centre.

							Angiosperms				
	Bryophytes		Pteridophytes		Gymnosperms		Monocotyledons		Dicotyledons		
	No.	%	No.	%	No.	%	No.	%	No.	%	Total
Families	47	23.0	21	10.2	3	1.5	29	14.1	105	51.2	205
Genera	114	14.6	34	4.4	3	0.4	205	26.2	425	54.4	781
Species	200	7.1	93	3.3	5	0.2	872	30.9	1648	58.5	2818

Table 2.4. Statistics relating to the native vascular floras of the Cape Floristic Region and southern Africa (from Goldblatt & Manning, 2002), KwaZulu-Natal (amended from Scott-Shaw, 1999) and the DAC (this survey). Inconsistencies with Tables 2.2 and 2.3 are due to figures for vascular plants being used here as opposed to angiosperms, to be consistent with Goldblatt & Manning (2002).

Region	Physical area (km^2)	Total species	Total genera	Species endemism (%)	Mean species/genus	Species/ 10^3 km^2	10 largest genera (%)
Southern Africa	2 674 000	20 367	2130	80.3	9.6	7.6	15.1
Cape Floristic Region	90 000	9030	990	68.7	9.1	100.3	21.4
KwaZulu-Natal	92 300	6000	1258	16.0	4.8	65.0	±15.0
DAC (this survey)	40 000	2618	667	15.7	3.9	65.0	17.2

monocotyledons, and lowest in the bryophytes and gymnosperms. The high proportion of bryophyte families relative to species is a reflection of the many small genera per family. By contrast, the monocotyledons are characterised by a large number of species relative to their number of families, possibly the result of rapid speciation in conjunction with the spread of the Grassland Biome (Meter *et al.*, 2002). The low overall contribution made by the gymnosperms is a feature common to southern Africa (see Arnold & De Wet, 1993).

The floristic diversity of the DAC approaches half of that in KwaZulu-Natal (c. 44%), almost a third of that in the CFR (c. 29%), and over a tenth of the diversity in southern Africa (c. 13%) (Table 2.4). The floras of the DAC and KwaZulu-Natal share many similarities, especially in terms of endemism, species/genus indices, species density and their 10 largest genera (Table 2.4). Species densities of the DAC and KwaZulu-Natal approach that of the CFR (Table 2.4), indicative of the richness of their floras relative to their physical area.

The number of exotic angiosperm taxa in the DAC is 166, or c. 6% of the total angiosperm flora (Appendix 2.2). The 166 taxa, 80% of which are dicotyledons, are placed in 32 families and 100 genera. Poaceae and Asteraceae contribute the most species, a reflection of the success of the two groups in general. Although not a true measure of species richness, amalgamating the native and exotic floras results in a flora of 2984 taxa. The spread of invasives has been accelerated by the accessibility of the DAC. Its many roads and mountain passes (e.g. Sani Pass) are disturbed sites that are easily colonized. Overgrazing by domestic animals and the predominance of agricultural lands within Lesotho has exacerbated the spread of invasives, all of which pose as serious threats to conservation efforts in the DAC.

2.4.6 LARGEST FAMILIES

The larger families contributing 1% or more species to the angiosperm flora are presented in Table 2.5. Collectively they contain c. 79% of the species and c. 65% of the genera. The seven largest families contribute over half of the angiosperm total (c. 52%). Monocotyledonous families form a large proportion of the seven largest angiosperm families (c. 47%) relative to their total representation in the angiosperm flora (c. 24%).

The Asteraceae are the largest contributor of species (c. 17%) and the second largest contributor of genera (c. 10%) to the angiosperm flora of the DAC (Table 2.5). Their dominance is a feature common to all floras of sub-regions within the DAC (Table 2.6) and to many other floras, including those of KwaZulu-Natal and the CFR (Goldblatt & Manning, 2002) and the Afromontane and Pondoland regions (Table 2.6). This family has readily speciated in the Grassland Biome (Meter *et al.*, 2002), the dominant habitat of the DAC. Radiation of the Poaceae in the DAC is not surprising in a grassland-dominated system. They are the second largest contributor of species (c. 11%) and the largest contributor of genera (c. 14%) to the angiosperm flora of the DAC (Table 2.5). The Poaceae also feature strongly in the flora of KwaZulu-Natal (Hilliard & Burtt, 1987), yet poorly in the CFR (Goldblatt & Manning, 2002).

Species/genus indices ≥ 10 are prevalent in six families (Ericaceae, Campanulaceae, Geraniaceae, Crassulaceae, Santalaceae and Asphodelaceae) (Table 2.5). These are medium-sized families dominated by the large genera *Erica*, *Wahlenbergia*, *Pelargonium*, *Crassula*, *Thesium* and *Kniphofia* respectively (Table 2.7).

Table 2.5. Ranking of the larger families that contribute 1% or more species to the native angiosperm flora of the DAC, together with the number of genera per family.

Rank	**Family**	**Total species**	**% of total**	**Total genera**	**% of total**	**Species/ genus**
1.	Asteraceae	430	17.1	65	10.3	6.6
2.	Poaceae	267	10.6	86	13.7	3.1
3.	Fabaceae	136	5.4	32	5.1	4.3
4.	Scrophulariaceae	133	5.3	31	4.9	4.3
5.	Orchidaceae	130	5.2	22	3.5	5.9
6.	Cyperaceae	122	4.8	20	3.2	6.1
7.	Iridaceae	97	3.8	14	2.2	6.9
8.	Asclepiadaceae	87	3.5	22	3.5	4.0
9.	Hyacinthaceae	55	2.2	16	2.5	3.4
10.	Asphodelaceae	50	2.0	5	0.8	10.0
11.	Lamiaceae	47	1.9	14	2.2	3.4
12.	Apiaceae	38	1.5	15	2.4	2.5
12.	Mesembryanthemaceae	38	1.5	5	0.8	7.6
13.	Geraniaceae	37	1.5	3	0.5	12.3
14.	Rubiaceae	36	1.4	20	3.2	1.8
15.	Ericaceae	35	1.4	2	0.3	17.5
15.	Hypoxidaceae	35	1.4	4	0.6	8.8
16.	Crassulaceae	34	1.3	3	0.5	11.3
17.	Santalaceae	32	1.3	3	0.5	10.7
18.	Euphorbiaceae	30	1.2	8	1.3	3.8
19.	Gentianaceae	28	1.1	3	0.5	9.3
20.	Brassicaceae	27	1.1	7	1.1	3.9
21.	Amaryllidaceae	26	1.0	9	1.4	2.9
21.	Campanulaceae	26	1.0	2	0.3	13.0
		$\sum$ = 1976	**$\sum$ = 78.5%**	**$\sum$ = 411**	**$\sum$ = 65.3%**	

Table 2.6. Comparisons of the five largest angiosperm families for a number of floras of the Eastern Region. See also details of the largest angiosperm families of the DAC (Table 2.5). Liliaceae have been used here by the various authors in the broadest sense. *The families of the Wolkberg Centre are those with the most endemics on quartzitic substrates only.

Eastern Cape Drakensberg (Bester, 1998)	**Southern KwaZulu-Natal Drakensberg (Hilliard & Burtt, 1987)**	**Northern KwaZulu-Natal Drakensberg (Killick, 1963)**	**Lesotho (Jacot Guillarmod, 1971)**
Asteraceae	Asteraceae	Asteraceae	Asteraceae
Poaceae	Poaceae	Poaceae	Poaceae
Fabaceae	Liliaceae	Liliaceae	Scrophulariaceae
Scrophulariaceae	Orchidaceae	Cyperaceae	Fabaceae
Orchidaceae	Scrophulariaceae	Scrophulariaceae	Liliaceae
Legalameeste (Stalmans *et al.*, 1997)	**Sabie (Deall & Backer, 1989)**	**Wolkberg Centre* (Matthews *et al.*, 1993)**	**Pondoland (Oribi Gorge & Umtamvuna) (Meter, 1998)**
Asteraceae	Asteraceae	Liliaceae	Asteraceae
Poaceae	Fabaceae	Iridaceae	Fabaceae
Fabaceae	Poaceae	Asteraceae	Poaceae
Liliaceae	Rubiaceae	Lamiaceae	Liliaceae
Rubiaceae	Liliaceae	Orchidaceae	Rubiaceae

An account of the five largest angiosperm families for regions within the DAC, and for regions of the northern Drakensberg Range and the Pondoland Centre, is presented in Table 2.6. The overlap of families is striking. The largest families of the Pondoland Centre are equally well represented in the Legalameeste and Sabie regions of the northern Drakensberg Range (Table 2.6). The largest families of the DAC (Table 2.5) are similar to the largest families of a number of localized regions within the DAC

(Table 2.6) and KwaZulu-Natal (Hilliard & Burtt, 1987). All these regions form part of the Eastern Region characterised by summer rainfall.

2.4.7 LARGEST GENERA

The 22 genera contributing 17 or more species comprise more than a quarter of the angiosperm flora (c. 27%), with 11 genera contributing 24 or more species (c. 18%) (Table 2.7). Eleven of the genera contributing 17 or more species are Cape elements (Carbutt & Edwards, 2001), emphasising the link between the floras of the DAC and CFR (see also Table 2.8). The 10 largest genera of the DAC are also prominent in the northern KwaZulu-Natal Drakensberg (Killick, 1963), the southern KwaZulu-Natal Drakensberg (Hilliard & Burtt, 1987), the Eastern Cape Drakensberg (Bester, 1998) and Lesotho (Jacot Guillarmod, 1971), thus emphasising their widespread dominance. The prominence of *Helichrysum* and *Senecio* (Table 2.7), a reflection of the dominance of the Asteraceae (Table 2.5), has been mentioned in numerous flora accounts, particularly with regard to the floras of the Afromontane and Eastern regions (citations as for Asteraceae aforementioned). The larger genera of the DAC differ from those of KwaZulu-Natal (Hilliard & Burtt, 1987) and the CFR (Goldblatt & Manning, 2002) because the former include more subtropical taxa and the latter typically fynbos taxa. The proportion of dicotyledons to monocotyledons is only slightly lower in the genera contributing 17 or more species (Table 2.7) than the angiosperm flora as a whole (Table 2.3).

Table 2.7. Ranking of the larger genera that contribute 17 or more species to the native angiosperm flora of the DAC.

Rank	Genus	Family	D = Dicotyledon M = Monocotyledon	Total species	% of total
1.	*Helichrysum*	Asteraceae	D	102	4.0
2.	*Senecio*	Asteraceae	D	100	4.0
3.	*Erica*	Ericaceae	D	34	1.3
4.	*Disa*	Orchidaceae	M	32	1.3
5.	*Crassula*	Crassulaceae	D	30	1.2
5.	*Delosperma*	Mesembryanthemaceae	D	30	1.2
5.	*Thesium*	Santalaceae	D	30	1.2
6.	*Eragrostis*	Poaceae	M	25	1.0
7.	*Hypoxis*	Hypoxidaceae	M	24	1.0
7.	*Lotononis*	Fabaceae	D	24	1.0
7.	*Sebaea*	Gentianaceae	D	24	1.0
8.	*Wahlenbergia*	Campanulaceae	D	22	0.9
9.	*Cyperus*	Cyperaceae	M	20	0.8
9.	*Kniphofia*	Asphodelaceae	M	20	0.8
9.	*Pelargonium*	Geraniaceae	D	20	0.8
10.	*Gladiolus*	Iridaceae	M	19	0.8
11.	*Berkheya*	Asteraceae	D	18	0.7
11.	*Moraea*	Iridaceae	M	18	0.7
11.	*Rhus*	Anacardiaceae	D	18	0.7
12.	*Euryops*	Asteraceae	D	17	0.7
12.	*Habenaria*	Orchidaceae	M	17	0.7
12.	*Hesperantha*	Iridaceae	M	17	0.7
				$\sum$ = 661	**$\sum$ = 26.5%**

Table 2.8. The generic elements of the angiosperm flora of the southern KwaZulu-Natal Drakensberg (adapted from Hilliard & Burtt, 1987).

Element	No. of taxa	Percentage of total (%)
Cape	88	26
Afrotropical (subtropical)	71	21
Eurasian	66	20
African	62	18
DAC endemics and near-endemics	25	8
Cosmopolitan	24	7
	$\sum$ = 336[a]	**$\sum$ = 100%**

Table 2.9. The specific elements of the angiosperm flora of the southern KwaZulu-Natal Drakensberg (adapted from Hilliard & Burtt, 1987).

Element	No. of taxa	Percentage of total (%)
DAC endemics	394	30.0
Submontane (midlands and uplands)	286	22.0
Southern African	187	15.0
Drakensberg-Sneeuberge	102	8.0
KwaZulu-Natal Midlands - NE & SW southern Africa	99	8.0
African	83	6.0
KwaZulu-Natal endemics	62	4.8
Cosmopolitan	46	4.0
Arid west	30	2.0
Northern KwaZulu-Natal	2	0.2
	$\sum$ = 1291[a]	**$\sum$ = 100%**

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[a] It was not possible to accommodate all 404 genera and 1375 species in the classes used for this analysis.

2.4.8 SPECIES ENDEMISM

An estimated 410 angiosperms are endemic to the DAC, resulting in c. 16% endemism. This is lower than previous accounts (Hilliard & Burtt, 1987; Carbutt & Edwards, 2001; Van Wyk & Smith, 2001) because of the diluting effect of a native flora that is larger than previously recognised.

The KwaZulu-Natal Drakensberg in particular is recognised as a major centre of rare and endemic species, accommodating c. 60% of the DAC's endemics, including c. 26% which are strictly endemic to this region (Porter *et al.*, 1999). The southern KwaZulu-Natal Drakensberg is colder and drier than that further north, forming the basis for distinguishing two sub-centres of endemism, the northern and southern KwaZulu-Natal Drakensberg (Hilliard & Burtt, 1987). Some 53% of the species of the southern KwaZulu-Natal Drakensberg are restricted to montane and submontane southern Africa and c. 75% are confined to the boundaries of southern Africa south of the Limpopo (Hilliard & Burtt, 1987), reiterating the southern affinities of the flora (Table 2.9).

2.4.9 GENERIC ENDEMISM

Five genera are endemic to the DAC, three of which are monotypic. *Dracomonticola* was erected by Linder & Kurzweil (1999) to accommodate *Neobolusia virginea* (Bolus) Schltr. as *Dracomonticola virginea* (Bolus) H. P. Linder & Kurzweil, a diminutive, white-flowered member of the Orchidaceae restricted to the wet basalt seeps of the DAC. This left *Neobolusia* with the single species, *N. tysonii* (Bolus) Schltr., a wider-ranging orchid that occurs in moist grasslands (Linder & Kurzweil, 1999). *Polevansia* (Poaceae), described in 1966, was then known only from the two collections of *P.*

rigida De Winter made in the Mokhotlong district of eastern Lesotho (De Winter, 1966). *Strobilopsis* (Scrophulariaceae) contains the annual or perennial herb *S. wrightii* Hilliard & Burtt, having a dense, terminal to sub-terminal, erect inflorescence of pale mauve flowers with orange centres (Hilliard & Burtt, 1977; Hilliard, 1994). It favours the shallow soils of sandstone outcrops of the Clarens Formation, and is particularly abundant in Lesotho's Sehlabathebe National Park. *Glumicalyx* (Scrophulariaceae) is a genus of six species, previously in *Zaluzianskya.* All species of *Glumicalyx* are characterised by a dense, terminal inflorescence of trumpet-shaped flowers, with variations of yellow, orange and red, that droop or hang downwards, except when in fruit (Hilliard & Burtt, 1977; Hilliard, 1994). They favour boulder-strewn gullies, wet gravel patches and the bases of rocky drip faces. *Heteromma* (Asteraceae) comprises three species of coarse, tall herbs and sub-shrubs with bright yellow, discoid heads (Hilliard & Burtt, 1973; Hilliard, 1977), often forming dense stands in mesic environments, ranging from *Leucosidea* boulder-bed scrub and forest margins to rank hygrophilous grasslands and drainage lines. The endemic genera of the DAC therefore occupy a wide spectrum of habitats typical of mountainous terrain.

2.4.10 GENERIC NEAR-ENDEMISM

Six genera are near-endemic to the DAC, three of which are monotypic. *Craterocapsa* (Campanulaceae) and *Rhodohypoxis* (Hypoxidaceae), although both centred in the DAC, have outliers both to the north and south (Hilliard & Burtt, 1973, 1978). *Guthriea* (Achariaceae) comprises *G. capensis* H. Bol. (Killick, 1976a). It is the only high-altitude member of the family and favours damp, rocky, grassy slopes leading up to the escarpment. Although centred in the DAC, outlying populations occur in the

Sneeuberge Mountains of the Eastern Cape, c. 350 km south-west of the Eastern Cape Drakensberg. *Huttonaea* (Orchidaceae) comprises five species of slender, terrestrial herbs, either of shaded forest or steep, damp grasslands, with outliers occurring to the north, south and east of the DAC (Linder & Kurzweil, 1999). *Saniella verna* Hilliard & Burtt (Hypoxidaceae) is a diminutive, crocus-like geophyte with white flowers coloured canary-yellow in the throat. It grows in wet, basalt gravel beds and along the marshy drainage lines of short, damp turf on the summit of the DAC, and is spring-flowering (October and November). The genus was considered endemic to the DAC (Hilliard & Burtt, 1978, 1987), until the rediscovery of *Empodium occidentale* (Nel) B. L. Burtt on the Roggeveld Escarpment in the south-western Cape led to the recircumscription of *Saniella* and other Hypoxidaceae (Burtt, 2000). The Roggeveld species was subsequently transferred to *Saniella*, which now contains two species, namely *S. occidentalis* (Nel) B. L. Burtt and *S. verna*, with disjunct distributions. The genus *Saniella* is therefore no longer endemic (and not considered near-endemic) to the DAC. *Thamnocalamus* is southern Africa's only endemic bamboo. It comprises *T. tessellatus* (Nees) Soderstrom & Ellis, favouring moist, sheltered ravines in mountainous areas (c. 1600 - 2700 m). Although confined mostly to the DAC, outlying populations occur near Harrismith and Ficksburg in the Free State to the north and north-west respectively, and in the Hogsback region of the Amatole Mountains in the Eastern Cape, to the south (Soderstrom & Ellis, 1982; Gibbs Russell *et al.*, 1990). *Glekia* was erected to accommodate the wide ranging *G. krebsiana* (Benth.) Hilliard, which inhabits bare cliffs and rocky mountainsides at altitudes between c. 1200 and 2150 m; it favours the drier regions of the DAC, especially western Lesotho and the Eastern Cape Drakensberg and Witteberge. It occurs as far west as Graaff Reinet in the Eastern Cape (Hilliard, 1994). The combined number of endemic and near-endemic genera in the DAC is 11. There are no endemic families.

2.5 STUDY REGION NO. 2: THE PONDOLAND CENTRE

2.5.1 GEOLOGY AND CLIMATE

The Maputaland-Pondoland Region (Van Wyk & Smith, 2001), of the Indian Ocean Coastal Belt of South Africa, is primarily associated with Karoo sediments, interspersed with (1) red sandstones of the Natal Group (previously referred to as Table Mountain Sandstone) (King, 1982; Thompson, 1993; Van Wyk, 1993), and (2) pale grey sandstones of the Msikaba Formation (SACS, 1980) (Fig. 2.8). Natal Group Sandstone previously included the Msikaba Formation, but on the basis of mineral properties, the two are now considered distinct (SACS, 1980). The Msikaba Formation was deposited 490 to 800 million years ago and comprises fine-grained, mono-mineralic quartzites which are fairly resistant to weathering and form the characteristic sandstone cliffs (Thompson, 1993; Whitmore *et al.*, 1999) (Figs 2.8C & D). This formation is geologically allied to quartzites of the Cape Supergroup, located 600 km further south (Van Wyk, 1989, 1990a); these edaphic similarities are of strategic phytogeographic importance (Van Wyk, 1990b, 1993).

The climate is subtropical with mild winters, warm summers and short periods of high humidity. The frost-free coastal plateau receives a mean annual rainfall in excess of 1000 mm, falling in spring and summer (Abbott *et al.*, 2000).

Fig. 2.8. Msikaba Formation environments of the Pondoland Centre. Seasons are indicated in parentheses. A. & B. Umtamvuna Nature Reserve (autumn); C. & D. Oribi Gorge Nature Reserve (summer), both of the southern KwaZulu-Natal coastal region.

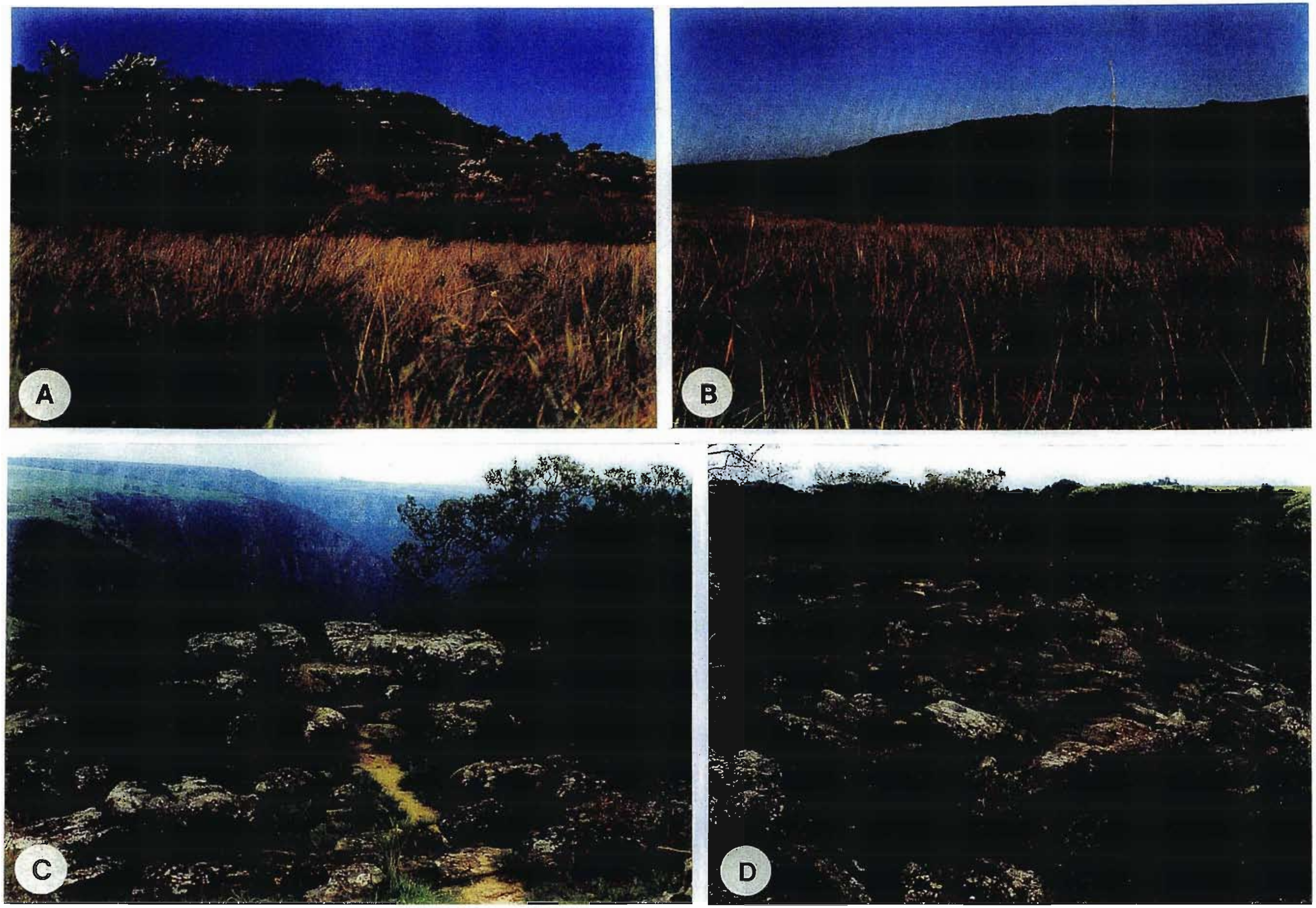

A
B
C
D

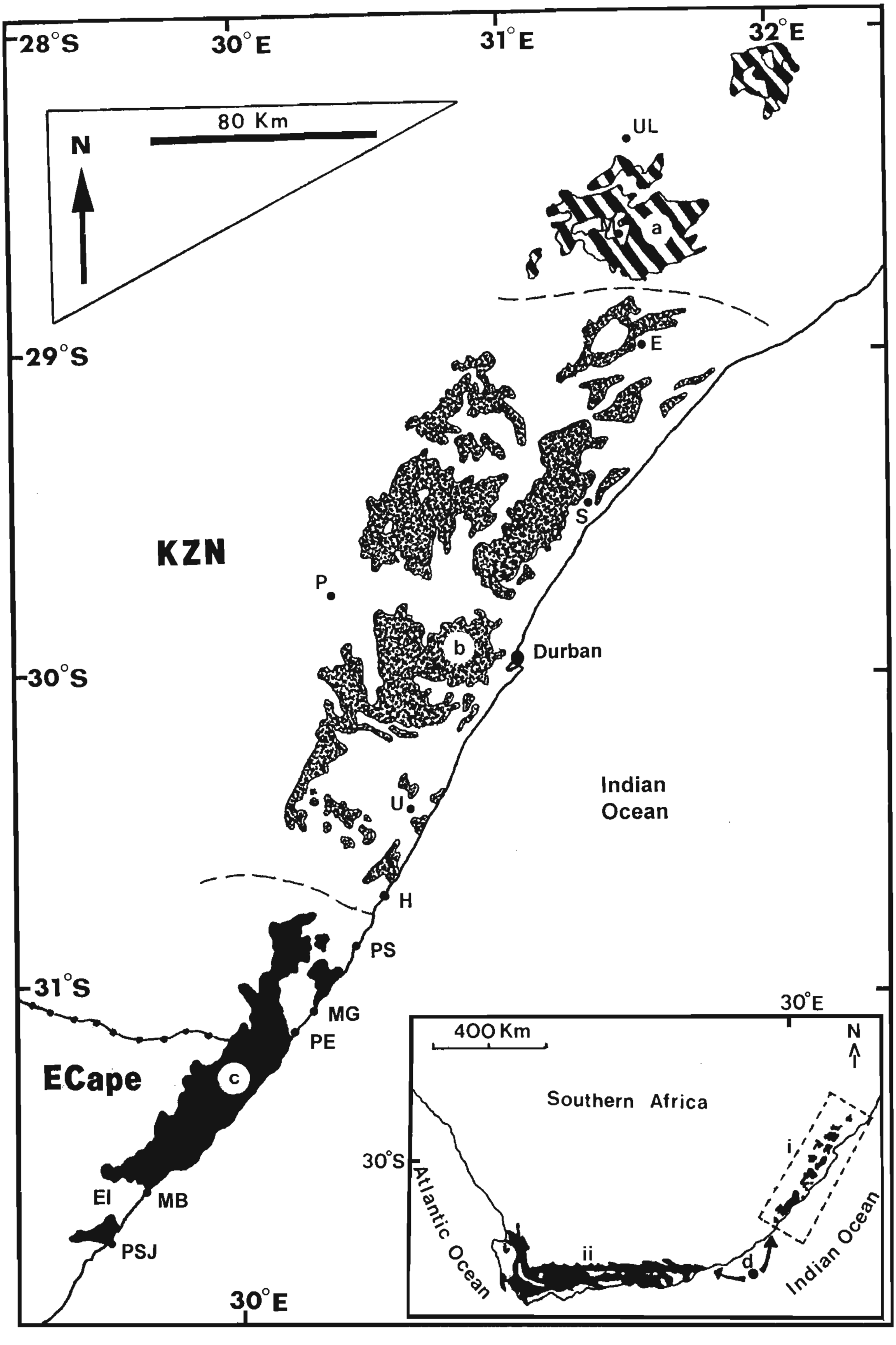
Fig. 2.9. Recorded distribution of outcrops of Natal Group Sandstone in KwaZulu-Natal (KZN) and Msikaba Formation Sandstone in KZN and the Eastern Cape (E. Cape). Adapted from Van Wyk (1990a) and Abbott *et al.* (2000).

Limits: a & b - Natal Group Sandstone (Red Beds). a, upper limit; b, lower limit; c, Msikaba Formation Sandstone (Grey Beds) - Pondoland Centre. Each delimitation is differentiated by a dashed line (— — —).

Abbreviations: Towns (●), from top to bottom: UL, Ulundi; M, Melmoth; E, Eshowe; S, Stanger; P, Pietermaritzburg; U, Umzinto; H, Hibberdene; PS, Port Shepstone; MG, Margate; PE, Port Edward; MB, Mbotyi; PSJ, Port St. Johns; EI, Egossa Interval; provincial boundary (-•-•-•-•-).

Inset: Comparative account showing the recorded distribution of outcrops of sandstone in southern Africa (■), comprising (i) Natal Group, Msikaba and (ii) Cape Supergroup Formations.

Discontinuity: d, sandstone discontinuity (interval) of some 600 kilometres comprising primarily Karoo Sequence sediments and doleritic intrusions.


28°S
30°E
31°E
32°E
80 Km
N
UL
a
E
29°S
KZN
S
P
b
Durban
30°S
Indian
Ocean
U
H
PS
31°S
MG
PE
ECape
c
EI
MB
PSJ
30°E
400 Km
30°E
N
Southern Africa
30°S
i
Atlantic Ocean
ii
d
Indian Ocean

2.5.2 FLORA AND VEGETATION

The Pondoland Centre (PC) (Van Wyk, 1996; Van Wyk & Smith, 2001) is an epicentre of botanical diversity closely affiliated with the Msikaba Formation (Fig. 2.9). It extends as a narrow wedge from the Mzimkulu River on the eastern seaboard of southern KwaZulu-Natal to the Egossa Fault (Ntsubane region) in the north-eastern region of the Eastern Cape (Abbott *et al.*, 2000). This relatively small area is considered to be one of southern Africa's premier centres of botanical diversity (Van Wyk, 1993). Of its vascular flora totalling c. 1800 spp., some 120 (6.7%) are considered endemic (Van Wyk & Smith, 2001). A comparison of the larger genera of Oribi Gorge and Umtamvuna Natures Reserves of the PC with those of the DAC revealed a poor overlap due to a stronger showing of subtropical taxa in the PC (Table 2.10). Only *Helichrysum* and *Senecio* are most prominent across the three floras, with *Crassula* also a common contributor. Oribi Gorge and Umtamvuna are floristically fairly similar as expected.

The PC comprises humid coastal grasslands and forest patches covering an area of c. 1880 km^2 (Abbott, 1993; Van Wyk, 1993; Le Roux, 1995). The high level of plant diversity is generally attributed to the overlap of fynbos, Transvaal Highveld and subtropical vegetation types (Acocks, 1988), overlayed on sandy, acidic, nutrient-poor outcrops of Msikaba Sandstone (Abbott *et al.*, 2000). The PC contains remnants of the rare and threatened Acocks' Veld Type 3 - Pondoland Coastal Plateau Sourveld (Acocks, 1988; Le Roux, 1995). Topographically, the region is characterised by gently undulating plateaus supporting short grasslands, stepped sandstone outcrops supporting woody (≈ fynbos) communities and steep-sided valleys and river gorges supporting forest (Nel, 2003).

Table 2.10. Comparative account of the larger angiosperm genera that contribute 1% or more species to the native angiosperm floras of the Drakensberg Alpine Centre (2520 spp.), Oribi Gorge (± 1002 spp.) and Umtamvuna (± 1265 spp.). Totals from: *Carbutt & Edwards (2004); ** Meter (1998).

DAC*			**Oribi Gorge****			**Umtamvuna****		
Genus	**Species**	**%**	**Genus**	**Species**	**%**	**Genus**	**Species**	**%**
Helichrysum	102	4.0	*Helichrysum*	24	2.4	*Helichrysum*	34	2.7
Senecio	100	4.0	*Senecio*	22	2.2	*Senecio*	27	2.1
Erica	34	1.3	*Crassula*	15	1.5	*Crassula*	15	1.2
Disa	32	1.3	*Plectranthus*	15	1.5	*Indigofera*	14	1.1
Crassula	30	1.2	*Cyperus*	14	1.4	*Plectranthus*	13	1.0
Delosperma	30	1.2	*Rhus*	14	1.4	*Rhus*	13	1.0
Thesium	30	1.2	*Indigofera*	11	1.1			
Eragrostis	25	1.0	*Eragrostis*	10	1.0			
Hypoxis	24	1.0	*Maytenus*	10	1.0			
Lotononis,	24	1.0	*Tephrosia*	10	1.0			
Sebaea	24	1.0						
$\sum =$	**455**	**18.2**		**145**	**14.5**		**116**	**9.1**

2.5.3 THE CAPE ELEMENTS OF PONDOLAND

Glen's (1996) and Meter's (1998) floristic accounts reported Cape elements (e.g. *Agathosma*, *Cliffortia*, *Disparago*, *Erica*, *Leucadendron*, *Protea*, *Relhania* and *Thesium*) from Oribi Gorge Nature Reserve, a 1725 ha reserve forming part of the Pondoland Centre, some 21 km inland from Port Shepstone on the southern KwaZulu-Natal coastal belt. Umtamvuna Nature Reserve, a 3257 ha species-rich centre of diversity and endemism, situated 35 km south of Oribi Gorge, is underlain by identical sediments and supports similar plant communities rich in Cape elements (Hilliard, 1978; Moll & Jarman, 1984b; Abbott, 1993; Le Roux, 1995; Meter, 1998;

Abbott *et al.*, 2000). Further south, along the coastal reaches of the Eastern Cape (the former Transkei), edaphic outcrops of the Msikaba Formation support Cape elements (largely as fynbos communities) in Mkambati Nature Reserve of north-eastern Pondoland (Shackleton *et al.*, 1991; Nel, 2003) and in the Dwesa Nature Reserve (McKenzie, 1979, cited in Moll & Jarman, 1984a). These fynbos communities in the PC (as for the DAC), have been considered as heathlands (Moll & Jarman, 1984b).

2.6 ENVIRONMENT AND FLORISTICS

2.6.1 INTRODUCTION

The primary constraints on terrestrial plant communities are climate, topography, substrate and biotic factors (Schulze & McGee, 1978), all of which are important in biogeographical and ecological studies (Bester, 1998). Climate, however, is generally perceived as the principal dynamic component and the obvious independent variable shaping vegetation and soil, on both micro and subcontinental scales (Daubenmire, 1947, 1968; Counts, 1993; Ellery *et al.*, 1995). It takes into account not only the prevailing weather conditions, but also the dynamic and intricate variations occurring diurnally, daily, monthly, seasonally and annually; these parameters operate in combination to produce the specific environment in which a plant grows (Schulze & McGee, 1978; Schulze, 1997).

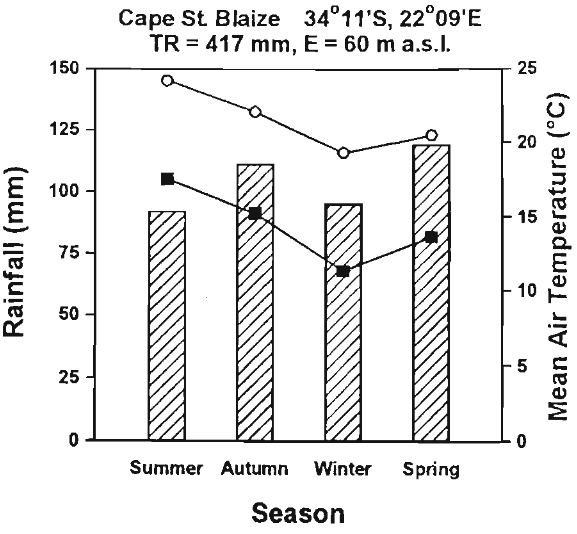
2.6.2 METHODOLOGY

2.6.2.1 THE CLIMATIC ENVIRONMENT

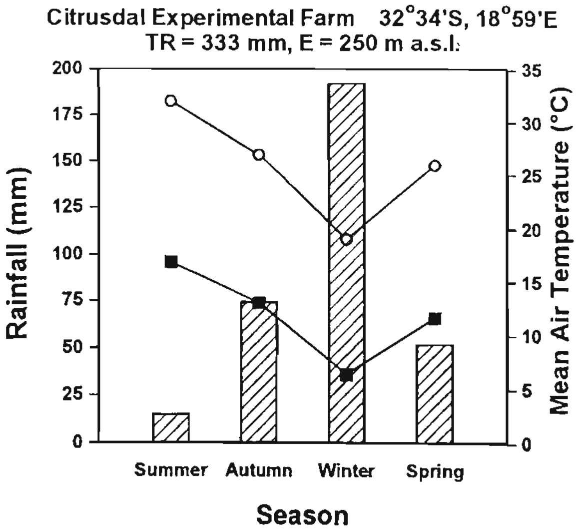
Rainfall and temperature data were collated for the CFR, DAC (represented mainly by the KwaZulu-Natal and Eastern Cape Drakensberg), PC and Sneeuberge. Data were collated from numerous sources as single weather databases are potentially erroneous. Grid references, mean annual rainfall and elevation accompany seasonal rainfall and temperature minima and maxima for each station (Figs 2.10 - 2.14).

(1) CFR, 14 stations (Fig. 2.10): Cape St. Blaize, Citrusdal Experimental Farm, Danger Point, Deepwalls, De Keur Experimental Farm, Elgin Experimental Farm, Grahamstown, Jakkalsrivier, Jonkershoek (Biesievlei), La Plaisante Experimental Farm, Misgund-Oos Experimental Farm, Port Elizabeth, Table Mountain House and Tygerhoek Experimental Farm. Data were sourced from the South African Weather Bureau, the Department of Agricultural Technical Services and from records of the Department of Forestry, as quoted by Kruger (1979); (2) Sneeuberge, six stations (Fig. 2.11): Cradock, Graaff Reinet, Hanover, Middelburg, Noupoort and Somerset East; (3) Eastern Cape Drakensberg and Witteberge, five stations (Fig. 2.12): Avoca, Barkly East, Lady Grey, Maclear and Rhodes; (4) PC, six stations (Fig. 2.13): Holy Cross Mission, Lusikisiki, Margate, Mkambati Nature Reserve, Oribi Flats and Port St. Johns. Data for (2), (3) and (4) were sourced from the Computing Centre for Water Research (CCWR, University of Natal, Pietermaritzburg) and from the Department of Meteorology (KwaZulu-Natal Department of Agriculture); (5) KwaZulu-Natal Drakensberg, 11 stations (Fig. 2.14): Bergville, Cathedral Peak (Mlambonja) Wilderness Area, Giant's Castle Game Reserve, Himeville, Kamberg Nature Reserve, Mokhotlong, Monk's Cowl (Mdedelelo) Wilderness Area, Qacha's Nek, Royal Natal National Park, Sani Pass (summit) and Witsieshoek. Data for (5) were sourced as in (2), (3) and (4) above, in consultation with published data of Tyson *et al.* (1976) and AGROMET (Pretoria).

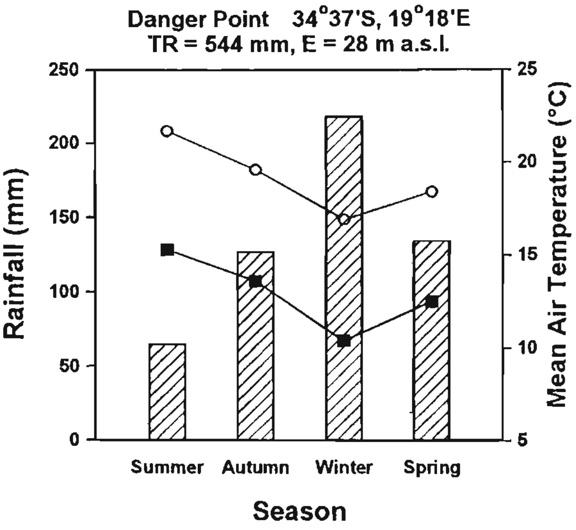
Fig. 2.10. Rainfall and temperature data for 14 stations in the CFR. Mean seasonal rainfall is represented by the Y1 axis (bar graphs) and mean air temperature by the Y2 axis (line graphs). Maxima, (○); minima, (■). TR, mean annual rainfall; E, elevation. Summer: December, January, February; Autumn: March, April, May; Winter: June, July, August; Spring: September, October, November. None of the above stations occur at an altitude exceeding 800 m; there is a shortage of high-altitude weather stations in the CFR.


Cape St Blaize 34°11'S, 22°09'E
TR = 417 mm, E = 60 m a.s.l.
Rainfall (mm)
0
25
50
75
100
125
150
Mean Air Temperature (°C)
0
5
10
15
20
25
Summer
Autumn
Winter
Spring
Season

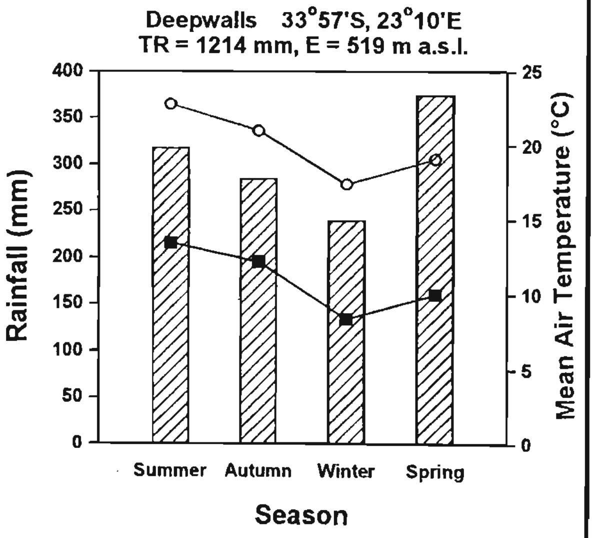
A.


Citrusdal Experimental Farm 32°34'S, 18°59'E
TR = 333 mm, E = 250 m a.s.l.
Rainfall (mm)
0
25
50
75
100
125
150
175
200
Mean Air Temperature (°C)
0
5
10
15
20
25
30
35
Summer
Autumn
Winter
Spring
Season

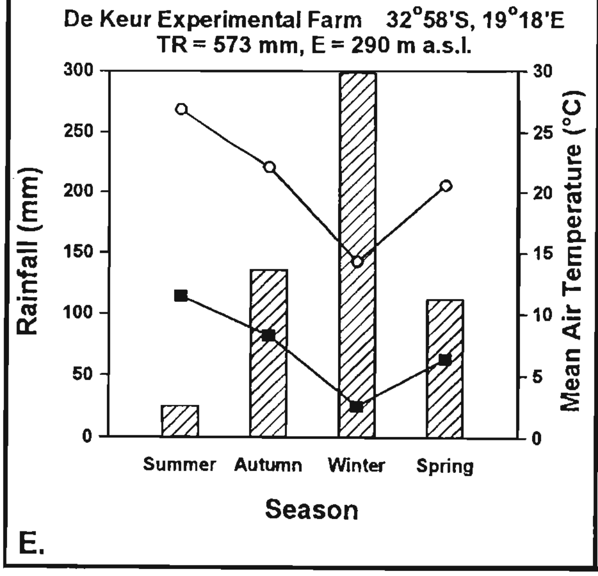
B.


Danger Point 34°37'S, 19°18'E
TR = 544 mm, E = 28 m a.s.l.
Rainfall (mm)
0
50
100
150
200
250
Mean Air Temperature (°C)
5
10
15
20
25
Summer
Autumn
Winter
Spring
Season

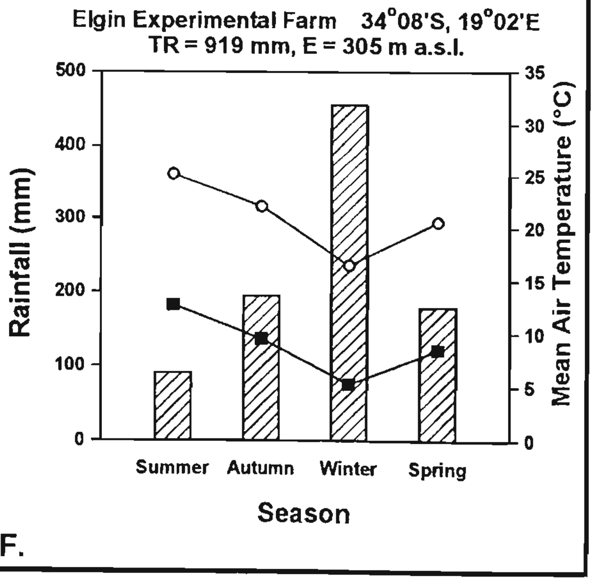
C.


Deepwalls 33°57'S, 23°10'E
TR = 1214 mm, E = 519 m a.s.l.
Rainfall (mm)
0
50
100
150
200
250
300
350
400
Mean Air Temperature (°C)
0
5
10
15
20
25
Summer
Autumn
Winter
Spring
Season

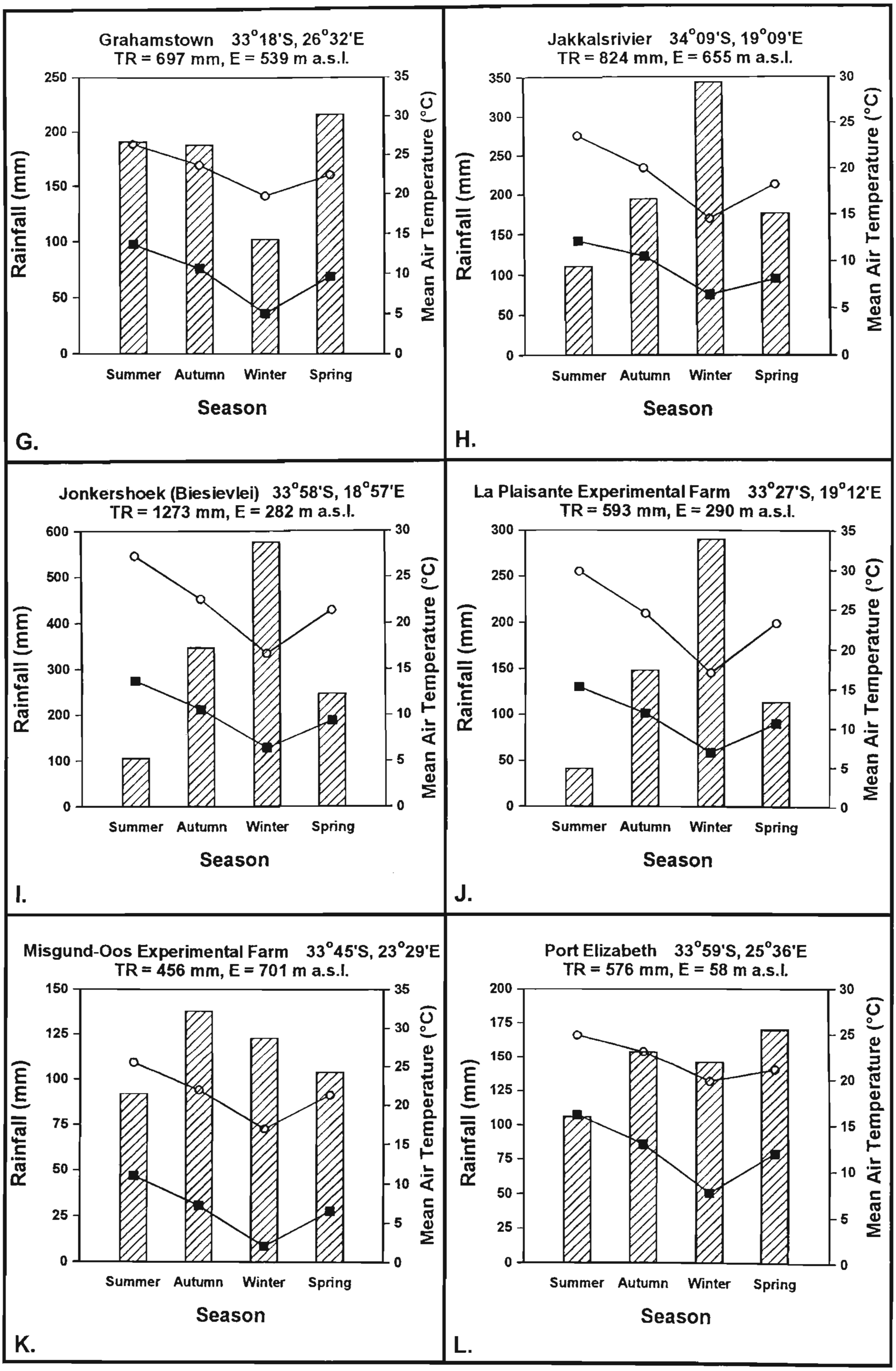
D.


De Keur Experimental Farm 32°58'S, 19°18'E
TR = 573 mm, E = 290 m a.s.l.
Rainfall (mm)
0
50
100
150
200
250
300
Mean Air Temperature (°C)
0
5
10
15
20
25
30
Summer
Autumn
Winter
Spring
Season

E.


Elgin Experimental Farm 34°08'S, 19°02'E
TR = 919 mm, E = 305 m a.s.l.
Rainfall (mm)
0
100
200
300
400
500
Mean Air Temperature (°C)
0
5
10
15
20
25
30
35
Summer
Autumn
Winter
Spring
Season

F.


Grahamstown 33°18'S, 26°32'E
TR = 697 mm, E = 539 m a.s.l.
Rainfall (mm)
0
50
100
150
200
250
Mean Air Temperature (°C)
0
5
10
15
20
25
30
35
Summer
Autumn
Winter
Spring
Season
G.
Jakkalsrivier 34°09'S, 19°09'E
TR = 824 mm, E = 655 m a.s.l.
Rainfall (mm)
0
50
100
150
200
250
300
350
Mean Air Temperature (°C)
0
5
10
15
20
25
30
Summer
Autumn
Winter
Spring
Season
H.
Jonkershoek (Biesievlei) 33°58'S, 18°57'E
TR = 1273 mm, E = 282 m a.s.l.
Rainfall (mm)
0
100
200
300
400
500
600
Mean Air Temperature (°C)
0
5
10
15
20
25
30
Summer
Autumn
Winter
Spring
Season
I.
La Plaisante Experimental Farm 33°27'S, 19°12'E
TR = 593 mm, E = 290 m a.s.l.
Rainfall (mm)
0
50
100
150
200
250
300
Mean Air Temperature (°C)
0
5
10
15
20
25
30
35
Summer
Autumn
Winter
Spring
Season
J.
Misgund-Oos Experimental Farm 33°45'S, 23°29'E
TR = 456 mm, E = 701 m a.s.l.
Rainfall (mm)
0
25
50
75
100
125
150
Mean Air Temperature (°C)
0
5
10
15
20
25
30
35
Summer
Autumn
Winter
Spring
Season
K.
Port Elizabeth 33°59'S, 25°36'E
TR = 576 mm, E = 58 m a.s.l.
Rainfall (mm)
0
25
50
75
100
125
150
175
200
Mean Air Temperature (°C)
0
5
10
15
20
25
30
Summer
Autumn
Winter
Spring
Season
L.

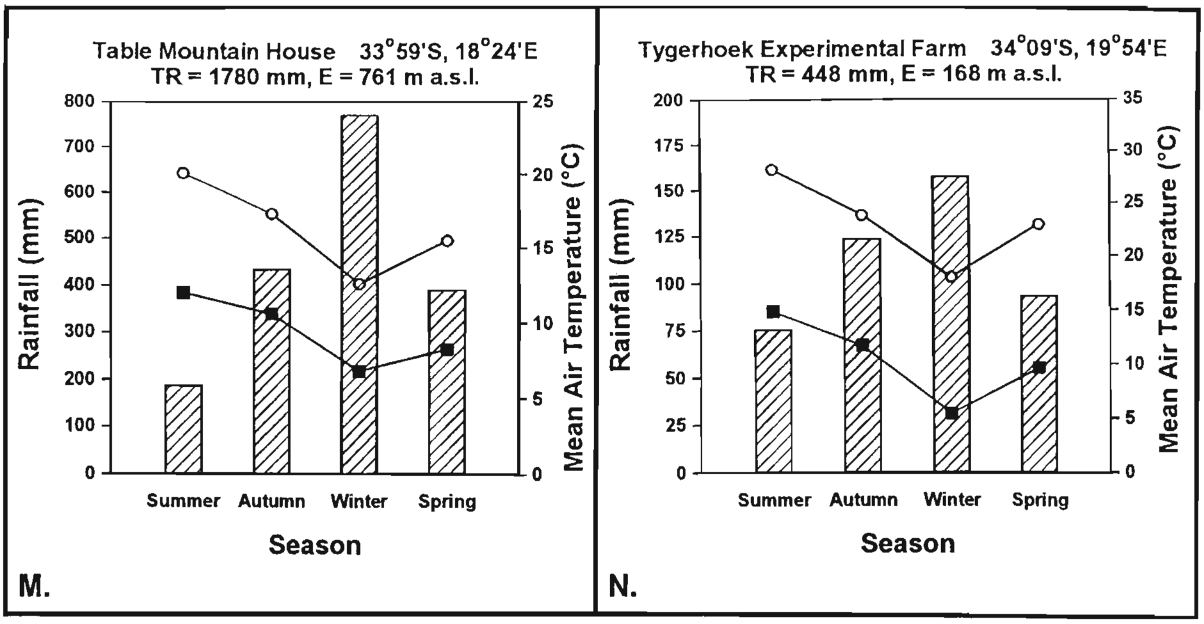


Table Mountain House 33°59'S, 18°24'E
TR = 1780 mm, E = 761 m a.s.l.
Rainfall (mm)
800
700
600
500
400
300
200
100
0
Mean Air Temperature (°C)
25
20
15
10
5
0
Summer
Autumn
Winter
Spring
Season
M.
Tygerhoek Experimental Farm 34°09'S, 19°54'E
TR = 448 mm, E = 168 m a.s.l.
Rainfall (mm)
200
175
150
125
100
75
50
25
0
Mean Air Temperature (°C)
35
30
25
20
15
10
5
0
Summer
Autumn
Winter
Spring
Season
N.

Fig. 2.11. Rainfall and temperature data for six stations in the Sneeuberge region. Mean seasonal rainfall is represented by the Y1 axis (bar graphs) and mean air temperature by the Y2 axis (line graphs). Maxima, (○); minima, (■). TR, mean annual rainfall; E, elevation. Summer: December, January, February; Autumn: March, April, May; Winter: June, July, August; Spring: September, October, November.

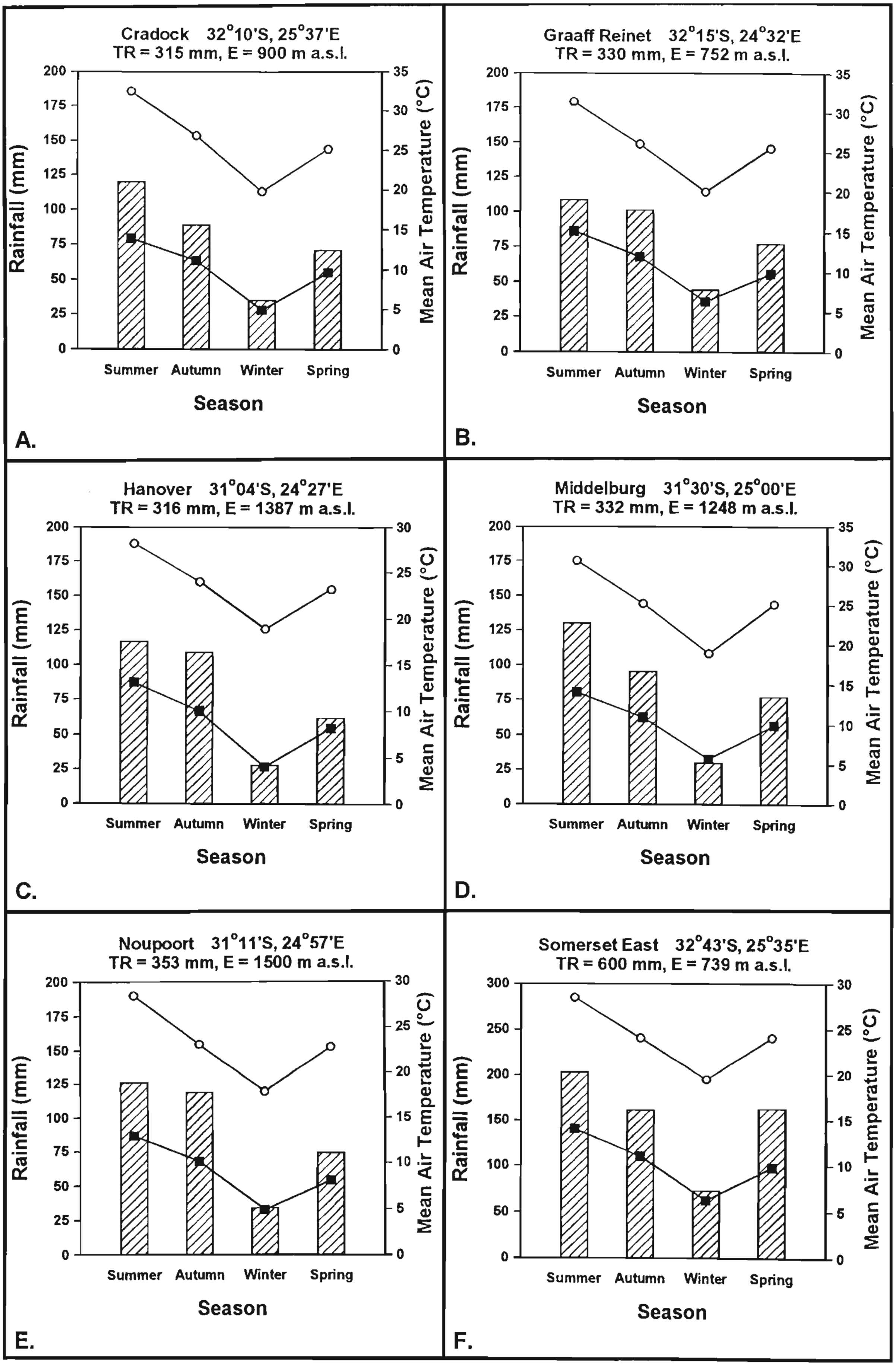

Cradock 32°10'S, 25°37'E
TR = 315 mm, E = 900 m a.s.l.
Rainfall (mm)
Mean Air Temperature (°C)
Summer
Autumn
Winter
Spring
Season
A.
Graaff Reinet 32°15'S, 24°32'E
TR = 330 mm, E = 752 m a.s.l.
Rainfall (mm)
Mean Air Temperature (°C)
Summer
Autumn
Winter
Spring
Season
B.
Hanover 31°04'S, 24°27'E
TR = 316 mm, E = 1387 m a.s.l.
Rainfall (mm)
Mean Air Temperature (°C)
Summer
Autumn
Winter
Spring
Season
C.
Middelburg 31°30'S, 25°00'E
TR = 332 mm, E = 1248 m a.s.l.
Rainfall (mm)
Mean Air Temperature (°C)
Summer
Autumn
Winter
Spring
Season
D.
Noupoort 31°11'S, 24°57'E
TR = 353 mm, E = 1500 m a.s.l.
Rainfall (mm)
Mean Air Temperature (°C)
Summer
Autumn
Winter
Spring
Season
E.
Somerset East 32°43'S, 25°35'E
TR = 600 mm, E = 739 m a.s.l.
Rainfall (mm)
Mean Air Temperature (°C)
Summer
Autumn
Winter
Spring
Season
F.

Fig. 2.12. Rainfall and temperature data for five stations in the Eastern Cape Drakensberg and Witteberge. Mean seasonal rainfall is represented by the Y1 axis (bar graphs) and mean air temperature by the Y2 axis (line graphs). Maxima, (○); minima, (■). TR, mean annual rainfall; E, elevation. Summer: December, January, February; Autumn: March, April, May; Winter: June, July, August; Spring: September, October, November.

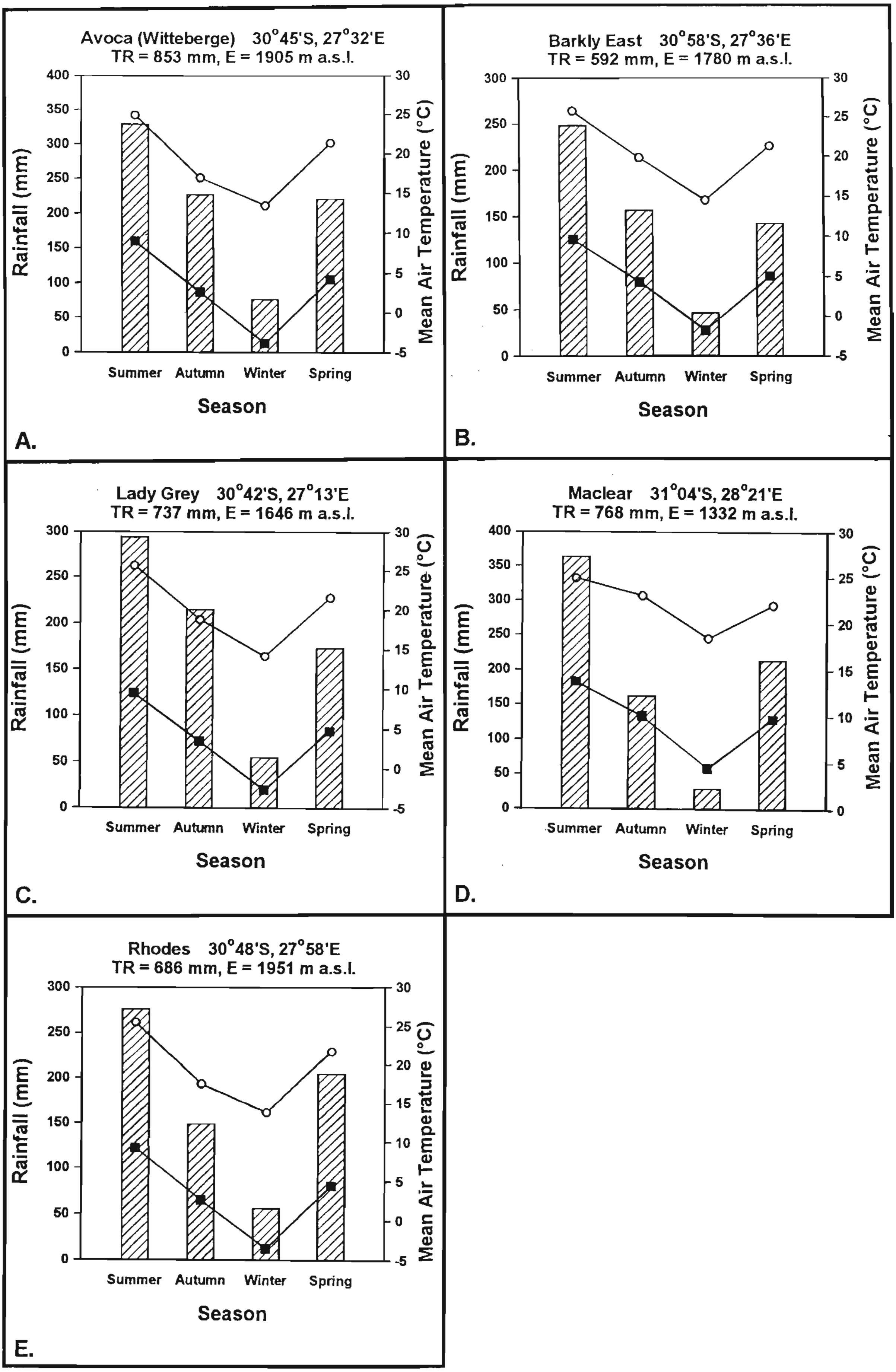
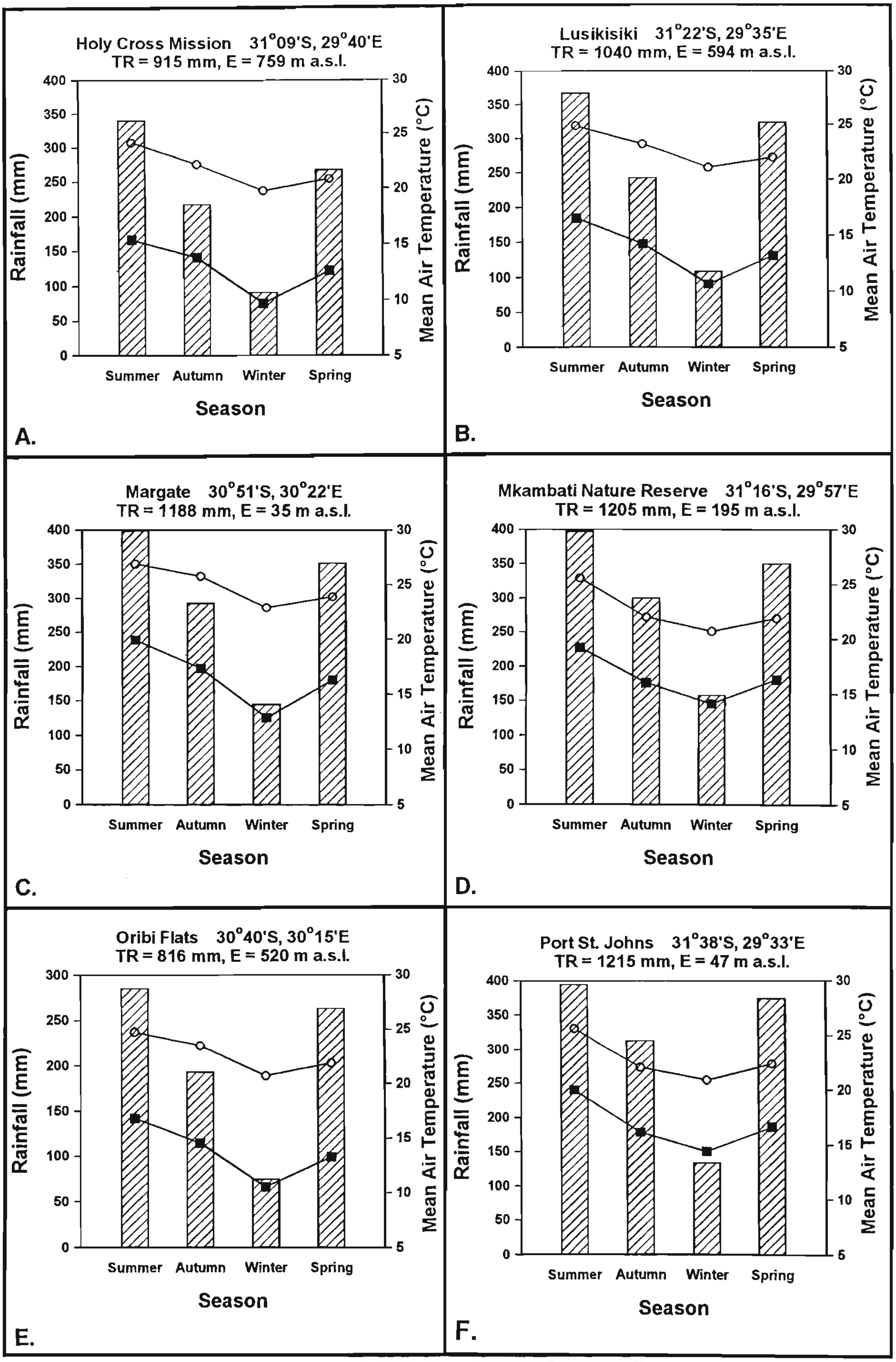

Avoca (Witteberge) 30°45'S, 27°32'E
TR = 853 mm, E = 1905 m a.s.l.
Rainfall (mm)
0
50
100
150
200
250
300
350
400
Mean Air Temperature (°C)
-5
0
5
10
15
20
25
30
Summer
Autumn
Winter
Spring
Season
A.
Barkly East 30°58'S, 27°36'E
TR = 592 mm, E = 1780 m a.s.l.
Rainfall (mm)
0
50
100
150
200
250
300
Mean Air Temperature (°C)
-5
0
5
10
15
20
25
30
Summer
Autumn
Winter
Spring
Season
B.
Lady Grey 30°42'S, 27°13'E
TR = 737 mm, E = 1646 m a.s.l.
Rainfall (mm)
0
50
100
150
200
250
300
Mean Air Temperature (°C)
-5
0
5
10
15
20
25
30
Summer
Autumn
Winter
Spring
Season
C.
Maclear 31°04'S, 28°21'E
TR = 768 mm, E = 1332 m a.s.l.
Rainfall (mm)
0
50
100
150
200
250
300
350
400
Mean Air Temperature (°C)
0
5
10
15
20
25
30
Summer
Autumn
Winter
Spring
Season
D.
Rhodes 30°48'S, 27°58'E
TR = 686 mm, E = 1951 m a.s.l.
Rainfall (mm)
0
50
100
150
200
250
300
Mean Air Temperature (°C)
-5
0
5
10
15
20
25
30
Summer
Autumn
Winter
Spring
Season
E.

Fig. 2.13. Rainfall and temperature data for six stations in the Pondoland Centre. Mean seasonal rainfall is represented by the Y1 axis (bar graphs) and mean air temperature by the Y2 axis (line graphs). Maxima, (○); minima, (■). TR, mean annual rainfall; E, elevation. Summer: December, January, February; Autumn: March, April, May; Winter: June, July, August; Spring: September, October, November.


Holy Cross Mission 31°09'S, 29°40'E
TR = 915 mm, E = 759 m a.s.l.

Lusikisiki 31°22'S, 29°35'E
TR = 1040 mm, E = 594 m a.s.l.

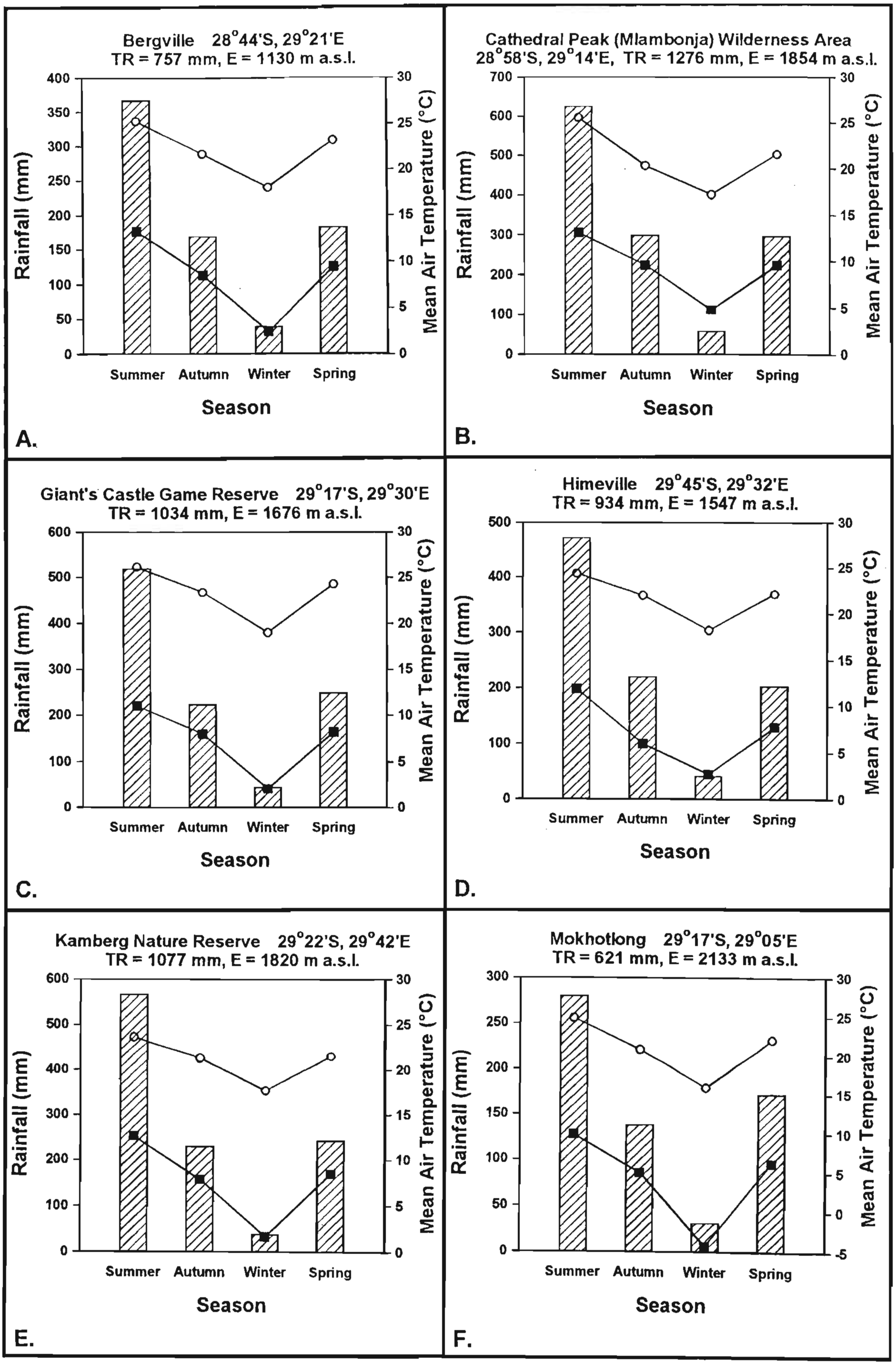
Margate 30°51'S, 30°22'E
TR = 1188 mm, E = 35 m a.s.l.

Mkambati Nature Reserve 31°16'S, 29°57'E
TR = 1205 mm, E = 195 m a.s.l.

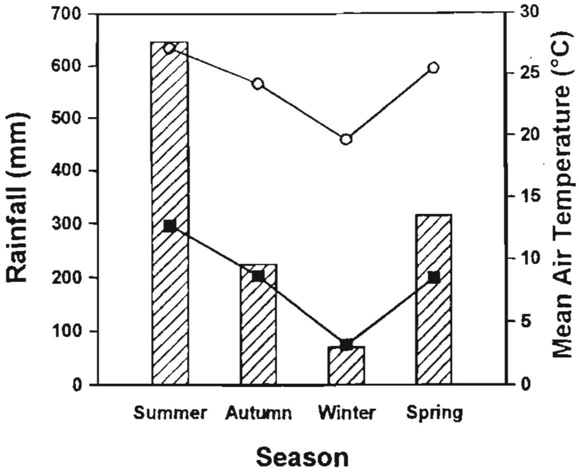
Oribi Flats 30°40'S, 30°15'E
TR = 816 mm, E = 520 m a.s.l.

Port St. Johns 31°38'S, 29°33'E
TR = 1215 mm, E = 47 m a.s.l.

Fig. 2.14. Rainfall and temperature data for 11 stations in the KwaZulu-Natal Drakensberg. Mean seasonal rainfall is represented by the Y1 axis (bar graphs) and mean air temperature by the Y2 axis (line graphs). Maxima, (○); minima, (■). TR, mean annual rainfall; E, elevation. Summer: December, January, February; Autumn: March, April, May; Winter: June, July, August; Spring: September, October, November.

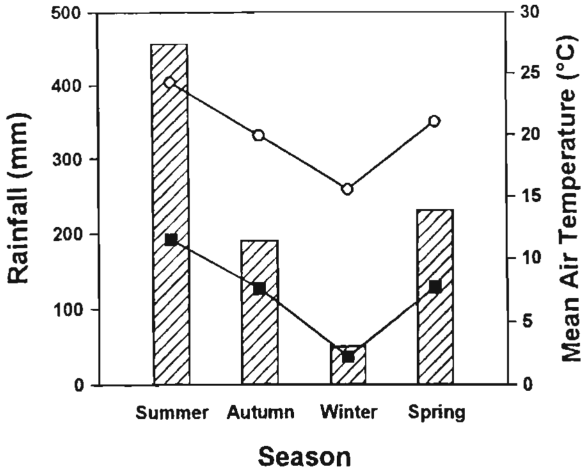

Bergville 28°44'S, 29°21'E
TR = 757 mm, E = 1130 m a.s.l.
Rainfall (mm)
Mean Air Temperature (°C)
0
50
100
150
200
250
300
350
400
0
5
10
15
20
25
30
Summer
Autumn
Winter
Spring
Season
A.
Cathedral Peak (Mlambonja) Wilderness Area
28°58'S, 29°14'E, TR = 1276 mm, E = 1854 m a.s.l.
Rainfall (mm)
Mean Air Temperature (°C)
0
100
200
300
400
500
600
700
0
5
10
15
20
25
30
Summer
Autumn
Winter
Spring
Season
B.
Giant's Castle Game Reserve 29°17'S, 29°30'E
TR = 1034 mm, E = 1676 m a.s.l.
Rainfall (mm)
Mean Air Temperature (°C)
0
100
200
300
400
500
600
0
5
10
15
20
25
30
Summer
Autumn
Winter
Spring
Season
C.
Himeville 29°45'S, 29°32'E
TR = 934 mm, E = 1547 m a.s.l.
Rainfall (mm)
Mean Air Temperature (°C)
0
100
200
300
400
500
0
5
10
15
20
25
30
Summer
Autumn
Winter
Spring
Season
D.
Kamberg Nature Reserve 29°22'S, 29°42'E
TR = 1077 mm, E = 1820 m a.s.l.
Rainfall (mm)
Mean Air Temperature (°C)
0
100
200
300
400
500
600
0
5
10
15
20
25
30
Summer
Autumn
Winter
Spring
Season
E.
Mokhotlong 29°17'S, 29°05'E
TR = 621 mm, E = 2133 m a.s.l.
Rainfall (mm)
Mean Air Temperature (°C)
0
50
100
150
200
250
300
-5
0
5
10
15
20
25
30
Summer
Autumn
Winter
Spring
Season
F.

Monk's Cowl (Mdedelelo) Wilderness Area
28°58'S, 29°19'E, TR = 1256 mm, E = 1480 m a.s.l.



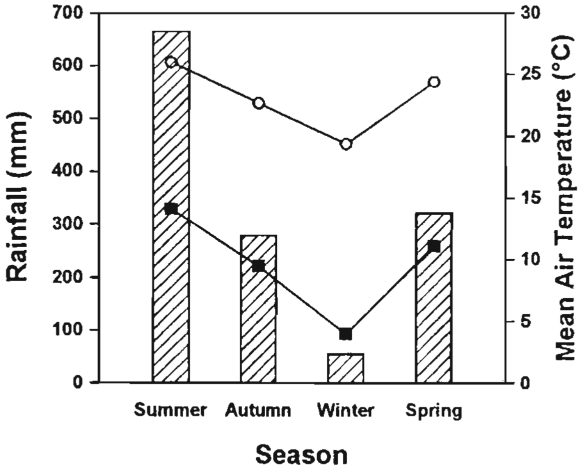
G.

Qacha's Nek 30°07'S, 28°42'E
TR = 927 mm, E = 1981 m a.s.l.



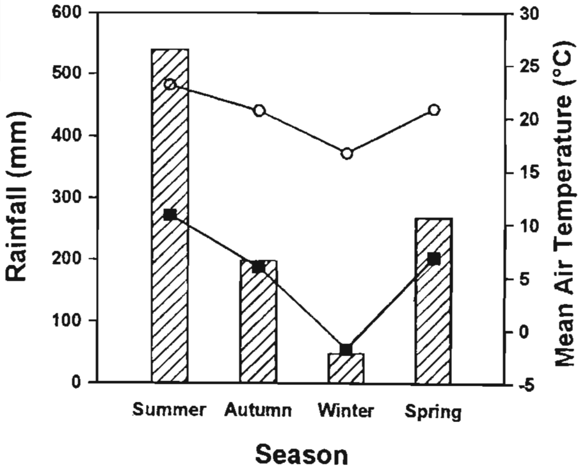
H.

Royal Natal National Park 28°41'S, 28°57'E
TR = 1321 mm, E = 1500 m a.s.l.



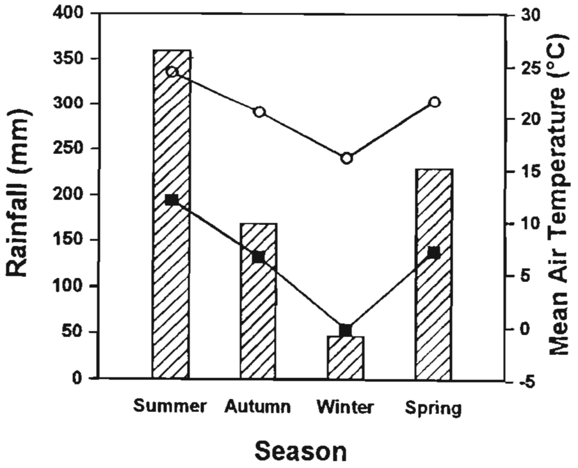
I.

Sani Pass (summit) 29°34'S, 29°18'E
TR = 1054 mm, E = 2874 m a.s.l.



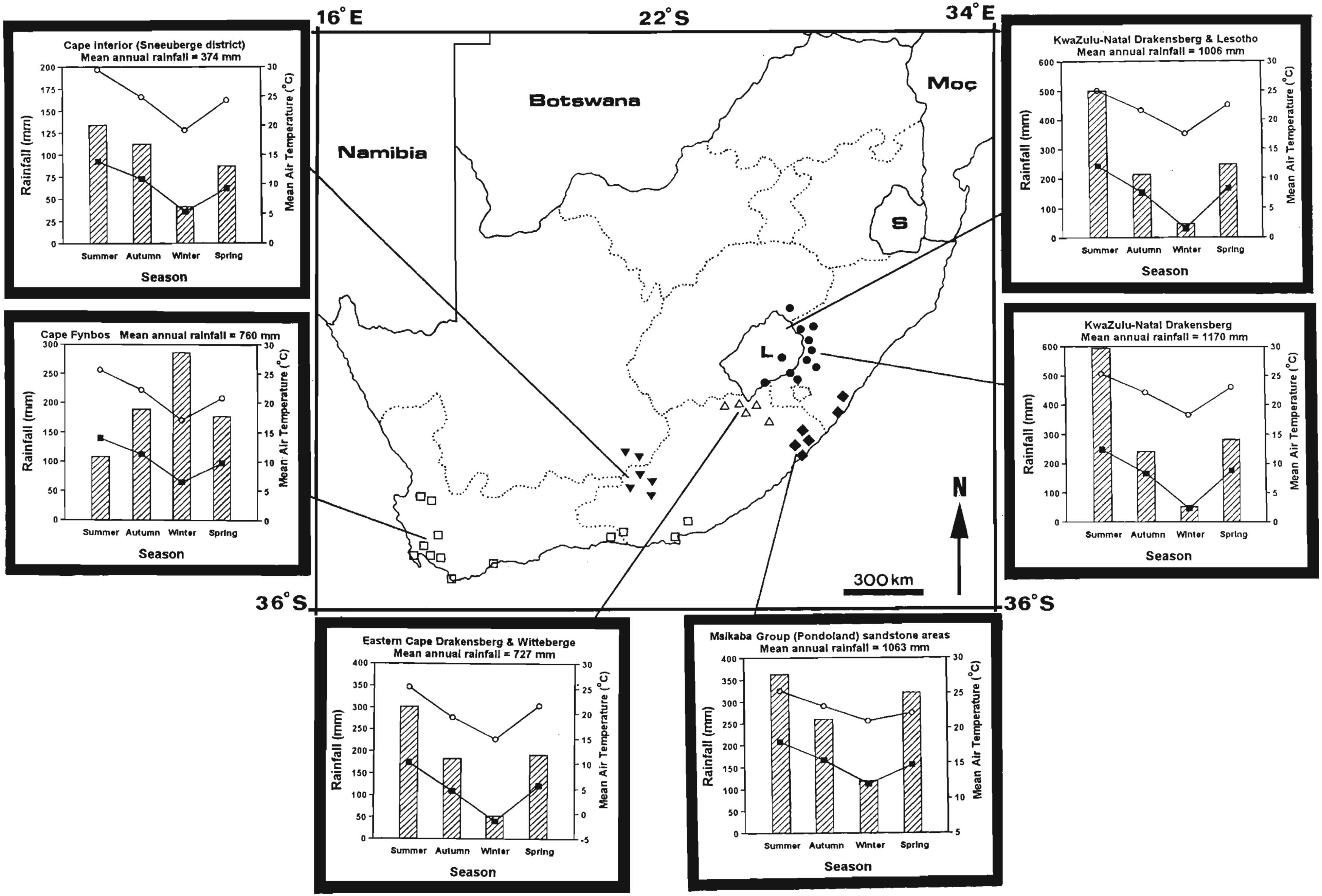
J.

Witsieshoek 28°32'S, 28°48'E
TR = 806 mm, E = 1676 m a.s.l.



K.

Fig. 2.15. The weather stations used to collate climate data for Lesotho and South and the climate regimes representing each of the study regions. Rainfall (Y1 axis) refers to mean seasonal rainfall. Open circles (○) refer to temperature maxima and closed squares (■) refer to temperature minima. Abbreviations: L, Lesotho; Moç, Moçambique; S, Swaziland.


16° E
22° S
34° E
36° S
36° S
Namibia
Botswana
Moç
S
L
N
300 km
Cape interior (Sneeuberge district)
Mean annual rainfall = 374 mm
Cape Fynbos Mean annual rainfall = 760 mm
KwaZulu-Natal Drakensberg & Lesotho
Mean annual rainfall = 1006 mm
KwaZulu-Natal Drakensberg
Mean annual rainfall = 1170 mm
Eastern Cape Drakensberg & Witteberge
Mean annual rainfall = 727 mm
Msikaba Group (Pondoland) sandstone areas
Mean annual rainfall = 1063 mm
Rainfall (mm)
Mean Air Temperature (°C)
Summer
Autumn
Winter
Spring
Season

The rainfall and temperature charts generated by Fig.P® for Windows® Version 2.98 (Biosoft, 1999) were preferred to the cumbersome Walter-Lieth climate diagrams (Walter & Lieth, 1960; Walter *et al.*, 1975). Finally, a climatic summary for each of the study regions was compiled using climate data from individual stations (Fig. 2.15).

2.6.2.2 HIGH-ALTITUDE FLORISTICS

The high-altitude regions of Lesotho and South Africa exceeding 2200 m were determined using two 1: 250 000 physical relief maps of Lesotho and the Eastern Cape (Department of Lands, Surveys & Physical Planning, 1987; Lesotho Government, 1994) and a 1: 500 000 topographical map of the Cape Provinces (Directorate of Surveys & Mapping, 1984) (Table 2.11). Species-level distributional inventories for quarter degree grids located within these areas were accessed from PRECIS and the number of Cape elements occurring within these grids were recorded (taxa recognised as Cape elements are listed in Table 2.12). It is appreciated that under normal circumstances distributional data gathered from PRECIS should be verified. This was, however, impossible due to the large phytogeographical scale of the study, so anomalous distributional patterns were considered spurious when single records could not be corroborated.

Furthermore, the high-altitude floras of South Africa and Lesotho were compared with those of southern and south-central Africa using a numerical analysis of their Cape elements. These numbers were derived from flora accounts for each region: Nyika Plateau (C. Willis *et al.*, unpublished data; Willis *et al.*, 2001); Mt. Mulanje (Whyte, 1894; Chapman & White, 1970; Strugnell, 2002); Chimanimani Mountains (Phipps & Goodier, 1962; Wild, 1964, 1968); Wolkberg Centre (Van der

Schijff & Schoonraad, 1971; Deall & Backer, 1989; Matthews *et al.*, 1993; Stalmans *et al.*, 1997); DAC (Carbutt & Edwards, 2001; Carbutt & Edwards, 2004); KwaZulu-Natal Drakensberg, Eastern Cape Drakensberg and Sneeuberge (all from PRECIS). The PC, although not a high-altitude region, was later referred to for comparative purposes.

2.6.3 RESULTS AND DISCUSSION

2.6.3.1 GENERAL FLORISTICS AND ENVIRONMENTAL GRADIENTS

Three regions with mean altitudes greater than 2200 m occur outside of the CFR (Table 2.11): (1) Lesotho/KwaZulu-Natal Drakensberg (± 2800 - 3482 m); (2) Lesotho/Eastern Cape Drakensberg and Witteberge (± 2400 - 3000 m); and (3) the Sneeuberge (± 2000 - 2500 m). The KwaZulu-Natal Drakensberg extends from Royal Natal National Park to Bushman's Nek and bisects KwaZulu-Natal and Lesotho. This range initially faces north-east and then shifts in a south-easterly direction, covering a distance of c. 300 km (Hilliard & Burtt, 1987; Irwin & Irwin, 1992) (Fig. 2.7). The higher-lying areas of the Eastern Cape Drakensberg are a southern extension of the Lesotho and KwaZulu-Natal Drakensberg and lie diagonally between Barkly East and Maclear (Fig. 2.7). The Witteberge Range lies approximately between Lady Grey and Rhodes. The Eastern Cape Drakensberg is colder and drier than the KwaZulu-Natal Drakensberg (Fig. 2.15). The Sneeuberge are a crescent-shaped range of mountains straddling the south-eastern Northern Cape and south-western Eastern Cape, between Graaff-Reinet, Cradock and Middelburg in the Great Karoo (Fig. 2.18).

The three high-altitude regions form a gradient of altitude increasing in a north-easterly direction (Fig. 2.16A). Closely associated with this directional increase in altitude is a climatic gradient of increasing rainfall (Fig. 2.16B) and a general

Table 2.11. The quarter degree grid squares used for the high-altitude analysis of Cape elements in Lesotho and South Africa (mean altitudes > 2200 m). Data courtesy of PRECIS (Gibbs Russel, 1985).

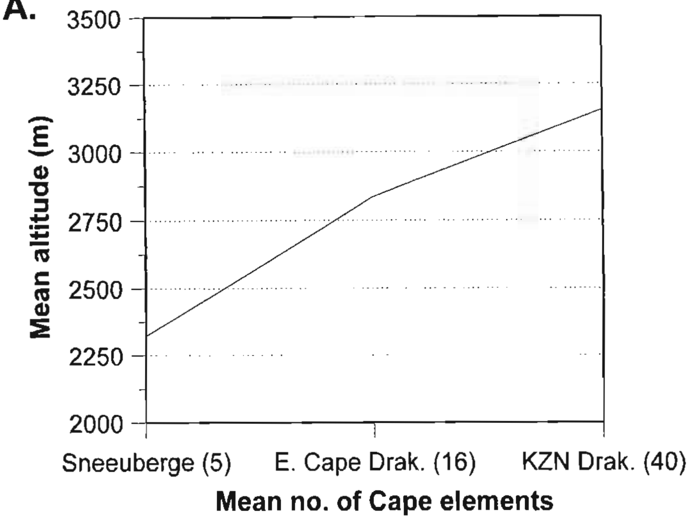
No.	**Grid reference**	**Lesotho/KwaZulu-Natal Drakensberg**		
		Major locality	**Minor locality**	**Altitude (m)**
1	2828 DD	Bethlehem	Mont-aux-Sources	3282
2	2829 CC	Harrismith	Cathedral Peak	3004
3	2929 AB	Underberg	Champagne Castle	3248
4	2929 AD	Underberg	Giant's Castle	3314
5	2929 CB	Underberg	Sani Top (border post)	2874
6	2929 CC	Underberg	Bushman's Nek summit	2500 - 3000

No.	**Grid reference**	**Lesotho/Eastern Cape Drakensberg and Witteberge**		
		Major locality	**Minor locality**	**Altitude (m)**
7	3027 BD	Lady Grey	Thaba-Ntšo	3015
8	3027 DA	Lady Grey	Avoca Peak	2769
9	3027 DB	Lady Grey	Ben Macdhui	3001
10	3027 DD	Lady Grey	Rotskop	2615
11	3028 AC	Matatiele	Makholo Mitre	2899
12	3028 AC	Matatiele	Tsatsane	2950
13	3028 AD	Lady Grey	Thaba-Putsoa	2938
14	3028 CC	Matatiele	Scobbel's Kop	2730
15	3127 BB	Lady Frere	Fern Tower	2675
16	3127 BB	Lady Frere	Ben Dearg	2770

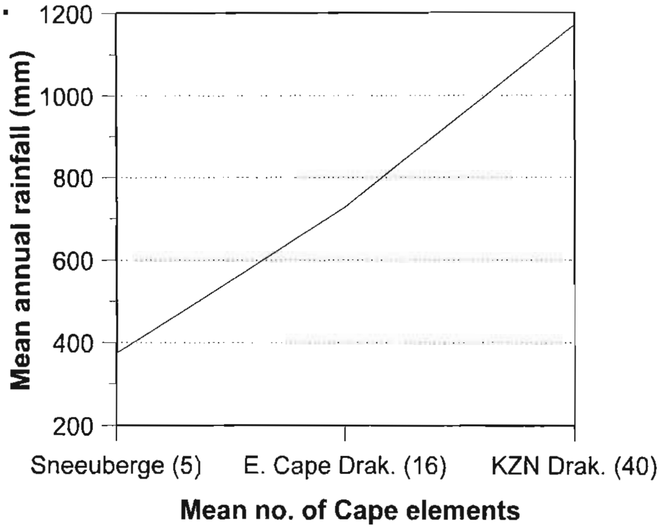
No.	**Grid reference**		**Sneeuberge**	
		Major locality	**Minor locality**	**Altitude (m)**
17	3124 CB	Hanover	Rooikop	2034
18	3124 DC	Hanover	Kompasberg	2502
19	3224 BB	Graaff Reinet	Nardousberg	2429

Fig. 2.16. The relationship between the mean number of Cape elements for three high-altitude regions ($\bar{x} \geq 2200$ m) and A. altitude, B. rainfall and C. temperature. Abbreviations: E. Cape Drak., Eastern Cape Drakensberg; KZN Drak., KwaZulu-Natal Drakensberg. Mean altitude was calculated as the mean of the highest altitudes for the three regions.

A.


Mean altitude (m)
3500
3250
3000
2750
2500
2250
2000
Sneeuberge (5)
E. Cape Drak. (16)
KZN Drak. (40)
Mean no. of Cape elements

B.


Mean annual rainfall (mm)
1200
1000
800
600
400
200
Sneeuberge (5)
E. Cape Drak. (16)
KZN Drak. (40)
Mean no. of Cape elements

C.

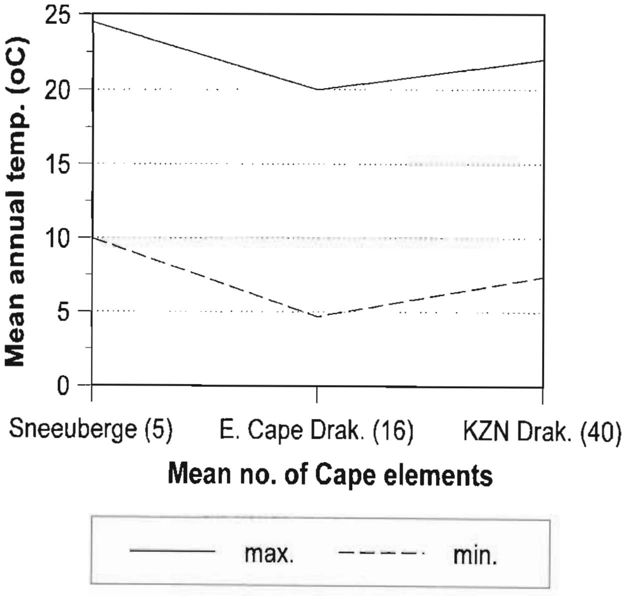

Mean annual temp. (oC)
25
20
15
10
5
0
Sneeuberge (5)
E. Cape Drak. (16)
KZN Drak. (40)
Mean no. of Cape elements
max.
min.

Fig. 2.17. The number of Cape elements per quarter degree grid square for selected high-altitude regions outside the CFR. Data from PRECIS (Gibbs Russell, 1985). Abbreviations: NC, Northern Cape; WC, Western Cape; EC, Eastern Cape; FS, Free State; KZN, KwaZulu-Natal; a, Sneeuberge; b, Eastern Cape Drakensberg and Witteberge; c, KwaZulu-Natal Drakensberg.

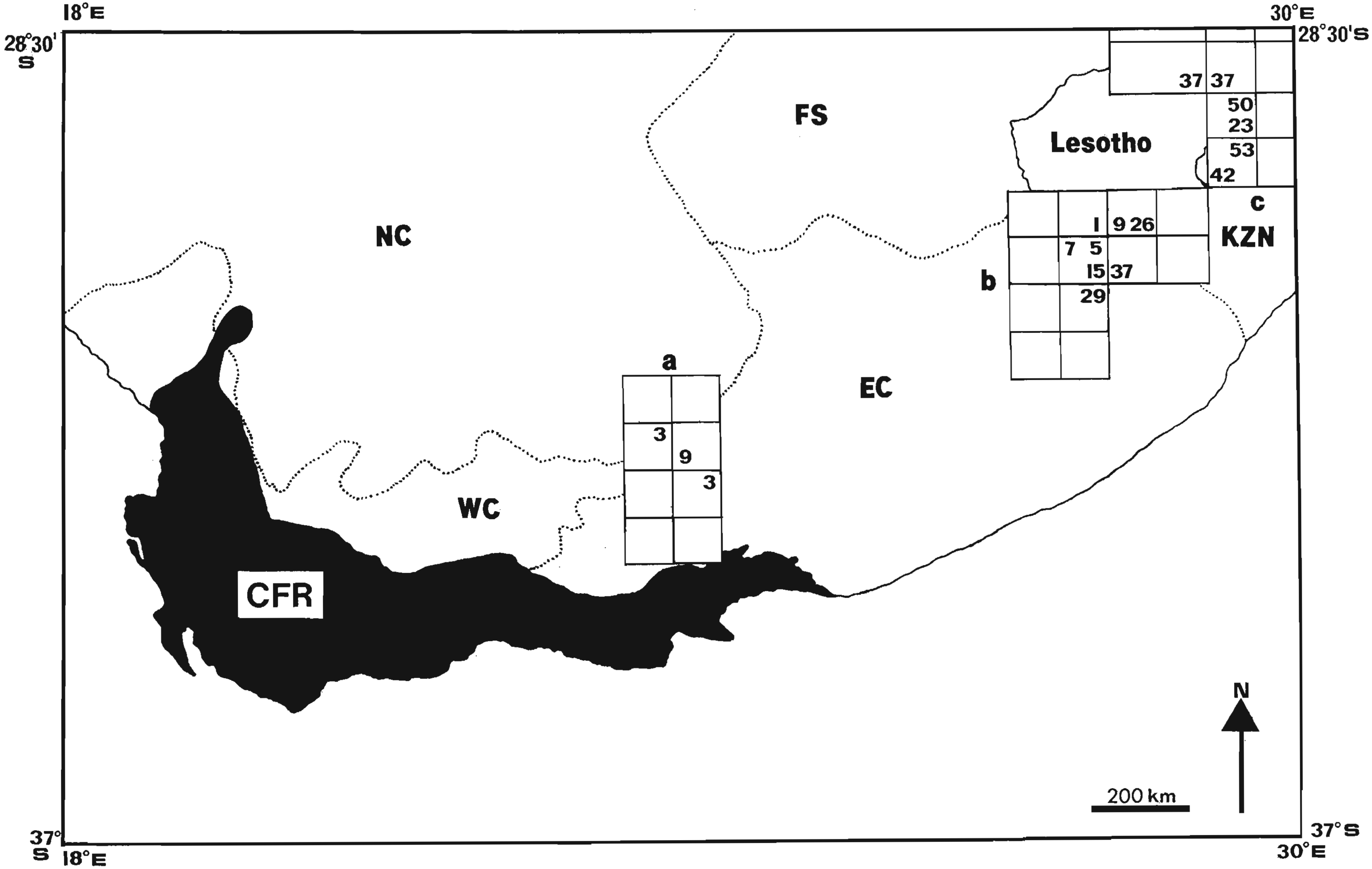
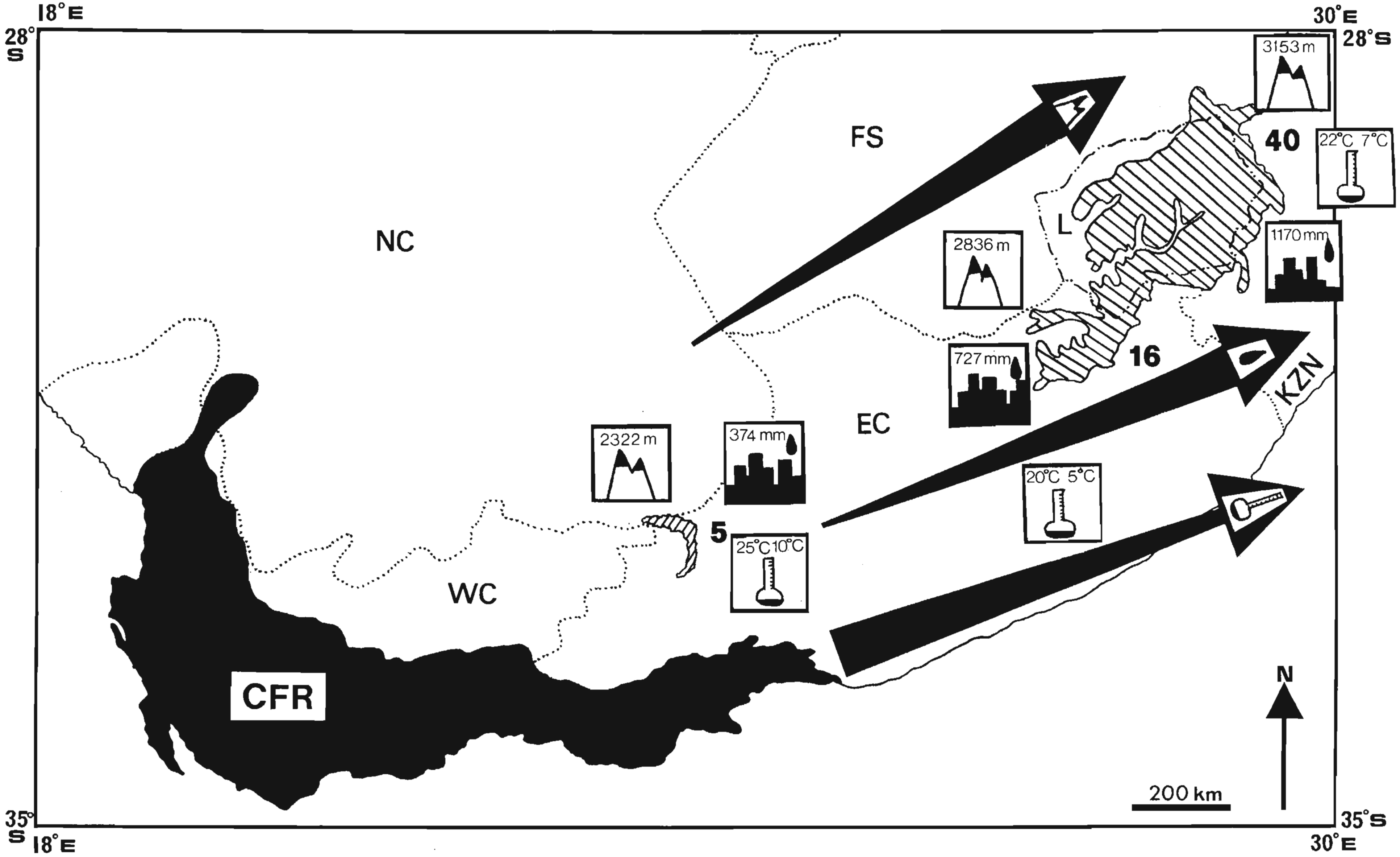

18°E
30°E
28°30' S
28°30'S
37° S
37°S
18°E
30°E
FS
Lesotho
NC
KZN
EC
WC
CFR
a
b
c
37 37
50
23
53
42
1 9 26
7 5
15 37
29
3
9
3
200 km
N

Fig. 2.18. Pictorial representation of the environmental gradients across selected high-altitude regions outside the CFR. The mean number of Cape elements are listed for each high-altitude region (hatched): the Sneeuberge Range (5); the Eastern Cape Drakensberg and Witteberge (16); the KwaZulu-Natal Drakensberg (40). Abbreviations: NC, Northern Cape; WC, Western Cape; EC, Eastern Cape; FS, Free State; KZN, KwaZulu-Natal; L, Lesotho.


18°E
28° S
30°E
28°S
3153 m
40
22°C 7°C
FS
NC
L
2836 m
1170 mm
727 mm
16
KZN
EC
2322 m
374 mm
5
25°C 10°C
20°C 5°C
WC
CFR
N
200 km
35° S
18°E
35°S
30°E

decrease in temperature (Fig. 2.16C) (although the Eastern Cape Drakensberg is slightly colder than the KwaZulu-Natal Drakensberg) (Fig. 2.15). It is important to note that the general decrease in temperature from south-west to north-east pertains specifically to the mountainous regions mentioned above. This does not apply for the country as a whole. Tyson *et al.* (1976) mentioned the decrease of mean January and July temperatures southward over the 13° of latitude covered by South Africa - the collective effects of latitude, continentality and ocean currents.

The increase in the number of Cape elements towards the KwaZulu-Natal Drakensberg (Figs 2.17 & 2.18) corresponded with the south-west to north-east gradient of increasing altitude and rainfall, and decreasing temperature (Fig. 2.16).

2.6.3.2 CAPE ELEMENTS OF THE SOUTHERN AND SOUTH-CENTRAL AFRICAN HIGHLANDS

Cape elements are useful subjects for comparing temperate floras because they often contribute the most taxa to these floras (e.g. Hilliard & Burtt, 1987). Cape elements increase in number from the Sneeuberge, with their numbers peaking in the DAC (72 genera); the majority of these taxa occur in the KwaZulu-Natal Drakensberg (67 genera) (Fig. 2.19). The Sneeuberge and Eastern Cape Drakensberg accommodate the fewest Cape elements south of the DAC, possibly because of their drier climates (Carbutt & Edwards, 2001) and their lower altitudes appear to make them less secure as refugia during episodes of climate change. Numbers decline northwards from the DAC toward south-central Africa (Fig. 2.19), a function of increasing distance from the CFR. The total for Mulanje is an underestimate because few inventories exist for the region. A comprehensive checklist of its spermatophyte flora is currently awaiting publication (A. Strugnell, 2003, pers. comm.). If the northward trend of decreasing

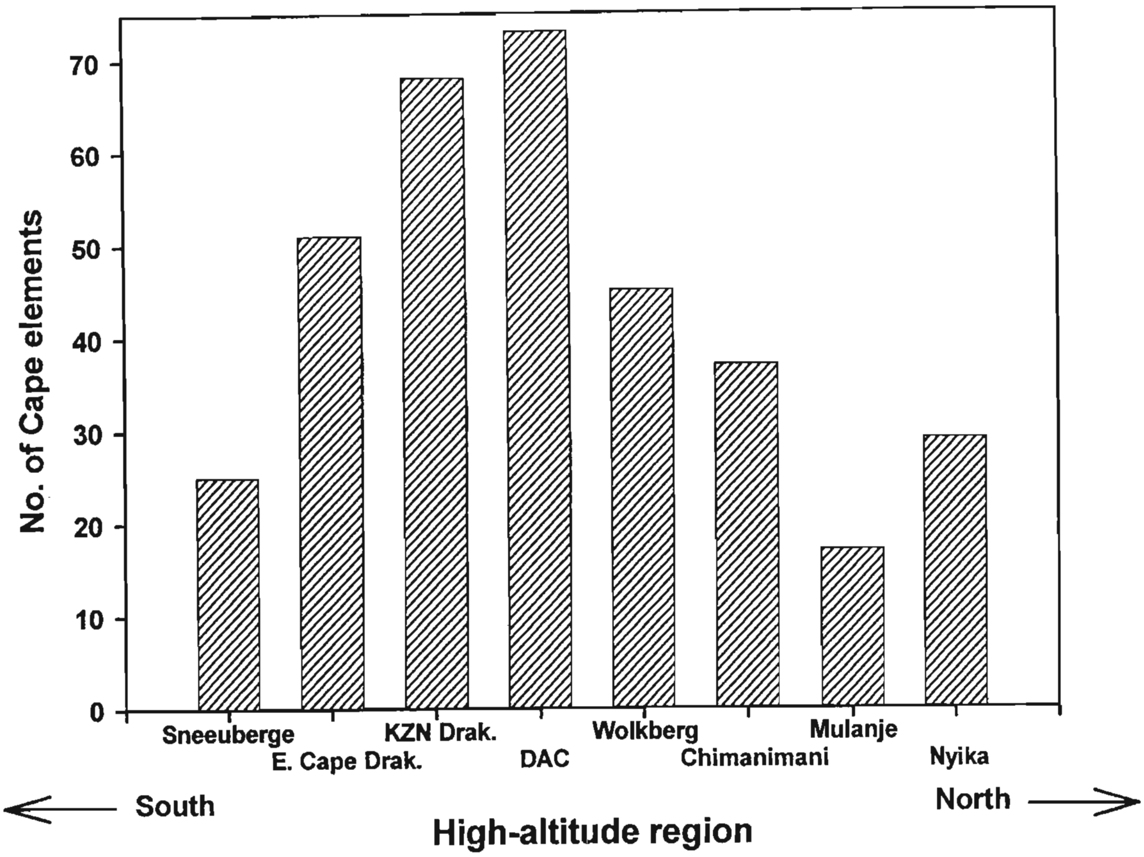


Fig. 2.19. The number of Cape elements for high-altitude regions in southern and south-central Africa[a]. Abbreviations: E. Cape Drak., Eastern Cape Drakensberg; KZN Drak., KwaZulu-Natal Drakensberg; DAC, Drakensberg Alpine Centre.

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[a] (1) These numbers do not equal those for the initial high-altitude analysis of Lesotho and South Africa (Figs 2.17 & 2.18) because the former analysis used only PRECIS data expressed as numbers of taxa per quarter degree grid (Fig. 2.17) and as a mean per region (Fig. 2.18) in order to determine basic environmental gradients. The current analysis covered a wider area and used data from many sources. (2) Most of these high-altitude regions are centres of plant diversity, as recognised by Van Wyk & Smith (2001), which coincidentally accommodate significant numbers of Cape elements. It is not implied that these regions are official centres for Cape elements.

Cape elements continues into tropical Africa as expected, this pattern would suggest either a southern origin in the Cape Region or extinction in the northern stations as taxa migrated southwards.

A botanical survey of the Klein Swartberg in the northern reaches of the Cape Fold Mountains (Linder *et al.*, 1993) corroborates the Cape element-environmental correlation expressed above. The high-altitude flora of the Klein Swartberg is closely allied to the Drakensberg flora of KwaZulu-Natal, Lesotho and the Free State, and less so to the proximal Sneeuberge. The latter range is floristically more similar to the Eastern Cape Drakensberg-Witteberge whose floras are probably both drought-adapted. Ties between the flora of the Klein Swartberg and those of mountains to the north of the Limpopo River are poor (Linder *et al.*, 1993).

2.6.3.3 CAPE ELEMENTS OF THE DAC AND PC

There is an overwhelming overlap of Cape-centred genera (≈ Cape elements) that occur in the DAC and PC. Collectively 89 genera occur in 37 families ($\bar{x}$ = 2.4 genera per family) (Table 2.12). Of these, 60 genera are shared between the DAC and PC, 17 are not recorded from the DAC, and 12 are not recorded from the PC (Table 2.12).

The total of 77 Cape elements for the PC is the highest recorded number of Cape elements in any flora. This is perhaps a function of its close proximity to the CFR and edaphically similar nutrient-poor substrates, as well as the ameliorating effect of its maritime climate on extinction events.

A number of genera (≈ potential candidates) were excluded from the analysis despite their radiation in the Cape Region, because their strict centre of diversity is not the CFR. These taxa and their centres of diversity are as follows: *Cyphia* -

Table 2.12. Cape elements occurring either as secondary centres in the Drakensberg Alpine Centre (DAC), in the Pondoland Centre (PC), or shared between both regions. Abbreviations: C-D, Cape-Drakensberg overlap; C-P, Cape-Pondoland overlap; SH, shared between Cape, Drakensberg and Pondoland floras. Note: *, distinct centre of radiation present in the CFR, but other significant centre(s) of radiation present elsewhere (i.e. DAC). $^{++}$, predominantly annuals in the CFR, weak perennials in the DAC. **, *Gladiolus*: Cape sections *Blandus*, *Homoglossum* and *Linearifolius* only.

Taxon	Authorities recognising 'Cape element' status	C-D	C-P	SH
Agathosma	Pillans, 1950; Glen, 1996			✓
Anisodontea	Dyer, 1975; Goldblatt & Manning, 2000			✓
Anthospermum	Puff, 1986			✓
Arctotis	Hilliard, 1977			✓
Aristea	Weimarck, 1940; Goldblatt, 1983, 1995; Vincent, 1985			✓
Aspalathus	Dahlgren, 1963, 1968			✓
Athanasia	Hilliard, 1978; Källersjö, 1985	✓		
Boophone	Goldblatt & Manning, 2000			✓
Bulbine	Baijnath, 1987; Van Jaarsveld & Baijnath, 1987			✓
Caesia	Obermeyer, 1973		✓	
Calopsis	Linder, 1984, 1985b		✓	
Centella	Adamson, 1951			✓
Cliffortia	Weimarck, 1934, 1948; C. Whitehouse, pers. comm, 2003			✓
Colpoon	Bean, 1990a		✓	
Corycium	Kurzweil *et al.*, 1991; Linder & Kurzweil, 1999			✓
Cotula^{++}	Hilliard, 1977, 1978			✓
Crassula	Tölken, 1985; Glen, 1996			✓
*Disa**	Linder, 1983; Linder & Kurzweil, 1999			✓
Diascia^{*++}	Hilliard & Burtt, 1984; Steiner, 1992			✓
Disparago	Levyns, 1936; Hilliard, 1978		✓	
Ehrharta	Gibbs Russell & Ellis, 1987; Gibbs Russell *et al.*, 1990			✓
Empodium	Burtt, 2000			✓

Taxon	Authorities recognising 'Cape element' status	C-D	C-P	SH
Erica	Oliver, 1989, 1991; Schumann & Kirsten, 1992			✓
Eriospermum	Perry, 1984, 1989			✓
*Euryops**	Nordenstam, 1969; Hilliard, 1978			✓
Felicia++	Levyns, 1950; Hilliard, 1977, 1978			✓
Ficinia	Arnold & Gordon-Gray, 1978; Gordon-Gray, 1995			✓
*Gladiolus***	Goldblatt & Manning, 1998			✓
Gnidia	Wright, 1915; A. Beaumont, pers. comm., 1999			✓
Hebenstretia++	Roessler, 1979			✓
Heliophila++	Marais, 1970; Bean, 1990b			✓
*Hesperantha**	Goldblatt, 1983, 1984, 1986a, 2003; Hilliard & Burtt, 1986a			✓
Holothrix	Linder & Kurzweil, 1999			✓
Homeria	Goldblatt, 1973, 1981	✓		
Hyobanche	Goldblatt & Manning, 2000; A. Wolfe, pers. comm., 2003	✓		
Ischyrolepis	Linder, 1984, 1985b			✓
Knowltonia	Rasmussen, 1979		✓	
Lampranthus	Pooley, 1998; Goldblatt & Manning, 2000		✓	
Leucadendron	Williams, 1972; Van Wyk, 1990a, 1990b; Glen, 1996		✓	
Leucospermum	Rourke, 1972; Van Wyk, 1990a, 1990b		✓	
Lichtensteinia	Burtt, 1991		✓	
Loxostylis	Killick, 1968; Van Wyk, 1990a		✓	
Macrochaetium	Levyns, 1947; Gordon-Gray, 1995		✓	
Manulea++	Hilliard, 1994			✓
Massonia	Jessop, 1976	✓		
*Merxmuellera**	Gibbs Russell *et al.*, 1990	✓		
Metalasia	Pillans, 1954; Levyns, 1964; Karis, 1989	✓		
Moraea	Goldblatt, 1983, 1986b			✓
Muraltia	Levyns, 1954, 1964			✓
Nemesia++	Hilliard & Burtt, 1986b; Steiner, 1989			✓
Nenax	Puff, 1986	✓		
Osteospermum	Hilliard, 1977, 1978			✓
Otholobium	Stirton, 1981, 1986			✓
Othonna	Hilliard, 1977, 1978			✓
Oxalis	Salter, 1944; Oberlander *et al.*, 2002			✓
Passerina	Thoday, 1924; Weimarck, 1941			✓

Taxon	Authorities recognising 'Cape element' status	C-D	C-P	SH
Pelargonium	Van der Walt & Vorster, 1983			✓
Pentaschistis	Linder & Ellis, 1990	✓		
Phylica	Pillans, 1942; Van Wyk, 1990a			✓
Plecostachys	Hilliard, 1983			✓
Podalyria	Harvey, 1862a; Hilliard, 1978; Schelpe, 1987		✓	
Prionium	Obermeyer, 1985; Van Wyk, 1990a, 1990b		✓	
Protea	Beard, 1958, 1963; Rourke, 1980			✓
Pseudoscolopia	Killick, 1976b; Glen, 1996		✓	
Psoralea	Salter, 1950; Van Wyk, 1990a			✓
Pterygodium	Kurzweil *et al.*, 1991; Linder & Kurzweil, 1999	✓		
Rafnia	Harvey, 1862b; Van Wyk, 1990a, 1990b		✓	
Raspalia	Pillans, 1947; Van Wyk, 1990a		✓	
Relhania	Bremer, 1976; Anderberg & Bremer, 1991			✓
Restio	Pillans, 1928; Linder, 1984, 1985b			✓
Rhodocoma	Linder, 1985b; Linder & Vlok, 1991			✓
Roella	Adamson, 1951		✓	
Romulea	De Vos, 1972, 1983a	✓		
Ruschia	Hartmann, 1991	✓		
Sebaea	Marais & Verdoorn, 1963			✓
Selago^{++}	Hilliard, 1999			✓
Stoebe	Levyns, 1937; Glen, 1996			✓
Struthiola	Wright, 1915; Levyns, 1964			✓
Sutera	Hilliard, 1994			✓
Tetraria	Gordon-Gray, 1995			✓
Thesium	Hill, 1915; Hendrych, 1970			✓
Trachyandra	Obermeyer, 1962			✓
Tritonia	De Vos, 1982, 1983b			✓
Troglophyton	Hilliard, 1983	✓		
Ursinia	Hilliard, 1977, 1978			✓
Wahlenbergia	Von Brehmer, 1915; Goldblatt & Manning, 2000			✓
Watsonia	Goldblatt, 1983, 1989			✓
Wurmbea	Nordenstam, 1978			✓
Zaluzianskya^{++}	Hilliard & Burtt, 1983; Hilliard, 1994			✓
$\sum$ = 89		**12**	**17**	**60**

southern Africa (Cupido & Conrad, 2003), *Cyrtanthus* - Eastern Cape (Reid & Dyer, 1984), *Haemanthus* - Namaqualand (Snijman, 1984), *Harveya* - the broader Cape Region (C. Randall, 2003, pers. comm.), *Ifloga* - arid regions of southern Africa (Hilliard, 1981), *Jamesbrittenia* - Namaqualand and Karoo (Hilliard, 1994), *Kniphofia* - South Africa (Codd, 1968), *Lotononis* - occupies marginal habitats seral to fynbos and shares strong ties with tropical Africa (Van Wyk, 1991), *Ornithogalum* - southern Cape to tropical Africa (Obermeyer, 1978) and *Saniella* - Hantam-Roggeveld Centre of the Succulent Karoo (Burtt, 2000).

The common occurrence of species and sections in the CFR, DAC and PC is notable in a number of vicarious Cape-centred genera (Tables 2.13 - 2.17). None of these species seem capable of long-distance dispersal. It must be pointed out, however, that most of the overlapping species are fairly widespread taxa (≈ generalists), undermining the floristic links shared between the DAC and PC at the specific level.

2.6.3.4 FAMILY-LEVEL FLORISTICS

Of the 37 families contributing Cape elements to both floras, 6 families (i.e. 16%) contribute 44 of the 89 genera (i.e. 49%) (Fig. 2.20). Families with the highest numbers of Cape elements common to both the DAC and PC are the Asteraceae, Scrophulariaceae, Iridaceae, Fabaceae, Orchidaceae, Restionaceae and Thymelaeaceae (Fig. 2.20). The Cape elements of the DAC that are not shared with the PC belong to the Asteraceae, Iridaceae, Poaceae (temperate grasses only), Orchidaceae and Scrophulariaceae (Fig. 2.20). Their members are mostly herbaceous taxa restricted to grassland habitats, typical of regions that form part of the Grassland Biome (Rutherford & Westfall, 1994; Low & Rebelo, 1996).

Table 2.13. Phytogeographical overview of *Aristea* in the Cape Floristic Region (CFR) and KwaZulu-Natal (KZN) (adapted from Weimarck, 1940; Goldblatt, 1983, 1995; Vincent, 1985). Note: * of the world total, ** of the regional total. Bolded taxa are those common to both the DAC and PC. Taxon numbers include subspecies and varieties.

***Aristea* Aiton (Iridaceae)**						
No. of species & centre of distribution	**No. of Cape taxa**	**No. of Cape high-altitude taxa**	**No. of KZN taxa**	**No. of KZN high-altitude taxa**	**Species shared between CFR & DAC (= 1)**	**Section**
c. 50 spp. in total, sub-Saharan Africa & Madagascar, mostly SW Cape	30 (60%*)	23 (77%**)	13 (26%*)	9 (69%**)	***A. abyssinica* Pax**	***Ancipites***
					Species shared between CFR & PC (= 3)	**Section**
					***A. abyssinica* Pax**	***Ancipites***
					A. ecklonii Baker	*Pseudaristea*
					A. schizolaena Harv.	*Euaristea*

Table 2.14. Phytogeographical overview of *Cliffortia* in the Cape Floristic Region (CFR) and KwaZulu-Natal (KZN) (adapted from Weimarck, 1934, 1948; Whitehouse, 2003). Note: * of the world total, ** of the regional total. Bolded taxa are those common to both the DAC and PC. Taxon numbers include subspecies and varieties.

Cliffortia **L. (Rosaceae)**

No. of species & centre of distribution	**No. of Cape taxa**	**No. of Cape high-altitude taxa**	**No. of KZN taxa**	**No. of KZN high-altitude taxa**	**Species shared between CFR & DAC (= 3)**	**Section**
c. 118 spp. in total, South Africa to tropical East Africa, mostly SW Cape mountains	112 (95%*)	86 (77%**)	10 (8%*)	7 (70%**)	***C. linearifolia*** **Eckl. & Zeyh.**	***Costatae***
					C. paucistaminea **Weim.**	***Costatae***
					C. repens Schltr.	*Simplices*
					Species shared between CFR & PC (= 5)	**Section**
					C. linearifolia **Eckl. & Zeyh.**	***Costatae***
					C. odorata L. f.	*Simplices*
					C. paucistaminea **Weim.**	***Costatae***
					C. serpyllifolia Cham. & Schlechtd.	*Costatae*
					C. strobilifera Murray	*Simplices*

Table 2.15. Phytogeographical overview of *Diascia* in the Cape Floristic Region (CFR) and KwaZulu-Natal (KZN) (adapted from Hilliard & Burtt, 1984; Steiner, 1992). Note: * of the world total, ** of the regional total. Taxon numbers include subspecies and varieties. †*Diascia* section *Racemosae* comprises 26 species, confined mostly to the Eastern Region, with five species reaching the CFR (Hilliard & Burtt, 1984).

***Diascia* Link & Otto (Scrophulariaceae)**						
No. of species & centre of distribution	**No. of Cape taxa**	**No. of Cape high-altitude taxa**	**No. of KZN taxa**	**No. of KZN high-altitude taxa**	**Study taxon selected**	**Section**
c. 67 spp. in total, southern Africa, mostly CFR & DAC	46 (69%*)	36? (78%**)	10 (15%*)	9 (90%**)	*D. mollis* Hilliard & Burtt (refer to Chapter 4)	*Racemosae*†

Table 2.16. Phytogeographical overview of *Erica* in the Cape Floristic Region (CFR) and KwaZulu-Natal (KZN) (adapted from Oliver, 1989, 1991; Schumann & Kirsten, 1992; Goldblatt & Manning, 2002). Note: * of the world total, ** of the South African total, *** of the regional total. Bolded taxa are those common to both the DAC and PC. Taxon numbers include subspecies and varieties.

***Erica* L. (Ericaceae)**						
No. of species & centre of distribution	**No. of Cape taxa**	**No. of Cape high-altitude taxa**	**No. of KZN taxa**	**No. of KZN high-altitude taxa**	**Species shared between CFR & DAC (= 5)**	**Section**
c. 770 spp. in total, Africa & Europe, mainly South Africa (c. 690 spp.), mostly SW Cape	657 (85%*, 95%**)	577 (88%***)	46 (6%*, 7%**)	33 (72%***)	**_E. caffra_ L. var. _caffra_**	***Ephebus***
					E. cerinthoides L. var. _cerinthoides_ FP	***Dasyanthes***
					E. leucopelta Tausch var. _leucopelta_	***Arsace***
					E. leucopelta Tausch var. *pubescens* H. Bol.	*Arsace*
					E. maesta H. Bol. var. *maesta*	*Chlorocodon*
					Species shared between CFR & PC (= 4)	**Section**
					E. caffra L. var. _caffra_	***Ephebus***
					E. cerinthoides L. var. _cerinthoides_ FP	***Dasyanthes***
					E. cubica L. var. *cubica*	*Melastemon*
					E. leucopelta Tausch var. _leucopelta_	***Arsace***

Table 2.17. Phytogeographical overview of *Romulea* in the Cape Floristic Region (CFR) and KwaZulu-Natal (KZN) (adapted from De Vos, 1972, 1983a). Note: * of the world total, ** of the regional total. Taxon numbers include subspecies and varieties. *Romulea* in KwaZulu-Natal is restricted to high-altitudes in the DAC, between c. 2100 - 3000 m, with an outlier at a slightly lower elevation on Ngeli Mountain (De Vos, 1983a).

***Romulea* Maratti (Iridaceae)**						
No. of species & centre of distribution	**No. of Cape taxa**	**No. of Cape high-altitude taxa**	**No. of KZN taxa**	**No. of KZN high-altitude taxa**	**Species shared between CFR & DAC (= 1)**	**Section**
c. 90 spp. in total, South Africa to southern Europe (Mediterranean Sea region), mostly SW Cape	70 (78%*)	52 (74%**)	6 (7%*)	6 (100%**)	*R. luteoflora* De Vos	*Roseae*

Interestingly, the Poaceae are more dominant in the Cape Fold Mountains than at lower elevations, replacing families such as the Proteaceae and Iridaceae (Linder *et al.*, 1993). The dominance of the C_3 grasses *Ehrharta*, *Festuca*[a], *Koeleria*[a], *Merxmuellera* and *Pentaschistis* on the summit of the DAC (Killick, 1978b, 1994) may be a helpful indicator of ecological constraints as C_3 grases in general have lower temperature optima for photosynthesis that C_4 taxa, and tend to favour infertile regions, particularly low in soil nitrogen (Cowling, 1983). Their dominance therefore testifies to the cool, impoverished nature of this high-altitude environment.

The Cape elements of the PC that are not shared with the DAC belong to the Fabaceae, Proteaceae, Asphodelaceae, Asteraceae, Cyperaceae and Restionaceae (Fig. 2.20). In the PC, the subtropical Poaceae occur in place of the cold-adapted temperate grasses from higher altitudes.

The success of the families contributing the most Cape elements is partly a result of their geophytic growth form. Subterranean storage organs and annual aerial parts are convergent in these families. Tunicated corms (Iridaceae), lignotubers (Asteraceae, Fabaceae and some Scrophulariaceae), tuberoid roots (Orchidaceae) and creeping rhizomes (Restionaceae) all represent efficient strategies for nutrient storage. Most of these families are able to survive cold winters (often with snow) and seasonal fires by dying back during the dry season.

2.6.3.5 COMBINING FLORISTICS WITH GROWTH AND LIFE FORMS

Most life form systems conveniently appropriate the following generalizations: (1) plants exhibit different ecological tolerances; (2) physiological adaptation to the

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[a] Not Cape elements, but are nonetheless included to reiterate the point.

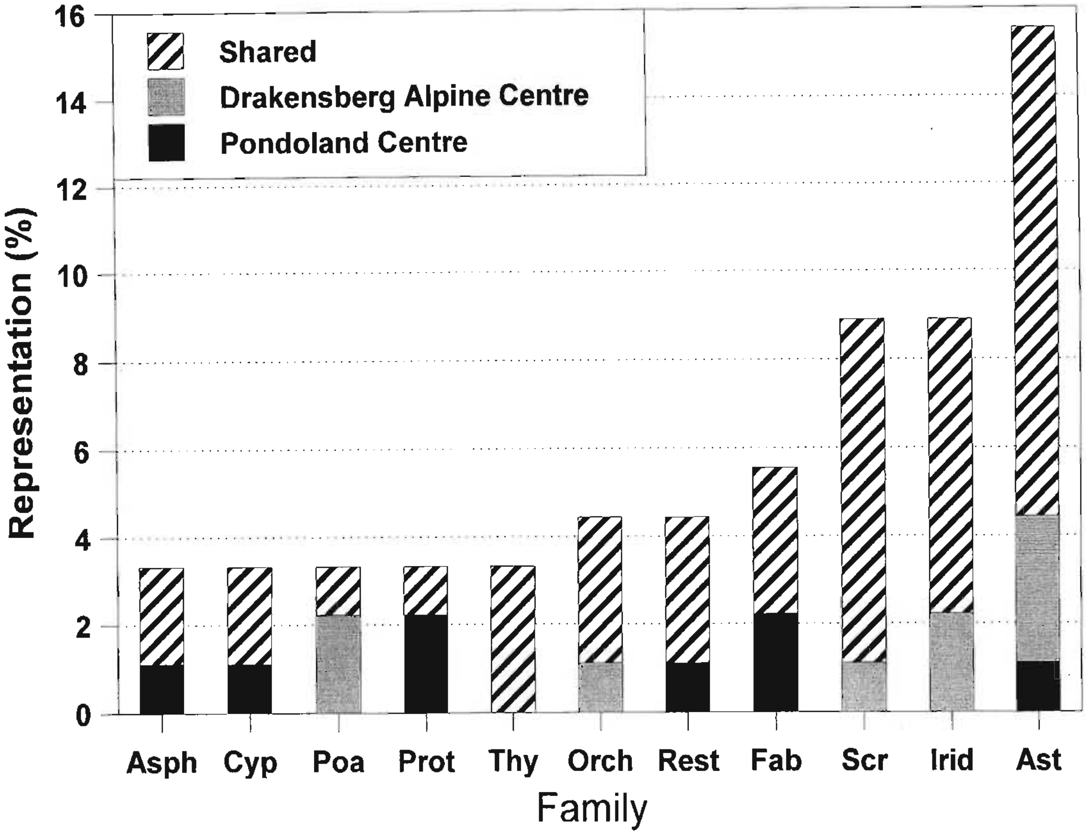

Fig. 2.20. Eleven of the 37 angiosperm families that contribute the most Cape elements occurring either as secondary centres in the Drakensberg Alpine Centre (DAC), in the Pondoland Centre (PC), or shared between both regions. Family abbreviations: Asph, Asphodelaceae; Cyp, Cyperaceae; Poa, Poaceae; Prot, Proteaceae; Thy, Thymelaeaceae; Orch, Orchidaceae; Rest, Restionaceae; Fab, Fabaceae; Scr, Scrophulariaceae; Irid, Iridaceae; Ast, Asteraceae.

Table 2.18. The growth and life form account of Cape elements occurring either as secondary centres in the Drakensberg Alpine Centre (DAC), in the Pondoland Centre (PC), or shared between both regions.

Taxon	Family	Growth and life form
Agathosma	Rutaceae	ericoid shrublets or shrubs
Anisodontea	Malvaceae	mesic perennial herbs, shrublets or shrubs
Anthospermum	Rubiaceae	herbs or shrublets
Arctotis	Asteraceae	mat-forming perennial herbs
Aristea	Iridaceae	evergreen geophytic perennial herbs
Aspalathus	Fabaceae	ericoid shrublets or shrubs
Athanasia	Asteraceae	mesic herbs, shrublets or shrubs
Boophane	Amaryllidaceae	deciduous bulbous herbs
Bulbine	Asphodelaceae	succulent perennial herbs or shrublets
Caesia	Asphodelaceae	grasslike geophtyic herbs
Calopsis	Restionaceae	rhizomatous sclerophyllous herbs
Centella	Apiaceae	perennial creeping herbs
Cliffortia	Rosaceae	sclerophyllous shrublets or shrubs
Colpoon	Santalaceae	shrubs or small trees
Corycium	Orchidaceae	tuberous herbs
Cotula	Asteraceae	mesic annual or perennial herbs
Crassula	Crassulaceae	succulent annual or perennial herbs or shrubs
Disa	Orchidaceae	tuberous herbs
Diascia	Scrophulariaceae	mesic annual or perennial herbs
Disparago	Asteraceae	ericoid shrublets
Ehrharta	Poaceae	annual or perennial herbs
Empodium	Hypoxidaceae	rhizomatous herbs
Erica	Ericaceae	ericoid shrublets or shrubs
Eriospermum	Eriospermaceae	perennial geophytic herbs
Euryops	Asteraceae	mesic shrublets or shrubs
Felicia	Asteraceae	mesic herbs or shrublets
Ficinia	Cyperaceae	erect leafy perennial herbs
Gladiolus	Iridaceae	cormous herbs
Gnidia	Thymelaeaceae	ericoid perennial shrublets or shrubs
Hebenstretia	Scrophulariaceae	mesic annual or perennial herbs or shrubs

Taxon	Family	Growth and life form
Heliophila	Brassicaceae	mesic annual or perennial herbs or shrubs
Hesperantha	Iridaceae	cormous deciduous herbs
Holothrix	Orchidaceae	tuberous terrestrial or lithophytic herbs
Homeria	Iridaceae	cormous deciduous herbs
Hyobanche	Scrophulariaceae	parasitic herbs
Ischyrolepis	Restionaceae	rhizomatous sclerophyllous herbs
Knowltonia	Ranunculaceae	erect perennial herbs
Lampranthus	Mesembryanthemaceae[a]	mat-forming succulent herbs, shrublets or shrubs
Leucadendron	Proteaceae	mesic dioecious shrubs or trees
Leucospermum	Proteaceae	mesic shrubs or small trees
Lichtensteinia	Apiaceae	erect perennial herbs
Loxostylis	Anacardiaceae	mesic dioecious small trees
Macrochaetium	Cyperaceae	rhizomatous perennial herbs
Manulea	Scrophulariaceae	mesic annual or perennial herbs or shrublets
Massonia	Hyacinthaceae	small geophytic herbs
Merxmuellera	Poaceae	tufted ericoid perennial herbs
Metalasia	Asteraceae	ericoid shrublets or shrubs
Moraea	Iridaceae	cormous deciduous herbs
Muraltia	Polygalaceae	ericoid shrublets or shrubs
Nemesia	Scrophulariaceae	mesic annual or perennial herbs or shrublets
Nenax	Rubiaceae	dwarf woody sclerophyllous shrubs
Osteospermum	Asteraceae	mesic perennial herbs or shrublets
Otholobium	Fabaceae	ericoid shrubs
Othonna	Asteraceae	herbs, sub-shrubs or shrubs
Oxalis	Oxalidaceae	cormous or tuberous annual or perennial herbs
Passerina	Thymelaeaceae	ericoid shrublets or shrubs
Pelargonium	Geraniaceae	tuberous herbs, undershrubs or shrubs
Pentaschistis	Poaceae	tufted perennial (rarely annual) herbs
Phylica	Rhamnaceae	ericoid shrublets or shrubs
Plecostachys	Asteraceae	mesic sub-shrubs
Podalyria	Fabaceae	mesic shrubs
Prionium	Juncaceae	stoloniferous semi-aquatic herbs
Protea	Proteaceae	sclerophyllous shrubs or small trees
Pseudoscolopia	Flacourtiaceae	mesic shrubs or small trees
Psoralea	Fabaceae	ericoid herbs, undershrubs or shrubs

Taxon	Family	Growth and life form
Pterygodium	Orchidaceae	terrestrial tuberous herbs
Rafnia	Fabaceae	mesic shrublets or shrubs
Raspalia	Bruniaceae	ericoid shrublets or shrubs
Relhania	Asteraceae	sclerophyllous herbs, shrublets or shrubs
Restio	Restionaceae	sclerophyllous rush-like perennial herbs
Rhodocoma	Restionaceae	mostly rhizomatous sclerophyllous herbs
Roella	Campanulaceae	ericoid herbs or shrublets
Romulea	Iridaceae	small cormous deciduous herbs
Ruschia	Mesembryanthemaceae[a]	dwarf perennial succulent geophytic shrubs
Sebaea	Gentianaceae	mesic annual or perennial herbs
Selago	Scrophulariaceae	ericoid annual or perennial herbs or shrublets
Stoebe	Asteraceae	ericoid shrubs
Struthiola	Thymelaeaceae	ericoid shrublets or shrubs
Sutera	Scrophulariaceae	mesic annual or perennial herbs or shrublets
Tetraria	Cyperaceae	coarse, tufted grass-like perennial herbs
Thesium	Santalaceae	ericoid hemiparasitic herbs or sub-shrubs
Trachyandra	Asphodelaceae	rhizomatous grasslike herbs
Tritonia	Iridaceae	deciduous cormous herbs
Troglophyton	Asteraceae	annual or perennial herbs
Ursinia	Asteraceae	mesic annual or perennial herbs or undershrubs
Wahlenbergia	Campanulaceae	mesic annual or perennial herbs or shrublets
Watsonia	Iridaceae	large evergreen or deciduous cormous herbs
Wurmbea	Colchicaceae	cormous perennial herbs
Zaluzianskya	Scrophulariaceae	mesic annual or perennial herbs

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[a] Mesembryanthemaceae is upheld over Aizoaceae (P. Burgoyne, 2003, pers. comm.).

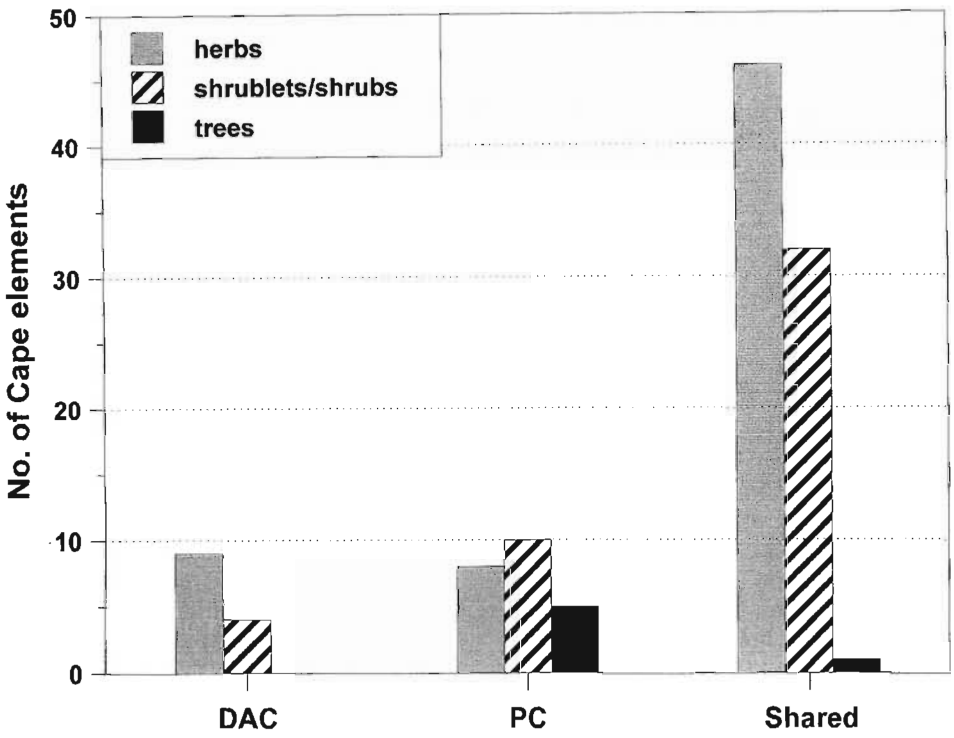

Fig. 2.21. The life forms of Cape elements occurring either as secondary centres in the Drakensberg Alpine Centre (DAC), in the Pondoland Centre (PC), or shared between both regions. Numbers presented graphically exceed those listed in Table 2.18 because simultaneous inclusion into a number of categories was possible.

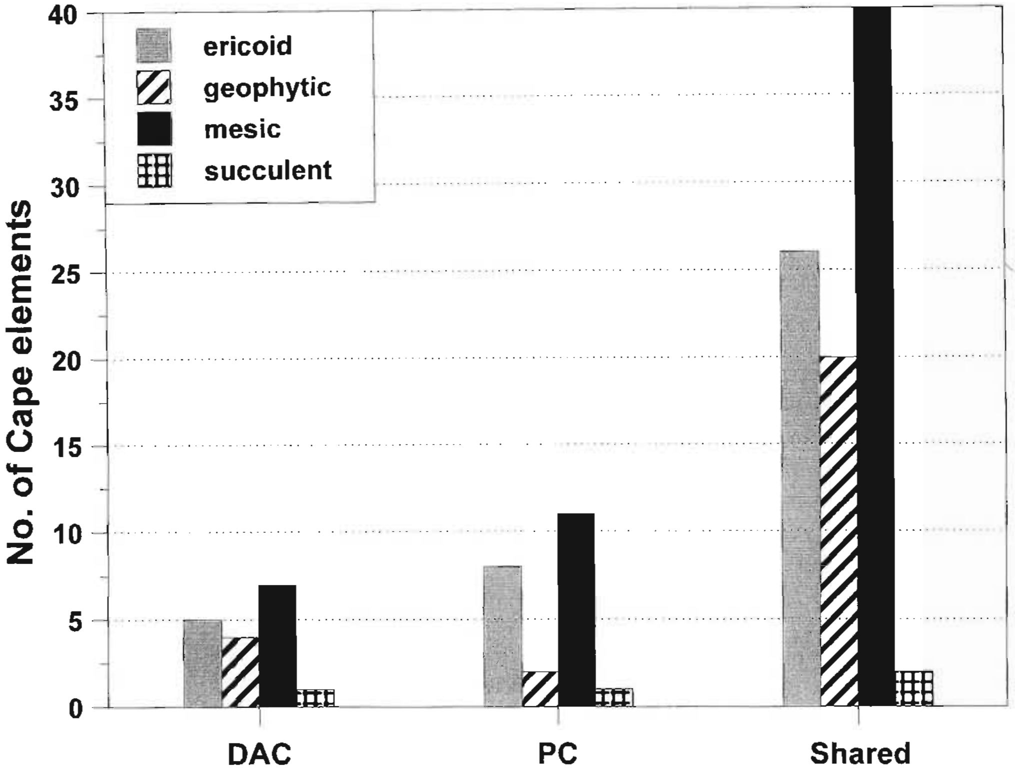

Fig. 2.22. The growth forms of Cape elements occurring either as secondary centres in the Drakensberg Alpine Centre (DAC), in the Pondoland Centre (PC), or shared between both regions. Numbers presented graphically exceed those listed in Table 2.18 because simultaneous inclusion into a number of categories was possible. Qualification: ericoid: leaves ericoid and/or sclerophyllous.

environment is a prerequisite for survival; and (3) there is often a correlation between morphology and adaptation (Cain & Castro, 1959). The life form system is determined by general physiognomy whereas growth form divisions are based on shoot architecture (Adamson, 1939; Rutherford & Westfall, 1994). There is no generally accepted classification of plants into growth forms (Rutherford & Westfall, 1994), hence the emphasis on life form systems such as that proposed by Raunkiaer (1934). Körner (1999) argued that 'growth form' is a 'general plan', whereas 'life form' is a phenotypic response to plant-environment interactions. Concise definitions are conflicting, hence the adopted approach to benefit this study.

The life form system of Raunkiaer (1934) was modified for this analysis. The initial framework (Table 2.18) was loosely dissected into life (Fig. 2.21) and growth forms (Fig. 2.22). In terms of life forms, most Cape elements of the summer rainfall region are herbs and shrubs, although the PC includes a number of trees (Fig. 2.21). Cape elements occurring as trees are poorly represented in the DAC, the single contributor being *Protea*. The endemic species of the southern KwaZulu-Natal Drakensberg (Hilliard & Burtt, 1987; Cowling & Hilton-Taylor, 1994, 1997) and the PC (Abbott *et al.*, 2000) follow similar patterns with respect to their life forms. The allotment of growth forms is as follows. Cape elements of the DAC and those shared between the DAC and PC are mostly either mesic or ericoid (and sclerophyllous) taxa, many of which are also geophytic (Fig. 2.22) (as for reasons mentioned in Section 2.6.3.4). A similar trend occurs in the PC, but with fewer geophytes (Fig. 2.22).

Sclerophylly has been interpreted as a functional response to a number of ecological constraints. It has been correlated with water conservation in both high-altitude tropical environments (Leuschner, 2000) and arid to semi-arid environments (Levitt, 1980), particularly those susceptible to summer drought (Axelrod, 1973, Beard, 1977). Sclerophylly is also thought to improve nutrient use efficiency in nutrient-poor environments (Loveless, 1961, 1962; Beadle, 1966, 1968; Small, 1972; Specht & Rundel, 1990; Stock *et al.*, 1992) by increasing carbon return per unit of nutrient invested that in turn makes photosynthesis more cost-effective (Orians & Solbrig, 1977; Mooney, 1983). The prevalence of sclerophylly in the Cape Region over the entire moisture spectrum is suggestive of nutrient deprivation (Campbell & Werger, 1988; Stock & Allsopp, 1992; Stock *et al.*, 1997). The high incidence of sclerophylly in Cape elements of the DAC and PC (Fig. 2.22), which are both mesic environments, also suggests that nutrient limitation is a factor, either the result of temperature and soil pH, or inherently nutrient-poor substrates respectively. The incidence of succulence is poor in both regions (Fig. 2.22), most probably the result of high fire frequency characteristic of grasslands (Rutherford & Westfall, 1994).

Some 25% of Cape elements possess supplementary mechanisms for acquiring nutrients, either in the form of host-specific or general (VA) mycorrhizae, capillaroid and proteoid roots, parasitic haustoria or N_2-fixing root nodules (Table 2.19). This statistic may be an underestimate and further research into the symbiotic relationships of the remaining Cape elements is necessary. These associations are effective strategies for maximising the uptake of limiting nutrients, especially nitrogen, phosphorus, and a range of micronutrients (Lamont, 1982, 1983a, 1983b).

Certain mycorrhizae are highly effective in acidic soils (Clark & Baligar, 2000); their infection of roots enhances the acquisition of phosphorus in particular due to the extensive surface areas of their fungal hyphae (Lamont, 1982; Binkley & Vitousek,

Table 2.19. The adaptive strategies[a] used by Cape elements of the Drakensberg Alpine Centre (DAC) and Pondoland Centre (PC) to maximise nutrient uptake through their association with microsymbionts (adapted from Lamont, 1981, 1982, 1983a, 1983b).

Strategy	Taxon	Family
Capillaroid root clusters	*Restio*	Restionaceae
Ericoid mycorrhizae	*Erica*	Ericaceae
Orchid mycorrhizae	*Corycium*	Orchidaceae
	Disa	Orchidaceae
	Holothrix	Orchidaceae
	Pterygodium,	Orchidaceae
Proteoid roots	*Leucadendron*	Proteaceae
	Leucospermum	Proteaceae
	Protea	Proteaceae
Root hemiparasites	*Colpoon*	Santalaceae
	Thesium	Santalaceae
Root holoparasites	*Hyobanche*	Scrophulariaceae
Root nodules infected with the *Rhizobium* bacterium	*Aspalathus*	Fabaceae
	Otholobium	Fabaceae
	Podalyria	Fabaceae
	Psoralea	Fabaceae
	Rafnia	Fabaceae
Vesicular-arbuscular (VA) mycorrhizae	*Cliffortia*	Rosaceae
	Oxalis	Oxalidaceae
	Phylica	Rhamnaceae
	Stoebe	Asteraceae

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[a] These adaptations have not necessarily evolved in response to the nutrient-poor soils of the CFR, but are mostly family-level adaptations prevalent in taxa across numerous floras that incidentally may confer a competitive advantage in nutrient-poor environments such as the CFR.

1989; Clark & Baligar, 2000). They also have the ability to transport nutrients over fairly long distances and their small diameters allow for intimate contact with soil particles (Lamont, 1983b; Clark & Baligar, 2000). Parasitic haustoria are particularly adept at absorbing phosphorus and potassium (Lamont, 1982).

Further insights into the nutritional economies of the DAC and PC are discussed in Chapter 4.

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APPENDIX 2.1. The native angiosperm flora of the Drakensberg Alpine Centre

Numbers in brackets after each family are the total number of genera and species. All taxa are arranged alphabetically.

ANGIOSPERMAE-MONOCOTYLEDONAE

AGAPANTHACEAE (1/2)
- Agapanthus (2)

ALLIACEAE (1/8)
- Tulbaghia (8)

AMARYLLIDACEAE (9/26)
- Ammocharis (1)
- Apodolirion (1)
- Boophone (1)
- Brunsvigia (4)
- Crinum (1)
- Cyrtanthus (10)
- Haemanthus (2)
- Nerine (5)
- Scadoxus (1)

ANTHERICACEAE (1/7)
- Chlorophytum (7)

APONOGETONACEAE (1/2)
- Aponogeton (2)

ARACEAE (1/2)
- Zantedeschia (2)

ASPARAGACEAE (1/11)
- Asparagus (11)

ASPHODELACEAE (5/50)
- Aloe (14)
- Bulbine (8)
- Haworthia (1)
- Kniphofia (20)
- Trachyandra (7)

COLCHICACEAE (4/12)
- Androcymbium (4)
- Littonia (1)
- Sandersonia (1)
- Wurmbea (6)

COMMELINACEAE (2/3)
- Commelina (2)
- Cyanotis (1)

CYPERACEAE (20/122)
- Ascolepis (1)
- Bulbostylis (7)
- Carex (13)
- Carpha (1)
- Cyperus (20)
- Eleocharis (3)
- Ficinia (8)
- Fimbristylis (1)
- Fuirena (4)
- Isolepis (9)
- Kyllinga (5)
- Lipocarpha (2)
- Mariscus (5)
- Pycreus (11)
- Rhynchospora (1)
- Schoenoplectus (6)
- Schoenoxiphium (10)
- Scirpus (7)
- Scleria (5)
- Tetraria (3)

DIOSCOREACEAE (1/4)
- Dioscorea (4)

ERIOCAULACEAE (1/3)
- Eriocaulon (3)

ERIOSPERMACEAE (1/5)
- Eriospermum (5)

HAEMODORACEAE (1/1)
- Barberetta (1)

HYACINTHACEAE (16/55)
- Albuca (9)
- Bowiea (1)
- Dipcadi (3)
- Drimia (4)
- Drimiopsis (1)
- Eucomis (5)
- Galtonia (3)

  - Lachenalia (1)
  - Ledebouria (5)
  - Litanthus (1)
  - Massonia (1)
  - Merwilla (3)
  - Ornithogalum (8)
  - Schizocarphus (1)
  - Thuranthos (1)
  - Urginea (8)
- **HYDROCHARITACEAE (1/2)**
  - Lagarosiphon (2)
- **HYPOXIDACEAE (4/35)**
  - Empodium (2)
  - Hypoxis (24)
  - Rhodohypoxis (8)
  - Saniella (1)
- **IRIDACEAE (14/97)**
  - Aristea (9)
  - Crocosmia (3)
  - Dierama (12)
  - Dietes (1)
  - Freesia (1)
  - Gladiolus (19)
  - Gynandriris (1)
  - Hesperantha (17)
  - Homeria (1)
  - Moraea (18)
  - Romulea (6)
  - Syringodea (1)
  - Tritonia (2)
  - Watsonia (6)
- **JUNCACEAE (2/12)**
  - Juncus (11)
  - Luzula (1)
- **LEMNACEAE (1/1)**
  - Lemna (1)
- **LUZURIAGACEAE (1/1)**
  - Behnia (1)
- **ORCHIDACEAE (22/130)**
  - Angraecum (2)
  - Bonatea (1)
  - Brachycorythis (2)
  - Brownleea (5)
  - Corycium (5)
  - Diaphananthe (1)
  - Disa (32)
  - Disperis (12)
  - Dracomonticola (1)
  - Eulophia (14)
  - Habenaria (17)
  - Holothrix (4)
  - Huttonaea (5)
  - Liparis (1)
  - Mystacidium (1)
  - Neobolusia (1)
  - Polystachya (1)
  - Pterygodium (4)
  - Satyrium (14)
  - Schizochilus (5)
  - Stenoglottis (1)
  - Tridactyle (1)
- **POACEAE (86/267)**
  - Agrostis (8)
  - Alloteropsis (2)
  - Andropogon (6)
  - Anthoxanthum (3)
  - Aristida (12)
  - Arundinella (1)
  - Axonopus (1)
  - Bewsia (1)
  - Bothriochloa (2)
  - Brachiaria (6)
  - Brachypodium (2)
  - Bromus (4)
  - Catalepis (1)
  - Chloris (3)
  - Colpodium (1)
  - Ctenium (1)
  - Cymbopogon (6)
  - Cynodon (5)
  - Deschampsia (1)
  - Diandrochloa (1)
  - Digitaria (14)
  - Diheteropogon (2)

Diplachne (2)
Echinochloa (4)
Ehrharta (3)
Eleusine (3)
Elionurus (1)
Enneapogon (2)
Eragrostis (25)
Eulalia (1)
Eustachys (1)
Festuca (8)
Fingerhuthia (2)
Harpochloa (1)
Helictotrichon (5)
Hemarthria (1)
Heteropogon (1)
Hordeum (1)
Hyparrhenia (8)
Imperata (1)
Ischaemum (1)
Karroochloa (2)
Koeleria (1)
Leersia (1)
Loudetia (2)
Melica (2)
Melinis (3)
Merxmuellera (7)
Microchloa (2)
Microstegium (1)
Miscanthus (2)
Monocymbium (1)
Oplismenus (2)
Oropetium (1)
Panicum (10)
Paspalum (6)
Pennisetum (5)
Pentaschistis (12)
Perotis (1)
Phacelurus (1)
Phragmites (2)
Poa (2)
Pogonarthria (1)
Polevansia (1)
Polypogon (1)
Rendlia (1)
Schismus (1)
Schizachyrium (1)
Schmidtia (1)
Setaria (9)
Sporobolus (9)
Stiburus (2)
Stipa (2)
Stipagrostis (3)
Streblochaete (1)
Styppeiochloa (1)
Tetrachne (1)
Thamnocalamus (1)
Themeda (1)
Trachypogon (1)
Tragus (3)
Tribolium (1)
Trichoneura (1)
Triraphis (1)
Tristachya (1)
Urochloa (2)

POTAMOGETONACEAE (1/3)

Potamogeton (3)

RESTIONACEAE (3/5)

Ischyrolepis (1)
Restio (3)
Rhodocoma (1)

TYPHACEAE (1/1)

Typha (1)

VELLOZIACEAE (2/3)

Talbotia (1)
Xerophyta (2)

XYRIDACEAE (1/2)

Xyris (2)

ANGIOSPERMAE-DICOTYLEDONAE

ACANTHACEAE (9/13)
- Adhatoda (1)
- Barleria (1)
- Blepharis (2)
- Chaetacanthus (1)
- Crabbea (2)
- Hypoestes (1)
- Isoglossa (3)
- Justicia (1)
- Thunbergia (1)

ACHARIACEAE (2/2)
- Ceratiosicyos (1)
- Guthriea (1)

AIZOACEAE (3/16)
- Limeum (5)
- Pharnaceum (4)
- Psammotropha (7)

AMARANTHACEAE (1/2)
- Cyathula (2)

ANACARDIACEAE (3/20)
- Protorhus (1)
- Rhus (18)
- Smodingium (1)

APIACEAE (15/38)
- Agrocharis (1)
- Alepidea (14)
- Anginon (1)
- Annesorhiza (1)
- Bupleurum (1)
- Centella (2)
- Conium (3)
- Dracosciadium (1)
- Heteromorpha (2)
- Lichtensteinia (1)
- Peucedanum (5)
- Pimpinella (2)
- Polemannia (2)
- Sanicula (1)
- Sium (1)

APOCYNACEAE (2/2)
- Carissa (1)
- Strophanthus (1)

AQUIFOLIACEAE (1/1)
- Ilex (1)

ARALIACEAE (2/3)
- Cussonia (2)
- Seemannaralia (1)

ASCLEPIADACEAE (22/87)
- Anisotoma (1)
- Asclepias (15)
- Aspidoglossum (6)
- Aspidonepsis (4)
- Brachystelma (10)
- Cordylogyne (1)
- Cynanchum (1)
- Fanninia (1)
- Gomphocarpus (1)
- Huernia (1)
- Miraglossum (3)
- Pachycarpus (8)
- Parapodium (1)
- Periglossum (3)
- Riocreuxia (3)
- Sarcostemma (1)
- Schizoglossum (13)
- Secamone (1)
- Sisyranthus (3)
- Stapelia (1)
- Stenostelma (1)
- Xysmalobium (8)

ASTERACEAE (65/430)
- Amellus (1)
- Arctotis (3)
- Artemisia (1)
- Aster (8)
- Athanasia (2)
- Athrixia (6)
- Berkheya (18)
- Callilepis (1)
- Cenia (1)
- Chrysanthemoides (2)

  - Chrysocoma (2)
  - Cineraria (11)
  - Comborhiza (1)
  - Conyza (6)
  - Cotula (9)
  - Crepis (2)
  - Delairea (1)
  - Denekia (1)
  - Dicoma (1)
  - Dimorphotheca (2)
  - Eriocephalus (2)
  - Eumorphia (3)
  - Euryops (17)
  - Felicia (12)
  - Garuleum (3)
  - Gazania (3)
  - Geigeria (2)
  - Gerbera (5)
  - Gnaphalium (5)
  - Gymnopentzia (1)
  - Haplocarpha (2)
  - Helichrysum (102)
  - Heteromma (3)
  - Hirpicium (2)
  - Ifloga (2)
  - Inulanthera (7)
  - Lactuca (4)
  - Lasiospermum (1)
  - Lepidostephium (1)
  - Macowania (7)
  - Metalasia (1)
  - Mikaniopsis (1)
  - Nidorella (6)
  - Nolletia (2)
  - Oncosiphon (1)
  - Osteospermum (7)
  - Othonna (3)
  - Pegolettia (1)
  - Pentzia (5)
  - Phymaspermum (4)
  - Plecostachys (1)
  - Printzia (3)
  - Pseudognaphalium (3)
  - Pterothrix (1)
  - Pulicaria (1)
  - Relhania (2)
  - Schistostephium (2)
  - Senecio (100)
  - Sonchus (7)
  - Stoebe (1)
  - Tarchonanthus (1)
  - Tolpis (1)
  - Troglophyton (1)
  - Ursinia (6)
  - Vernonia (6)
- **BALSAMINACEAE (1/1)**
  - Impatiens (1)
- **BASELLACEAE (1/1)**
  - Anredera (1)
- **BEGONIACEAE (1/1)**
  - Begonia (1)
- **BORAGINACEAE (6/15)**
  - Afrotysonia (1)
  - Anchusa (1)
  - Cynoglossum (5)
  - Ehretia (1)
  - Lithospermum (4)
  - Myosotis (3)
- **BRASSICACEAE (7/27)**
  - Aplanodes (1)
  - Erucastrum (2)
  - Heliophila (6)
  - Lepidium (8)
  - Matthiola (1)
  - Rorippa (4)
  - Sisymbrium (5)
- **BUDDLEJACEAE (2/5)**
  - Buddleja (4)
  - Gomphostigma (1)
- **CAMPANULACEAE (2/26)**
  - Craterocapsa (4)
  - Wahlenbergia (22)
- **CAPPARACEAE (1/1)**
  - Cleome (1)

CARYOPHYLLACEAE (5/21)
- Cerastium (4)
- Dianthus (6)
- Drymaria (1)
- Silene (7)
- Stellaria (3)

CELASTRACEAE (5/10)
- Gymnosporia (3)
- Hippocratea (1)
- Lauridia (1)
- Maytenus (3)
- Pterocelastrus (2)

CHENOPODIACEAE (1/1)
- Chenopodium (1)

CLUSIACEAE (1/5)
- Hypericum (5)

COMBRETACEAE (1/2)
- Combretum (2)

CONVOLVULACEAE (5/13)
- Convolvulus (5)
- Falkia (1)
- Ipomoea (5)
- Merremia (1)
- Turbina (1)

CORNACEAE (1/1)
- Curtisia (1)

CRASSULACEAE (3/34)
- Cotyledon (1)
- Crassula (30)
- Kalanchoe (3)

CUCURBITACEAE (7/11)
- Citrullus (1)
- Coccinia (1)
- Cucumis (3)
- Kedrostis (2)
- Mukia (1)
- Peponium (1)
- Zehneria (2)

DIPSACACEAE (2/7)
- Cephalaria (5)
- Scabiosa (2)

DROSERACEAE (1/4)
- Drosera (4)

EBENACEAE (2/7)
- Diospyros (5)
- Euclea (2)

ERICACEAE (2/35)
- Erica (34)
- Ericinella (1)

ESCALLONIACEAE (1/1)
- Choristylis (1)

EUPHORBIACEAE (8/30)
- Acalypha (5)
- Adenocline (2)
- Andrachne (1)
- Chamaesyce (1)
- Clutia (8)
- Euphorbia (11)
- Micrococca (1)
- Phyllanthus (1)

FABACEAE (32/136)
- Acacia (5)
- Amphithalea (1)
- Argyrolobium (15)
- Aspalathus (3)
- Calpurnia (4)
- Chamaecrista (1)
- Crotalaria (1)
- Dalbergia (1)
- Desmodium (1)
- Dichilus (3)
- Dolichos (4)
- Dumasia (1)
- Elephantorrhiza (2)
- Eriosema (6)
- Erythrina (2)
- Hoffmannseggia (1)
- Indigofera (15)
- Lessertia (6)
- Lotononis (24)
- Medicago (2)
- Melolobium (6)
- Otholobium (2)

- Pearsonia (1)
- Pseudarthria (1)
- Psoralea (2)
- Rhynchosia (9)
- Sphenostylis (1)
- Sutherlandia (3)
- Tephrosia (5)
- Trifolium (4)
- Vigna (3)
- Zornia (1)

FLACOURTIACEAE (5/10)
- Casearia (1)
- Dovyalis (3)
- Kiggelaria (1)
- Scolopia (3)
- Trimeria (2)

FUMARIACEAE (1/1)
- Cysticapnos (1)

GENTIANACEAE (3/28)
- Chironia (3)
- Sebaea (24)
- Swertia (1)

GERANIACEAE (3/37)
- Geranium (13)
- Monsonia (4)
- Pelargonium (20)

GESNERIACEAE (1/5)
- Streptocarpus (5)

GREYIACEAE (1/1)
- Greyia (1)

GUNNERACEAE (1/1)
- Gunnera (1)

HALORAGACEAE (1/1)
- Laurembergia (1)

HAMAMELIDACEAE (1/1)
- Trichocladus (1)

ICACINACEAE (2/2)
- Apodytes (1)
- Cassinopsis (1)

ILLECEBRACEAE (3/4)
- Corrigiola (1)
- Herniaria (2)
- Pollichia (1)

LAMIACEAE (14/47)
- Acrotome (1)
- Aeollanthus (1)
- Ajuga (1)
- Becium (2)
- Hemizygia (2)
- Leonotis (4)
- Mentha (3)
- Plectranthus (5)
- Pycnostachys (1)
- Salvia (6)
- Satureja (4)
- Stachys (14)
- Syncolostemon (1)
- Teucrium (2)

LAURACEAE (2/3)
- Cryptocarya (2)
- Ocotea (1)

LENTIBULARIACEAE (1/5)
- Utricularia (5)

LINACEAE (1/1)
- Linum (1)

LOBELIACEAE (3/18)
- Cyphia (7)
- Lobelia (9)
- Monopsis (2)

LYTHRACEAE (1/1)
- Rotala (1)

MALVACEAE (5/13)
- Abutilon (1)
- Anisodontea (3)
- Hibiscus (7)
- Pavonia (1)
- Sida (1)

MELIACEAE (1/1)
- Ekebergia (1)

MELIANTHACEAE (2/2)
- Bersama (1)
- Melianthus (1)

- **MENISPERMACEAE (2/2)**
  - Cissampelos (1)
  - Stephania (1)
- **MENYANTHACEAE (1/1)**
  - Nymphoides (1)
- **MESEMBRYANTHEMACEAE (5/38)**
  - Chasmatophyllum (2)
  - Delosperma (30)
  - Mossia (1)
  - Rabiea (1)
  - Ruschia (4)
- **MORACEAE (1/2)**
  - Ficus (2)
- **MYRICACEAE (1/3)**
  - Morella (3)
- **MYRSINACEAE (3/4)**
  - Maesa (1)
  - Myrsine (2)
  - Rapanea (1)
- **MYRTACEAE (2/2)**
  - Eugenia (1)
  - Syzygium (1)
- **OCHNACEAE (1/2)**
  - Ochna (2)
- **OLEACEAE (2/4)**
  - Chionanthus (2)
  - Olea (2)
- **OLINIACEAE (1/1)**
  - Olinia (1)
- **ONAGRACEAE (2/5)**
  - Epilobium (4)
  - Ludwigia (1)
- **OXALIDACEAE (1/8)**
  - Oxalis (8)
- **PAPAVERACEAE (1/1)**
  - Papaver (1)
- **PERIPLOCACEAE (1/2)**
  - Raphionacme (2)
- **PHYTOLACCACEAE (1/3)**
  - Phytolacca (3)
- **PIPERACEAE (1/2)**
  - Peperomia (2)
- **PITTOSPORACEAE (1/1)**
  - Pittosporum (1)
- **PLANTAGINACEAE (1/1)**
  - Plantago (1)
- **PODOSTEMACEAE (1/1)**
  - Sphaerothylax (1)
- **POLYGALACEAE (2/17)**
  - Muraltia (4)
  - Polygala (13)
- **POLYGONACEAE (4/16)**
  - Fallopia (1)
  - Persicaria (3)
  - Polygonum (3)
  - Rumex (9)
- **PORTULACACEAE (2/4)**
  - Anacampseros (3)
  - Talinum (1)
- **PRIMULACEAE (2/2)**
  - Anagallis (1)
  - Lysimachia (1)
- **PROTEACEAE (1/6)**
  - Protea (6)
- **PTAEROXYLACEAE (1/1)**
  - Ptaeroxylon (1)
- **RANUNCULACEAE (4/9)**
  - Anemone (2)
  - Clematis (1)
  - Ranunculus (4)
  - Thalictrum (2)
- **RESEDACEAE (2/2)**
  - Oligomeris (1)
  - Reseda (1)
- **RHAMNACEAE (4/5)**
  - Phylica (2)
  - Rhamnus (1)
  - Scutia (1)
  - Ziziphus (1)
- **RHIZOPHORACEAE (1/1)**
  - Cassipourea (1)

- **ROSACEAE (7/20)**
  - Agrimonia (1)
  - Alchemilla (5)
  - Cliffortia (9)
  - Geum (1)
  - Leucosidea (1)
  - Prunus (1)
  - Rubus (2)
- **RUBIACEAE (20/36)**
  - Anthospermum (5)
  - Burchellia (1)
  - Canthium (3)
  - Cephalanthus (1)
  - Conostomium (1)
  - Galium (6)
  - Galopina (1)
  - Hyperacanthus (1)
  - Kohautia (1)
  - Nenax (1)
  - Oldenlandia (1)
  - Pachystigma (1)
  - Pavetta (2)
  - Pentanisia (3)
  - Psydrax (1)
  - Pygmaeothamnus (1)
  - Rothmannia (2)
  - Rubia (2)
  - Spermacoce (1)
  - Tricalysia (1)
- **RUTACEAE (5/6)**
  - Agathosma (1)
  - Calodendrum (1)
  - Clausena (1)
  - Vepris (1)
  - Zanthoxylum (2)
- **SALICACEAE (1/2)**
  - Salix (2)
- **SANTALACEAE (3/32)**
  - Osyridicarpos (1)
  - Osyris (1)
  - Thesium (30)
- **SAPINDACEAE (2/3)**
  - Allophylus (2)
  - Hippobromus (1)
- **SCROPHULARIACEAE (31/133)**
  - Alectra (6)
  - Aptosimum (1)
  - Bartsia (1)
  - Bowkeria (1)
  - Buchnera (3)
  - Cycnium (1)
  - Diascia (10)
  - Diclis (2)
  - Glekia (1)
  - Glumicalyx (6)
  - Graderia (1)
  - Halleria (1)
  - Harveya (8)
  - Hebenstretia (5)
  - Hyobanche (3)
  - Jamesbrittenia (11)
  - Limosella (7)
  - Lindernia (2)
  - Manulea (7)
  - Melasma (1)
  - Mimulus (1)
  - Nemesia (11)
  - Phygelius (2)
  - Selago (12)
  - Sopubia (2)
  - Striga (4)
  - Strobilopsis (1)
  - Sutera (5)
  - Teedia (1)
  - Veronica (2)
  - Zaluzianskya (14)
- **SOLANACEAE (3/12)**
  - Lycium (2)
  - Solanum (9)
  - Withania (1)
- **STERCULIACEAE (2/16)**
  - Dombeya (2)
  - Hermannia (14)

THYMELAEACEAE (6/20)
- Dais (1)
- Englerodaphne (1)
- Gnidia (13)
- Passerina (2)
- Peddiea (1)
- Struthiola (2)

TILIACEAE (3/4)
- Grewia (2)
- Sparrmannia (1)
- Triumfetta (1)

TRIMENIACEAE (1/1)
- Xymalos (1)

ULMACEAE (1/1)
- Celtis (1)

URTICACEAE (5/9)
- Didymodoxa (2)
- Droguetia (1)
- Laportea (2)
- Parietaria (1)
- Urtica (3)

VAHLIACEAE (1/1)
- Vahlia (1)

VALERIANACEAE (1/3)
- Valeriana (3)

VERBENACEAE (2/3)
- Clerodendrum (2)
- Lantana (1)

VIOLACEAE (1/2)
- Hybanthus (2)

VISCACEAE (1/3)
- Viscum (3)

VITACEAE (1/3)
- Rhoicissus (3)

ZYGOPHYLLACEAE (1/1)
- Tribulus (1)

APPENDIX 2.2. The exotic angiosperm flora of the Drakensberg Alpine Centre

Numbers in brackets after each family are the total number of genera and species. All taxa are arranged alphabetically.

ANGIOSPERMAE-MONOCOTYLEDONAE

AGAVACEAE (1/1)

- Agave (1)

POACEAE (17/33)

- Aira (1)
- Arundo (1)
- Avena (2)
- Briza (1)
- Bromus (5)
- Cortaderia (1)
- Dactylis (1)
- Holcus (1)
- Hordeum (1)
- Lamarckia (1)
- Lolium (5)
- Pennisetum (2)
- Phalaris (4)
- Poa (2)
- Sorghum (2)
- Vulpia (2)
- Zea (1)

ANGIOSPERMAE-DICOTYLEDONAE

AMARANTHACEAE (5/10)

- Achyranthes (2)
- Alternanthera (2)
- Amaranthus (4)
- Gomphrena (1)
- Guilleminea (1)

APIACEAE (7/7)

- Ammi (1)
- Anthriscus (1)
- Apium (1)
- Caucalis (1)
- Chamarea (1)
- Ciclospermum (1)
- Daucus (1)

ASTERACEAE (20/32)

- Acanthospermum (2)
- Achillea (1)
- Ambrosia (2)
- Anthemis (1)
- Bidens (4)
- Carduus (1)
- Chrysanthellum (1)
- Chrysanthemum (1)
- Cichorium (1)
- Cirsium (1)
- Coreopsis (1)
- Galinsoga (2)
- Gamochaeta (1)
- Hypochoeris (2)
- Schkuhria (1)
- Tagetes (1)
- Taraxacum (5)
- Tragopogon (1)
- Xanthium (2)
- Zinnia (1)

BORAGINACEAE (3/4)

- Buglossoides (1)
- Echium (2)
- Lappula (1)

BRASSICACEAE (7/8)

- Barbarea (1)
- Capsella (1)
- Cardamine (2)
- Coronopus (1)
- Crambe (1)
- Raphanus (1)
- Turritis (1)

CACTACEAE (1/1)

- Opuntia (1)

CANNABACEAE (1/1)

- Cannabis (1)

- **CARYOPHYLLACEAE (1/1)**
  - Spergula (1)
- **CHENOPODIACEAE (2/7)**
  - Atriplex (1)
  - Chenopodium (6)
- **CONVOLVULACEAE (1/1)**
  - Cuscuta (1)
- **EUPHORBIACEAE (1/1)**
  - Ricinus (1)
- **FABACEAE (2/2)**
  - Melilotus (1)
  - Vicia (1)
- **FUMARIACEAE (1/1)**
  - Fumaria (1)
- **GERANIACEAE (1/1)**
  - Erodium (1)
- **ILLECEBRACEAE (1/1)**
  - Paronychia (1)
- **LAMIACEAE (2/2)**
  - Lamium (1)
  - Marrubium (1)
- **MALVACEAE (1/4)**
  - Malva (4)
- **NYCTAGINACEAE (1/1)**
  - Boerhavia (1)
- **ONAGRACEAE (1/8)**
  - Oenothera (8)
- **PAPAVERACEAE (1/1)**
  - Argemone (1)
- **PLANTAGINACEAE (1/2)**
  - Plantago (2)
- **POLYGONACEAE (2/3)**
  - Emex (1)
  - Persicaria (2)
- **PORTULACACEAE (1/1)**
  - Portulaca (1)
- **ROSACEAE (5/7)**
  - Cotoneaster (1)
  - Duchesnea (1)
  - Pyracantha (1)
  - Rosa (2)
  - Rubus (2)
- **RUBIACEAE (2/2)**
  - Richardia (1)
  - Sherardia (1)
- **RUTACEAE (1/1)**
  - Ruta (1)
- **SALICACEAE (1/3)**
  - Salix (3)
- **SCROPHULARIACEAE (2/2)**
  - Linaria (1)
  - Verbascum (1)
- **SOLANACEAE (5/11)**
  - Datura (1)
  - Nicandra (1)
  - Nicotiana (2)
  - Physalis (3)
  - Solanum (4)
- **VERBENACEAE (2/6)**
  - Lantana (1)
  - Verbena (5)

'Changing climatic conditions and the advance of the African flora have led to the isolation of the old temperate type on the mountains (of tropical Africa).'

Rennie (1936)

'The extension of several Cape genera into the coastal districts of Pondoland and Natal, and along the Drakensbergen and the mountains of the Rhodesian border into East Africa, has frequently led to the assumption that migration was essentially, if not entirely, along an eastern route.'

Rennie (1936)

CHAPTER 3

BIOGEOGRAPHICAL IMPLICATIONS OF THERMAL CYCLES ON THE DISTRIBUTION OF CAPE ELEMENTS IN SUB-SAHARAN AFRICA

3.1 INTRODUCTION

Climates over the past two million years have been influenced by the expansion and contraction of northern hemisphere ice sheets every 100 000 years. Each cycle comprises a short, warmer interglacial lasting c. 10 000 years and a cooler glacial lasting c. 90 000 years (Deacon, 1983; Tyson, 1986; Deacon & Lancaster, 1988). These climatic vicissitudes are believed to have triggered speciation by facilitating vicariance and allopatry events (Midgley *et al.*, 2001), and are possibly partly responsible for the high species richness of the CFR (Midgley *et al.*, 2001), particularly during the shift to a Mediterranean-type climate during the late Pliocene and Pleistocene (Cowling *et al.*, 1999).

Hypothermal (≈ glacial) periods are generally characterised by cold and dry climates during which time temperate vegetation expands[a]. Alternating hyperthermal (≈ interglacial) periods are generally characterised by warmer, moister climates which favour the expansion of tropical vegetation and forests (Eeley *et al.*, 1999), and the retreat of temperate vegetation into refugia (Rennie, 1936), as currently shown by fynbos vegetation of the CFR (Midgley *et al.*, 2001). Such

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[a] This generalisation does not apply to all Cape elements. The drought-adapted taxa (e.g. *Cliffortia*) will most probably expand in distribution during glacials, while mesic taxa such as *Diascia* and *Nemesia* will most probably expand in distribution during interglacials.

responses to cyclical environmental conditions ('hot and wet', 'cold and dry') are thought to govern plant productivity and their persistence over time (Duncan, 2000).

3.2 POSTULATES CONCERNING SUB-SAHARAN AFRICA'S CLIMATIC HISTORY

3.2.1 INTERPRETING THE ORIGIN(S) OF THE CAPE FLORA

Numerous theories have been proposed on the origin(s) of the Cape flora (Rennie, 1936; Adamson, 1947; Levyns, 1952, 1964; Goldblatt, 1978; Taylor, 1978; Linder *et al.*, 1992). Adamson (1947) alluded to a recent, northern origin from tropical Africa. Others suggest a southern, Gondwanan origin for the Cape flora (Rennie, 1936; Specht, 1979; Goldblatt, 1983), when climatic conditions favoured the spread of temperate species (Rennie, 1936), most probably after the onset of a Mediterranean-type climate in the mid- to late Pliocene (Cowling *et al.*, 1999). Additional proposals include evidence for a boreal origin from Laurasia (Taylor, 1978; Linder *et al.*, 1992; Linder, 1994). Van der Schijff & Schoonraad (1971) proposed that the strong ties shared between the floras of the CFR and the northern Drakensberg (Mariepskop) and the Chimanimani Mountains point towards an eastern migration route for Cape taxa from the Western Cape. However, closer ties between the Mariepskop forests and those of tropical Africa infer that the Drakensberg Range is a migration route for both southern and tropical elements (Van der Schijff & Schoonraad, 1971).

Van Zinderen Bakker (1978) hypothesised that the Cape flora (or its direct ancestors) covered a large continuous area of Africa during the relatively stable Early Caenozoic (Eocene) until the early Tertiary, supporting Wild's (1968) hypothesis that the centres and subcentres within the Cape flora were once continuous. Van

Zinderen Bakker (1978) added that its great wealth of species were the result of repeated fragmentation of its area caused by drastic climate changes during the late-Tertiary and Quaternary times. Vicariance events are believed to be important agents responsible for shaping the Afromontane flora (Friis, 1983), although this seems less so for its forest component (Chapman & White, 1970) and more so for the grassland component, particularly grass taxa (Clayton, 1983). The deposition of Kalahari Sands over southern Africa in the Middle and Later Tertiary and subsequent aridification are believed to have fragmented the Cape flora into refugia (Wild, 1964). Quaternary climate changes were sufficiently great to have allowed the Cape elements to bridge the Limpopo and Zambezi Intervals (Van Zinderen Bakker, 1978, 1983).

Van Zinderen Bakker (1978) recognised a Cape component in many elevated regions of the eastern escarpment and believed that the progenitors of the Cape flora migrated southwards from the mountainous areas in central Africa as the continent moved northward. This idea was supported by Levyns (1952, 1958, 1964), whose studies of some typical Cape genera (e.g. *Aristea, Muraltia, Phylica, Protea, Stoebe*) in central Africa refuted a recent, southern origin because of their plesiomorphic characters and discontinuous ranges. By contrast, the limited distribution and absence of range disjunctions of *Protea* species in the CFR supposedly indicates a more recent origin (Beard, 1963), with a gradual accumulation of species from around 30 MYA (Reeves, 2001). Furthermore, Proteaceae pollen dating to the Tertiary in the Northern Hemisphere also corroborates the theory of a northern origin (Levyns, 1958). Linder (1994), however, supported the 'reduction series' hypothesis for Africa, stating that Cape 'outliers' in tropical Africa indicate southern origins, corroborated by a reduction series southwards of boreal taxa concentrated more heavily in the north.

Modern revisions and the generation of species-level cladograms from morphological and molecular data are necessary for the comprehensive understanding of the Afrotemperate flora and its history.

3.2.2 INTERPRETING THE ORIGIN(S) OF CAPE ELEMENTS IN PONDOLAND

The PC is believed to be a refuge for taxa which were formerly more widespread in Africa (White & Moll, 1978). These edaphic palaeoendemics (referring to genera and not species) were unable to migrate due to climatic and geological constraints (Van Wyk, 1989, 1990a, 1990b, 1993; Jacobs, 1996). Their inability to compete with the current regional flora on nutrient-rich substrates has probably reduced them to small, isolated populations (Van Wyk, 1993). However, their superior competitive ability on nutrient-impoverished sandstone islands may well have ensured their survival (cf. Major, 1988).

Van Wyk (1989, 1990a) hypothesised that the Natal Group, Msikaba and Cape Supergroup formations were once a continuum before the break-up of Gondwanaland owing to the presence of the Falkland Plateau. Discontinuities arose during the separation of Africa and South America (King, 1978; Raven, 1983; Partridge & Maud, 1987). The resulting disjunction between Port St. Johns and the Cape Supergroup in the Eastern Cape approximates the area described by Weimarck (1941: 85) as 'the area between the south-eastern Cape Centre and the Drakensberg Centre', referred to as the 'Kaffraria Interval', more or less congruent with the Albany Centre (Van Wyk

& Smith, 2001). Range contractions through vicariance events (i.e. geological and climatic changes) of once widespread floras therefore seems most likely (Cowling, 1986; Van Wyk, 1990b; Geldenhuys, 1992). Midgley (1986), referring in particular to the anomalous distribution of *Leucadendron* (Proteaceae), suggested that climate change is the most plausible explanation of the Cape-Pondoland disjunction. Congruency in distribution patterns of a range of plant species, genera and families exhibiting disjunct distributions suggests that a general explanation may apply to all taxa concerned (Van Wyk 1989, 1990a, 1990b).

3.3 METHODOLOGY

The methods employed is this chapter draw partly on cladistic biogeography and Global Information Systems (GIS). In addition, an overview of the centres and intervals of Cape elements in sub-Saharan Africa is presented (updated from Weimarck, 1941), as well as the geological affinities of Cape elements in southern and south-central Africa.

3.3.1 HISTORICAL CLADISTIC BIOGEOGRAPHY

Historical biogeography is concerned with range description, speciation, endemism, disjunctions and vicariance versus dispersal theory as plausible explanations for distribution (Bond, 1989), rather than using environmental or biological correlates (cf. Linder, 1983; Kurzweil *et al.*, 1991). The scale of study is usually at the regional level and a sound understanding of the taxonomy and phylogeny of species is crucial (Wild, 1964; Bond, 1989). Historical biogeography was based on the principles of centres of origin and was supported by Wallace and others (Humphries & Parenti, 1986). Croizat *et al.* (1974), however, rejected such theories because taxa known to be distributed by passive dispersal make poor subjects for biogeograpical enquiry. Another reason for rejecting chance dispersal *a priori* as a causal factor in biogeography is that it leads to poorly formulated and untestable hypotheses (Ball, 1976). Instead, Croizat *et al.* (1974) proposed the concepts of 'panbiogeography', 'tracks', 'vicariance' and 'differential form-making'.

A phylogenetic background is essential to any biogeographical study (Ball, 1976), particularly in the absence of fossil evidence (Linder, 1983). Cladistic biogeographers search for congruent patterns from multiple taxa distributed disjunctly over a common area. A common pattern is likely to be caused by a single historical event, rather than several independent ones (Linder & Crisp, 1995). A number of temperate taxa renowned for their Cape-centres were used to determine their biogeographic relationships with other, more secondary, centres of diversity (e.g. the DAC).

In order to reconstruct the historic relationships among their various centres of diversity, species were substituted by their centres of distribution, thereby forming an area cladogram (e.g. Nelson & Platnick, 1981; Humphries & Parenti, 1986; Humphries *et al.*, 1988; Kurzweil *et al.*, 1991; Van Soest & Hajdu, 1997). Ancestral affiliations were determined by correlating congruent centres of distribution with a common node, because the sum of congruent areas on one cladogram is equivalent to a track (Humphries & Parenti, 1986).

Four temperate taxa characterised by sound taxonomy and phylogeny were selected for such an assessment. Species-level cladograms of *Cliffortia* (Rosaceae) (Whitehouse, 2003), *Disa* (Linder & Kurzweil, 1999; Bellstedt *et al.*, 2001) and *Pterygodium* (Orchidaceae) (Kurzweil *et al.*, 1991; Linder & Kurzweil, 1999) and *Moraea* (Iridaceae) (Goldblatt *et al.*, 2002) were used. A simplified area cladogram was generated for one of the four taxa (*Pterygodium*) as its cladogram was well resolved and represented all but one of its suite of species. *Diascia*, a most suitable choice in the context of this study (refer to Chapter 4), was rejected based on the poor resolution of its molecular phylogeny based on the ITS region. Crisper resolution using matK sequences was undermined by an incomplete data set (K. Steiner, 2003, pers. comm.).

3.3.2 MAPPING TEMPERATURE CORRIDORS THROUGH GIS

In order to relate the distributions of Cape elements to physical factors, the temperature regimes experienced by taxa in the CFR, DAC and PC were collated and presented using the GIS programme ArcView version 3.3 (Environmental Systems Research Institute, 2002). All data were sourced from Schulze (1997). Two criteria were set as the framework within which temperature data were extracted and later superimposed. 1. Geology. All regions characterised by geologies of (a) the Drakensberg Group (Stormberg Series) and (b) the Natal Group were selected. The analysis was not able to differentiate between sandstones of the Natal Group and Msikaba Formation, but all Natal Group Sandstone was deleted (i.e. by deleting all except the PC region). 2. Altitude. All regions belonging to 1(a) at an elevation ≥ 1800 m meant that the 'Drakensberg' analysis left only the DAC as the region fulfilling both criteria. The two outputs were overlain onto a common base map that also highlighted all regions characterised by Table Mountain Sandstone of the CFR. The GIS generated temperature minima, maxima and means for each month of the year from a temperature data base (Table 3.1). Temperature data representing only the growing season for each of the regions were used. The growing season of the DAC is a contracted one and so temperature data from November to March (five months) was used, while that of the PC is more protracted, from October to April (seven months). A six month period was used for the CFR (October - March). Temperature data were compared between regions to determine the precise temperature ranges experienced by their floras, with special reference to Cape elements.

3.4 RESULTS AND DISCUSSION

3.4.1 CASE STUDIES - EVIDENCE FROM CLADISTICS

3.4.1.1 *CLIFFORTIA* L.

Cliffortia is a speciose member of the Rosaceae, comprising c. 118 species confined to sub-Saharan Africa, the majority of which (c. 112 species) are centred in the CFR (Whitehouse, 2003). The DAC, however, is considered a secondary centre of endemism for the group (Whitehouse, in press). Members of the genus are anemophilous (Whitehouse, 2001) with a tendency to hybridise (C. Whitehouse, 2003, pers. comm.). Its ancestors must therefore have been in close proximity to generate the diversity currently displayed, making the assumptions of the group more credible. Its recent systematic treatment resulted in molecular phylogenies using cpDNA and nDNA (Whitehouse, 2003). Unfortunately, congruency between the two series of trees was poor. This is possibly the result of reticulate evolution because sexual inheritance is only evident in nDNA. Furthermore, the tendency of *Cliffortia* to hybridise means that use of only a single specimen per sequence may result in the sequencing of only maternal traits, making its placement on the cladogram variable. However, an area cladogram generated from the nDNA tree showed fairly poor correlation with regions of endemism and diversity. The cpDNA tree was more informative.

Cliffortia appears to have originated in the Western Cape, and to a lesser degree the Karoo, with evidence for repeated invasions into KwaZulu-Natal. The three endemic species of the DAC (*C. dracomontana* C. M. Whitehouse, *C. filicauloides* Weim. and *C. spathulata* Weim.), along with two other species recorded for the greater Drakensberg Range (*C. browniana* Burtt Davy and *C. nitidula* (Engl.) R.E.Fr. & T.C.E.Fr. subsp. *pilosa* Weim.) occur in close proximity in the cpDNA tree (four of these taxa are monophyletic, with *C. filicauloides* as a close ally). Species more widespread in KwaZulu-Natal form another grouping. The DAC endemics are probably derived from Cape ancestors.

3.4.1.2 *DISA* BERG.

Disa is a genus of c. 162 species, confined mostly to sub-Saharan Africa, with outliers in Madagascar, Réunion and the Arabian Peninsula (Linder & Kurzweil, 1999). The genus is well represented in southern Africa, where 131 species occur; these species are placed in five sub-genera and 19 sections (Linder & Kurzweil, 1999). The primary centre of distribution for *Disa* is the CFR, with a secondary centre in the greater

Drakensberg Range (Linder & Kurzweil, 1999). Thirty-two species have been recorded from the DAC, making it the fourth largest genus for this region (Carbutt & Edwards, 2004).

Determining the origins of *Disa* has proved problematic (Linder, 1983). Historical reconstruction of the Disinae using vicariance biogeography (area cladograms in particular), using morphological characters, has been unsuccessful due to the vagility of the taxa (Linder, 1983). Examination of a molecular phylogeny for 41 species of *Disa* (Bellstedt *et al.*, 2001) revealed numerous polytomies, making conclusive judgements difficult. Use of *D. galpinii* Rolfe (a narrow DAC endemic) as an outgroup for section *Disella* (all CFR taxa) (Linder & Kurzweil, 1999), however, infers a relationship between the two centres. Further evidence from *Disa* is scant and tentative; the lack of strong correlations between taxa and their geography are possibly the result of long-distance dispersal events (cf. Linder, 1983).

3.4.1.3 *PTERYGODIUM* Sw.

Pterygodium is a genus of 18 species centred in southern Africa, with a single species (*P. ukingense* Schltr.) endemic to the highlands of southern Tanzania. Most of the southern African species are centred in the CFR, with the exception of three species (*P. hastatum* H. Bol., *P. leucanthum* H. Bol. and *P. magnum* Reichb. f.) centred in the greater Drakensberg Range, and one species (*P. cooperi* Rolfe) confined entirely to the DAC (Linder & Kurzweil, 1999).

Neatly resolved cladograms of the genus distinguish two sub-groups and four sections (Kurzweil *et al.*, 1991; Linder & Kurweil, 1999). The area cladogram revealed

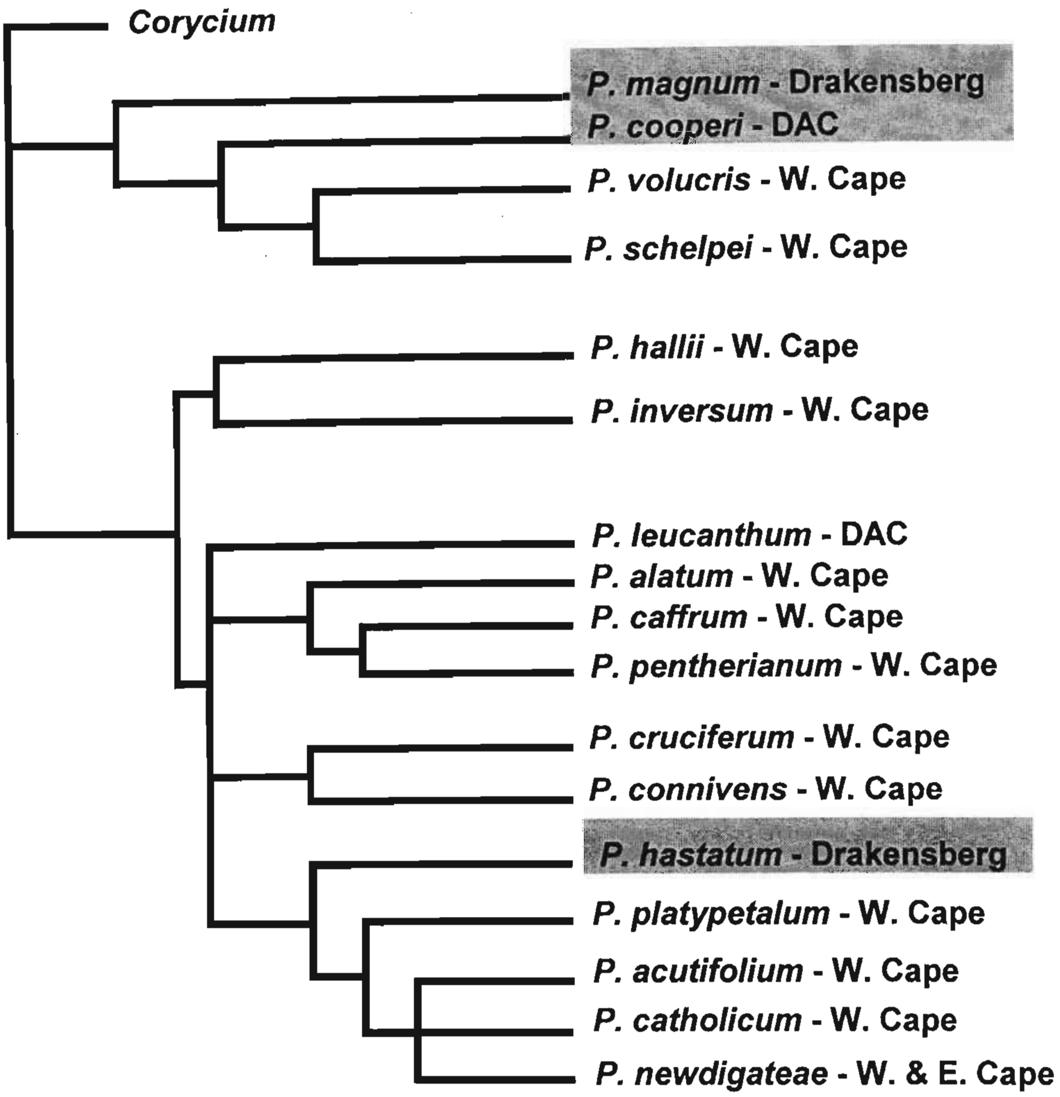


Fig. 3.1. Cladistic biogeographic analysis of *Pterygodium*. Areas referencing a primary centre of distribution were correlated with individual species to determine the historical relationships between centres. The analysis used the morphological phylogeny of Linder & Kurzweil (1999). Abbreviations: DAC, Drakensberg Alpine Centre; E. Cape, Eastern Cape; W. Cape, Western Cape. 'Drakensberg' refers to the Drakensberg Range in the broadest sense. Drakensberg taxa basal to their clade are highlighted.

that most of the Drakensberg species are basal to CFR clades (Fig. 3.1), suggesting a more recent derivation for species of the CFR.

Inclusion of the tropical species *P. ukingense* in a phylogenetiic overview of the *Coryciinae* (Kurzweil *et al.*, 1991), and its basal placement with *P. cooperi* (DAC) as a sister species, suggests a close relationship between the DAC and tropical Africa, and a long speciation history in the Drakensberg (Kurzweil *et al.*, 1991). The invasions into the CFR from the Drakensberg has led to the speciation of a number of neoendemics.

3.4.1.4 *MORAEA* MILL.

Moraea is a large genus of herbaceous geophytes (c. 200 species) confined to sub-Saharan Africa (Goldblatt, 1986; Goldblatt *et al.*, 2002). Its principal centre of diversity is the CFR (Goldblatt, 1986; Goldblatt *et al.*, 2002), with a secondary centre in the Drakensberg Range (Goldblatt, 1986). Eighteen species have been recorded from the DAC (Goldblatt, 1986). These patterns are reflected by a number of taxa within the Iridaceae (Goldblatt, 1983).

The molecular phylogeny of 73 species of *Moraea*, based on four cpDNA regions, was used in the cladistic biogeographic analysis. Two tightly clustered and derived clades, subgenus *Polyanthes* and a portion of subgenus *Vieusseuxia*, have provided evidence for at least two invasion events into the summer rainfall region from the CFR. These invasions include the DAC, with subgenera *Polyanthes* and *Vieusseuxia* represented by the DAC endemics *M. alpina* Goldbl. and *M. dracomontana* Goldbl. respectively. A third summer rainfall clade includes the DAC endemic *M. alticola* Goldbl., and is derived from a clade of tropical African species, that includes *M. bella* Harms and *M. schimperi* (Hochst.) Pichi-Sermolli. Both clades comprise subgenus *Grandiflora*. This analysis provides evidence for both a northern (tropical) and southern (Cape) origin for the Drakensberg species of *Moraea*, and therefore the north-south/south-north reciprocal exchange of taxa between these centres.

3.4.2 CAPE ELEMENT CENTRES AND INTERVALS

A comprehensive summary of the centres and sub-centres of Cape elements is presented (Fig. 3.2). Four primary centres are recognised: the Drakensberg Centre, Madagascar Centre, Pondoland Centre and Tropical Mountain Centre, with a number of individual high-altitude regions in the tropics considered as sub-centres because they represent smaller strongholds for Cape elements, with numbers, once having peaked in the DAC, decreasing in a northerly direction (refer also to Fig. 2.19, Chapter 2).

The Drakensberg Centre is considered a significant route for both temperate and tropical elements (Van der Schijff & Schoonraad, 1971). Its position between the sub-tropics and the temperate Cape region, and its high altitudes, make it a likely corridor. The DAC houses more temperate elements than the lower-lying regions of the Drakensberg Range (refer also to Fig 2.19; Chapter 2).

An evaluation of the possible floristic ties shared between the southern KwaZulu-Natal Drakensberg and a number of its smaller enclaves, and further south with the PC, was undertaken using Sørenson's indices of similarity (Granger, unpublished data) (Fig. 3.3). These ties, as expected, were strongest between the

Fig. 3.2. Pictorial representation of the centres and sub-centres of Cape elements in sub-Saharan Africa (updated from Weimarck, 1941). The high-altitude sub-centres in particular are often fragmented, hence the need for two hyphenated names when considering two dominant enclaves of close proximity. The most modern and geographically accurate names have been used. For example, 'Abessinian Sub-centre' is now 'Ethiopian Sub-centre'; 'Rungwe Sub-centre' is now 'Nyika-Rungwe Sub-centre'; 'Mitumba-Ruwenzori Sub-centre' is an amalgamation of Weimarck's (1941) 'Katanga' and 'Kivu' Sub-centres, named after the Mitumba Highlands, and the dominant Ruwenzori Mountains (5109 m) further north. The double-sided arrows denote possible dual-direction migration events that may have resulted in reciprocal exchange of taxa between centres.

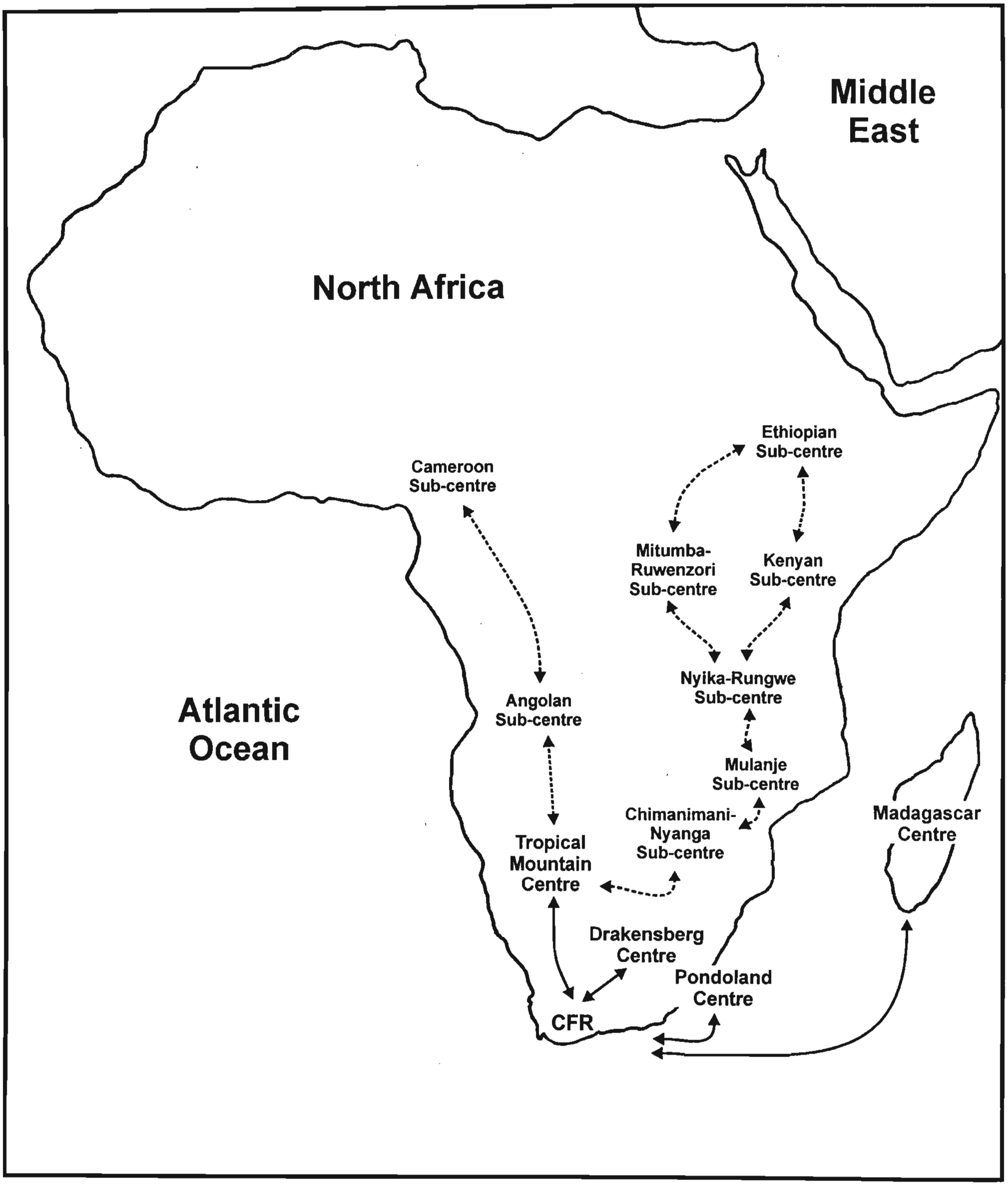

Middle East
North Africa
Atlantic Ocean
Ethiopian Sub-centre
Cameroon Sub-centre
Mitumba-Ruwenzori Sub-centre
Kenyan Sub-centre
Nyika-Rungwe Sub-centre
Angolan Sub-centre
Mulanje Sub-centre
Chimanimani-Nyanga Sub-centre
Madagascar Centre
Tropical Mountain Centre
Drakensberg Centre
Pondoland Centre
CFR

Fig. 3.3. The putative angiosperm migration tracks and floristic links across southern KwaZulu-Natal. Flora counts and Sørensen's similarity indices are listed for four high-altitude study regions above c. 1800 m and a Pondoland locality. The value in each circle refers to the number of angiosperm species and infraspecific taxa reported for each region. Values bridging the inter-connecting stippled lines are Sørensen's similarity indices (Mueller-Dombois & Ellenberg, 1974) between adjacent sites. Data courtesy of Granger (unpublished data).

KEY:

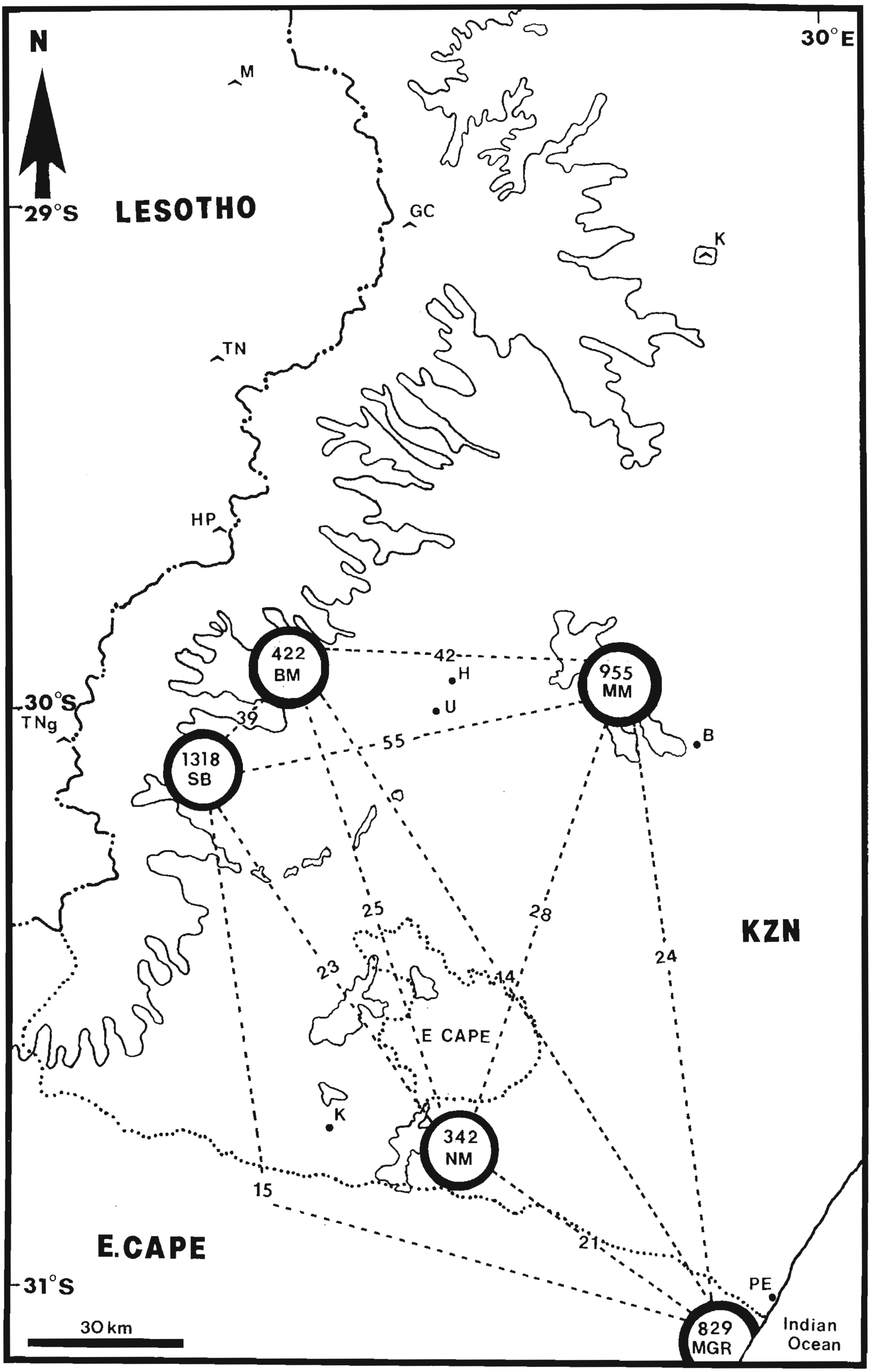
Provinces: KZN, KwaZulu-Natal; E. Cape, Eastern Cape

Study Regions: SB, southern KwaZulu-Natal Drakensberg; BM, Bamboo Mountain (2421 m); MM, Mahwaqa Mountain (2083 m); NM, Ngele Mountain (2268 m); MGR, Mkambati Game Reserve.

Towns (●): B, Bulwer; H, Himeville; K, Kokstad; PE, Port Edward; U, Underberg.

Peaks (^): GC, Giant's Castle (3314 m); HP, Hodgson's Peaks (3256 m & 3244 m respectively); K, Kamberg (2095 m); M, Makheka (3461 m); TN, Thabana Ntlenyana (3482 m); Tng, Thaba Ngwangwe (3068 m).

·························· = provincial boundary
——●●—— = international boundary
————— = 1800 m contour line

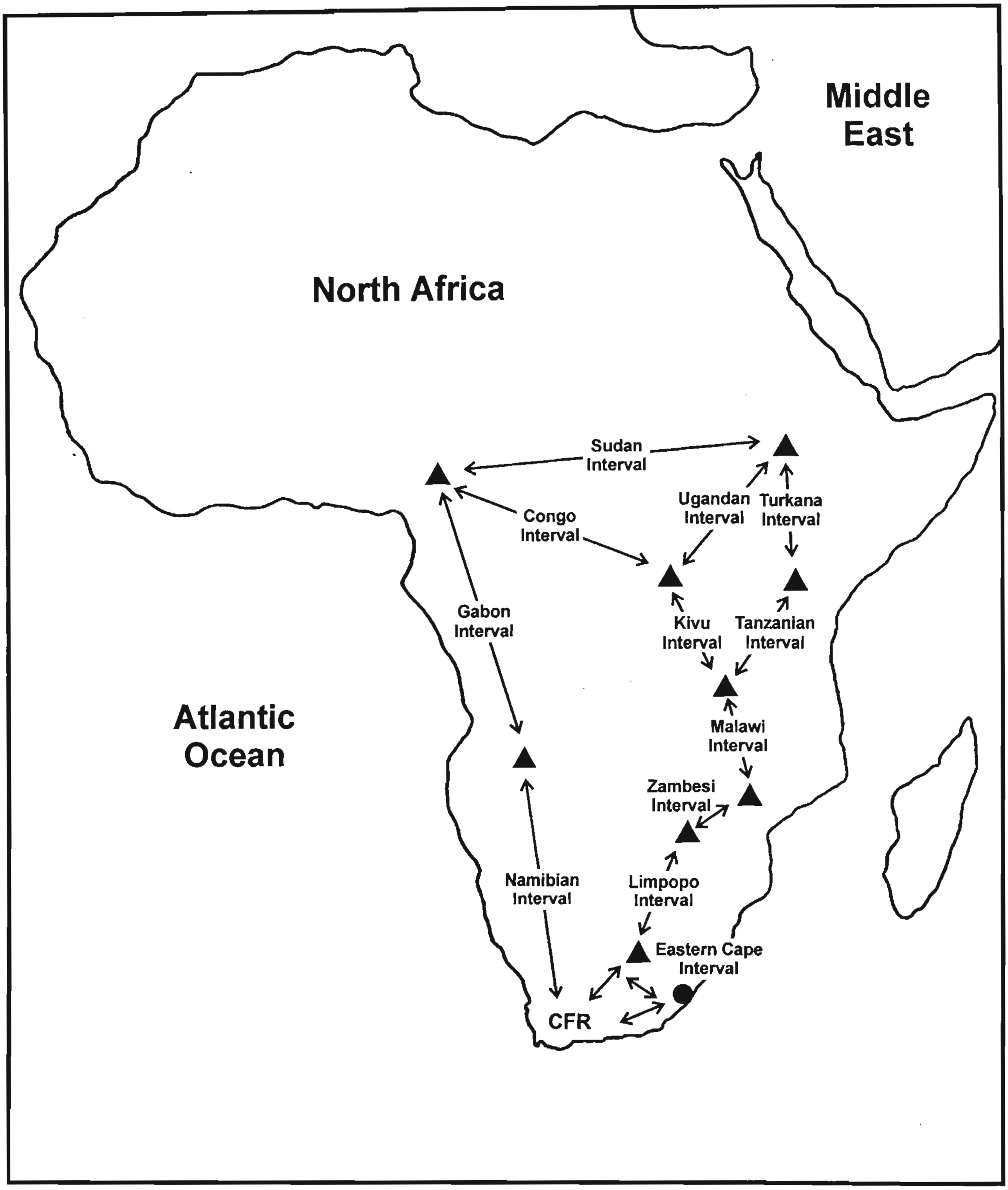

N
30°E
M
29°S
LESOTHO
GC
K
TN
HP
422
BM
42
H
955
MM
30°S
TNg
U
39
1318
SB
55
B
25
28
23
14
24
KZN
E CAPE
K
342
NM
15
21
E.CAPE
31°S
PE
30 km
829
MGR
Indian
Ocean

southern KwaZulu-Natal Drakensberg and its immediate outliers (Bamboo Mountain, 2421 m; Mahwaqa Mountain, 2083 m). The fewer number of species recorded in the latter is the result of a geographical size bias. Ties diminish, however, towards Ngele Mountain (2268 m), and further south towards the PC. Ngele Mountain is believed to have served as a high-altitude migration corridor between the DAC and PC (Granger, unpublished data). This migration corridor may have served as a passage for Cape elements, facilitating the exchange of taxa between the DAC and PC. A noteworthy example is found in *Disa tysonii* H. Bol. This rare orchid occurs either only at high-altitude (DAC) or on sandstone substrates at low-altitude (Linder & Kurzweil, 1999).

This evidence, however, supports one possibility concerning the migration of temperate taxa involving the DAC and PC. This idea is not generally well supported by phylogeny, although it is appreciated that the taxa selected for the historical biogeographical analyses did not involve taxa having the PC as their centre of diversity or endemism. Cladograms show that species alliances between the DAC and PC are often poor (e.g. *Cliffortia* - Whitehouse, 2003; *Watsonia* - Goldblatt, 1989). Another possibility therefore relates to two separate routes of migration: the *reciprocal* exchange of taxa between the CFR and DAC, and a one-way transfer from the CFR to the PC. Lateral exchange between the DAC and the PC may not be as significant as previously suggested.

Centres for one particular phytogeographic element are generally intervals for another. For example, the intervals for Cape elements are coincidentally centres for tropical and subtropical elements positioned in between temperate stations (Fig. 3.4).

Fig. 3.4. Pictorial representation of the intervals between centres and sub-centres of Cape elements in sub-Saharan Africa (updated from Weimarck, 1941). Symbols: ▲, high-altitude centres and sub-centres of Cape elements; ●, low-altitude centre of Cape elements (Pondoland Centre). Most names are derived from the geographic regions in which the intervals occur.

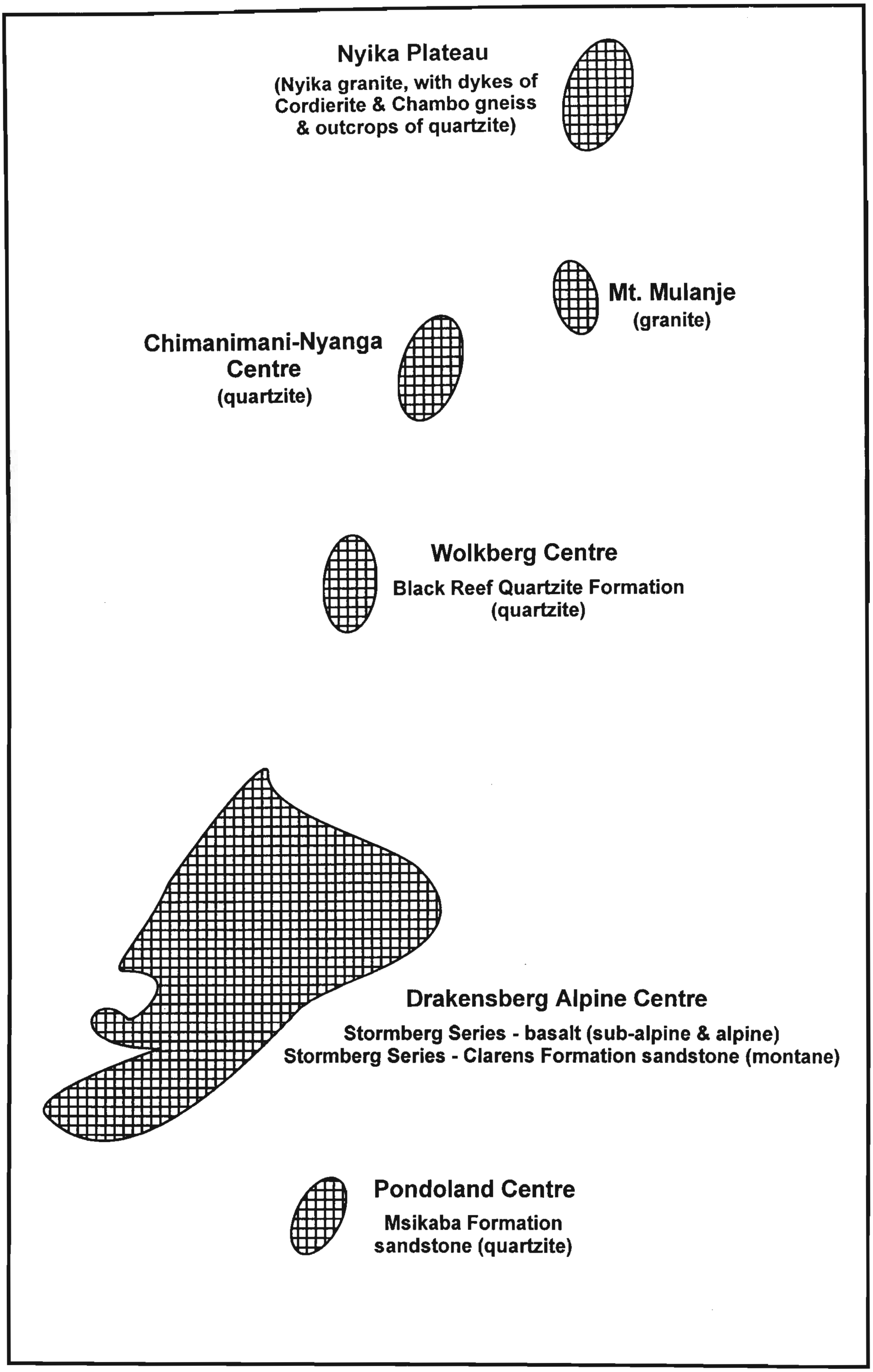

Middle East
North Africa
Atlantic Ocean
Sudan Interval
Congo Interval
Ugandan Interval
Turkana Interval
Gabon Interval
Kivu Interval
Tanzanian Interval
Malawi Interval
Zambesi Interval
Namibian Interval
Limpopo Interval
Eastern Cape Interval
CFR

3.4.3 THE GEOLOGICAL AFFINITIES OF CAPE ELEMENTS

The primary affinity of Cape elements appears to be with sandstone deposits, often with a high quartz content (Fig. 3.5). These substrates resemble ‘edaphic islands’ in that they are isolated areas that underpin and enrich local habitat diversity (Mason, 1946; Kruckeberg, 1986). The result is the proliferation of a number of neoendemic species. Examples include *Watsonia bachmannii* L. Bol., *W. mtamvunae* Goldbl., *W. pondoensis* Goldbl. (Goldblatt, 1989), *Leucadendron pondoense* Van Wyk, *Leucospermum innovans* Rourke and *Raspalia trigyna* (Schltr.) Dümmer (Van Wyk & Smith, 2001), all of the PC.

Cape elements of the Wolkberg Centre of floristic endemism (Van Wyk & Smith, 2001) are associated with nutrient-poor quartzitic sandstones, while its nutrient-rich dolomitic substrates house tropical and subtropical species (Matthews *et al.*, 1993). Soils also influence the distribution of plant communities in the Chimanimani Mountains (Phipps & Goodier, 1962; Wild, 1964). Its soils derived from quartzite are white, sandy and nutrient-poor, giving rise to sclerophyllous shrublands (≈ Cape elements). Schists are also common in the Chimanimani Mountains, and give rise to fertile red soils with a strong presence of tropical vegetation. Mt. Mulanje, further north, is an inselberg consisting of granite, quartz-syenite and syenite (Porembski, 1996; Strugnell, 2002). Its documentation of Cape elements is based on either the endemic flora (Strugnell, 2002) or outdated accounts (Whyte, 1894; Chapman & White, 1970), that suggest there are fewer Cape elements on Mt. Mulanje than in the Chimanimani Mountains (Wild, 1964). However, the complete spermatophyte flora of Mt. Mulanje is pending (A. Strugnell, 2003, pers. comm.). The geology of the Nyika Plateau in northern MalaŴi is diverse, ranging from

Fig. 3.5. The geological associations of Cape elements in southern and south-central Africa. Use of the term 'centres' refers to formal centres of floristic diversity and endemism (*sensu* Van Wyk & Smith, 2001) and not formal centres of Cape elements. Direction of migration of Cape elements is not implied.


Nyika Plateau
(Nyika granite, with dykes of Cordierite & Chambo gneiss & outcrops of quartzite)
Mt. Mulanje
(granite)
Chimanimani-Nyanga Centre
(quartzite)
Wolkberg Centre
Black Reef Quartzite Formation
(quartzite)
Drakensberg Alpine Centre
Stormberg Series - basalt (sub-alpine & alpine)
Stormberg Series - Clarens Formation sandstone (montane)
Pondoland Centre
Msikaba Formation sandstone (quartzite)

dykes of granite and gneiss, to outcrops of quartzite (Willis *et al.*, unpublished data; Willis *et al.*, 2001). Although numerous Cape elements have been reported for the region, their precise geological affinities were not outlined. Furthest north, Cape elements have been documented for the flora of the Ethiopian Highlands (Hedberg, 1961, 1965). These highlands are volcanic plateaus comprising 'flood basalt' lavas (Mohr, 1983). Although the basalts of Ethiopia are alkaline, largely a function of high Na_2O content (Mohr, 1983), and those of the Drakensberg Formation in southern Africa are acidic, both appear to be (potentially) nutrient-rich systems that differ from the general association of Cape elements with nutrient-poor substrates.

3.4.4 TEMPERATURE INCREASE AND ITS POSSIBLE EFFECT ON CAPE ELEMENTS OF THE DRAKENSBERG ALPINE CENTRE

The present-day distributions of taxa are determined by their ecological compatibility with present-day climate. However, due to changing climatic conditions, taxa with a specific set of adaptive characteristics may not be suited to the new conditions they face (Deacon *et al.*, 1992; Stock *et al.*, 1997).

The DAC, characterised by diverse topography and steep altitudinal gradients, is an ideal region in which to study the effects of palaeoclimate change. These effects translate into the movement of vegetation communities along altitudinal gradients in order to remain within their optimal growth environment. Ultimately, species that are similarly affected occupy similar habitats (Van Zinderen Bakker & Coetzee, 1988; Hill, 1996; Midgley *et al.*, 2001).

Mountains systems are renowned for their sensitivity to climate change (e.g.

Hill, 1996; Midgley *et al.*, 2001), especially changes to temperature. Speculations concerning the potential effects of glacial-interglacial fluctuations on the Cape elements of the DAC are made. It is suggested that warming during interglacials may cause wide-scale extirpation of Cape elements from mountain systems characterised by inherently nutrient-rich soils (e.g. the basalt-derived soils of the DAC). These elements are able to occupy nutrient-rich soils only during hypothermals because of the ameliorating influence of cooler temperatures on nutrient availability. If temperature increases during hyperthermals were sufficient to release the true fertility of nutrient-rich soils previously constrained by cooler temperatures, then these elements may have survived on the adjacent nutrient-poor sandstones of the Clarens Formation at lower elevations. The ideas relating to temperature-effects are thoroughly explored in Chapter 4.

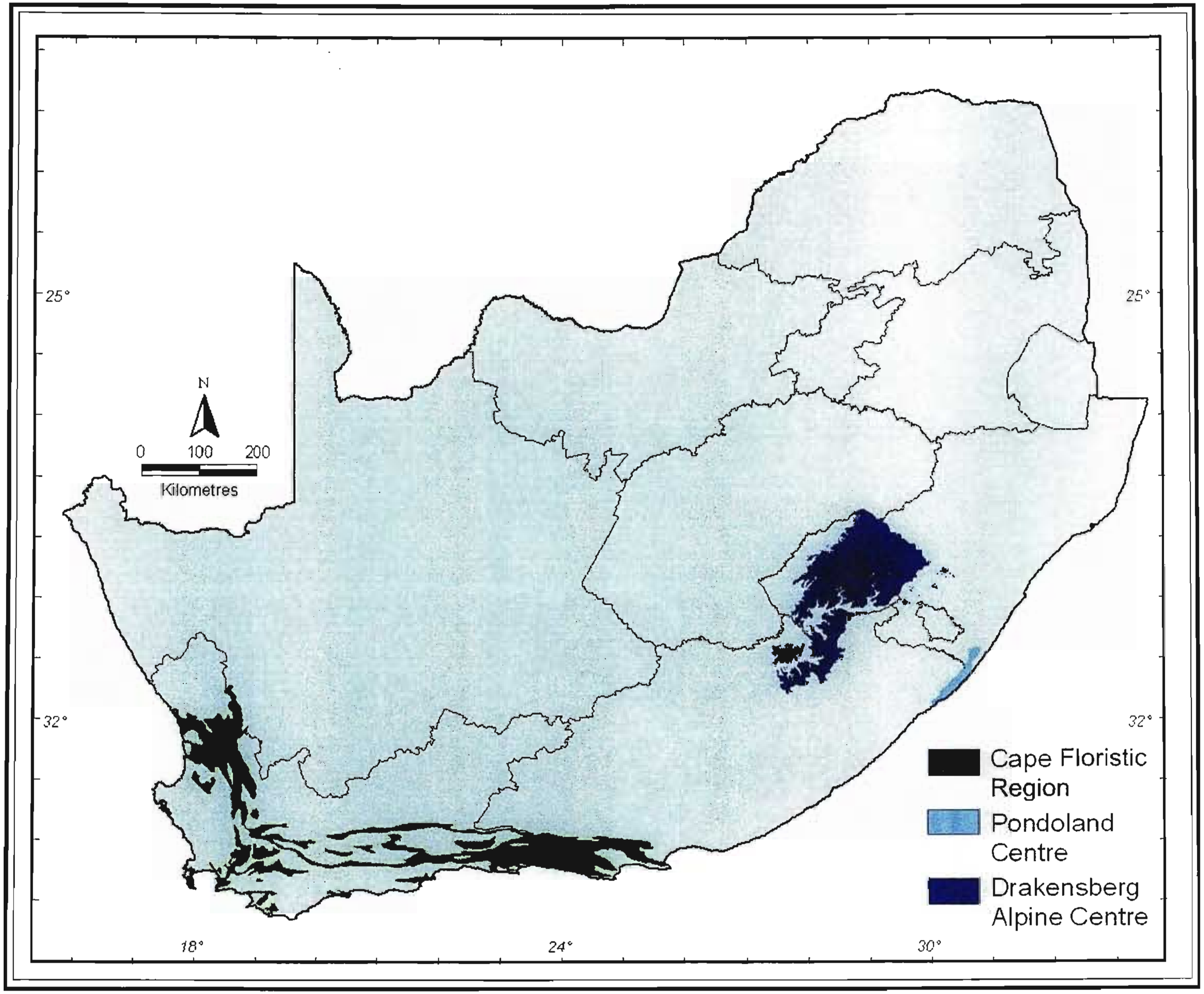
Subsequent hypothermals have possibly allowed reinvasion by Cape elements onto high-altitude basalt substrates. Their ability to remain on Clarens Formation Sandstones during warm cycles, and subsequent expansion onto basalt substrates during cool cycles, lies in their capacity to compete in nutrient-poor environments, thereby occupying suitable niches that non-Cape (non-preadapted) taxa have not been able to occupy. Studies on plant-climate relationships therefore need to consider both the current selection pressures as well as future ones, as currently nonadaptive traits may preadapt taxa to future environmental conditions (Stock *et al.*, 1997).

The purpose of the GIS analysis was simply to highlight the current temperature regimes favouring Cape elements in regions of contrasting geology (Fig. 3.6). The DAC is able to retain Cape elements on its inherently nutrient-rich substrates because of its cooler temperatures (Table 3.1). Pondoland, subject to warmer temperatures (Table 3.1), is able to retain Cape elements because of its inherently nutrient-poor soils.

Table 3.1. Temperature data derived from a GIS analysis of three phytogeographic centres of diversity. Months represent the growing season of each region.

Region	Lowest temperatures (°C)			Highest temperatures (°C)		
	Min.	Max.	Mean	Min.	Max.	Mean
1. **Cape Floristic Region**						
October	2.1	12.8	9.0	12.7	27.8	22.3
November	4.8	14.8	11.0	15.4	30.7	24.9
December	6.5	16.8	12.6	17.3	32.0	26.7
January	7.7	17.4	13.6	18.2	33.3	27.9
February	8.2	18.2	14.1	18.5	34.2	28.2
March	6.7	16.8	12.9	17.6	31.7	26.4
2. **Drakensberg Alpine Centre**						
November	-2.8	11.2	5.7	6.2	25.0	18.7
December	-1.6	12.8	7.2	7.6	26.8	20.4
January	0.1	13.7	8.2	9.1	27.5	21.0
February	-0.3	13.8	7.9	8.4	26.5	20.2
March	-1.8	12.9	6.3	7.2	25.0	18.5
3. **Pondoland Centre**						
October	12.7	15.8	14.2	21.7	23.6	22.5
November	14.1	17.2	15.6	22.3	24.7	23.3
December	15.6	18.8	17.1	24.1	26.4	25.1
January	16.6	19.8	18.2	25.1	26.9	25.8
February	16.8	20.0	18.3	25.4	27.3	26.1
March	16.0	19.2	17.5	24.9	26.8	25.6
April	13.4	16.8	15.1	23.6	25.4	24.4

Fig. 3.6. Three regions of floristic endemism and diversity relevant to this investigation. Temperature regimes were compiled for each region to determine the temperature constraints on their Cape elements. Boundaries of the Cape Floristic Region (CFR) refer to its association with Table Mountain Sandstone.


25°
25°
N
0
100
200
Kilometres
32°
32°
Cape Floristic Region
Pondoland Centre
Drakensberg Alpine Centre
18°
24°
30°

3.5 CONCLUSION

Cladistic biogeographic analyses have provided evidence of exchange between the CFR and DAC, and the subsequent proliferation of neoendemics in both floras. These sites are possible refugia during interglacials, when warmer temperatures are responsible for the contraction of temperate vegetation. The likelihood of both north-south and south-north migration events is supported by a limited number of phylogenies, as suggested by the close relationship between taxa from the DAC and tropical Africa in *Pterygodium* and *Moraea*.

The reciprocal exchange of temperate taxa between the CFR and DAC, and from the CFR to the PC, and from tropical Africa to the DAC, has resulted in a distinct distribution pattern common to the Afromontane highlands, most notably the sharing of Cape-centred genera called Cape elements.

The generation of sound phylogenies and the search for congruent patterns across a broad spectrum of Cape elements will aid in the comprehensive reconstruction of their origins and relationships. Generalisations at this stage are still tentative as they are based on very few taxa.

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'There is little empirical work to test the new theoretical speculations on what limits membership of plant communities.'

Bond *et al.* (1992)

CHAPTER 4

A biogeochemical appraisal of Cape elements on high-altitude corridors and edaphic islands

4.1 INTRODUCTION

4.1.1 BACKGROUND

The vegetation patterns of southern Africa are well documented (e.g. Acocks, 1988; Rutherford & Westfall, 1994; Low & Rebelo, 1996). In particular, many descriptive accounts have been published on the classification, distribution and community organisation of the vegetation of the Cape Region (e.g. Campbell, 1986; Campbell & Werger, 1988). Furthermore, several investigations have shown that nutrients, when in limited supply, are responsible for shaping the boundaries of this vegetation (e.g. Dahlgren, 1968; Stock & Lewis, 1986; Cowling & Holmes, 1992; Richards *et al.*, 1997).

Cape elements occupy certain habitats in the summer rainfall region of southern Africa, particularly the Drakensberg Alpine Centre (DAC) and Pondoland Centre (PC) (Carbutt & Edwards, 2001). Their prominence in the latter region is not surprising because its nutrient-poor soils produce similar nutritional niches to the quartzitic sandstones of the Cape Region, some 600 km further south (Van Wyk, 1990). Numerous outliers of the Cape flora occur in the PC, including members of the genera *Leucospermum* and *Leucadendron*, as well as a member of the relict *Raspalia* of the near-endemic family Bruniaceae (Abbott, 1993; Van Wyk & Smith, 2001). More surprising is the prominence of Cape elements associated with the mountainous regions of southern Africa, particularly the DAC. This high-altitude region borders the eastern periphery of the southern African plateau (Partridge & Maud, 1987), ~~and~~ ~~has~~ its alpine and sub-alpine soils are derived from nutrient-rich basalt that overlie nutrient-poor sandstones of the Clarens Formation (Killick, 1994). Almost 70% of the Cape-centred genera in the summer rainfall region of southern Africa occur both in the DAC and PC (Carbutt & Edwards, 2001). This is a surprising overlap for regions separated by a horizontal disjunction of between 280 to 400 km, which differ in altitude, precipitation, temperature and substrate. The factors responsible for the occurrence of Cape elements in summer rainfall areas of southern Africa are poorly understood.

4.1.2 THE ROLE OF PREADAPTATION

Mason (1946) used the term 'preadaptation' (or more recently 'exaptation' *sensu* Gould & Vrba, 1982) to refer to adaptations that provide the potential for extending the range of a species through their serendipitous suitability to a different set of ecological constraints. For example, taxa adapted to stressful edaphic conditions may become founder members of stress tolerance in the new environment to which they are preadapted (Kruckeberg, 1986).

It is hypothesized that Cape elements are preadapted to high-altitude habitats. These habitats experience nutrient deprivation due to low temperatures, which reduce metabolic rates and the movement of ions in cold soils. Nutrient-related stresses are also associated with the Cape Floristic Region (CFR) (Goldblatt & Manning, 2000) and the PC; these regions are characterized by nutrient-poor soils. Taxa that are adapted to the nutrient-poor soils of the CFR and PC are preadapted to the temperature-induced 'nutrient-poor' soils of the DAC and vice versa. This 'compatibility' has allowed the reciprocal exchange of taxa between regions, resulting in the sharing of Cape elements with (and between) the DAC and PC.

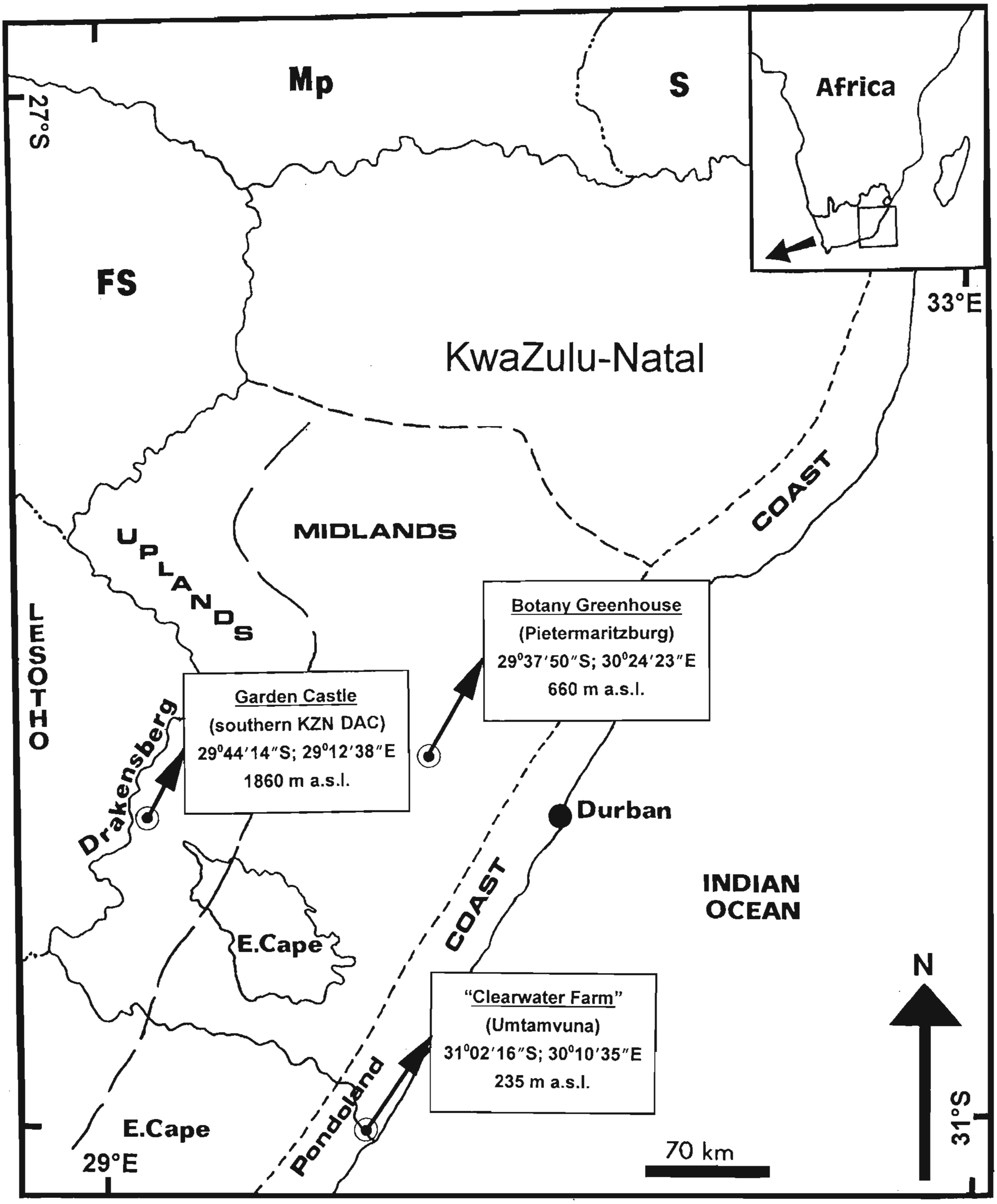
The primary aim of this study was to determine which aspect(s) of the edaphic environment of the DAC were most influenced by temperature; these interactions most probably have contributed to its nutrient-poor soil economy to which Cape elements are simultaneously preadapted.

4.2 METHODOLOGY

4.2.1 SELECTION OF STUDY SITES

Three study sites were chosen in KwaZulu-Natal, South Africa (Fig. 4.1), collectively representing a gradient of temperature (coastal hinterland to mountain): (1) Garden Castle, southern KwaZulu-Natal Drakensberg; (2) 'Clearwater Farm', Umtamvuna, southern KwaZulu-Natal; and (3) Pietermaritzburg, KwaZulu-Natal Midlands. Garden Castle is located in the southern KwaZulu-Natal Drakensberg. Its pot experiment was established at c. 1860 m, compliant with the 1800 m altitude that characterizes the DAC (Hilliard & Burtt, 1987; Van Wyk & Smith, 2001). A second pot experiment was established on the border of Umtamvuna Nature Reserve (UNR), situated on Msikaba Formation sandstone (Abbott, 1993). Study sites (1) and (2) occurred within regions supporting many Cape elements, while the third site, in the KwaZulu-Natal Midlands, supports few Cape elements, allowing the comparison of productivity in sites both favouring and excluding Cape elements. Calibrated HOBO®-H8 data loggers (Onset, 1998) were placed with each pot experiment to record temperature and relative humidity (RH) on an hourly basis (Fig. 4.2). Rainfall was recorded daily at each site using standard rain gauges. Meteorological data were

Fig. 4.1. Overview of KwaZulu-Natal, South Africa, highlighting the relevant study sites and their localities within natural bioregions which accommodated the reciprocal pot experiments. Precise localities and altitudes were generated with a Global Positioning System (GPS). Abbreviations: E. Cape, Eastern Cape; FS, Free State; Mp, Mpumalanga; S, Swaziland.


Mp
S
Africa
27°S
FS
33°E
KwaZulu-Natal
COAST
MIDLANDS
UPLANDS
LESOTHO
Botany Greenhouse
(Pietermaritzburg)
29°37′50″S; 30°24′23″E
660 m a.s.l.
Garden Castle
(southern KZN DAC)
29°44′14″S; 29°12′38″E
1860 m a.s.l.
Drakensberg
Durban
INDIAN OCEAN
E.Cape
COAST
"Clearwater Farm"
(Umtamvuna)
31°02′16″S; 30°10′35″E
235 m a.s.l.
N
Pondoland
E.Cape
29°E
70 km
31°S

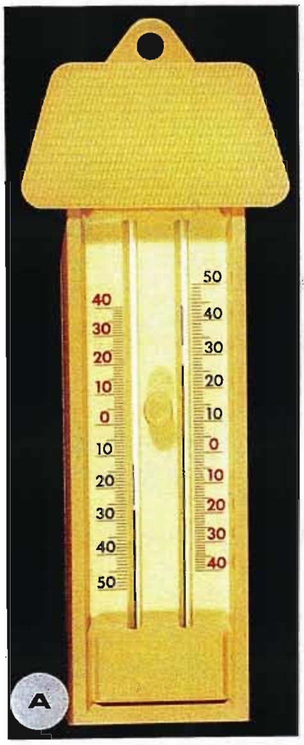
collated as weekly and monthly means.

4.2.2 THE TEST TAXON

Diascia (Scrophulariaceae) was selected as the test taxon because of its temperate affinities - its main centres of distribution lie within the Cape Region (Steiner, 1992) and the DAC (Hilliard & Burtt, 1984). The perennial herb *D. mollis* Hilliard & Burtt (Fig. 4.2) was selected because it has a widespread distribution, extending from Port St. Johns to Hogsback in the Eastern Cape, with a broad altitudinal range from sea level to 1500 m (Hilliard & Burtt, 1984). Most of the KwaZulu-Natal species of *Diascia* are DAC endemics, which are likely to display aberrant growth at lower altitudes. Attempts at using *Cliffortia*, which characterises sclerophyllous Cape vegetation, were unsuccessful. They propagated poorly and grew too slowly to be useful test subjects.

Equal-sized clonal cuttings of *D. mollis* (each c. 12 cm in length with 2 - 3 nodes) were struck following the recommendations of Clausen *et al.* (1940). Prolific rooting was induced in perlite after eight days in a mist shed, using the synthetic auxin powder indolbutyric acid (IBA) (trademark Seradix® B No. 1 for softwood plant cuttings). After determining their initial fresh weights, cuttings were transferred to pots containing Drakensberg, Pondoland and Midlands-derived soils. A total of 30 individuals were used per soil type (n = 90) in the local Midlands experiment, while the Drakensberg and Pondoland experiments, further afield, used 20 individuals per soil type (n = 60). Experiments were laid out as either ten 3 X 3 Latin Squares (Midlands site) or ± seven 3 X 3 Latin Squares (Drakensberg and Pondoland sites) (cf. Gomez & Gomez, 1984; Mead *et al.*, 1993) (Appendix 4.1). All pot experiments were placed on tables of equal height and were conducted for 100 days during the

Fig. 4.2. Snapshots of the *D. mollis* reciprocal pot experiments. A. minimum-maximum thermometer used to calibrate HOBO® data logger; B. & C. front view of *D. mollis* flower; D. lateral view of *D. mollis* flower; E. cuttings established in moist perlite; F. HOBO® data logger that recorded temperature and relative humidity data; G. Midlands greenhouse experiment; H. serial jack and serial com ports for downloading HOBO® data; I. rain-proof device that housed a HOBO® data logger at each site.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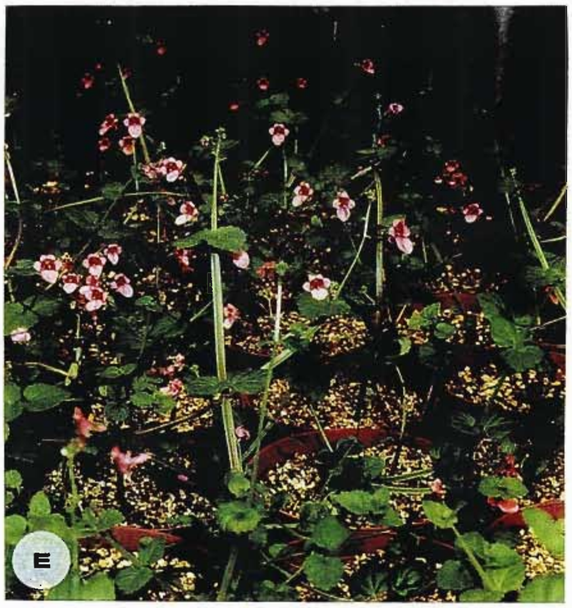
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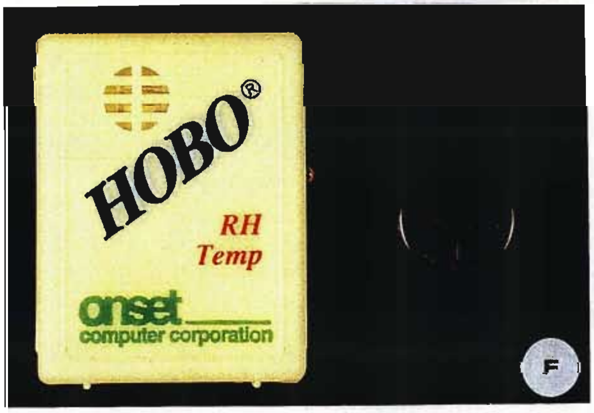
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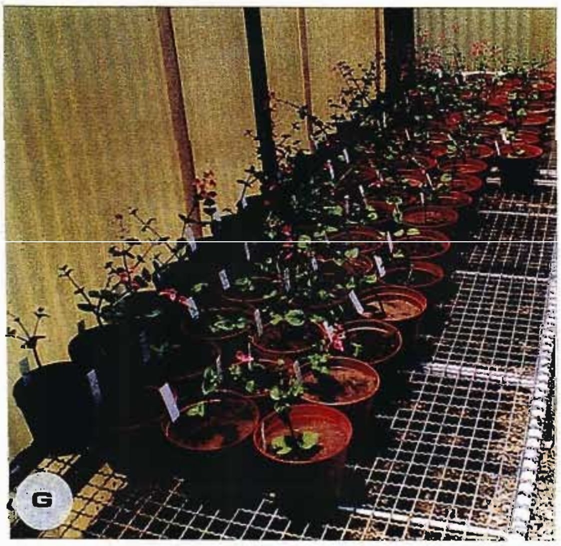
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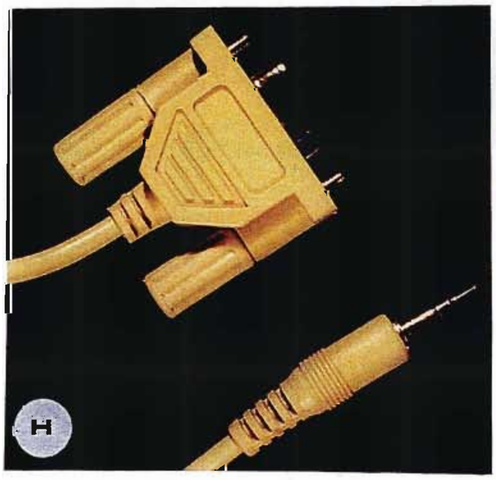
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summer (December 1999 to February 2000).

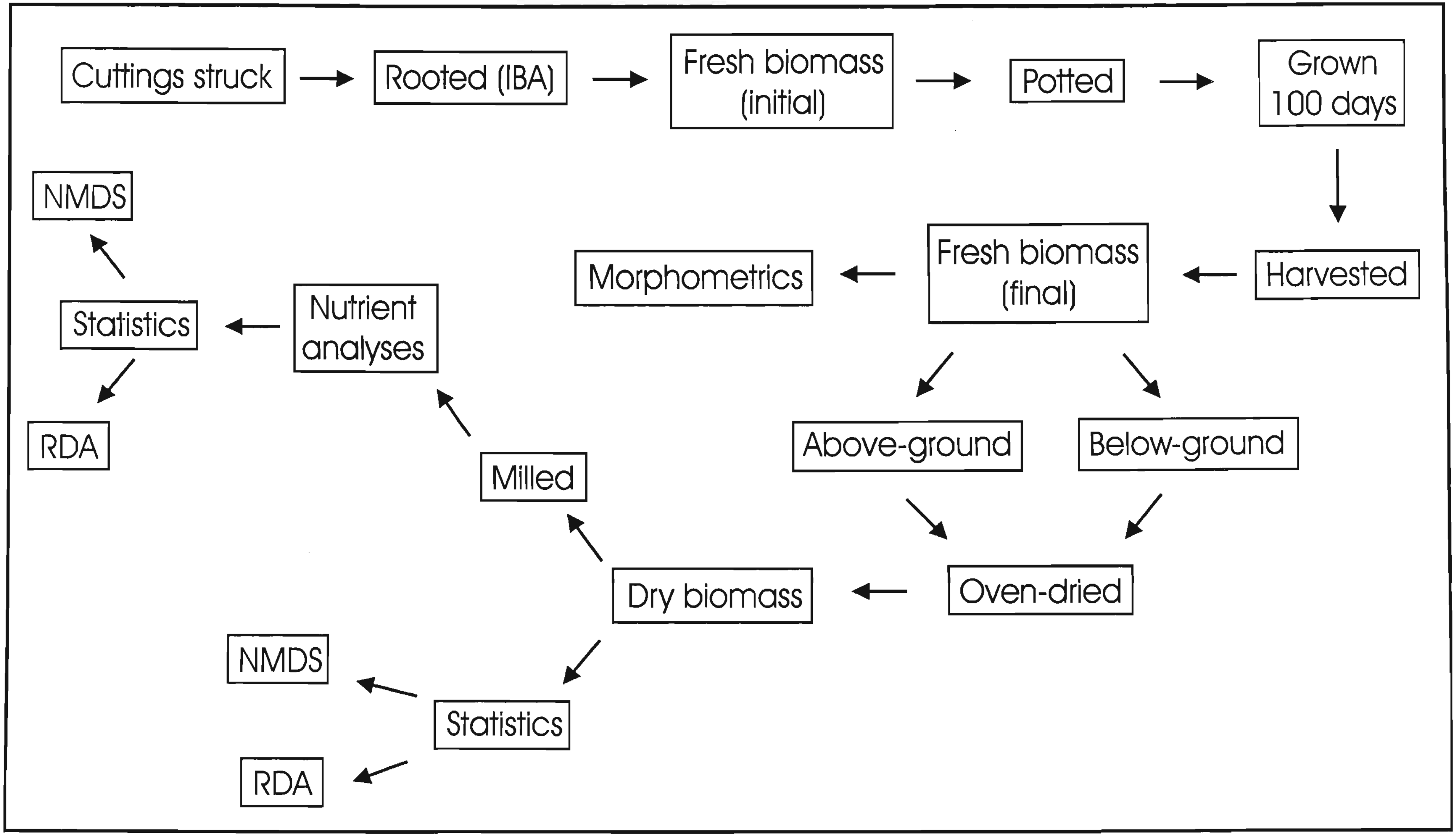
Protection from hail using netting in the Drakensberg experiment and clear polycarbonate in the Midlands experiment was necessary. Photosynthetic photon fluence rate (PPFR) was measured using the Parkinson leaf chamber of an ADC LCA3 portable infra red gas analysis (IRGA) at midday under a cloudless sky. PPFR measurements relating to 'shaded' and unshaded treatments are provided (Appendix 4.2). All pot experiments were kept moist for the duration of the study. Hand-watering was necessary during dry spells; samples were analysed by the Analytical Services Department of Umgeni Water (Appendix 4.3).

All individuals were analysed morphometrically after 100 days. Measurements of shoot height, leaf length and breadth (five of the largest, healthiest leaves), and internode length were recorded. Fresh and dry below- and above-ground biomass was also recorded; dry biomass was determined after 48 hours of oven drying at 80°C. A summary of the methods used in the preparation, harvesting and final analyses of *D. mollis* is provided (Fig. 4.3).

4.2.3 POST-HARVEST ANALYSES

The dried material was milled to pass through a 0.84 mm sieve. Subsamples were then dry ashed at 450°C overnight and taken up in 1 M HCl. Phosphorus (P) concentration was determined colorimetrically using the modified molybdenum blue procedure (Hunter, 1974) and calcium (Ca), copper (Cu), potassium (K), magnesium (Mg), manganese (Mn), sodium (Na) and zinc (Zn) were determined by atomic absorption (Hunter, 1975). Carbon (C), nitrogen (N) and sulfur (S) concentrations were determined by Dumas dry combustion using a LECO CNS-2000 automated analyser. N was verified using the macro-Kjeldahl digestion method (Bremner, 1965).

Fig. 4.3. Summary of the methods used in the preparation, harvesting and final analyses of *D. mollis* used in the reciprocal pot experiments at three sites.


Cuttings struck
Rooted (IBA)
Fresh biomass (initial)
Potted
Grown 100 days
Harvested
Fresh biomass (final)
Morphometrics
Above-ground
Below-ground
Oven-dried
Dry biomass
Milled
Nutrient analyses
Statistics
NMDS
RDA
Statistics
NMDS
RDA

Data were analysed using both one-way and two-way ANOVA in conjunction with Tukey's multiple range test. The two-way ANOVA tested the significance of site, soil and site-soil interactions on productivity.

4.2.4 SOILS: COLLECTION AND PREPARATION

Soils from the three study regions were used in the pot experiments: (1) basalt-derived soil supporting Cape elements at high-altitude ('Drakensberg'); (2) sandstone-derived soil supporting Cape elements at low-altitude ('Pondoland'); (3) shale-derived soil supporting few Cape elements at intermediate altitude ('Midlands').

Topsoils for both the pot experiments and chemical/physical soil analyses were collected to a depth of c. 20 cm in the rooting zone of the O/A-horizon. Specific collection sites were: (1) the summit of Mike's Pass, Cathedral Peak (Mlambonja) wilderness area, northern KwaZulu-Natal Drakensberg, altitude 2000 m ('Drakensberg soil'); (2) the sandstone pavements in the Oribi Flats area, southern KwaZulu-Natal, altitude 350 m ('Pondoland soil'); and (3) Pietermaritzburg, altitude 660 m ('Midlands soil').

All soils were air-dried at room temperature; soils for the pot experiments were sieved through a 2 mm sieve and stored in open sacks in a dry laboratory until required; soils for the chemical/physical analyses were crushed between rubber belts in a soil crusher and passed through a 1 mm sieve.

4.2.5 SOILS: NUTRIENT-RELATED PROTOCOLS

Total C, N and S were determined by Dumas dry combustion using a LECO CNS-2000 automated analyser. Available N was determined twice, firstly in a number of non-incubated soils and secondly in a number of incubated soils after mineralisation. N (NH_4^+) and N (NO_3^-) were determined from five replications of 20 g air-dried soil extracted in 50 ml 2M KCl (Bremner, 1965). Samples were shaken for 2 hours, filtered and analysed in a Bran+Luebbe TRAACS 2000 continuous-flow automated analyser. Mineralisable N was determined after 10 days of closed aerobic incubation with soils moistened to field capacity (Appendix 4.4) in sealed Erlenmeyer flasks. This protocol is regarded as one of the most useful methods for evaluating N mobilisation (Read & Mitchell, 1983); the release rates of NH_4^+ and NO_3^- under these conditions are closely correlated with plant N uptake (Stanford *et al.*, 1973a). Five replications per soil type were placed in a controlled environment (CONVIRON) set at their mean native spring temperature (Drakensberg, 12°C - 1800 m isotherm; Midlands and Pondoland, 19°C) (Schulze, 1981), because major peaks of mineralisation activity are found in spring and autumn for both Mediterranean-type (Read & Mitchell, 1983) and mountain systems (Morecroft *et al.*, 1992). However, use of spring temperatures seemed best suited to the summer rainfall conditions experienced in the study sites: spring is characterised by increasing soil temperature after a cooler winter and also the first rains of the new season; both temperature and water availability are important controls of microbial activity (Read & Mitchell, 1983). The amount of N mineralized during incubation was the difference in available N between incubated and non-incubated soils, and served as the index of N availability at each site.

KCl-extractable Ca and Mg were determined by atomic absorption; KCl-extractable pH was measured using a gel-filled combination glass electrode. Ambic-2-extractable Cu, K, Mn and Zn were determined by atomic absorption (Hunter, 1975) and available P determined by the modified molybdenum blue procedure (Hunter, 1974). Cation exchange capacity (CEC) was determined using the copper acetate titration method (Cornfield, 1952). Percent acid saturation was derived from effective CEC and extractable acidity, once KCl-extractable acidity was titrated against 0.005 M NaOH (Farina, 1981).

4.2.6 SOILS: PHYSICAL PROPERTIES

Soil density was analysed on a volume basis. For the particle size distribution, suspended clay and fine silt were determined after dispersion and sedimentation, while sand fractions were determined by sieving (Day, 1965). Texture classes were determined from a textural triangle diagram (Macvicar *et al.*, 1977). Soil colour followed the Munsell soil colour chart (1975) determined under full afternoon lighting. Diagnostic topsoils followed the classification of Macvicar *et al.* (1977). Estimates of clay content were made using near-infrared spectroscopy (Hunter, 1975). The chemical and physical properties of all soils were compared using a one-way ANOVA and LSD test.

4.2.7 PHENETIC ANALYSES

Phenetic analyses compared a range of characters relating to plant morphology, plant nutrients and soil nutrients in the context of treatment-effects ('soil-site interactions'). The plant morphology data set was initially analysed using Principal Components Analysis (PCA). This ordination method, however, has sometimes proved ineffective due to curvilinear distortion (Minchin, 1987). The more robust non-metric multidimensional scaling (NMDS) (Minchin, 1987) has superceded PCA as the preferred method for ecological ordination, enabling the interpretation of complex interactions between environmental and vegetation gradients (Whittaker, 1987).

Exploratory analyses of the data sets relating to plant morphology (133 individuals scored for 11 quantitative characters) and plant nutrient concentrations (37 profiles, of which 25 relate to above-ground biomass and 12 relate to below-ground biomass, each scored for 13 nutrient-related characters) were undertaken using the computer program PATN (Belbin, 1987). The fewer replicates in the plant nutrient analyses were due to combinations of c. 3 - 4 individuals of the same soil and site, similarly positioned within the LS experiment, in order to acquire sufficient material for analysis. The NMDS ordinations were arranged such that individuals (or groups of individuals) from all sites and soil types were grouped within a single data matrix, following the standard order: Drakensberg, Pondoland and Midlands.

Ordinations were undertaken in two dimensions (cf. Faith *et al.,* 1987; Whittaker, 1987; Mac Nally, 1989); those with the lowest stress were selected. All characters were equally weighted through transformation using the 'TRND' option. Furthermore, a dissimilarity matrix was produced using the 'ASO' function (association estimate). The best association measures (lowest stress values and most highly resolved groupings) were achieved using the 'Minkowski' option which includes the Manhattan Series (sub-type Manhattan Metric; $p = q = 1$) following range standardisation. The ordination procedure 'SSH' (semi-strong hybrid multidimensional scaling) was undertaken in two (not three) dimensions as the stress values were sufficiently low. Finally, the 'PCC' function (correlation of extrinsics) correlated the characters used to construct the association matrix with the distribution of points. Correlation values greater than 0.7 are considered informative (Belbin, 1987). Meteorological data, with the exception of rainfall because experiments were sometimes watered by hand, and altitude, were correlated with the NMDS morphology ordination using vector fitting.

The significance of treatments was tested using redundancy analysis (RDA) of plant morphology, plant nutrients (concentrations and total nutrient content) and soil nutrients (cf. Rao, 1964) using CANOCO for Windows version 4.0 (Ter Braak & Smilauer, 1998). RDA is the canonical form of PCA that extracts gradients directly derived (or, directly attributable to treatments) from the environment (i.e. 'treatment effects'). The data sets used for plant morphology and plant nutrients were identical to those used in the NMDS ordinations. Nutrient content for above- and below-ground biomass was calculated as 'nutrient concentration x dry mass'. Soils were scored for 21 chemical and physical properties from 15 samples (five samples per soil type). All data were centred and standardised to zero mean and unit standard deviation to account for different scales of measurement and variance. Three questions were addressed through the plant-related RDA's: (1) did the treatment combinations have a significant effect on morphology and nutrient allocation patterns, (2) and if so, what are these effects? (3) Which treatments had a similar effect on morphology and nutrient allocation patterns? A single question was addressed through the soils-related RDA: (1) can differences in soil nutrients be explained in terms of soil type?

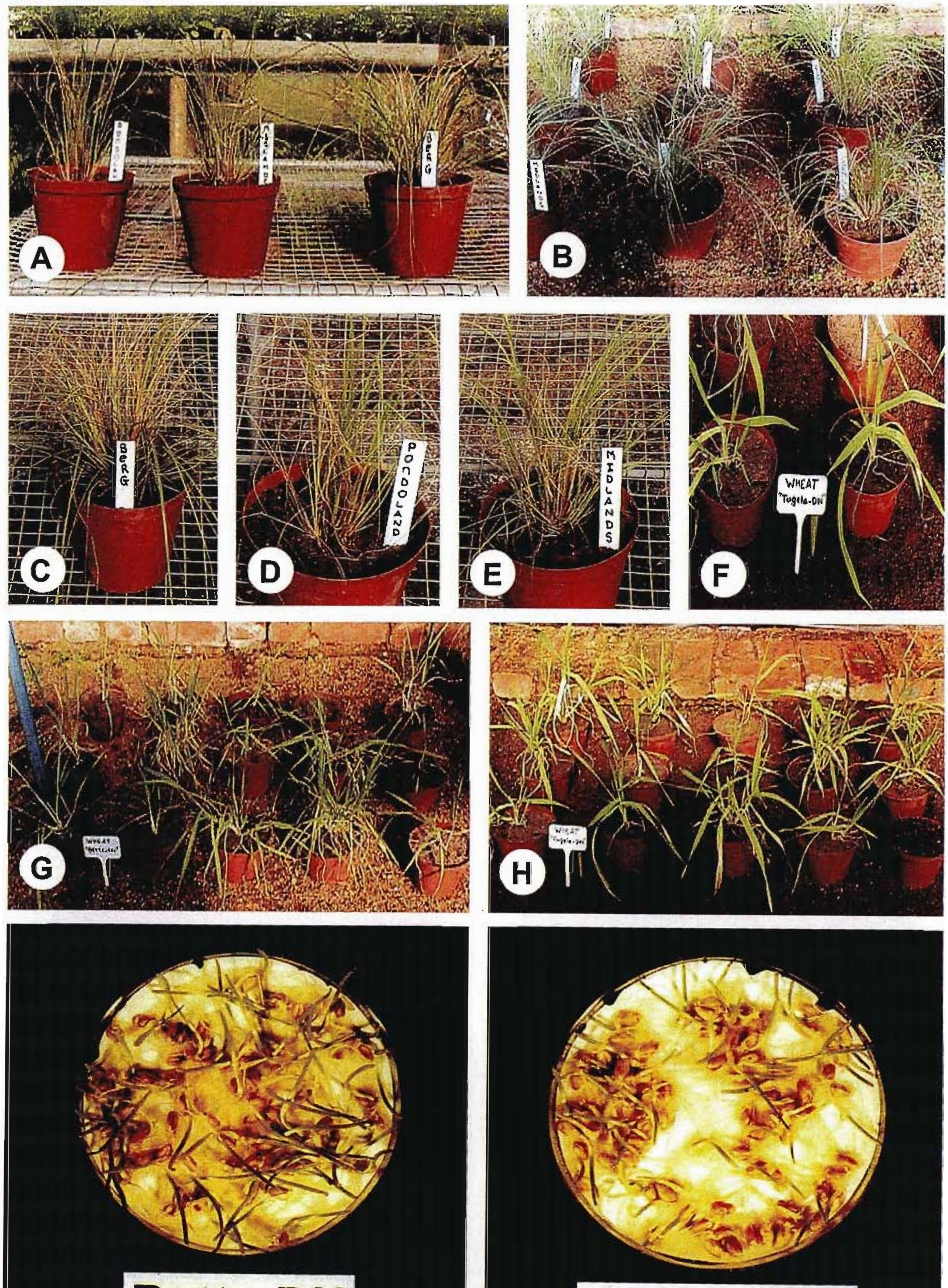
4.2.8 ADDITIONAL POT EXPERIMENTS

Two additional pot experiments were simultaneously undertaken in a greenhouse at the University of KwaZulu-Natal, Pietermaritzburg, during the autumn of 2003, due to the poor performance of *D. mollis* in Drakensberg soil at low altitudes (warm sites).

The possibility of N toxicity prompted an experiment that involved growing a C_4 subtropical grass in the same range of soils prepared for *D. mollis* (Fig. 4.4A-E). *Eragrostis curvula* (Schrad.) Nees (Weeping Lovegrass) is readily available, easily propagated and responds favourably to elevated levels of N (Le Roux & Mentis, 1986), making it an ideal test subject. Equal-sized plugs of *E. curvula* variety 'Ermelo', each c. 20 cm in height, were established in medium-sized pots on a mist bed in a well ventilated greenhouse in the three soils. Five replications were established in each soil type (n = 15) and arranged in a randomized complete block design. Above- and below-ground biomass was harvested after 100 days, then subjected to 48 hours oven drying at 80°C and weighed. The dried material was milled in a Wiley Mill (< 1 mm) and its N concentration determined by Dumas dry combustion using a LECO FP-2000 nitrogen analyser. Above- and below-ground plant N uptake was calculated as 'N concentration x dry mass'. Its productivity was compared to the herb *D. mollis* grown in the same range of soils for an equal period of time.

The second additional pot experiment tested the possibility of aluminium (Al) toxicity, because low pH increases the solubility and hence availability of heavy metals (e.g. Al^{3+}) that may become toxic (Woolhouse, 1981; Wilkinson, 1994; Sparks, 1995). Seeds from two cultivars of wheat (*Triticum aestivum* L.), the one Al-tolerant ('Tugela-DN'), the other Al-sensitive ('Betta-DN'), were germinated in a sterile medium (Fig. 4.4I&J) and planted out singly in small pots filled with Drakensberg soil (Fig. 4.4F-H). Five replications per cultivar were arranged in a randomized complete block design (n = 10). Productivity was compared between cultivars.

Fig. 4.4. Snapshots of the *Eragrostis curvula* (A - E) and *Triticum aestivum* (wheat) (F - J) pot experiments.


A
BERG
B
C
BERG
D
PONDOLAND
E
MIDLANDS
F
WHEAT "Tugela-DN"
G
H
I
Betta-DN
J
Tugela-DN

4.3 RESULTS

4.3.1 PRODUCTIVITY

Meteorological data collected throughout the duration of the pot experiments showed that the high-altitude site ('Drakensberg') experienced higher rainfall, lower temperature and intermediate RH (Table 4.1; Fig. 4.5). The low-altitude site ('Pondoland') experienced intermediate rainfall and temperature and higher RH (Table 4.1; Fig. 4.5). The mid-altitude site ('Midlands') experienced the lowest rainfall and RH and highest maximum temperatures (Table 4.1; Fig. 4.5).

The nine soil-site treatments exercised varying effects on the productivity of *D. mollis* (Table 4.2; Fig. 4.6). For example, plants grown at the Drakensberg site in different soils had the most similar biomass (Fig. 4.6). At the two lower altitude sites lower productivity and higher mortality characterised individuals grown in Drakensberg soil (Table 4.2; Fig. 4.6). Above- and below-ground biomass was consistently greatest in Midlands and Pondoland soils respectively (Fig. 4.6). The Midlands site was the most productive and gave rise to the largest shoot:root ratios; the Pondoland site was least productive, giving rise to the smallest shoot:root ratios (Table 4.2; Fig. 4.7). Productivity differences resulting from shading and water chemistry differences between sites cannot be negated (Appendix 4.2 & 4.3). Results of a two-way ANOVA showed that site, soil and all soil-site interactions significantly affected productivity ($p \leq 0.001$, Table 4.3), with temperature a significant factor affecting biomass at all sites (Fig. 4.8).

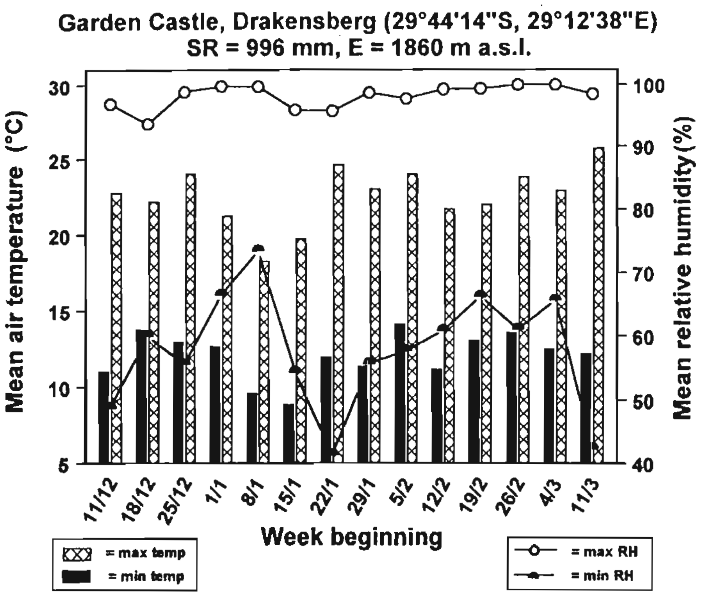
Biomass of the subtropical grass *E. curvula* was affected by soil type ($p < 0.05$), with Drakensberg soil resulting in the highest productivity (Fig.4.4A-E & 4.9A). Patterns of N uptake for above- and below-ground biomass (Fig. 4.9B) correlated to productivity in all three soils (Fig. 4.9A). Above-ground biomass accumulated the

Table 4.1. Meteorological data recorded during the summer months of 1999/2000 from three sites relevant to the *D. mollis* reciprocal pot experiments. Site abbreviations: D, Drakensberg; P, Pondoland; M, Midlands. For rainfall data, monthly totals are given; for other variables, monthly means.

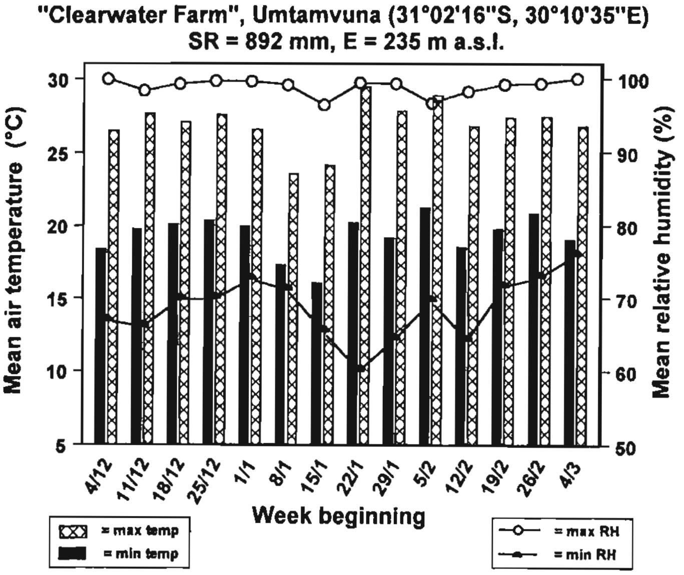
Month	**Rainfall (mm)**			**Min. temp. (°C)**			**Max. temp. (°C)**			**Mean temp. (°C)**			**Min. RH (%)**			**Max. RH (%)**			**Mean RH (%)**		
	D	**P**	**M**	**D**	**P**	**M**	**D**	**P**	**M**	**D**	**P**	**M**	**D**	**P**	**M**	**D**	**P**	**M**	**D**	**P**	**M**
December	204	164	289	12.5	19.6	19.0	23.0	27.2	32.2	17.8	23.4	25.6	54.8	68.2	55.9	96.6	99.4	96.7	75.7	83.8	76.3
January	463	393	124	10.8	18.3	18.3	21.2	26.4	30.8	16.0	22.4	24.6	58.5	64.4	55.9	98.2	98.9	96.5	78.4	81.7	76.2
February	329	335	58	12.6	20.1	20.0	22.9	27.7	32.6	17.8	23.9	26.3	59.4	68.9	54.7	98.9	98.8	96.9	79.2	83.9	75.8
Total/Mean	**996**	**892**	**471**	**12.0**	**19.3**	**19.1**	**22.4**	**27.1**	**31.9**	**17.2**	**23.2**	**25.5**	**57.6**	**67.2**	**55.5**	**97.9**	**99.0**	**96.7**	**77.8**	**83.1**	**76.1**

Fig. 4.5. Mean temperature and relative humidity (RH) data recorded on a weekly basis throughout the *D. mollis* reciprocal pot experiments at three sites. A. Drakensberg site; B. Pondoland site; C. Midlands site. Abbreviations: E, elevation; SR, summer rainfall.

A.


Garden Castle, Drakensberg (29°44'14"S, 29°12'38"E)
SR = 996 mm, E = 1860 m a.s.l.

B.


"Clearwater Farm", Umtamvuna (31°02'16"S, 30°10'35"E)
SR = 892 mm, E = 235 m a.s.l.

C.

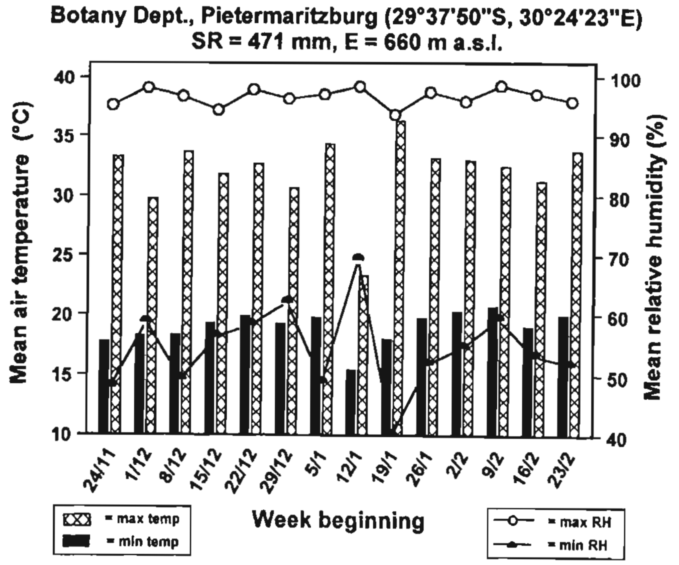

Botany Dept., Pietermaritzburg (29°37'50"S, 30°24'23"E)
SR = 471 mm, E = 660 m a.s.l.

Table 4.2. The effect of site and soil on 12 quantitative characters (mean ± SD) and survival of *D. mollis*.

Character		**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**
Site	no. of survivors	shoot height (mm)	leaf length (mm)	leaf breadth (mm)	internode length (mm)	increase in fresh mass (g)	total fresh mass (g)	root fresh mass (g)	shoot fresh mass (g)	total dry mass (g)	root dry mass (g)	shoot dry mass (g)	shoot:root ratio (dry mass)
Drakensberg	**(n = 20)**												
soil type													
Drakensberg	7	21±6	37±5	29±4	38±14	1.9±1.1	4.0±1.5	2.1±0.9	1.9±0.6	0.7±0.3	0.3±0.1	0.4±0.1	1.3±0.4
Pondoland	18	27±4	32±3	27±3	26±7	4.4±1.0	6.1±1.1	3.0±0.7	3.1±0.7	1.1±0.3	0.5±0.2	0.6±0.2	1.2±0.5
Midlands	18	26±5	32±7	25±6	27±6	4.0±1.8	5.8±2.1	1.9±0.8	3.9±1.4	1.0±0.4	0.3±0.2	0.7±0.3	2.3±0.7
Pondoland	**(n = 20)**												
soil type													
Drakensberg	4	12±4	10±4	9±1	6±2	-0.4±0.2	1.0±0.0	0.3±0.0	0.7±0.0	0.2±0.1	0.1±0.0	0.1±0.0	1.0±0.3
Pondoland	10	21±5	31±8	25±5	13±5	2.1±0.9	3.8±1.3	2.0±0.8	1.8±0.5	0.9±0.4	0.5±0.3	0.4±0.1	0.8±0.3
Midlands	19	25±4	30±8	26±5	20±5	4.6±1.4	6.5±1.5	1.8±0.6	4.7±1.0	1.3±0.3	0.4±0.1	0.9±0.2	2.3±0.9
Midlands	**(n = 30)**												
soil type													
Drakensberg	10	22±8	14±7	11±5	22±8	0.3±0.4	1.3±0.6	0.4±0.2	0.9±0.4	0.5±0.2	0.1±0.0	0.4±0.2	4.0±0.6
Pondoland	21	56±6	26±6	22±5	43±7	8.6±3.2	10.0±3.3	4.6±2.3	5.4±1.1	2.3±1.0	1.0±0.7	1.3±0.4	1.3±0.7
Midlands	26	44±12	27±7	22±4	40±9	6.6±2.6	7.7±2.7	1.6±0.7	6.1±2.3	1.9±0.6	0.4±0.2	1.5±0.5	3.8±1.9

Table 4.3. Two-way ANOVA of the effect of site, soil and site-soil interactions on the productivity of *D. mollis* grown for 100 days in a series of reciprocal pot experiments subject to nine site-soil treatments. Refer to Table 4.2 for character descriptions.

Source of variation	**Characters**											
	1	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**
Site	***	***	***	***	***	***	***	***	***	***	***	***
Soil	***	***	***	***	***	***	***	***	***	***	***	***
Site x Soil	***	***	***	***	***	***	***	***	***	***	***	***

Note for probability: * = $p \leq 0.05$; ** = $p \leq 0.01$; *** = $p \leq 0.001$

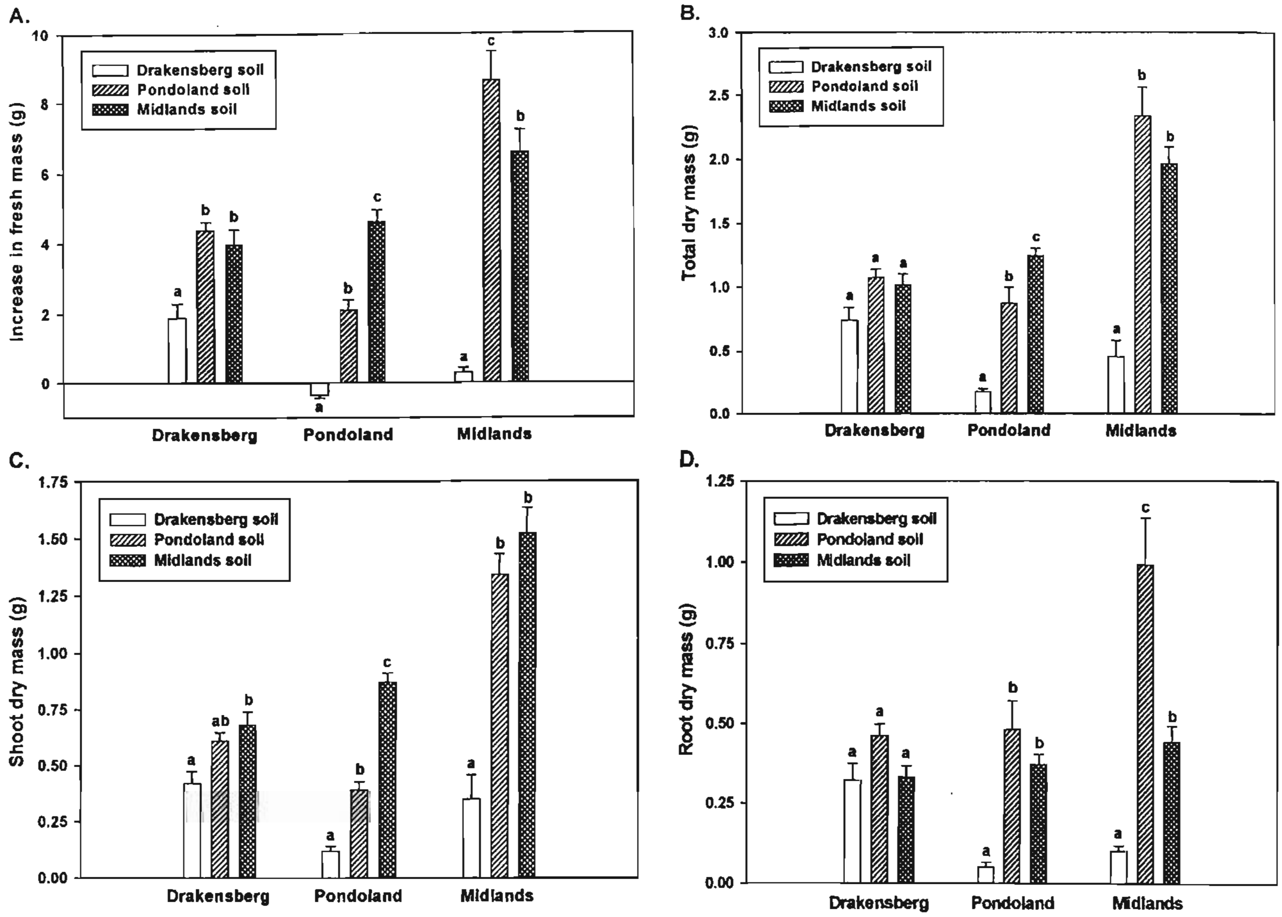


Fig. 4.6. The effect of soil and site on the biomass of *D. mollis* grown for 100 days in a series of reciprocal pot experiments subject to nine soil-site treatments. A. Increase in fresh mass; B. dry mass of shoots; C. dry mass of roots; D. total dry mass. Within each site, columns with the same letter on top are not significantly different using Tukey's multiple range test ($p > 0.05$). Error bars represent the standard error of the mean.

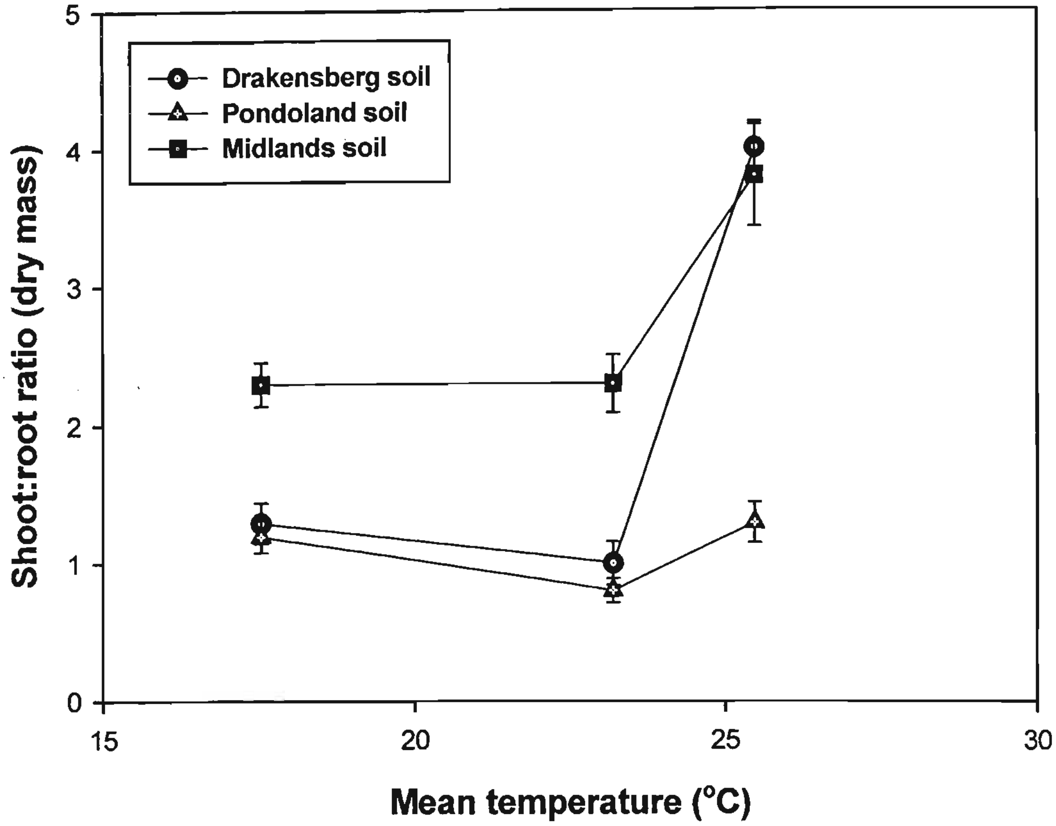


Fig. 4.7. The effect of temperature on the shoot:root ratios of *D. mollis* grown for 100 days in a series of reciprocal pot experiments subject to nine soil-site treatments. Data plots (mean ± SE) refer to three sites, the coolest of which is the Drakensberg and the warmest being the Midlands. Pondoland lies in between. Error bars represent the standard error of the mean. Confidence limits set at 95%.

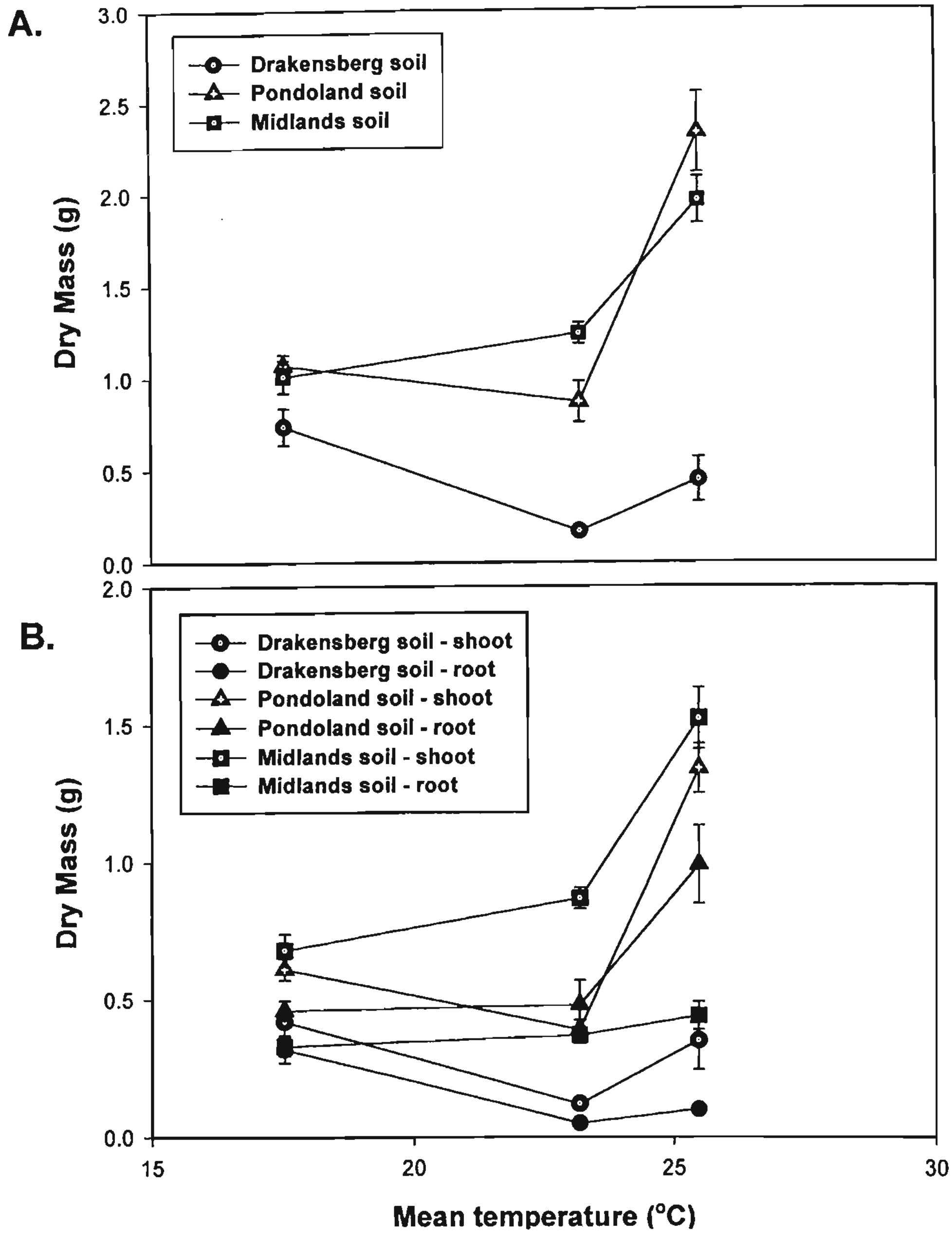


Fig. 4.8. The effect of temperature on the biomass of *D. mollis* grown for 100 days in a series of reciprocal pot experiments subject to nine soil-site treatments. Data plots (mean ± SE) refer to three sites, the coolest of which is the Drakensberg and the warmest being the Midlands. Pondoland lies in between. A. Whole plant analysis. B. Above- and below-ground biomass analysed separately. Error bars represent the standard error of the mean. Confidence limits set at 95%.

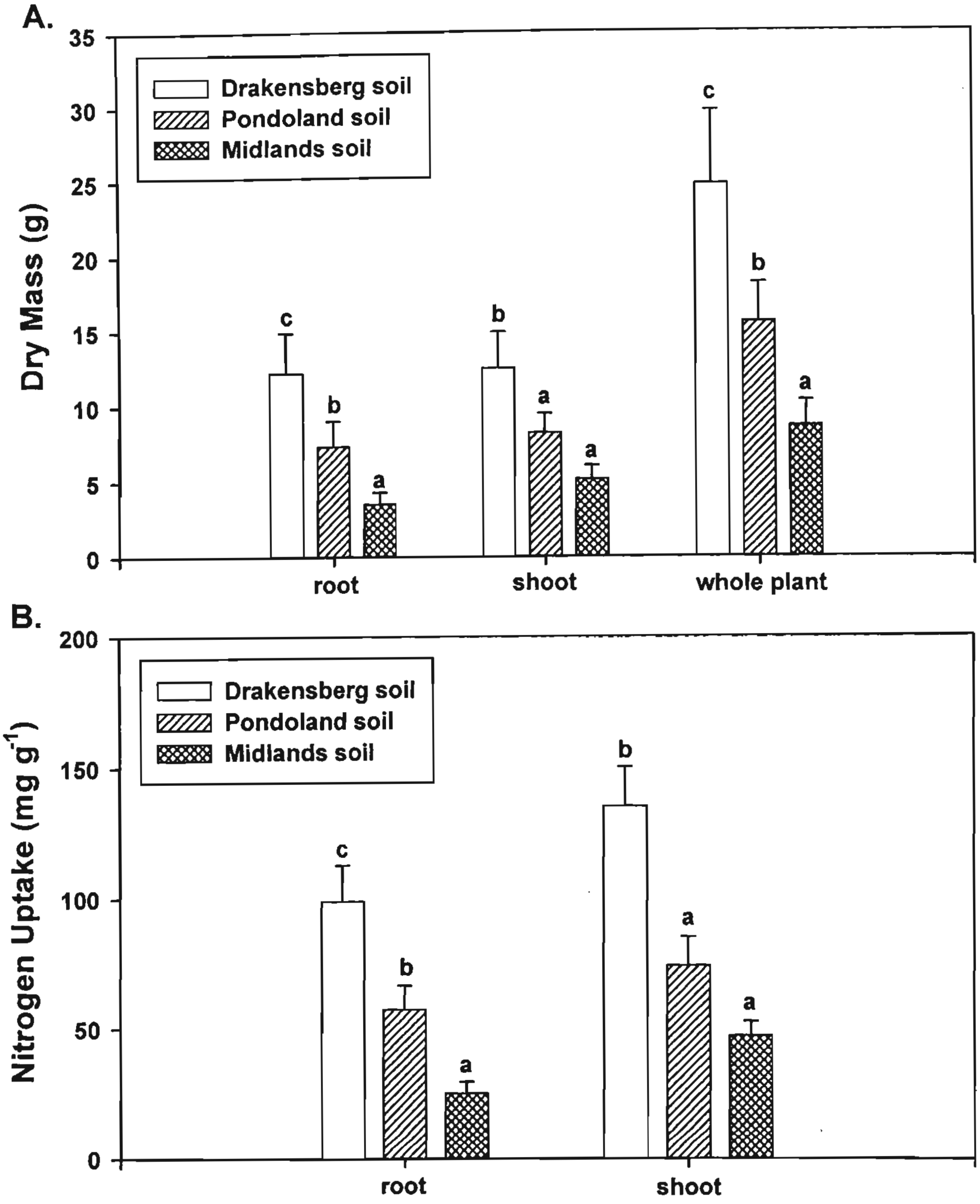


Fig. 4.9. The effect of soil on the productivity of *E. curvula* at the Midlands site. A. Biomass. B. Nitrogen uptake. Within each plant trait, columns with the same letter on top are not significantly different using Tukey's multiple range test ($p > 0.05$). Error bars represent the standard error of the mean.

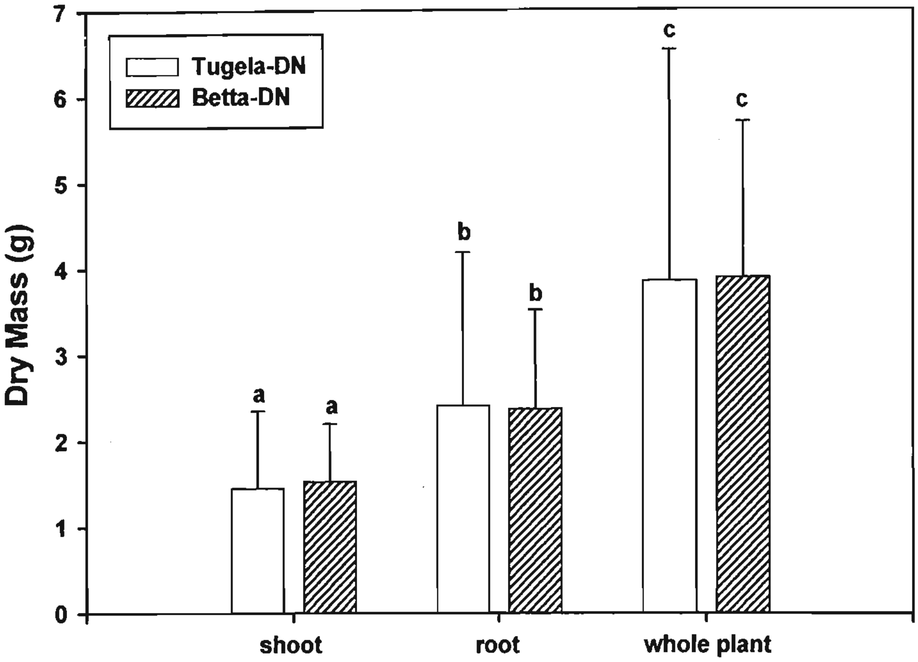


Fig. 4.10. Biomass of two wheat cultivars grown in Drakensberg soil at the Midlands site. The 'Tugela-DN' cultivar was bred to withstand Al^{3+} toxicity, while the 'Betta-DN' cultivar is Al-sensitive. Within each plant trait, and across cultivars, columns with the same letter on top are not significantly different using Tukey's multiple range test ($p > 0.05$). Error bars represent the standard error of the mean.

N (Fig. 4.9B). The Al-sensitive and Al-tolerant wheat cultivars performed equally well in Drakensberg soil (Fig. 4.4G&H & 4.10).

4.3.2 TISSUE NUTRIENT ALLOCATION IN *D. MOLLIS*

Tissue nutrient concentrations and amounts differed between above- and below-ground biomass and between soils and sites (Tables 4.4 - 4.7). Macro-nutrients (e.g. C and N) were more concentrated in the above-ground biomass and micro-nutrients (i.e. Cu, Mn, and Zn) were more concentrated in the below-ground biomass (Tables 4.4 & 4.5). Differences between above- and below-ground biomass allocation were least apparent in Pondoland soil (all sites) and in Drakensberg soil at high-altitude, particularly with regard to N (Tables 4.4 - 4.7). Nutrient content was a reflection of plant size, with either large or small biomass (Table 4.2) translating into high or low nutrient amounts respectively (Tables 4.6 & 4.7).

Plants grown in Drakensberg soil at high-altitude had lower N concentrations than plants from the same soil at the warmer sites, especially in the above-ground biomass (Tables 4.4 & 4.5). Plants grown in Drakensberg soil at the warmer sites, however, had small amounts of nutrients (Tables 4.6 & 4.7) owing to their small size (Table 4.2). Nutrient concentrations in the above- and below-ground biomass were generally lowest in Pondoland soil at all sites (Tables 4.4 & 4.5).

4.3.3 ORDINATION OF TREATMENT-EFFECTS

4.3.3.1 MORPHOLOGY DATA

The two dimensional NMDS ordination of 133 individuals, each scored for 11 morphological characters (excluding shoot:root ratios), resolved three data clusters and a stress value of 0.09 after 30 iterations (Fig. 4.11A). Correlation values for all characters exceeded 0.7. Vectors representing soil-temperature interactions were the most informative predictors of biomass differences between sites (Fig. 4.11B).

Table 4.4. Mean nutrient concentrations (± SD) in the above-ground biomass of *D. mollis* with respect to nine soil-site treatments. Protein concentrations were based on Kjeldahl N. A dash indicates insufficient material for analysis. A lack of SD indicates single sample numbers.

Site	No. of samples	Dumas N	Kjeldahl N	Protein	C	S	Ca	K	Mg	Na	P	Cu	Mn	Zn
		(% of dry mass)										(ppm)		
Drakensberg														
soil type														
Drakensberg	1	1.7	1.6	10	36.1	0.3	1.0	0.8	0.5	0.1	0.1	25	255	25
Pondoland	2	0.7±0.1	0.7±0.1	4±1	37±3	0.2±0.0	0.8±0.1	0.7±0.1	0.3±0.0	0.1±0.0	0.2±0.0	8±0	167±2	19±3
Midlands	2	1.6±0.3	1.4±0.1	9±1	41±1	0.4±0.1	1.9±0.2	1.2±0.2	0.4±0.1	0.2±0.0	0.3±0.0	15±3	136±4	17±0
Pondoland														
soil type														
Drakensberg	1	-	1.9	12	-	-	0.7	0.1	0.3	0.2	0.1	30	230	60
Pondoland	1	0.8	0.8	5	33	0.4	1.1	0.6	0.5	0.5	0.1	8	97	21
Midlands	3	1.1±0.1	1.0±0.1	6±0	40±1	0.6±0.0	2.0±0.3	0.5±0.2	0.5±0.0	0.4±0.1	0.3±0.1	16±2	140±18	17±0
Midlands														
soil type														
Drakensberg	1	3.0	2.6	16	47	0.4	1.1	1	0.4	0.2	0.1	18	219	35
Pondoland	7	0.7±0.1	0.6±0.0	4±0	41±5	0.2±0.0	0.5±0.1	0.9±0.1	0.2±0.0	0.3±0.1	0.1±0.0	7±2	98±11	36±9
Midlands	7	1.8±0.1	1.4±0.2	9±1	46±2	0.6±0.1	1.3±0.1	1.2±0.1	0.3±0.0	0.3±0.0	0.1±0.0	15±4	120±44	27±6

Table 4.5. Mean nutrient concentrations (± SD) in the below-ground biomass of *D. mollis* with respect to nine soil-site treatments. Protein concentrations were based on Kjeldahl N. A dash indicates insufficient material for analysis. A lack of SD indicates single sample numbers.

Site	**No. of samples**	**Dumas N**	**Kjeldahl N**	**Protein**	**C**	**S**	**Ca**	**K**	**Mg**	**Na**	**P**	**Cu**	**Mn**	**Zn**
		(% of dry mass)										**(ppm)**		
Drakensberg														
soil type														
Drakensberg	1	1.7	1.5	9	36	0.1	0.3	1	0.2	0.1	0.1	29	231	29
Pondoland	2	0.7±0.1	0.7±0.0	4±0	32±0	0.1±0.0	0.3±0.0	1.2±0.2	0.2±0.0	0.1±0.0	0.2±0.0	25±0	121±6	36±4
Midlands	1	0.8	0.8	5	24	0.1	0.5	0.9	0.3	0.2	0.1	54	434	33
Pondoland														
soil type														
Drakensberg	0	-	-	-	-	-	-	-	-	-	-	-	-	-
Pondoland	1	0.7	0.6	4	21	0.1	0.2	0.1	0.1	0.1	0.1	12	53	20
Midlands	1	0.7	0.8	5	22	0.1	0.6	0.4	0.3	0.2	0.1	104	405	25
Midlands														
soil type														
Drakensberg	1	1.8	1.6	10	30	0.1	0.3	0.9	0.3	0.1	0.1	28	215	45
Pondoland	3	0.7±0.1	0.6±0.1	4±1	21±4	0.1±0.0	0.2±0.0	0.5±0.2	0.2±0.0	0.2±0.0	0.1±0.0	15±3	96±27	33±7
Midlands	2	1.0±0.3	0.8±0.1	5±0	25±8	0.1±0.0	0.6±0.0	0.5±0.1	0.5±0.1	0.4±0.1	0.1±0.0	67±11	510±128	28±0

Table 4.6. Mean nutrient amounts (± SD) in the above-ground biomass of *D. mollis* with respect to nine soil-site treatments. Protein amounts were based on Kjeldahl N. A dash indicates insufficient material for analysis. A lack of SD indicates single sample numbers.

Site	No. of samples	Dumas N	Kjeldahl N	Protein	C	S	Ca	K	Mg	Na	P	Cu	Mn	Zn
		(mg g^{-1})										(µg g^{-1})		
Drakensberg														
soil type														
Drakensberg	1	7.2	6.7	42	151	1.1	4.4	3.4	2.0	0.5	0.3	11	107	11
Pondoland	2	4.0±0.1	3.9±0.6	24±4	224±19	1.0±0.1	5.1±0.3	4.3±0.7	1.9±0.1	0.5±0.2	1.3±0.1	5±0	102±1	12±2
Midlands	2	11.2±1.9	9.5±1.0	59±6	279±5	2.9±0.4	12.6±1.3	8.2±1.3	2.8±0.4	1.4±0.1	2.0±0.1	10±2	92±2	12±0
Pondoland														
soil type														
Drakensberg	1	-	2.2	14	-	-	0.8	0.1	0.4	0.3	0.1	4	28	7
Pondoland	1	3.1	2.8	18	127	1.5	4.1	2.3	1.8	2.0	0.4	3	38	8
Midlands	3	9.7±0.6	9.0±0.4	56±3	351±9	5.2±0.4	17.6±2.5	4.2±1.8	4.0±0.2	3.1±0.8	2.8±0.0	14±2	122±16	15±0
Midlands														
soil type														
Drakensberg	1	10.6	9.1	57	163	1.2	3.7	3.5	1.3	0.6	0.1	6	77	12
Pondoland	7	9.8±1.1	8.0±0.4	50±3	551±69	3.3±0.4	6.7±1.3	12.7±1.9	3.1±0.5	4.6±0.8	1.1±0.1	9±2	131±14	48±12
Midlands	7	26.7±2.3	21.9±2.6	137±16	694±32	9.4±0.8	19.7±1.2	17.9±2.1	5.1±0.3	4.1±0.6	1.0±0.1	23±6	182±67	41±9

Table 4.7. Mean nutrient amounts (± SD) in the below-ground biomass of *D. mollis* with respect to nine soil-site treatments. Protein amounts were based on Kjeldahl N. A dash indicates insufficient material for analysis. A lack of SD indicates single sample numbers.

Site	No. of samples	Dumas N	Kjeldahl N	Protein	C	S	Ca	K	Mg	Na	P	Cu	Mn	Zn
		(mg g^{-1})										(µg g^{-1})		
Drakensberg														
soil type														
Drakensberg	1	5.5	4.9	31	116	0.4	0.9	3.1	0.7	0.3	0.3	9	74	9
Pondoland	2	3.4±0.3	3.1±0.2	19±1	147±1	0.5±0.0	1.4±0.1	5.6±0.9	0.9±0.1	0.6±0.0	0.7±0.1	12±0	56±3	16±2
Midlands	1	2.5	2.5	16	80	0.3	1.5	2.9	1.0	0.7	0.3	18	143	11
Pondoland														
soil type														
Drakensberg	0	-	-	-	-	-	-	-	-	-	-	-	-	-
Pondoland	1	3.5	3.3	21	102	0.5	0.9	0.6	0.4	0.4	0.5	6	25	10
Midlands	1	2.7	2.8	18	82	0.4	2.1	1.4	1.1	0.7	0.5	38	150	9
Midlands														
soil type														
Drakensberg	1	1.8	1.5	9	30	0.1	0.3	0.9	0.3	0.1	0.1	3	22	5
Pondoland	3	6.7±0.7	5.9±0.7	37±5	207±41	1.0±0.1	1.8±0.4	4.8±1.6	1.6±0.3	2.2±0.4	0.5±0.2	15±3	95±27	33±7
Midlands	2	4.7±1.2	3.7±0.3	23±2	110±34	0.6±0.1	2.4±0.0	2.2±0.5	2.2±0.2	1.6±0.4	0.2±0.0	29±5	224±56	12±0

Fig. 4.11. A. Two dimensional NMDS ordination of 133 individuals scored for 11 quantitative characters. Values along axes are excluded because they are arbitrary points in ordination space. Individuals were grown in pots subject to nine soil-site treatments. Data were arranged such that the three soil types used in each experiment were grouped according to their respective sites, in the order: Drakensberg, Pondoland and Midlands sites. Symbols representing the nine soil-site treatments are provided. B. Vector fitting analysis of six meteorological variables and altitude. Vectors were derived from the correlation of environmental variables and altitude with the NMDS morphological ordination (A). Environmental variables with the longest arrow have the greatest influence on plant productivity. Variables are positively correlated if their arrows subtend a small angle, orthogonal if their arrows are at 90°, and negatively correlated if their arrows point in opposite directions.

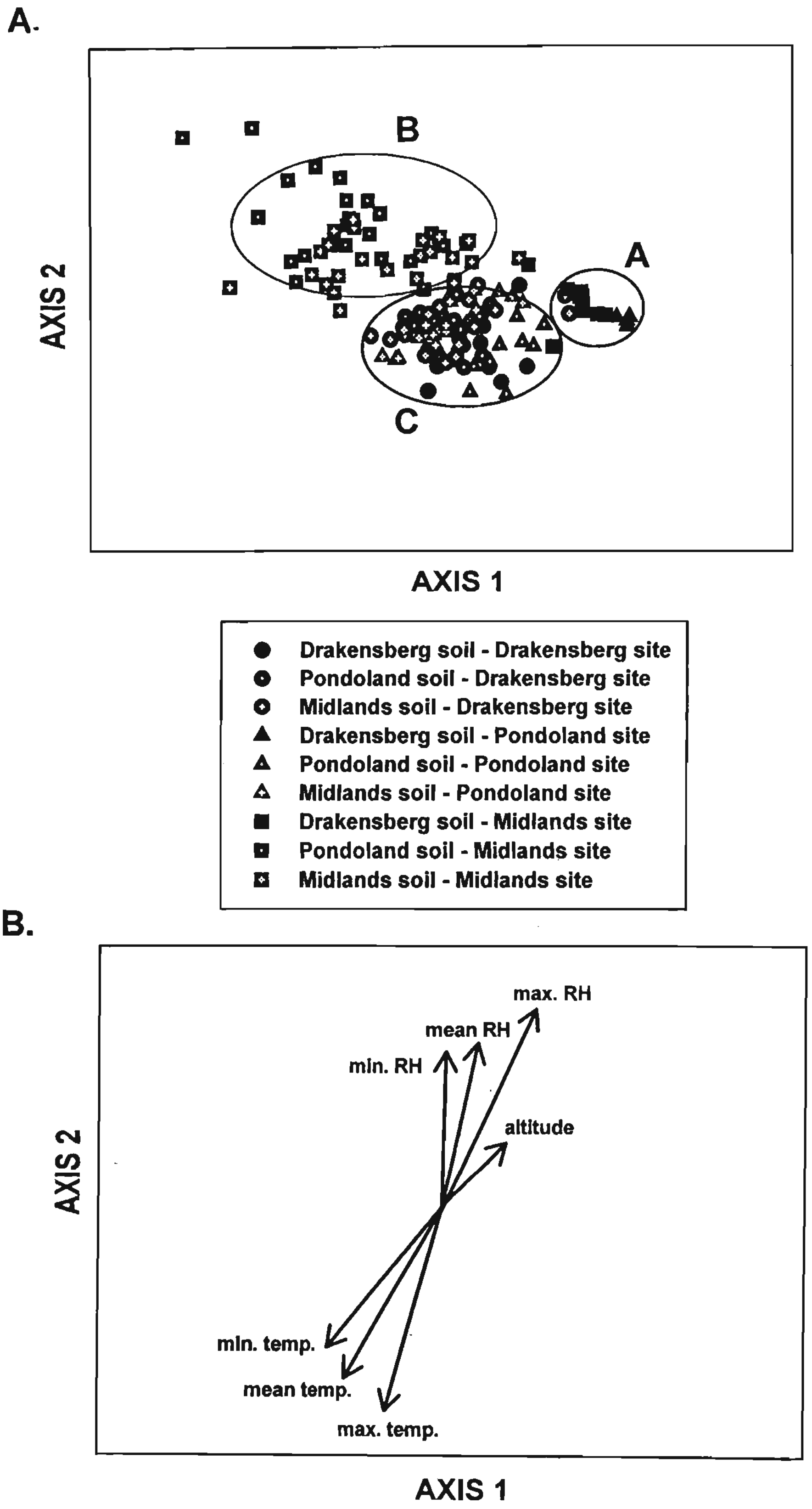
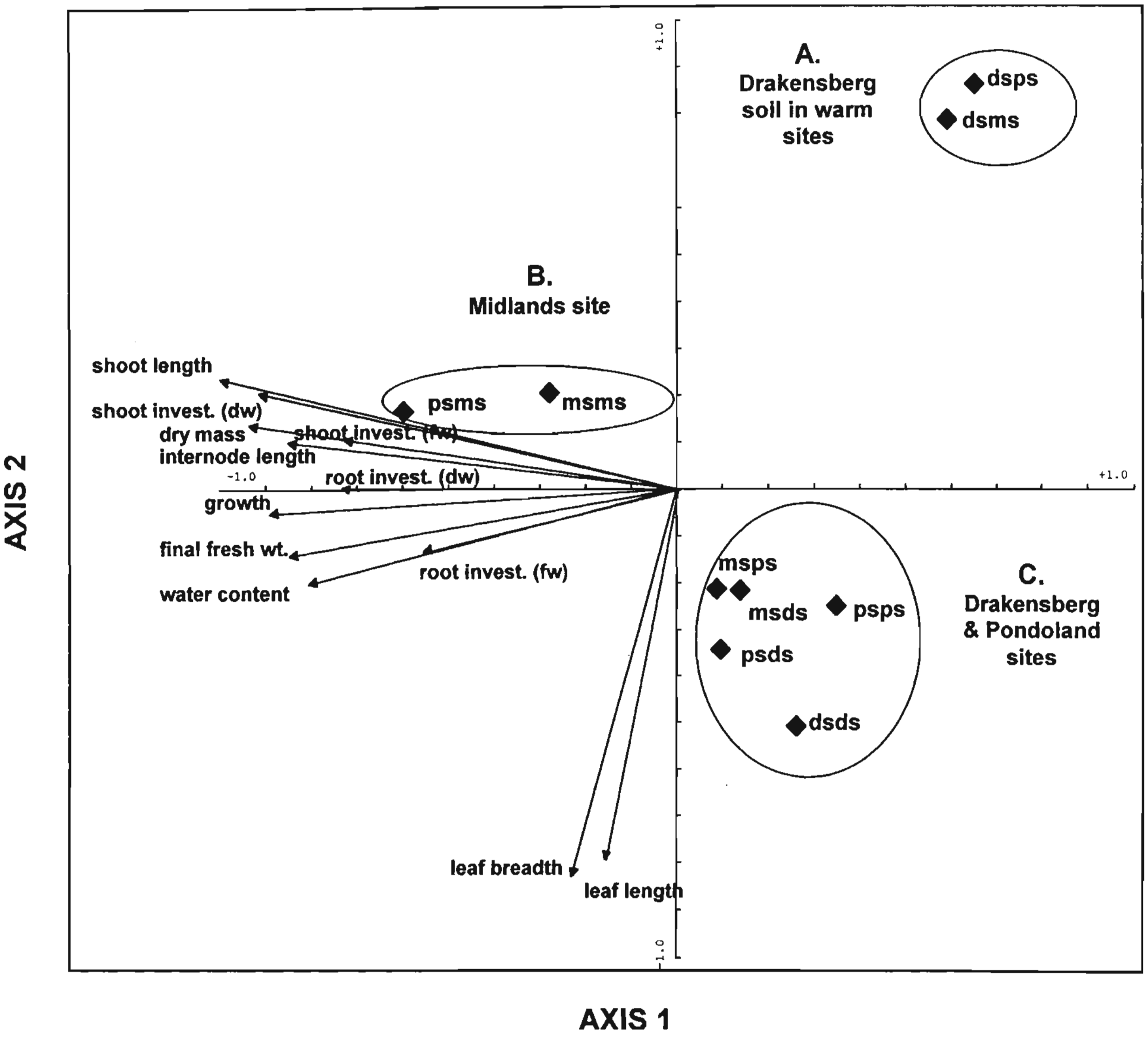

A.
B
A
C
AXIS 2
AXIS 1
● Drakensberg soil - Drakensberg site
● Pondoland soil - Drakensberg site
○ Midlands soil - Drakensberg site
▲ Drakensberg soil - Pondoland site
▲ Pondoland soil - Pondoland site
△ Midlands soil - Pondoland site
■ Drakensberg soil - Midlands site
■ Pondoland soil - Midlands site
□ Midlands soil - Midlands site
B.
max. RH
mean RH
min. RH
altitude
min. temp.
mean temp.
max. temp.
AXIS 2
AXIS 1

Fig. 4.12. Plots of the first two axes of a redundancy analysis (RDA) of morphology data relating to 11 quantitative characters scored for 133 individuals grown in a series of pot experiments subject to nine soil-site treatments. Eigenvalues: Axis 1 = 0.455; Axis 2 = 0.099; 88% of the cumulative variance. Key to treatments: A, the low performing plants grown in N-rich soil in warm sites (dsms, Drakensberg soil-Midlands site; dsps, Drakensberg soil-Pondoland site); B, the high performing plants grown in N-poor soil in the Midlands site (msms, Midlands soil-Midlands site; psms, Pondoland soil-Midlands site); and C, a larger grouping of below-par performing plants grown in all soil combinations in the Drakensberg site and those grown in N-poor soils in the Pondoland site (dsds, Drakensberg soil-Drakensberg site; msds, Midlands soil-Drakensberg site; psds, Pondoland soil-Drakensberg site; msps, Midlands soil-Pondoland site; psps, Pondoland soil-Pondoland site). Accompanying the treatments (◆) are a number of productivity-related vectors. Vectors with the longest arrow relative to an axis have the greatest influence on productivity on that axis. Vectors are positively correlated if their arrows subtend a small angle, orthogonal if their arrows are at 90°, and negatively correlated if their arrows point in opposite directions.


+1.0
A.
Drakensberg
soil in warm
sites
dsps
dsms
B.
Midlands site
shoot length
shoot invest. (dw)
dry mass
internode length
shoot invest. (fw)
psms
msms
-1.0
root invest. (dw)
+1.0
growth
final fresh wt.
water content
root invest. (fw)
msps
msds
psps
psds
dsds
C.
Drakensberg
& Pondoland
sites
leaf breadth
leaf length
-1.0
AXIS 2
AXIS 1

Axis 1 of the RDA (eigenvalue = 0.455) accounted for 72% of the variation in morphology that was due to treatment effects, represented by productivity-related measures such as total dry mass, above- and below-ground biomass (fresh and dry) and growth per se (Fig. 4.12). Axis 2 (eigenvalue = 0.099) accounted for a further 16% of this variation, represented by leaf length and breadth (Fig. 4.12). The cumulative variance was 88%. Morphology patterns relating to treatments were significant (Monte Carlo permutation test; $p < 0.01$). The three groupings of centroids (Fig. 4.12) were consistent with the NMDS ordination (Fig. 4.11A).

4.3.3.2 NUTRIENT DATA

The two dimensional NMDS ordination of 37 nutrient concentration profiles relating to the above- ($n = 25$) and below-ground ($n = 12$) biomass of individuals from various soil-site combinations resolved a number of data clusters grouped according to both soil and site factors (Fig. 4.13). The strong dichotomy between above- and below-ground allocation patterns was least apparent in Pondoland soil and in Drakensberg soil in the Drakensberg site (Fig. 4.13). The ordination generated a stress value of 0.17 after 25 iterations. Correlation values for six of the 13 nutrient characters were high (> 0.8), with N (Dumas N, Kjeldahl N and protein) accounting for most of the variation that resulted from treatment effects (correlation values > 0.9).

Axis 1 of the RDA relating to nutrient concentrations (eigenvalue = 0.669) accounted for 71.5% of the variation in nutrient allocation that was due to treatment effects (Fig. 4.14). Axis 2 (eigenvalue = 0.104) accounted for a further 11% of this variation (Fig. 4.14). The cumulative variance was c. 83%. Nutrient concentration patterns relating to treatments were significant (Monte Carlo permutation test; $p < 0.01$). Above-ground concentrations were generally higher than those below-ground,

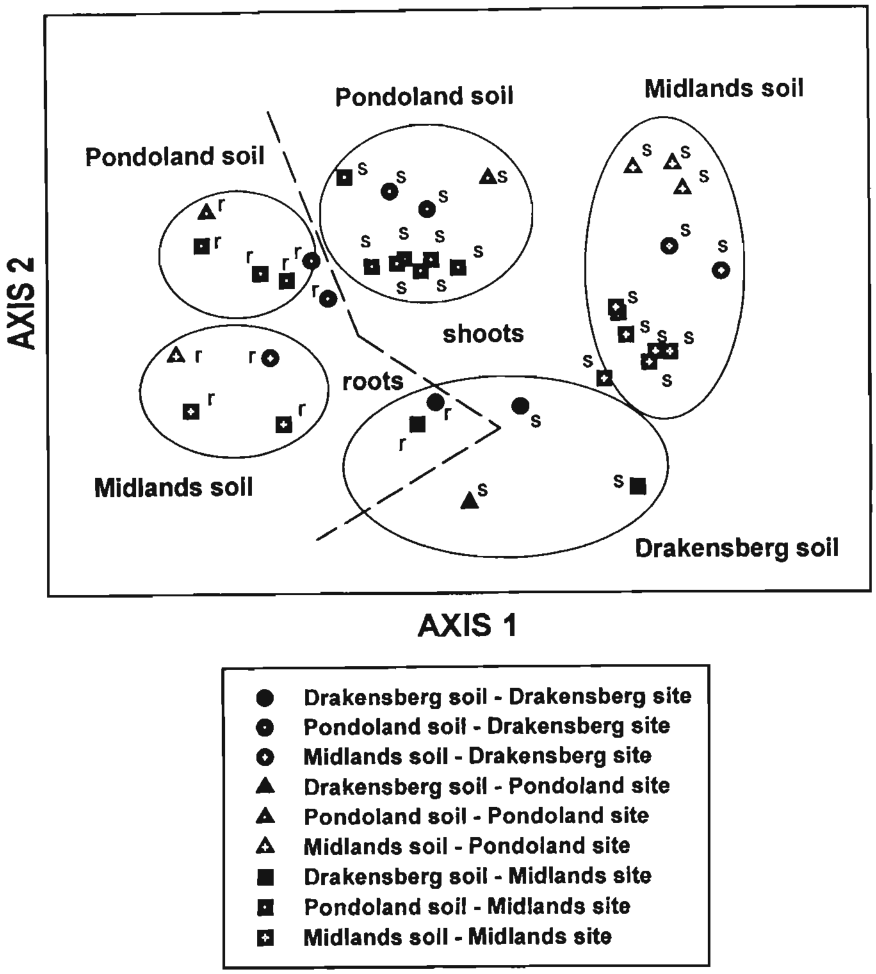


Fig. 4.13. Two dimensional NMDS ordination of 37 nutrient concentration profiles relating to the above- ('s') and below-ground ('r') biomass of individuals grown in a series of reciprocal pot experiments subject to nine soil-site treatments. Nutrient profiles were scored as concentrations from 13 plant nutrient-related characters. Values along axes are excluded because they are arbitrary points in ordination space. Data were arranged such that the three soil types used in each experiment were grouped according to their respective sites, in the order: Drakensberg, Pondoland and Midlands sites. Symbols representing the nine soil-site treatments are provided.

Fig. 4.14. Plots of the first two axes of a redundancy analysis (RDA) of 37 nutrient concentration profiles relating to the above- and below-ground biomass of individuals grown in a series of reciprocal pot experiments subject to nine soil-site treatments. Eigenvalues: Axis 1 = 0.669; Axis 2 = 0.104; 83% of the cumulative variance. Key to treatments: dsds, Drakensberg soil-Drakensberg site; psds, Pondoland soil-Drakensberg site; msds, Midlands soil-Drakensberg site; psps, Pondoland soil-Pondoland site; msps, Midlands soil-Pondoland site; dsms, Drakensberg soil-Midlands site; psms, Pondoland soil-Midlands site; msms, Midlands soil-Midlands site. Omitted: dsps, Drakensberg soil-Pondoland site (insufficient material). 'N' refers to both Dumas and Kjeldahl-derived N. Accompanying the plots are a number of nutrient-related vectors. Vectors with the longest arrow relative to an axis have the greatest influence on that axis. Vectors are positively correlated if their arrows subtend a small angle, orthogonal if their arrows are at 90°, and negatively correlated if their arrows point in opposite directions.

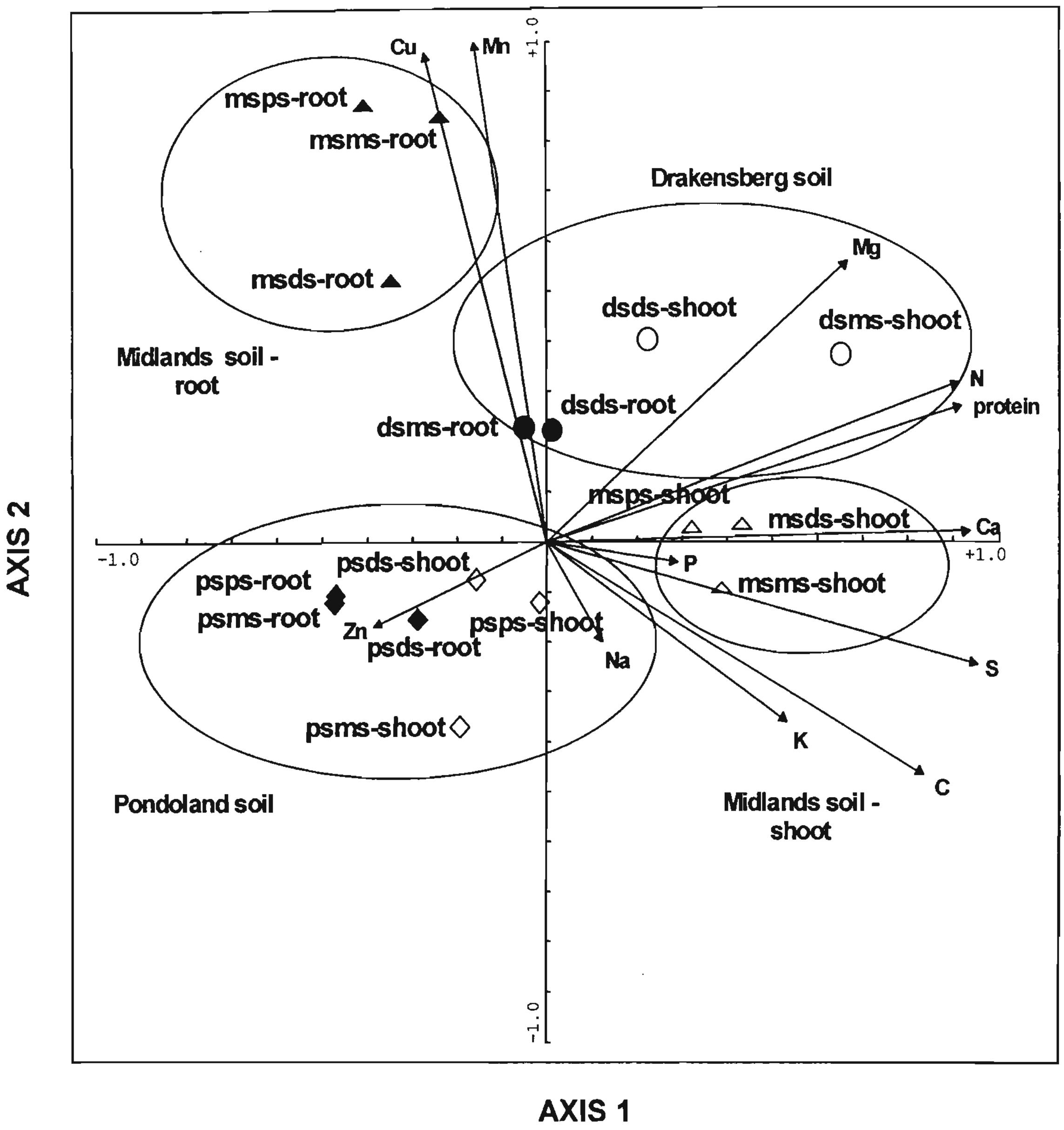
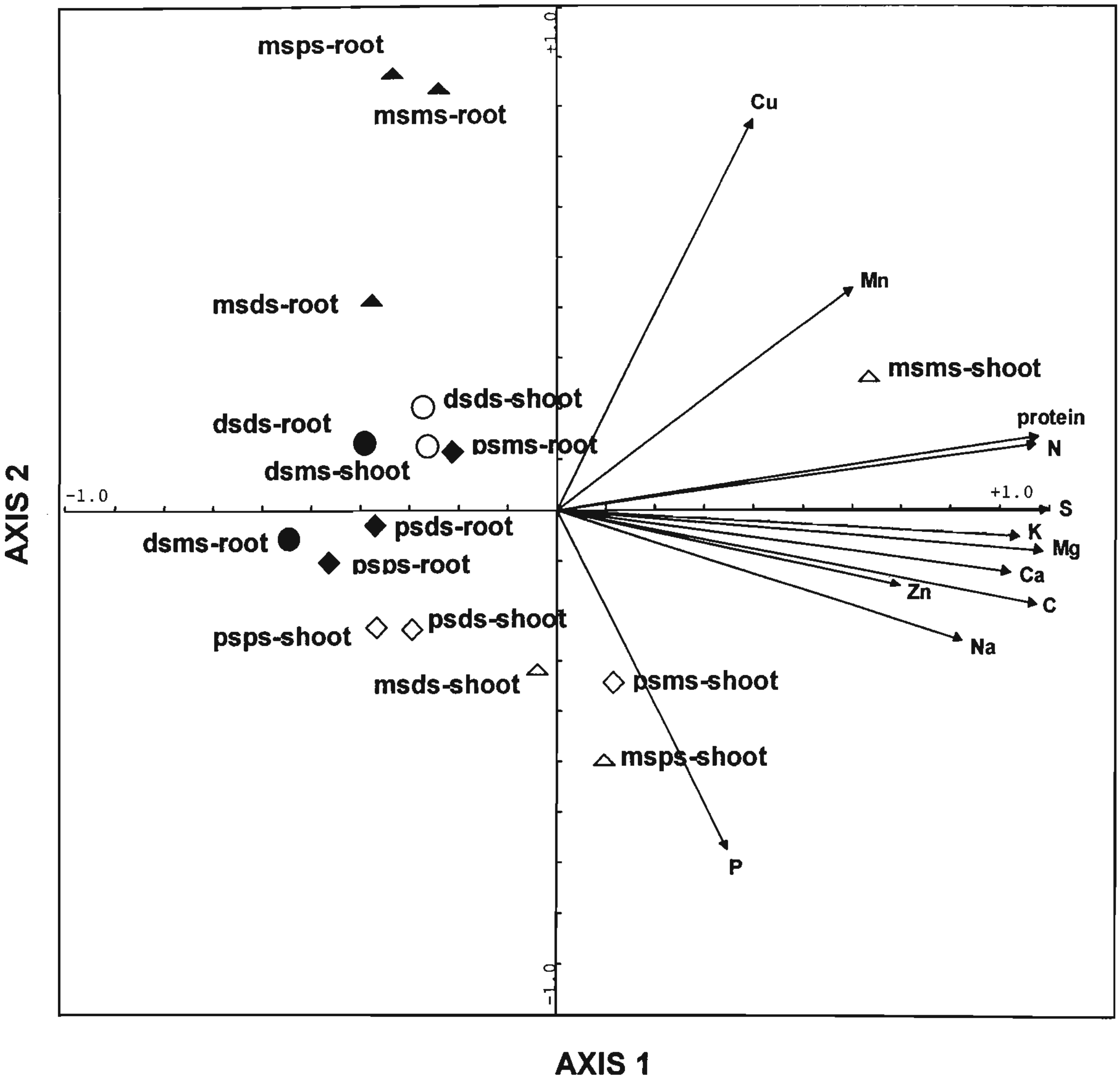

Cu
Mn
+1.0
msps-root
msms-root
Drakensberg soil
Mg
msds-root
dsds-shoot
dsms-shoot
Midlands soil - root
N
protein
dsds-root
dsms-root
msps-shoot
msds-shoot
Ca
-1.0
+1.0
psds-shoot
P
psps-root
msms-shoot
psms-root
Zn
psps-shoot
psds-root
Na
S
psms-shoot
K
C
Pondoland soil
Midlands soil - shoot
-1.0
AXIS 2
AXIS 1

Fig. 4.15. Plots of the first two axes of a redundancy analysis (RDA) of 37 nutrient content profiles relating to the above- and below-ground biomass of individuals grown in a series of reciprocal pot experiments subject to nine soil-site treatments. Eigenvalues: Axis 1 = 0.376; Axis 2 = 0.187; 61% of the cumulative variance. Key to treatments: dsds, Drakensberg soil-Drakensberg site; psds, Pondoland soil-Drakensberg site; msds, Midlands soil-Drakensberg site; psps, Pondoland soil-Pondoland site; msps, Midlands soil-Pondoland site; dsms, Drakensberg soil-Midlands site; psms, Pondoland soil-Midlands site; msms, Midlands soil-Midlands site. Omitted: dsps, Drakensberg soil-Pondoland site (insufficient material). 'N' refers to both Dumas and Kjeldahl-derived N. Accompanying the plots are a number of nutrient-related vectors. Vectors with the longest arrow relative to an axis have the greatest influence on that axis. Vectors are positively correlated if their arrows subtend a small angle, orthogonal if their arrows are at 90°, and negatively correlated if their arrows point in opposite directions.


msps-root
msms-root
msds-root
dsds-root
dsds-shoot
dsms-shoot
psms-root
dsms-root
psds-root
psps-root
psps-shoot
psds-shoot
msds-shoot
psms-shoot
msps-shoot
msms-shoot
Cu
Mn
protein
N
S
K
Mg
Ca
Zn
C
Na
P
-1.0
+1.0
+1.0
-1.0
AXIS 1
AXIS 2

which accounted for their separate groupings. These differences were least evident, however, in Pondoland soil, because the nutrient concentrations of plants grown in Pondoland soil (all sites), with the exception of Zn, were below-average (Fig. 4.14). Drakensberg soil resulted in high above-ground concentrations of Ca, Mg and N, particularly in the warm Midlands site (Fig. 4.14). High below-ground biomass concentrations of Cu and Mn, and high above-ground concentrations of C and S, were noted for plants grown in Midlands soil at all sites (Fig. 4.14).

Axis 1 of the RDA relating to nutrient contents (eigenvalue = 0.376) accounted for 40.6% of the variation in nutrient allocation that was due to treatment effects (Fig. 4.15). Axis 2 (eigenvalue = 0.187) accounted for a further 20.2% of this variation (Fig. 4.15). The cumulative variance was c. 61%. Nutrient content patterns relating to treatments were significant (Monte Carlo permutation test; $p < 0.01$). Groupings were not as resolved as those for the RDA relating to nutrient concentrations. Above-ground nutrient profiles reflected both the size of the plant and the nutrient status of the soil (with the exception of N in Midlands soil). Nutrient contents, particularly above-ground N levels, were highest in individuals grown in Midlands soil in the Midlands site (Fig. 4.15), correlating to plants larger than average (Fig. 4.12). Nutrient contents for plants grown in the Drakensberg and Pondoland sites were lowest (Fig. 4.15), correlating to plants smaller than average (Fig. 4.12).

4.3.3.3 SOIL DATA

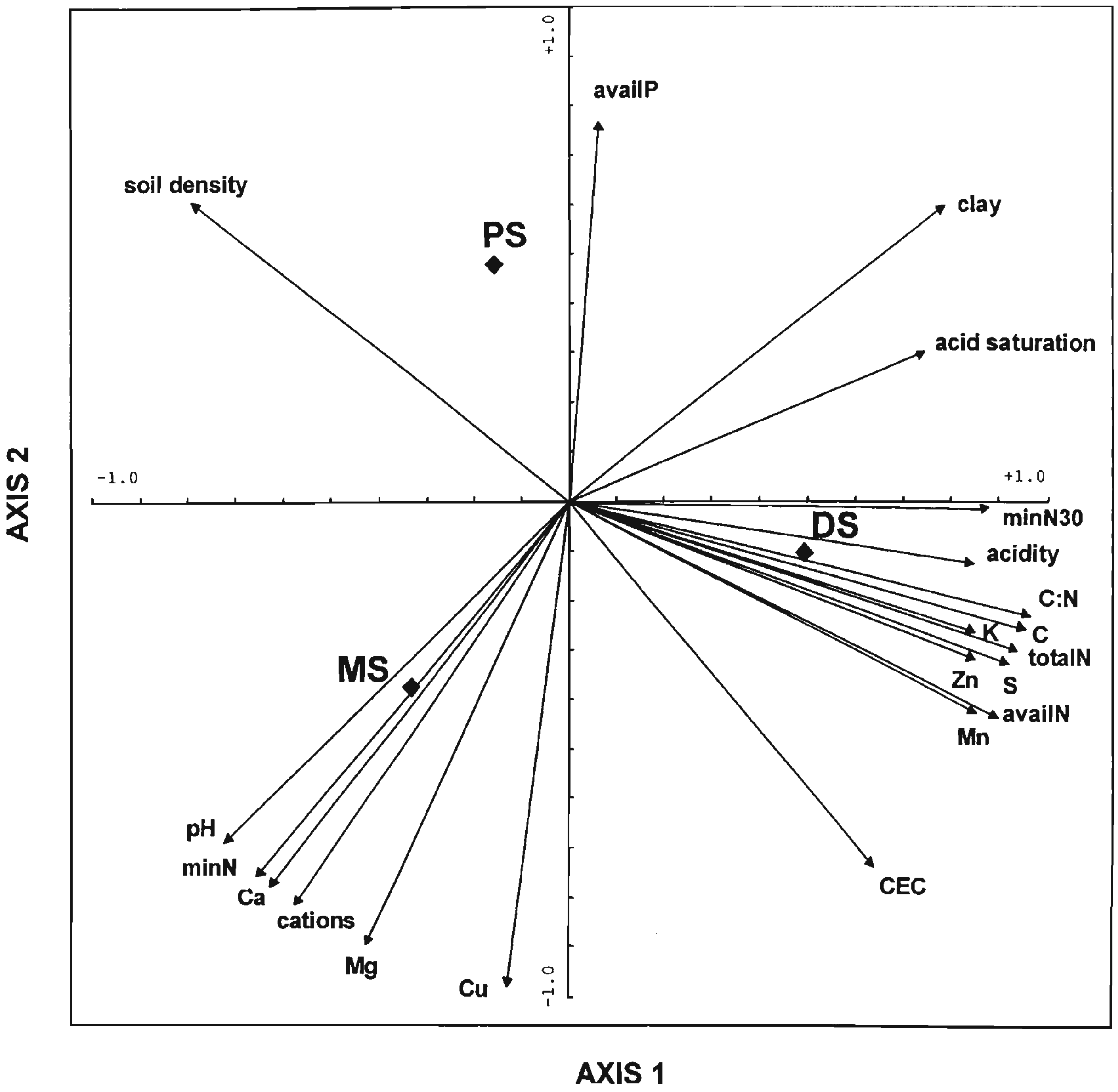
The three soils used in the pot experiments differed physically and chemically (Fig. 4.16). The result of the Monte Carlo permutation test showed that 'treatments' (i.e. the three soils) were responsible for the differences in soil nutrients ($p < 0.01$). Axis 1 of the RDA (eigenvalue = 0.568) accounted for 62.2% of the variation between soils, and axis 2 (eigenvalue = 0.345) accounted for a further 37.8% of this variation (Fig. 4.16). The cumulative variance was 100%. Drakensberg soil was distinguished by its higher exchangeable acidity, Al (indexed by acid saturation), C, N, C:N ratio, K, Mn, S, and Zn (Fig. 4.16). It also had the highest clay fraction and was the least dense (Table 4.8). Midlands soil was distinguished by its higher pH, cations, Ca, Cu, Mg and mineralisable N (Fig. 4.16; Tables 4.9 & 4.10). Pondoland soil was distinguished by its dense, sandy composition (Fig. 4.16), having the lowest clay fraction (Table 4.8) and, with the exception of P, was the most nutrient-poor soil (Tables 4.9 & 4.10). Drakensberg and Pondoland soils were very acidic, while the pH of Midlands soil approached neutrality (Table 4.9). Results of the one-way ANOVA and LSD test of the chemical and physical properties of all soils used in the reciprocal pot experiments are provided (Table 4.11).

Soils of the Cape Region are acidic and generally nutrient-poor, particularly the colluvial sands (Tables 4.9 & 4.10). C:N ratios are higher than those of the experimental soils of the summer rainfall region (Table 4.10).

4.3.4 NITROGEN MINERALISATION

N mineralisation is the microbially-mediated breakdown and conversion of organic matter to inorganic N (Wedin & Tilman, 1990) and, with the exception of communities dominated by legumes, is the most significant process by which N is made available to plants (Lee & Stewart, 1978). Drakensberg and Pondoland soils had very different levels of total N, yet mineralized similar amounts of N at their native spring temperatures (Table 4.10). Mineralisation in the disturbed Midlands soil was zero, yet high when pristine soils were tested (Table 4.10). Mineralisation levels at 30°C were greater than when tested at the lower spring temperatures (Table 4.10). Although this

Fig. 4.16. Plots of the first two axes of a redundancy analysis (RDA) of the three soils used in the *D. mollis* reciprocal pot experiments: DS, Drakensberg soil; PS, Pondoland soil; MS, Midlands soil. Each soil plot (◆) represents the mean of five samples. Eigenvalues: Axis 1 = 0.568; Axis 2 = 0.345; 100% of the cumulative variance. Accompanying the plots are 21 soil variables represented as vectors. Abbreviations (clockwise): availP, available P; minN30, mineralizable N at 30°C; acidity, exchangeable acidity; availN, available N; CEC, cation exchange capacity; minN, mineralizable N at mean spring temperature. Soil vectors with the longest arrow relative to an axis have the greatest influence on that axis. Soil vectors are positively correlated if their arrows subtend a small angle, orthogonal if their arrows are at 90°, and negatively correlated if their arrows point in opposite directions.



AXIS 2
AXIS 1
+1.0
-1.0
-1.0
+1.0
availP
soil density
PS
clay
acid saturation
minN30
DS
acidity
C:N
K
C
totalN
Zn
S
availN
Mn
MS
CEC
pH
minN
Ca
cations
Mg
Cu

Table 4.8. The physical soil properties of the soils used in the reciprocal pot experiments of *D. mollis* at three sites (mean ± SD). Analyses were based on five samples per soil type.

Site	Geology	Diagnostic topsoil (A horizon)	Soil colour	Soil density (g ml^{-1})	Clay (%)	Texture class	Intrinsic soil fertility
Drakensberg Alpine Centre	- upper limit (2200 m - >3300 m); basalt & dolerite of Drakensberg Group (Karoo Supergroup)	melanic (with humic tendencies in wetter parts)[a]	**dry**: 3/4 dark yellowish brown **wet**: 3/3 dark reddish brown (Lesotho soil: 2/2 very dark brown - dry & wet)	0.8±0.1	65±4	clay	highly fertile
	- lower limit (1500 m - 2200 m); Clarens Formation sandstone (Karoo Supergroup)	n/a	n/a	n/a	n/a	n/a	infertile
Pondoland Centre	quartzitic sandstones of Msikaba Formation	orthic A	**dry**: 3/1 dark reddish gray **wet**: 3/1 dark reddish gray	1.4±0.0	9±1	sand	infertile
KwaZulu-Natal Midlands	shales and sandstones (dolerite-amended) of Ecca Series	orthic A	**dry**: 3/4 dark brown **wet**: 3/3 dark reddish brown	1.2±0.0	40±5	clay-loam	fertile

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[a] The alpine soils of the DAC do not conform well to the current soil classification system because of their unique properties and the climatic conditions in which they occur. Theoretically they are 'humic', yet in reality they appear more 'melanic' because of their high base cations. A new classification system is pending (C. Bester, 2003, pers. comm.).

Table 4.9. The mineral soil properties relating to the soils used in the reciprocal pot experiments of *D. mollis* at three sites (mean ± SD). Analyses were based on five samples per soil type. Comparative values for two transects in colluvial sands and two transects in sandstone soils of the Soetanysberg, Cape Agulhas (Cape Floristic Region), are included (mean ± SE) (after Richards *et al.*, 1997). A dash means 'not determined'.

Site	pH (KCl)	Exchangeable acidity	Total cations	Acid saturation (%)	CEC (m.e. per 100g dry soil)	P	K	Ca	Mg	Zn	Mn	Cu
		(µmol l^{-1})				*Available		(mg l^{-1})				
Drakensberg												
soil collection locality												
Cathedral Peak	4.3±0.1	1.6±0.8	9±1	19.0±9.9	63±1	3±2	214±66	701±155	361±104	1.0±0.4	72±17	5.3±0.6
Pondoland												
soil collection locality												
Oribi Flats	4.4±0.1	0.2±0.1	2±0	10.6±4.8	39±3	6±2	62±12	200±42	59±12	0.1±0.1	5±2	0.3±0.1
Midlands												
soil collection locality												
Scottsville	6.1±0.1	0.1±0.0	57±4	0.2±0.4	53±4	1±1	78±3	9409±252	1114±45	0.2±0.1	23±4	9.1±0.8
Soetanysberg						***Total**						
Colluvial 1	4.8±0.1	-	-	-	-	62±0	38±0	284±45	80±0	-	-	-
Colluvial 2	4.7±0.0	-	-	-	-	62±0	37±3	195±12	62±5	-	-	-
Sandstone 1	5.2±0.1	-	-	-	-	69±1	93±6	1104±105	307±12	-	-	-
Sandstone 2	5.0±0.1	-	-	-	-	69±0	58±9	688±46	166±5	-	-	-

Table 4.10. The mineral soil properties (carbon, nitrogen and sulfur) relating to the soils used in the reciprocal pot experiments of *D. mollis* at three sites (mean ± SD). Analyses were based on five samples per soil type. Mineralisable N was determined for the mean spring temperatures ('spring') experienced by the soils in their native sites (Drakensberg soil, 12°C; Pondoland and Midlands soil, 19°C) and for all soils at 30°C. Mineralisation values were derived from means as it was not possible to pair incubated and non-incubated samples (and therefore no SD). Comparative values for two transects in colluvial sands and two transects in sandstone soils of the Soetanysberg, Cape Agulhas (Cape Floristic Region) are included (mean ± SE) (after Richards *et al.*, 1997). A dash means 'not determined'.

Soil	Total N (g kg^{-1})	Mineralisable N (mg kg^{-1}) Spring	Mineralisable N (mg kg^{-1}) 30°C	Total C (g kg^{-1})	C:N ratio	Total S (mg kg^{-1})
Drakensberg						
soil collection locality						
Cathedral Peak	4.0±0.4	6.7	31.4	53±6	13.3±0.3	5.0±1.0
Pondoland						
soil collection locality						
Oribi Flats	0.7±0.0	6.3	8.6	6±1	8.6±0.4	0.9±0.1
Midlands						
soil collection locality						
Scottsville (disturbed)	1.4±0.0	0.0	1.9	11±1	7.9±0.1	1.0±0.0
Hayfields (undisturbed)	-	32.8	43.4	-	-	-
Q.E. Park (undisturbed)	-	41.5	83.9	-	-	-
Soetanysberg						
Colluvial sand 1	0.4±0.0	-		21±2	52.5	-
Colluvial sand 2	0.3±0.0	-		17±1	56.7	-
Sandstone 1	2.1±0.2	-		64±4	30.5	-
Sandstone 2	1.3±0.1	-		50±3	38.5	-

Table 4.11. One-way ANOVA and LSD test of the chemical and physical properties of soils used in the reciprocal pot experiments of *D. mollis* at three sites. Analyses were based on five samples per soil type. Soil abbreviations: D, Drakensberg; P, Pondoland; M, Midlands. The number of soil variables tested (19) do not match the total number (21) because the mineralisation values (spring temperature and 30°C) were derived from means. Soils with the same lettering per character are not significantly different at 5% probability ($p > 0.05$).

Soil character	**F-ratio**	**Probability (p)**	**Significant difference of soils**		
			D	**P**	**M**
Soil density	486	$p < 0.01$	a	b	c
Clay	241	$p < 0.01$	a	b	c
Organic carbon	278	$p < 0.01$	a	b	b
Total nitrogen	197	$p < 0.01$	a	b	c
Available nitrogen	1326	$p < 0.01$	a	b	c
C:N ratio	460	$p < 0.01$	a	b	c
Sulfur	118	$p < 0.01$	a	b	b
pH	698	$p < 0.01$	a	b	c
Exchangeable acidity	17	$p < 0.01$	a	b	b
Total cations	938	$p < 0.01$	a	b	c
Acid saturation	11	$p < 0.01$	a	a	b
Cation exchange capacity	109	$p < 0.01$	a	b	c
Available phosphorus	9	$p < 0.01$	a	b	a
Potassium	23	$p < 0.01$	a	b	b
Calcium	4500	$p < 0.01$	a	b	c
Magnesium	340	$p < 0.01$	a	b	c
Zinc	28	$p < 0.01$	a	b	b
Manganese	62	$p < 0.01$	a	b	c
Copper	296	$p < 0.01$	a	b	c

increase in Drakensberg soil was a five-fold one, and that in Midlands soil was up to double, the amount of N mineralized in Drakensberg soil at 30°C was much lower than that mineralized in the pristine Midlands soils (Table 4.10).

Available N was more present as NH_4^+ than NO_3^- for all soils. This ratio, however, varied with temperature and so the ranges quoted below have taken the differences between the 'spring' and 30°C incubation experiments into account: Drakensberg soil: 4:1 - 33:1; Pondoland soil: 13:1 - 17:1; Midlands soil - pristine: 100:1 - 160:1; Midlands soil - disturbed: 5:1 - 8:1.

4.4 DISCUSSION

4.4.1 SOIL-SITE INTERACTIONS

Both 'soil' (soil N in particular) and 'site' (temperature in particular) factors determined productivity because differences in plant traits were quantified within and between sites (Table 4.2). Productivity of *D. mollis* in Drakensberg soil was highest in the Drakensberg site, with a larger below-ground biomass, in particular, characteristic of cold climates (Clarkson *et al.*, 1988; Körner & Larcher, 1988). Productivity in Drakensberg soil was lower in the warmer, low-altitude sites because the temperate herb was unable to tolerate high N levels (see Table 4.10), which probably resulted in the stunted plants with small leaves. The few remaining survivors had abnormally high shoot N concentrations (Table 4.4) which were significantly lower in the cooler Drakensberg site (Table 4.4). Shoot N concentrations increased as more soil N was made available for uptake, due to increased rates of mineralisation and diffusion associated with warmer temperatures. This effect lead to shoot N concentrations being toxic to plants grown in N-rich soil at the warmer sites.

Plants of the cooler Drakensberg site were characterised by similar productivity, tissue nutrient concentrations and amounts across all soils (Tables 4.4 - 4.7). The Midlands site was the most productive (with the exception of low biomass in Drakensberg soil). Its high temperatures also translated into the most diverse tissue nutrient concentrations and amounts across all soils (Tables 4.4 - 4.7) because warm sites enhance nutrient release (Van Cleve *et al.*, 1983). Plants grown in Midlands soil were robust with dark green leaves, and mortalities were low (Table 4.2). Plants grown in Pondoland soil were chlorotic, a general indication of nutrient deficiency (Lamont, 1983) and acidic soils (Newton *et al.*, 1991).

Comparatively lower productivity at the Drakensberg and Pondoland sites than the Midlands site was the unavoidable result of abnormally high rainfall and decreased sunlight hours at these sites during the experiments (cf. Shreve, 1924). The weather station closest to the Pondoland region (Mzimkhulu; 30°41′S, 30°26′E) recorded a 44% decrease in the number of daily sunlight hours during this period compared to its mean (J. Chetty, 2002, pers. comm.). Pondoland's climate is also buffered by the Indian Ocean (Table 4.1; Fig. 4.5). Unfortunately no weather station was able to verify the decrease in sunlight hours for the duration of the Drakensberg pot experiment.

Below-ground biomass and shoot:root ratios were suitable indicators of soil fertility. Irrespective of site, plants grown in the nutrient-poor Pondoland soil were characterised by small shoot:root ratios (Fig. 4.7) because shoot:root ratios of nutrient-poor soils are genetically fixed and seldom respond to changes in the environment (Bloom *et al.*, 1985). Increased below-ground allocation increases nutrient uptake by increasing the volume of soil available for the absorption of diffusion-limited elements (Lamont, 1983; Aerts & Chapin, 2000; Orcutt & Nilsen, 2000) and in particular increases a plant's ability to compete for soil N (Chapin, 1980;

Robinson & Rorison, 1987; Tilman, 1990a; Gleeson & Tilman, 1990; Tilman & Wedin, 1991a). Small shoot:root ratios have also been reported from the heathland vegetation growing on nutrient-poor soils of Australia (Groves, 1983) and California and Chile (Shaver, 1983). Larger shoot:root ratios in the Midlands site (Fig. 4.7) were associated with higher temperatures (e.g. Clausen *et al.*, 1940; Farrar, 1988) that influenced the nutrient economy of the soil.

Plants grown in Pondoland soil at all sites had low tissue nutrient concentrations and contents (Tables 4.4 - 4.7), being a direct reflection of the soil's nutrient-poor status (Tables 4.9 & 4.10). Low nutrient concentrations and contents, particularly N and P, are also a feature of fynbos litter (Van Wilgen & Le Maitre, 1981; Stock & Allsopp, 1992) and live biomass (Lewis & Stock, 1978; Van Wilgen & Le Maitre, 1981; Stock *et al.*, 1992) from a range of sites, especially those with acidic, highly leached soils derived from Table Mountain sandstone (Van Wilgen & Le Maitre, 1981). The above-mentioned results also compare favourably with the nutrient composition of heathland vegetation in Australia (Groves, 1983) and California and Chile (Shaver, 1983).

4.4.2 ORDINATION OF TREATMENT-EFFECTS

4.4.2.1 MORPHOLOGY DATA

The low stress (0.09) generated by the NMDS morphology ordination was the result of highly resolved groupings, suggesting a comprehensive sorting of treatment effects (soil-site interactions). Correlation values for all morphological characters were high (> 0.7), indicating their significant contributions to the variation in morphology. Both the unconstrained NMDS ordination and the RDA ordination constrained by treatments were consistent - the same combinations of soil-site interactions were evident in both analyses (Fig. 4.11 & 4.12), indicating that the main factors affecting variation in morphology were accounted for. Results of the two-way ANOVA confirmed that all treatments (soil-site interactions) exerted a statistically significant effect on plant morphology (Table 4.3). Variation in morphology resulting from productivity-related characters was almost five times greater than the contribution from leaf parameters (Fig. 4.12). Leaves are determinate organs and their characteristics are less influenced by growth, hence the poor contribution to morphological variation in axis 1 (Fig. 4.12). Vector fitting of meteorological data onto the growth ordination confirmed that temperature was the most significant contributor from a climatic point of view (Fig. 4.11B), probably due to its effects on the nutritional economy of the rhizosphere.

Highly significant is the occurrence of group ‘C’ (Fig. 4.11 & 4.12). Plant productivity in the Drakensberg and Pondoland sites was most similar (Fig. 4.11 & 4.12). This result suggests that localised interactions of the climatic environment (‘site’) and soil type in the DAC and PC have independently generated a similar growth response in *D. mollis*, which are probably responsible for high numbers of Cape elements in both regions.

4.4.2.2 NUTRIENT DATA

The allocation of nutrients either to above- or below-ground biomass is the response to providing the most strongly limiting resources (Bloom *et al.*, 1985). Groupings generated by the NMDS ordination with respect to nutrient allocation for above- and below-ground biomass (Fig. 4.13) were the results of treatment effects, as the RDA nutrient ordinations confirmed that both ‘soil’ and ‘site’ were significant contributors to these patterns ($p < 0.01$) (Fig. 4.14 & 4.15). The differences in allocation between above- and below-ground biomass were least apparent in Pondoland soil and in Drakensberg soil in the Drakensberg site (Fig. 4.13 & 4.14) because they were both nutrient-poor scenarios resulting in higher nutrient allocation to below-ground biomass, which correlated with higher below-ground biomass (Table 4.2). The significant role of N in accounting for most of the variation in nutrient allocation was supported by the high correlation values generated in the 'PCC' analysis of the NMDS ordination (correlation values > 0.9).

4.4.3 SOILS

4.4.3.1 CLAY AND ORGANIC MATTER-RELATED CONSTRAINTS

Drakensberg soil had the highest clay (Table 4.8) and total C content (Table 4.10). C levels are also generally high in the Agulhas soils (Table 4.10) because fynbos is a carbon-rich ecosystem (Stock *et al.*, 1992). Since C accounts for up to c. 60% of soil organic matter (SOM) (Sparks, 1995), it may be deduced that Drakensberg soils are high in SOM. This accumulation of SOM is evidence for its non-labile pool of nutrients (cf. Read & Mitchell, 1983) and represents a self-perpetuating system which maintains low soil nutrient levels (Vitousek, 1982). The main factors contributing to high C and SOM in the DAC are its cool climate that retards microbial activity (Ellery *et al.*, 1995) and the predominance of grasslands. The DAC forms part of the Grassland Biome (Rutherford & Westfall, 1994; Low & Rebelo, 1996) and grassland soils are high in SOM (Sparks, 1995) - a function of high biomass coupled with quick growth rates and short life spans, particularly in systems with a strong dormancy cycle.

Clay and SOM are important sorbents (sequestrators) of plant macro- and micronutrients and heavy metal cations (Hausenbuiller, 1985; Sparks, 1995; Tate, 2001), which resulted in higher CEC's (e.g. Drakensberg soil; Table 4.9), compared to sandy soils low in clay and SOM (e.g. Pondoland soil; Table 4.9). Soils with a high CEC resulted in low P availability and vice versa (Table 4.9).

Total N was highest in Drakensberg soil and lowest in Pondoland soil and the colluvial sands of the Agulhas region (Table 4.10). Drakensberg soil had the highest C:N ratio (Table 4.10), which is slightly higher than the average of 10 - 12 (Sparks, 1995), and approaches values recorded for the *Calluna*-dominated heathlands of Europe (Duchaufour, 1950, cited in Groves, 1981a) and the heathlands of Australia (Specht *et al.*, 1958), indicating retarded nitrification processes (i.e. slow turnover of SOM) and limiting N. However, all C:N ratios related to the soil fractions as a whole, and not the microbial biomass or light fractions of the soil, the latter probably being more informative (e.g. Bardgett *et al.*, 2002; Fynn *et al.*, 2003).

4.4.3.2 PH AND PH-RELATED CONSTRAINTS

Soil pH exerts a significant influence on chemical reactions and processes, particularly the availability of plant nutrients and the occurrence of soil microorganisms (Lucas & Davis, 1961; Sparks, 1995; Binkley & Vitousek, 1989). Most mineral nutrients are optimally available within the pH range of 5.6 - 7.0, provided other environmental conditions remain favourable (Wilkinson, 1994).

Drakensberg and Pondoland soils are 'extremely acidic' (mean pH < 4.5) according to the pH scale of Sparks (1995) (Table 4.9). Acid soils result from leaching that occurs when precipitation exceeds evapotranspiration (Clark & Baligar, 2000). Such leaching effects are typical of mountainous regions with high precipitation, particularly in areas with markedly seasonal climates prone to intense thunderstorms (e.g. the DAC) (Read & Mitchell, 1983). The darkly coloured 'stains' on Clarens

Formation sandstone in the DAC are evidence of leaching. Ferric and manganese cations are removed from the overlying basaltic soils by organic acids as water percolates through its SOM and are then precipitated as iron and manganese oxides (H. Beckedahl, 2002, pers. comm.). Losses through leaching are exacerbated by the minimisation of evapotranspiration through cooler temperatures and the maximisation of run-off by steep topography (i.e. both result in increased transport of dissolved minerals; Jeffrey, 1987).

Acid soils are not optimal for plant growth (Wilkinson, 1994) because low pH increases the solubility of heavy metals (e.g. Al, Fe and Mn) that may be toxic to plants (Taylor, 1989; Sparks, 1995). Low pH also results in deficiencies of Ca, K and Mg because these elements bind with Al and Fe oxides under acidic conditions (Lucas & Davis, 1961; Clark & Baligar, 2000). This may explain the low Ca and Mg levels in the Drakensberg and Pondoland soils, and low K in Pondoland soil (Table 4.9). Low Ca and Mg concentrations have also been reported from the acidic, quartz-derived soils of the Wolkberg Centre; these soils are favoured by calcifuges such as Cape elements (Matthews *et al.*, 1993). Soil acidity also affects the type of clay mineral (Sparks, 1995). For example, Drakensberg and Pondoland soils generate 1:1 layer clay minerals which have poor exchange capacities (Sparks, 1995; Clark & Balligar, 2000) which further impairs soil fertility.

The soils of Cape Agulhas are also acidic, lacking in Ca, K, Mg and N, particularly in the colluvial sands (Tables 4.9 & 4.10). Highly leached, nutrient-poor acidic soils are the common denominator underpinning heathland vegetation around the world (Groves, 1981a), particularly that of Australia (Groves, 1981a; Read & Mitchell, 1983; Stewart & Schmidt, 1999) and South Africa (Stock & Lewis, 1986; Richards *et al.*, 1997).

Midlands soil is 'slightly acid to neutral' (mean pH = 6.1; Table 4.9) according to the pH scale of Sparks (1995). The higher pH of Midlands soil is more likely to generate 2:1 clays; they have higher ion-exchange soil properties (Sparks, 1995; Clark & Balligar, 2000) which improves soil fertility. The warm, mesic Midlands climate is more likely to produce neutral soils because evapotranspiration often exceeds precipitation under these conditions (Clark & Baligar, 2000), and are therefore typically Ca- and Mg-rich (Table 4.9); high Ca in particular indicates high soil fertility (Jordan & Herrera, 1981). The dolomitic soils of the Wolkberg Centre are also Ca- and Mg-rich; these soils are favoured by sub-tropical calcicoles (Matthews *et al.*, 1993). Nutrient deficiencies associated with these soils include P and Zn deficiencies (Clark & Baligar, 2000), with P highly lacking in Midlands soil and Zn moderately so (Table 4.9). Drakensberg soil had the highest levels of Zn, which may affect the translocation of NO_3^- to the leaves (Smirnoff & Stewart, 1987).

4.4.3.3 ALUMINIUM TOXICITY AND/OR PHOSPHORUS LIMITATION?

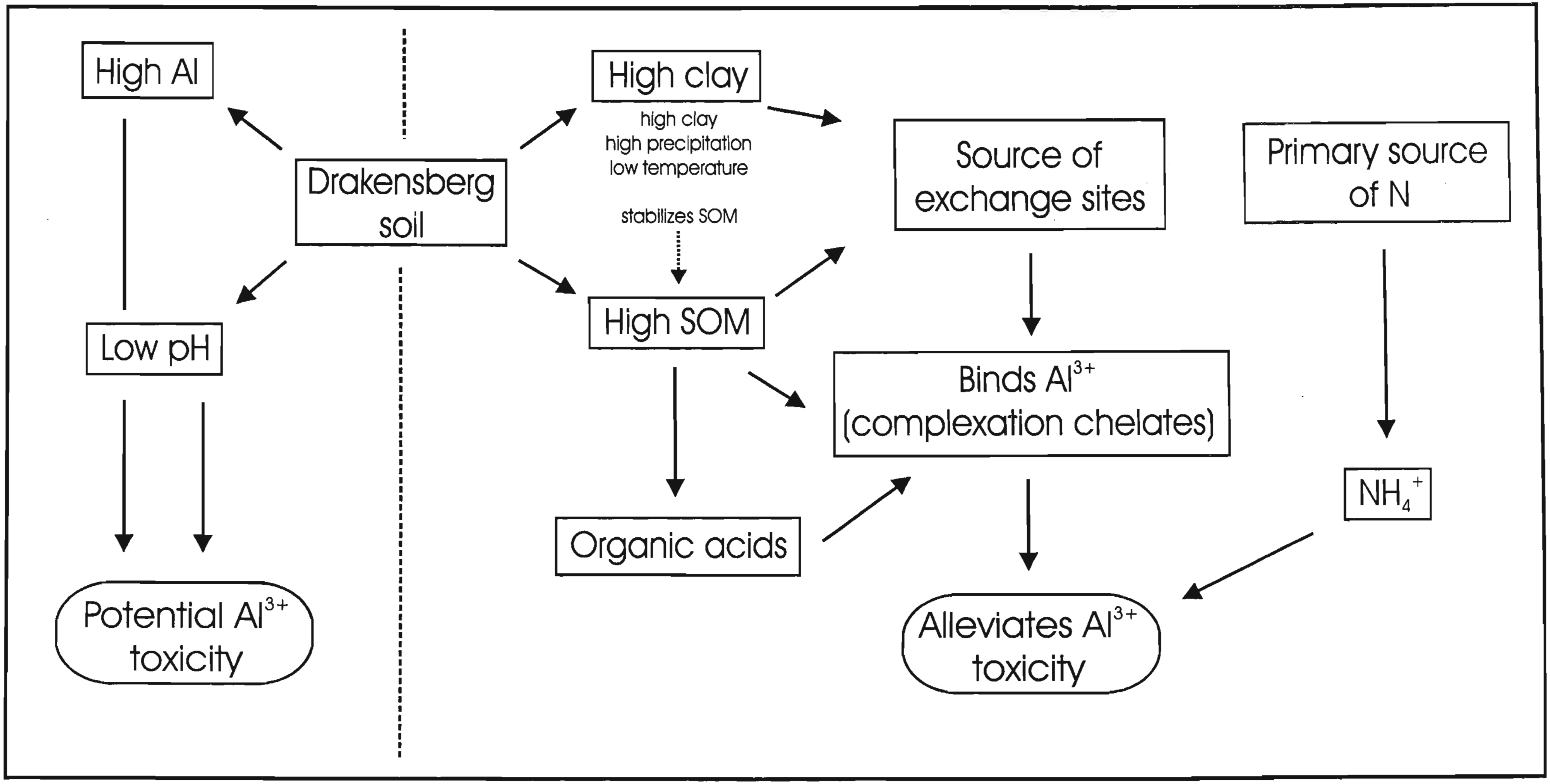
Al^{3+} toxicity is regarded as the primary growth-limiting factor in low pH soils (Clark & Baligar, 2000) because of its solubility in acidic media (Lucas & Davis, 1961; Wilkinson, 1994; Sparks, 1995). The details of Al rhizotoxicity are presented by Bennet (1998) and Bennet & Granger (2000). Drakensberg soil had high exchangeable acidity and high acid saturation (Table 4.9), with the latter in particular inferring high levels of Al. The possibility of Al^{3+} toxicity in Drakensberg soil at the low altitude sites was investigated because of the low biomass of *D. mollis* when grown under these conditions. However, Al^{3+} toxicity was dismissed due to the similar performance of Al-sensitive and Al-tolerant cultivars of wheat (Fig. 4.4G&H & 4.10) when grown under similar conditions to *D. mollis*. A number of factors relating to the chemical and physical properties of Drakensberg soil may have accounted for this result. Its high clay and SOM fractions are rich sources of exchange sites that bind with Al^{3+} and render it nonexchangeable (cf. Sparks, 1995). SOM is also a source of organic acids, which bind with Al^{3+} and reduce its availability (Clark & Baligar, 2000). The N source is also known to influence the Al^{3+} concentration; this metal is less toxic when NH_4^+ is the primary N source (McGrath & Rorison, 1982; Rorison, 1985; Smirnoff & Stewart, 1987). These effects are summarized in the form of a biogeochemical model (Fig. 4.17).

The possibility of P being a significant factor was negated because its availability was limited across *all* sites, but particularly so in the Midlands site that generally excludes Cape taxa (that are adapted to low available P soils). The P economy does, however, warrant further investigation because nutrients such as N may be affected by other nutrients (Groves, 1981b). For example, Hannon (1961; cited in Groves, 1981b), referring to the N economy of heathland communities in Australia, concluded by saying that 'the N economy of these communities is controlled by an efficient P regime'.

4.4.4 THE EFFECT OF TEMPERATURE ON NITROGEN MINERALISATION

Plant productivity and species' ranges in high-altitude systems are often temperature-limited (Scott & Billings, 1964; Nielsen, 1974; Grime, 1977; Craine & Lee, 2003) because high altitudes are temperature barriers that exclude non-adapted taxa (Janzen, 1967) following temperature decreases with altitude according to the adiabatic lapse rate of ± 0.6 °C/100 m (Jones, 1983). The DAC summit area experiences low temperatures, with the mean annual temperature being 5.7°C and the lowest recorded temperature -20.4°C (Killick, 1997). The experimental site,

Fig. 4.17. Biogeochemical model depicting the characteristics of Drakensberg soil that may contribute to Al^{3+} toxicity, particularly at low-altitude (left of dotted line) and the processes most likely responsible for the alleviation of Al^{3+} toxicity in Drakensberg soil under these conditions (right of dotted line).


High Al
Low pH
Potential Al3+ toxicity
Drakensberg soil
High clay
high clay
high precipitation
low temperature
stabilizes SOM
High SOM
Organic acids
Source of exchange sites
Binds Al3+ (complexation chelates)
Alleviates Al3+ toxicity
Primary source of N
NH4+

although only at the lower limits of the DAC (1840 m), was the coolest of all sites used in the pot experiments (Table 4.1; Fig. 4.5).

The soil temperatures that govern soil activities (Jeffrey, 1987) are generally lower than air temperatures (McMichael & Burke, 1996) and become increasingly important with increasing altitude (Shreve, 1924; Shanks, 1956). Soils of the DAC above 3000 m have frigid or cryic temperature regimes, with mean annual temperatures for cryic soils ranging from 0°C to 8°C (Schmitz & Rooyani, 1987; Grab, 1997). These low temperatures are expected to impact significantly on N availability, particularly by affecting N mineralisation (cf. Körner & Larcher, 1988; Klingensmith & Van Cleve, 1993; Craine & Lee, 2003), and in the case of NH_4^+, by decreasing its diffusion coefficient (Tisdale *et al.*, 1985). This effect on nutrient limitation (Chapin *et al.*, 1986; Berendse & Elberse, 1990) is regarded by some as a stress-inducing one (e.g. Grime, 1977), although others (e.g. Körner, 1999) have argued that alpine plants are adapted to their environmental constraints, rather than being stressed by them. Low soil temperatures also alter root membrane permeabilities (Nye & Tinker, 1977), retard translocation in phloem (Farrar, 1988), affect ion transport fluxes (Clarkson *et al.*, 1988) and impede water uptake by altering both water vapour pressure and surface tension (Nye & Tinker, 1977).

Measurements of total or available N are poor benchmarks for determining the dynamics of N release (Harmsen & Van Schreven, 1955), although it is thought that mineralisation is generally higher in soils with high total N contents (Lucas & Davis, 1961; Binkley & Vitousek, 1989). Although total N in Drakensberg soil was high, almost six times higher than Pondoland soil (Table 4.10), both soils mineralized similar low levels of N at their respective 'spring' temperatures (Table 4.10). The result for Drakensberg soil (simulated so as to include the effect of altitude) meant that only 1.7% of its total N was mineralisable at 12°C (Table 4.10), a statistic on par with soils of the Californian chaparral (0.1 to 4.4%), yet lower than the 4 to 41% reported for agricultural soils (Read & Mitchell, 1983). Low N availability suggests that nutrient limitation is a factor (cf. Chapin *et al.*, 1986); Drakensberg soil at high-altitude is therefore only *potentially* fertile. This outcome is probably exacerbated by the poor thermal conductivity typical of soils high in SOM (Jeffrey, 1987). Quartz sands, however, typical of Pondoland, have high thermal conductivities (Jeffrey, 1987) but this trait is not expected to exert a positive effect on soils so nutrient-poor.

The low level of N mineralisation in Drakensberg soil at 12°C was probably the result of impaired microbial activity; their functioning is strongly temperature-dependent (Nielsen, 1974; Grime, 1977; Bardgett & Leemans, 1996; Bardgett *et al.*, 2002). N mineralisation has a high temperature optimum, ranging from 25°C to 40°C for general microbe activity (Stanford *et al.*, 1973b; Read & Mitchell, 1983; MacDuff & White, 1985) because temperature is a major determinant of biological activity (Sutcliffe, 1977; Grace, 1988), influencing the rates of metabolic processes through its effects on the kinetics of biochemical reactions (Sutcliffe, 1977; Körner & Larcher, 1988; Bowers, 1994). This also explains the higher levels of N mineralisation at 30°C than at the spring temperatures. The low soil temperatures quoted for the DAC (Grab, 1997; Killick, 1997) and the mean spring temperature of 12°C used in the incubation experiment are therefore sub-optimal for microbial activity. Temperature is also a significant factor determining the levels of N mineralisation in soils of the Cape Region (Stock *et al.*, 1988). The major factors contributing to nutrient-impoverishment in the DAC and PC are summarized in the form of two biogeochemical models (Fig. 4.18 & 4.19).

N mineralisation was significantly greater in pristine Midlands soil than in

Fig. 4.18. Biogeochemical model depicting the various ecological processes that are responsible for creating a nutrient-poor economy in the Drakensberg Alpine Centre.

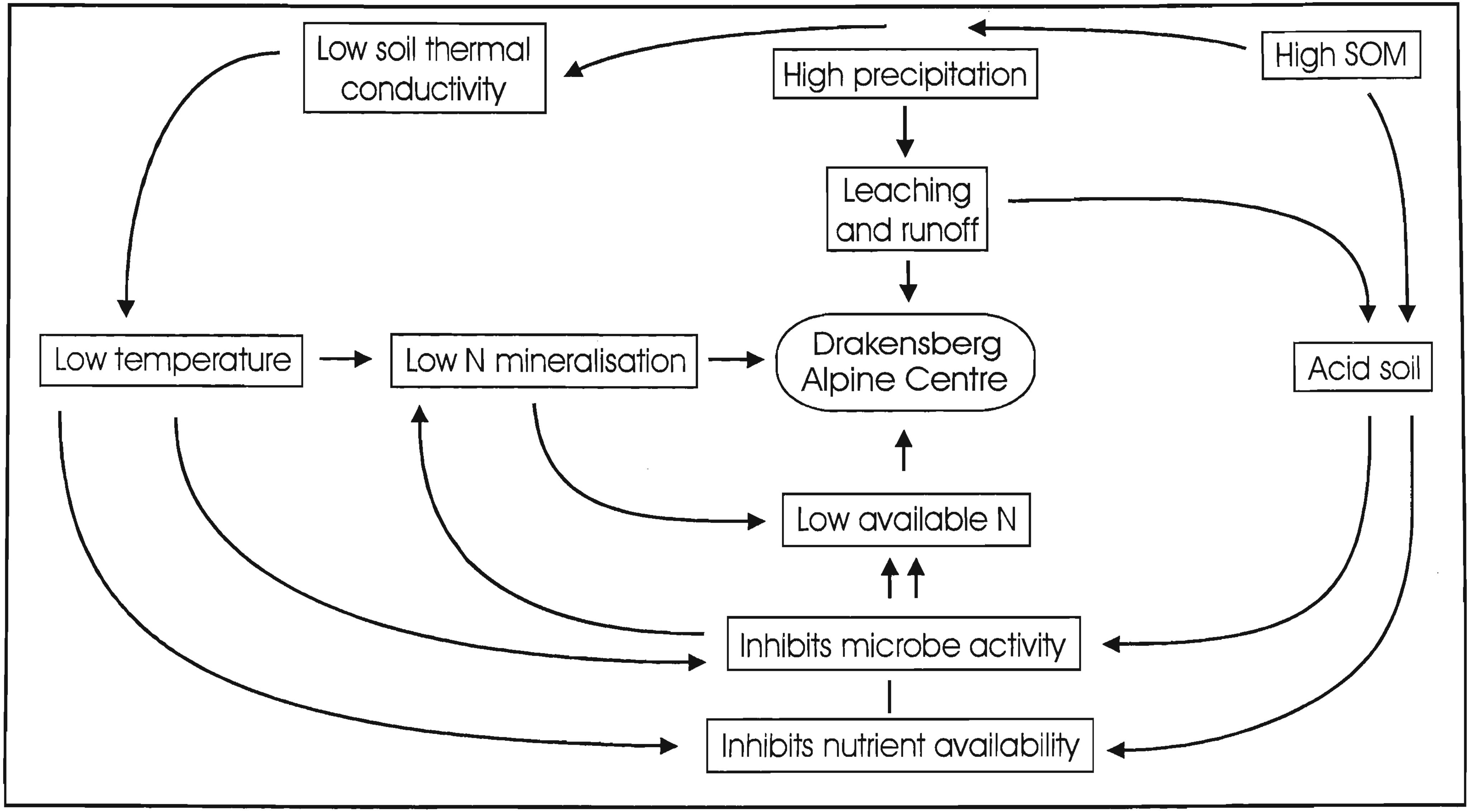
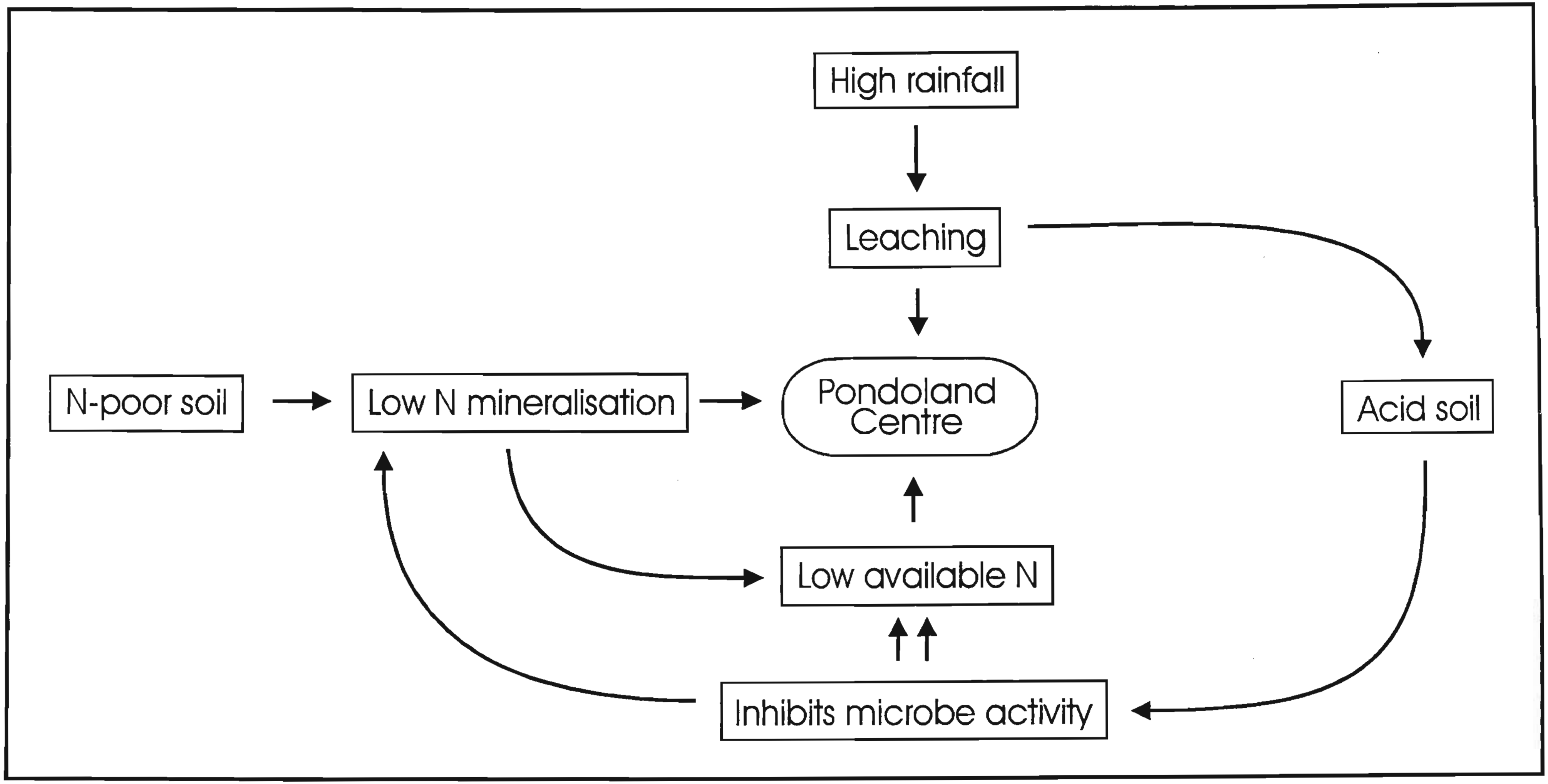

Low soil thermal conductivity
High precipitation
High SOM
Leaching and runoff
Low temperature
Low N mineralisation
Drakensberg Alpine Centre
Acid soil
Low available N
Inhibits microbe activity
Inhibits nutrient availability

Fig. 4.19. Biogeochemical model depicting the various ecological processes that are responsible for creating a nutrient-poor economy in the Pondoland Centre.


High rainfall
Leaching
N-poor soil
Low N mineralisation
Pondoland Centre
Acid soil
Low available N
Inhibits microbe activity

pristine Drakensberg and Pondoland soils (Table 4.10). Midlands soil is generally nutrient-rich when pristine, particularly with regard to N (Fynn *et al.*, 2003). However, N mineralisation was significantly lower in the Midlands soil used in the pot experiments (Table 4.10) because it was disturbed for a period of two months prior to collection. Perturbations that break the soil surface increase N mineralisation and deplete the N pool (e.g. Schimel *et al.*, 1985). Concentrations of the other (less volatile) nutrients in Midlands soil remained unaffected (Table 4.9). Remembering that Cape taxa are adapted to N-poor soils, high productivity of *D. mollis* in the nutrient-rich Midlands soil with depleted N suggests that N was the key factor. In summary, best growth occurred in a variety of N-poor scenarios (all soils at high-altitude; Midlands soil - previously disturbed; Pondoland soil - inherently N-poor), indicating that *D. mollis* favours N-deficient soils.

Although the two principal N sources for higher plants are NO_3^- and NH_4^+ (Haynes & Goh, 1978; Stewart & Schmidt, 1999), all soils at all sites yielded more NH_4^+ than NO_3^-. This was also noted for soils from a range of natural ecosystems (Lamont, 1982), including fynbos soils under mature *Protea* stands (Stock & Lewis, 1984). NH_4^+ is the major N source for plants in acid soils because low pH favours ammonification (Read & Mitchell, 1983), although Clark & Baligar (2000) have suggested that plants preferably absorb NH_4^+ at higher pH. Eviner & Chapin (1997) have suggested that species differ in their preference for particular N sources and that these preferences reflect the dominant form of available N.

NH_4^+ has the lowest energetic requirements of any inorganic form of N as no chemical transformation is required before assimilation (Gutschick, 1981), an important feature considering the high cost of producing N-containing tissues in infertile soils (Bloom *et al.*, 1985). A constraint on NH_4^+ uptake, however, is the high cost of producing sufficient root mass for its uptake as NH_4^+ is less mobile than NO_3^- (Gutschick, 1981; Bazzaz, 1996). Although its chances of being leached are therefore less, it may be less available to the plant (Bazzaz, 1996). This constraint is overcome, for example, by the seasonal production of proteoid roots in the Proteaceae (Lamont, 1982, 1983).

The NH_4^+:NO_3^- ratios, however, became smaller at lower temperatures, corroborated by data from the laboratory soil incubation experiments using the mean spring temperatures of the respective sites, as well as from soils collected in the field and their N content extracted immediately. The mean NH_4^+:NO_3^- ratio for a number of soils collected from Black Mountain in Lesotho (3240 m) was 4:1, and that of soils sampled from Garden Castle (1800 m) at the lower altitudinal limit of the DAC was 32:1. The NH_4^+ contribution of the former, higher site was therefore eight times less than the NH_4^+ contribution of the latter. Nutrient-impoverishment at high-altitude is further exacerbated as NO_3^- requires chemical transformation through nitrate reductase before it becomes available to a plant (e.g. Stock & Lewis, 1982).

4.4.5 FERTILITY CONSTRAINTS AND TRADE-OFFS

Soil N is an important nutrient affecting the distribution of species (Wherry, 1926; Bradshaw *et al.*, 1964; Nye & Tinker, 1977; Stock & Lewis, 1986; Gleeson & Tilman, 1990; Tilman & Wedin, 1991b; Berendse *et al.*, 1994; Richards *et al.*, 1997). Four productivity-soil fertility interactions were assessed, relating mostly to the variable N requirements of plants. (1) Infertile sites generally result in low productivity; this relationship is known as the 'Montgomery effect' (Crawford, 1976). (2) Low productivity, however, also occurs in highly fertile sites, particularly when plants adapted to infertile sites are grown in highly concentrated media (Chapin *et al.*, 1986).

In the present study, the temperate herb *D. mollis* was unproductive in the N-rich Drakensberg soil at the warmer sites, probably because the high levels of N mineralisation were deleterious (Fig. 4.6). Similar responses were reported for the C_4 subtropical grass *Trachypogon spicatus* (L. f.) Kuntze (= *T. plumosus* Nees) (Roux, 1954); a number of upland grass species (Bradshaw *et al.*, 1964) and Australian Proteaceae, when treated with high levels of N and P (Groves & Keraitis, 1976). Increases in soil fertility have also caused European heathlands to contract, as grasses are better competitors when soil nutrients are high (Heil & Diemont, 1983; Berdowski & Zeilinga, 1987), particularly N (Berendse & Elberse, 1990; Berendse *et al.*, 1994). (3) High productivity in N-poor soils have been reported for the grass *T. spicatus* (Roux, 1954) and *D. mollis* (Table 4.2; Fig. 4.6). Their tradeoff for high productivity in N-poor, often acidic soils (i.e. more cost-effective usage of limiting resources; Bloom *et al.*, 1985; Berendse & Elberse, 1990) probably allows them to outperform species that favour N-rich soils. The stronger performance of *D. mollis* in Drakensberg soil at the high-altitude site compared to the low-altitude sites suggests that low rates of N mineralisation occur when temperatures are cool. (4) High productivity in N-rich soils are a further possibility. For example, the strong performance of the subtropical grass *E. curvula* in Drakensberg soil at low altitude (Fig. 4.4A-E & 4.9) is the result of its preference for elevated levels of N (Roux, 1954; Le Roux & Mentis, 1986). Similar results were noted for a number of lowland grass species (Bradshaw *et al.*, 1964).

The relationship between productivity and fertility appears to be as follows. The taxon adapted to high N (*E. curvula*) was able to tolerate low N (e.g. Pondoland soil), but the taxon adapted to low N (*D. mollis*) was not able to tolerate high N, even in the absence of competitors (cf. Newton *et al.*, 1991). Similar antagonistic results have been documented for calcicole and calcifuge species (Newton *et al.*, 1991). These results serve to illustrate the particular nutrient requirements of different taxa for optimal growth.

4.4.6 COMPETITION-EFFECTS

Plant competition has often been used to explain productivity and compositional gradients (e.g. Wilson & Tilman, 1991). Grime (1977) is a proponent of the 'stress tolerance school' - species occupying infertile sites are those most able to tolerate nutrient stress; competition is only an important factor in fertile sites. Tilman (1990a, 1990b), however, is a student of the 'trade-off school' - species make trade-offs for below-ground (nutrient) competition in infertile sites and trade-offs for above-ground (light) competition in fertile sites. However, it is erroneous to attribute all differences in plant productivity to competition as these differences may also be accounted for by the physical or biotic environment (Gankin & Major, 1964; Grime, 1977; Bond *et al.*, 1992). Competition-effects were not included in the experiments; all results regarding the interactions of climate and soil were based entirely on productivity.

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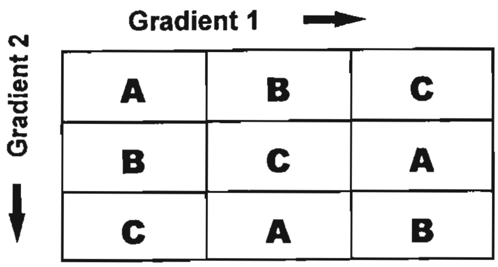

A	B	C
B	C	A
C	A	B

Appendix 4.1. The Latin Square (LS) design used during the *D. mollis* reciprocal pot experiments subject to nine soil-site treatments. Abbreviations: A, pot containing Drakensberg soil; B, pot containing Pondoland soil; C, pot containing Midlands soil. Gradients refer to the simultaneous light and temperature differences that may arise between pots in a large pot experiment.

Appendix 4.2. The effects of shading on photosynthetic photon fluence rate (PPFR), either the result of hail netting (Drakensberg site) or clear polycarbonate (Midlands site).

Treatment	PPFR (μmol photons m^{-2} s^{-1})	Shade (%)	Conditions and Time
Full sun - no shading effects	1717	-	cloudless sky; noon
Hail netting	1266	26	cloudless sky; noon
Greenhouse - clear polycarbonate	1033	40	cloudless sky; noon

Appendix 4.3. The chemical characteristics of water used in the watering of the reciprocal pot experiments at three sites: Drakensberg site (Mahai Stream), Pondoland site ('Clearwater Dam'), and the Midlands site (Midmar Waterworks). Due to the wet season experienced during 1999/2000, only the Midlands experiment under clear polycarbonate was regularly hand-watered; the remaining two sites were rarely hand-watered. Water analyses were undertaken by the Analytical Services Department, Umgeni Water. Abbreviations: Al, aluminium; N, nitrogen.

Supply source	Total Al	Soluble Al	Ammonium	Nitrate	Nitrite	Total N
	(μg l^{-1})			(mg l^{-1})		
Garden Castle (Mahai Stream)	< 0.05	< 0.05	< 0.01	10.8	< 10	0.59
Umtamvuna ('Clearwater Dam')	140	113	0.09	< 0.05	< 0.05	0.33
Midmar Waterworks	35.06	-	0.29	0.2	0.05	-

Appendix 4.4. The volume of distilled water required to bring 25 g of air-dried soil to field capacity.

Soil	Volume (ml)
Drakensberg	17.25
Pondoland	4.75
Midlands	10.00

‘If such conjectures stimulate the imagination and lead to fresh approaches, they will have served a useful purpose.’

Levyns (1964)

CHAPTER 5

CONCLUSION

5.1 NUTRIENT ECONOMIES

The DAC is characterised by a nutrient-poor economy superimposed on nutrient-rich substrates. This system is constrained by climatic boundaries that set the basic limits for their biota (cf. Mason, 1946). Further enrichment of local and regional diversity is attained through the effects of 'geo-edaphics' *sensu* Kruckeberg (1986), a collective term which encompasses soils, geology and topography.

The reciprocal pot experiments compared the productivity of a Cape element in a number of sites and soils that differed in temperature and soil N respectively, in order to determine the ecological factor(s) most responsible for the sharing of Cape elements between two contrasting summer rainfall sites. The results suggest that (1) the effect of temperature on N mineralisation rate was the key growth-limiting factor in the DAC, exacerbated by a number of complex interactions with soil pH and SOM. The low temperatures in the DAC result in low rates of N mineralisation, even though total N is high. Further evidence for the effects of the DAC's cooler temperatures were similar biomass across its range of soils, higher below-ground biomass in Drakensberg soil than the warmer sites, and lower tissue N concentrations and amounts than the warmer sites. (2) The outcome of tradeoffs between climate and soil in the DAC and PC probably result in similar nutrient stresses and probably therefore a similar flora and vegetation, which challenges the general view (as did Axelrod, 1975) that regions sharing similar species composition and vegetation structure are those constrained by similar selection pressures (Mueller-Dombois & Ellenberg, 1974). (3) Sensitivity to the amount of mineralisable N is an important controlling factor in the in the maintenance of species boundaries and probably the membership of communities, particularly the interface between communities either favouring or excluding Cape elements. Taxa adapted to the N-poor soils of the CFR are most likely preadapted to other soils low in available N. This criterion is met in the DAC and the PC, two disjunct centres of diversity characterized by N-poor economies, resulting either from temperature-effects or inherently nutrient-poor soils. The Midlands region excludes most Cape elements because its intermediate altitudes and mesic climate, nutrient-rich soils and high summer temperatures favour taxa that are able to out-perform Cape elements in such a productive environment. Such effects are manifest on a phytogeographical scale.

5.2 APPRAISAL

This study has hopefully provided further insights into the phytogeographical and ecological relationships shared between the floras and vegetation of the CFR, DAC and PC, as well as the dynamics of nutrient-poor systems. The results of the reciprocal pot experiments may help to infer how Cape taxa have responded to temperature changes in the past and help predict how they will respond in the future because the temperature differences generated by altitude were a small-scale replica of climate change.

5.3 FUTURE PROSPECTS

The opportunities for long-term field-based projects in the DAC and PC are many because knowledge of the DAC's and PC's physiological plant ecology is still in its infancy. Further work into their P budgets is necessary because soil P is often a limiting nutrient (Allard, 1942; Beadle, 1966; Richards *et al.*, 1997) and is highly dependent on temperature and mineralization of SOM (O'Connor *et al.*, 1986). Competition-based experiments will be helpful in refining knowledge on whether or not 'the preadaptive response is mediated through tolerance to nutrient-poor conditions or by below-ground competition for the most limiting resources?'

The topical issue of the effects of global warming, specifically in alpine regions because their low-temperature environment is particularly sensitive to elevated temperature, will soon be explored through the establishment of the Global Observation Research Initiative in Alpine Environments (GLORIA), most likely at Sani Top, Lesotho. A trial test for GLORIA-South Africa is soon to be undertaken with the assistance of a team of plant scientists from New Zealand in January 2004. This long-term field-based monitoring project will help assess the effects of global warming on the DAC, particularly its effects on the DAC's plant species composition and vegetation structure.

5.4 FINAL COMMENTS

The DAC forms of corridor for sources of temperate genetic material between the CFR and tropical Africa. The PC is surrounded by subtropical lowland vegetation and is therefore not an equivalent source of genetic material (≈ cul-de-sac). The distribution of Cape elements along the Afromontane axis of sub-Saharan Africa and on quartzitic outcrops of the PC highlights their affinity for both high-altitude corridors and nutrient-poor edaphic islands. These are remarkable examples of survival and preadaptation.

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