# Biogeographic patterns and the driving variables

S. J. Milton and W. R. J. Dean

More species of plants are packed into the small succulent karoo landscape than in any other desert on earth, yet the vegetation is strangely homogeneous in appearance. This pattern is not repeated in the Nama-karoo, or reflected in the vertebrates of either karoo biomes.

The geological history of the two biomes is similar, being sedimentary, but influenced by folding along the southern and western edges of the karoo, and by igneous intrusions in the northern and eastern parts. The soils of both biomes are typical of arid regions, and are poorly developed with little organic matter. Folding, endorrheic drainage and wind-blown movement of sand has resulted in localized patchiness in substrata which influences the biota.

Anomalous soils developed along the present inland boundary between the winter and summer rainfall regions indicate past shifts in rainfall seasonality (Watkeys, this volume). Pollen core data for the past 10 000 years that indicate fluctuations between grass and shrub dominance have occurred repeatedly throughout the karoo (Meadows and Watkeys, this volume). The grass : shrub ratio still follows patterns in present-day rainfall seasonality (Palmer et al., this volume). There can, however, be little doubt that the climate of the western succulent karoo has fluctated less in the recent past and is currently more predictable than that of the Nama-karoo (Desmet and Cowling, this volume).

The biota of the Succulent and Nama-karoo appear to have different geographical origins (Cowling and Hilton-Taylor, this volume; Vernon, this volume). Desert and fynbos genera are prevalent among succulent karoo plants, arachnids, insects and reptiles, whereas Nama-karoo genera have been drawn from savanna, grassland and forest, as well as from the adjacent succulent karoo and desert biomes.

Climatic patterns offer some insight into reasons for the explosive speciation of succulent plants and geophytes in the western parts of the succulent karoo. In their chapter on plant biogeograhy, Cowling and Hilton-Taylor point out that the predictability of the winter rainfall in the succulent karoo is unique among desert regions. This peculiar climate has favoured short-lived shrubs that store winter

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# 2 Part one

moisture in their leaves but die when drought-stressed. Limited lifespan and continuous turnover in populations result in lottery replacement and minimize competitive interactions resulting in structural similarity among species. Short seed dispersal distances and dependence on insect pollinators has favoured speciation. Succulent karoo plant communities are thus species-rich, but uniform in structure. Insects and the invertebrates and reptiles that prey on them show centres of species-richness in the succulent karoo that may reflect patterns of plant speciation. For example, Vernon (this volume) shows that indigenous solitary bee assemblages are most species-rich in Namaqualand, and species forage on a limited array of plants. Similarly, the masarid wasps and vespid wasps include many geographically restricted species that forage on the pollen of Mesembryanthema.

Some of the ideas discussed in the next five chapters are of necessity speculative, because the disciplines of soil science, palynology and metereology are undergoing rapid development in the karoo. Analyses of biogeographic patterns are severely hampered by systematic problems in the most speciose groups, and by many undescribed taxa among the invertebrates. Nevertheless, as the following five chapters show, advances in knowledge and techniques over the past few years have changed our perception of the ways in which climates and soils are influencing the evolution and distribution of karoo biota.

# 1 The climate of the karoo – a functional approach

P.G. Desmet and R.M. Cowling

# 1.1. Introduction

The arid lands of southern Africa occupy the area west of approximately 27 °E and north of 34 °S. North of approximately 27 °S, the arid zone becomes confined to coastal belt and plateau of southern Namibia. North of 22 °S, this zone is confined to the hyper-arid coastal belt of the Namib Desert and stretches as far north as 12 °S in southern Angola. The climate is dominated by, and indeed, the aridity is largely caused by, the southern subtropical highpressure (anticyclone) belt. To the south, the region is influenced by the circumpolar westerly airstream (Schulze, 1965). Only the southern and south-western arid regions are influenced by this belt of temperate cyclones. Local modifications occur as a result of the Cape Fold Mountains in the south, the mountains of the Great Escarpment, the raised interior plateau and the cold, north-flowing Benguela current that washes the west coast of the subcontinent. Incursions of moisture into the region are associated with the advection of air across the warm Indian Ocean (maximum precipitation from this source is largely confined to the eastern parts of the subcontinent) and the circumpolar westerlies to the south. Southern African arid lands are geographically marginal to these rain-producing systems.

The first part of this chapter provides an overview of the contemporary climate of the region. The second part provides a description of the weather systems that influence the karoo. This approach is taken to highlight the great diversity of systems that are responsible for the varied karoo climates, something which has not been appreciated by earlier reviews. This functional understanding of the weather patterns in the karoo is essential for understanding the landscape-vegetation patterns (i.e. at the level of biome and veld type). In the final part of this chapter, we present a new analysis of the climate of the karoo, which comprises a multivariate model that illustrates vegetation-climate relationships quantitatively. We do not, however, discuss long- and medium-term changes in climate, nor predictions of future climate change.

# 1.2. A general overview of the climate of the karoo

The climate of the karoo is summarized in the form of climate diagrams (Figs. 1.1(a) and 1.1(b)). The focus of this section is a discussion of the three primary limiting climatic factors which influence plant growth in arid lands, namely precipitation, temperature and light (Schulze and McGee, 1978).

# 1.2.1. Precipitation

# Rainfall

The overall feature apparent from the distribution of mean annual rainfall in the karoo is that south of the Tropic of Capricorn, precipitation decreases uniformly westwards from the eastern escarpment across the plateau. Only in the extreme south do the isohyets follow an east-west trend. This is due to the topographic irregularities of the Cape Fold Belt and associated orographic rain linked to westerly frontal and post-frontal systems. In the west, north of the tropic, the isohyets follow a similar north–south trend, although steeper; thus, in the Namib Desert of southern Angola, coastal stations receive <100 mm rainfall, whereas stations 200 km to the east on top of the escarpment receive in excess of 800 mm

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4 P. G. Desmet and R. M. Cowling



Figure 1.1(a) Map of southern Africa showing the localities of numbered weather stations from which climate data were obtained to generate the climate diagrams shown in Fig. 1.1(b) on p. 6. The boundary of the karoo sensu lato is shown as a dotted line. L = Lesotho, S = Swaziland

annually (Figs. 1.1(a) and 1.1(b)). The desert biome, namely the Namib Desert, occupies a narrow range of mean annual rainfall (<100 mm) whereas the succulent and Nama-karoo experience a broader range in rainfall, between 50 and 500 mm and 50 and 600 mm respectively (Fig. 1.2).

At a finer scale, the distribution of mean monthly rainfall across the subcontinent highlights two import trends in the annual march of rainfall, namely, summer and winter maxima regimes. Over most of the eastern parts of the country, summer rainfall regimes dominate. Over the western interior, to the east of the escarpment, and north of the Cape Fold Belt, this summer maximum is less marked and grades into a predominately winter-rainfall regime, or Mediterranean climate, in the south and southwest mountains and coastal belt.

At an even finer scale, considered much more meaningful in terms of the distribution and characteristics of plant cover than the general patterns already discussed, are the duration, time of occurrence, and the degree of intensity of the rainy season and dry season; particularly when viewed from the perspective of plant available soil moisture being able to meet evaporative demand. The annual march of mean monthly rainfall across the karoo shows a number of distinct patterns (Figs. 1.1(a) and 1.1(b)). These patterns can be summarized in terms of three distinct parameters, namely amplitude, phase and shape:

- a change in amplitude, thus higher or lower peaks in monthly rainfall, or more pronounced seasonality;
- a shift in phase (winter- or summer-rainfall maxima or minima), which is essentially a change in seasonality;
- and, alternatively, a change of curve shape from the general parabolic curve to sinusoidal or aseasonal.

Thus, within the karoo, for the same given mean annual rainfall there are a number of different possible combinations of rainfall distribution (Figs. 1.1(a) and 1.1(b)). Coupled to this variation are differences in reliability and intensity of rainfall events. This diversity in the occurrence of rainfall regimes arises as a result of the location of the southern African arid zone between two weather systems. The regional weather patterns that are responsible for this variation are discussed in more detail in the following sections of the chapter. The biogeographical implications of this diversity in rainfall regimes is discussed in section 1.7.

### Fog

Fog is an important alternative source of moisture for plants. Although there is generally no direct precipitation of water on the soil surface, interception by vegetation may lead to significant amounts of water entering the soil below the plant. Fog 'precipitation', although recognized as significant (Schulze and McGee, 1978; Walter, 1986; Werger, 1986; Lancaster et al., 1984; Pietruszka and Seely, 1985: Olivier, 1995), is not measured by standard rain gauges, and thus its importance in ecological studies has been very difficult to estimate. The measurement of moisture derived from fog is dependent on the type of obstacle used to catch fog moisture (Walter, 1986). Finely branched structures that transmit wind, such as a fine mesh or the canopy of a shrub, are much more efficient at combing out fog moisture than a smooth, solid structure.

Advective sea fog is characteristic of the entire west coast of the subcontinent, essentially the coastal Namib Desert (including both winter-rainfall strandveld, lowland succulent karoo (Low and Rebelo, 1996) and summer-rainfall portions of the desert) (Schulze and McGee, 1978; Olivier, 1995). Locally, fog is referred to by a number of different names: *Cacimbo* in Angola (Jackson, 1951), *Nieselregen* in Namibia (Walter, 1986) and *Mal-mokkie* in Namaqualand (A. Kotze, personal communication). We do not know of any studies on the occurrence or significance of fog (radiation fog) elsewhere in the karoo.

Clouds form when air is supersaturated with respect to water or ice (Preston-Whyte and Tyson, 1988). One manner in which this can occur is by the mixing of air. Advection fog occurs when warm air with high relative humidity is advected over a cool surface. The temperature differential

# The climate 5

between air and surface must be sufficiently large to enable the air to reach saturation after a small amount of cooling. Medium velocity winds are also necessary in the advection process, since strong winds would cause too much turbulence and vertical mixing to maintain the fog, whereas low wind speeds would provide too little advection and mixing. When air over the Atlantic Ocean moves across the leading edge of the cold Benguela current, temperature is depressed to dew point and fog forms. The coastline constitutes another leading edge with air moving over a hot, arid desert. Inland movement of fog is therefore limited by the arid nature of the new surface conditions, and the fog thins and evaporates downwind. By day, this process is hastened by surface heating.

The predominance of colder coastal ocean surface temperatures during summer, as a result of the seasonal intensification of the mid-Atlantic Ocean high, creates conditions more favourable for fog formation. The dominant flow of air during this period is westerly, thus warm moist air from the mid-Atlantic is cooled near the coast and fog forms. As midsummer wind velocities are too high to maintain the integrity of the fog bank, the coast experiences fog predominantly during spring and autumn, when the wind velocities are lower, but the flow of air is still predominately onshore.

The frequency of fog occurrence along and perpendicular to the coast varies considerably (Olivier, 1995). Using Meteosat images, Olivier (1995) estimated the highest occurrence to be between Sandwich Bay and Cape Cross in the central Namib with an excess of 100 days per year. South of the Orange River, the value is less than 75 days and in southern Angola less than 50 days. Fog also penetrates as far inland as the foothills of the escarpment and beyond where less than 10 fog days may be expected. Major river courses, such as that of the Orange River allow fog to penetrate deeper into the valleys and foothills of the escarpment mountain ranges than elsewhere. There is, however, little quantitative understanding of how fog is distributed in the landscape south of the Orange River.

Fog also plays an important amelioratory role in the local climate. From South African Weather Bureau data, the average total number of days per annum during which fog is recorded at Port Nolloth is 148, or 41% of the total days. As a result, the sunshine duration averages less than 70% of the possible total and this has a significant ameliorating effect (Burns, 1994).

The potential amount of water that can be derived from a fog event, relative to the mean annual rainfall, is substantial. For Swakopmund, with 121 fog days per annum, the amount of water intercepted in 1958 was equivalent to 130 mm of rainfall. More than seven times the mean annual rainfall (Schulze and McGee, 1978), but this amounts to an average of <1.0 mm (average of 0.2 mm) per fog event (Walter, 1986). Minimum and maximum annual fog-water totals along a latitudinal transect from Walvis Bay to Gobabeb were 49–158 mm (Rooibank, 20 km inland); 88–271 mm (Swartbank 40 km inland); and 8–48 mm (Gobabeb 60 km inland). The annual coefficient of variation for fog at the three same stations was 29%, 29%, and 36%, respectively, whereas that for rainfall was 123% at Gobabeb and 106% at Walvis Bay (Pietruszka and Seely, 1985). These coefficients for rainfall and fog are similar to those for the southern Namib (Desmet, 1996). Fog is a potentially significant source of water in the desert environment, and also a far more predictable source of moisture than rainfall (Pietruszka and Seely, 1985).

If and how desert plants derive any benefit from fog moisture is unclear. There is, however, no evidence for direct uptake of fog condensation on leaves by plants (Danin, 1991). A notable exception is Trianthema hereroensis from the sand erg of the central Namib Desert (Louw and Seely, 1982). Von Willert et al. (1990, 1992) argue that any leaf structure capable of absorbing water on the leaves is also a potential route via which water can evaporate. Thus, there would be little benefit for plants in a hyper-arid environment to absorb fog moisture directly from the leaves. A more likely route whereby plants could benefit from fog moisture would be by absorbing condensation on the sand surface (Danin, 1991) and as a result of stem flow. This route would facilitate the uptake of both fog and dew condensation on the soil surface. Louw and Seely (1982) sprayed tritiated water on the top 1 cm of soil near Salsola subulicola growing in the Namib, and found efficient water absorption by the plant. Certain plants growing in the fog zone of the Namib have well-developed superficial root networks (Danin, 1991) or efficient mycorrhizal relationships to be able to benefit from alternative moisture sources such as fog and dew (see below).

### Dew

In the absence of coastal advection fog, the potential still exists for plants to obtain moisture from heavy dews. Within the karoo, the occurrence of dew is a more widespread phenomenon than fog (Werger, 1986). Although it is a parameter that is difficult to quantify, moisture derived from dew condensation on plants and the ground is probably significant and worthy of some investigation.

Dew-point temperature is that to which air at a constant pressure and water vapour content must be cooled in order to become saturated and for dew to precipitate (Preston-Whyte and Tyson, 1988). At night, radiative cooling of the air to below dew-point temperature causes dew to form on the ground. The extraction of water vapour from the overlying air causes an inversion to form in the water vapour profile. The depth and strength of this inversion is determined by the downward flux of water vapour

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3. NAMIBE 1. LUBANGO 2. LOBITO 4. WALVIS-BAY 14°56' 13°34' 1761m 12°22' 13°32' 15°12' 12°09' 1m 45m 22°57' 14°30' 2m 904.0mm 18.4° 239.0mm 24.1° 20.7° 17.3° 43mm 15.2mm 6. DIAZ-POINT 5. GOBABEB 7. PORT NOLLOTH 8. OKIEP 29'15' 16"52' 29°36' 17°53' 915m 23°34' 15°03' 26°38' 15°06' 407m 16m 5m 27.2 21.1 17.3mm 15 9° 14 9° 159 6mm 17 9 66 1mm 9. GARIES 10. LAMBERTS BAY 12. ELANDSVLEI 11. VREDENDAL 30°34' 18°00' 240m 32°02' 18°20' 32°19' 19°34' 92m 31°40' 18°30' 30m 121m 141.4mm 18.7° 222.3 mm 16.3° 94.7mm 20.5° 145.5mm 18.8 13. AAN-DE-DOORNS 14. RIVERSDALE 15. OUDTSHOORN 16. WILLOWMORE 33°42' 19°29' 34°06' 21°16' 33'35' 22°12' 33°18' 23°29' 220m 128m 315m 831m 247mm 17.6 433.6mm 17 2 248 8 mm 17.5 272.7mm 16.1 . 18. QUEENSTOWN 17. JANSENVILLE 19. CRADOCK 20. BEAUFORT WEST 32°56' 24°40' 31°54' 26°52' 427m 32"10' 25°37' 32°21' 22°35' 1067m 875m 899m 264.8mm 18.7 496.5 mm 16.4 315.7mm 16.8 240.8 mm 17 5

# 6 P. G. Desmet and R. M. Cowling

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The climate 7

Figure 1.1(b) Climate diagrams for selected weather stations in the karoo and Namib Desert, and surrounding non-arid zone vegetation types. The title for each diagram contains the town name, co-ordinates, altitude (m), mean annual rainfall (mm) and mean annual temperature (°C). Points on each graph represent mean monthly maximum and minimum temperature, and the curve mean monthly rainfall. In all cases, the rainfall scale (mm), in increments of 10 units, equals 2 x that of temperature (°C). Months on the horizontal axis are from January to December

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# 8 P. G. Desmet and R. M. Cowling

Mean annual rainfall (mm)

Figure 1.2 The relative frequency distribution of mean annual rainfall for rainfall stations in the arid zone of southern Africa in relation to surrounding biomes. The data used in this figure were obtained from the Computing Centre for Water Research (University of Natal) database for South Africa weather stations. Additional data for Angola and Namibia were obtained from Lebedev (1970) and the South African Weather Bureau, respectively. Stations were classified according to biome and Veld Type

in a suitable turbulent environment. Thus, the level of turbulence is critical. If it is too low (i.e. calm conditions), dew ceases to form since the ground cannot be replenished by water vapour from above. If the turbulence is too high, mixing inhibits surface radiative cooling to below dewpoint temperature.

The probability of occurrence of heavy dews would be highest when the difference between mean minimum monthly temperature and dew-point temperature is smallest combined with the highest mean monthly relative humidity values and lowest mean monthly night-time wind speeds. These conditions are most frequent during the autumn (April–May) in summer-rainfall areas, and during mid winter (July–August) in winter-rainfall areas. Overall, dew as a phenomenon, and especially as a potential source of water not only for higher plants, but more so for the lower plant components of soil crusts (e.g. algae), has received little investigation.

The amount of moisture delivered by dew and its utilization is uncertain, but dew differs measurably from rain in terms of its predictability. Long-lived perennial plants would only be able to survive in a desert receiving less than 50 mm yr<sup>-1</sup> if there was some form of predictability in the moisture regime. Low rainfall is highly variable. Dew is a common occurrence, but how much water this makes available to plants is unknown. Fog is potentially a substantial water source and its predictability is far greater than that of rainfall. Plants inhabiting the fog zone of the southern Namib Desert should possess a unique suite of ecological characteristics of morphological/physiological features which enable them to utilize these alternative sources of moisture. This is a ripe area for further research.

# 1.2.2. Reliability of sources of moisture

The reliability of different sources of moisture across the karoo has important ecological implications. In 1.2.1. (Fog), it was shown that, for the west coast, fog as a source of moisture for plant growth is far more reliable in terms of frequency or predictability of occurrence than rainfall. It is not known if the same holds true for dew.

Rainfall across the karoo decreases from east to west and from south to north. Similarly, rainfall variability, expressed as co-efficient of variation (CV), follows a similar trend. This is to be expected, since cv is log-linearly related to mean annual rainfall (Fisher, 1994). What is more interesting to compare is cv for different stations with the same mean annual rainfall. In Fig. 1.3, the cv of mean annual rainfall is compared between stations in the Nama- (summer rain) and succulent (winter rain) karoo. On average, the rainfall in the winter rainfall karoo is 1.15 times more reliable than corresponding rainfall in the summer-rainfall karoo. This difference has important implications for the type of plant life-history strategies and plant community structure and dynamics prevalent in the different regions of the karoo (e.g. Hoffman and Cowling, 1987; Cowling and Hilton-Taylor, this volume).

# 1.2.3. El Niño in southern Africa

El Niño is a phenomenon that usually begins with the relaxation of the normally intense easterly trade winds that drive the westward equatorial surface currents and expose cold waters to the eastern Pacific surface (Philander, 1992; Preston-Whyte and Tyson, 1988). When these winds relax, they allow the warm surface waters, that have piled up in the western Pacific, to surge eastwards taking with them the region of heavy rainfall. Thus, the central Pacific, usually an arid zone, receives abnormally high torrential rains. In contrast, eastern Australia and the western Pacific islands, the usual recipients of these rains, experience drought. However, this effect is not restricted to the Pacific, but is linked to similar phenomena in both the Indian and Atlantic Oceans by what has been termed the Southern Oscillation (Philander, 1992),



Figure 1.3 Co-efficient of variation (CV) of mean annual rainfall for the succulent karoo vs. Nama-karoo. Equations for the curves are y = 0.0008148x + 1.71868 and y = 0.0006154x + 1.778731, respectively. The slopes are not significantly different (p = 0.1004) but the intercepts are significantly different (p = < 0.0001)

an irregular, interannual fluctuation in ocean air pressure.

The implications for southern Africa are profound. With the relaxation of the easterly Trades, the inflow of moist tropical air over the subcontinent subsides. Thus, regions of the karoo that rely on this tropical source of moisture, essentially the summer-rainfall karoo, experience abnormally low rainfalls. By contrast, the belt of westerly cyclones that brings winter rain to the region remains unaffected by the Southern Oscillation. This, in part, could explain the differences in reliability of annual rainfall in the Nama- and succulent karoo discussed in the previous section.

# 1.3. Temperature

There are five major characteristics in the distributions of mean annual temperature across the subcontinent (Schulze and McGee 1978):

- an expected overall temperature increase towards the equator;
- isotherms parallel to the coast over most of the area, which exhibit decreasing values with distance inland, reflecting the effects of continentality;
- the effects of the cold Benguela and warm Agulhas currents moving northwards and southwards on the west and east coast, respectively;
- the temperature irregularities induced by topographic variation on the subcontinent, for instance the lower temperatures along the escarpments on the perimeter of the subcontinent (<14 °C) or the higher temperatures along the Orange River valley (>22 °C);
- highest mean annual temperatures which occur in areas with highest continentality, namely the Orange River trough. These areas also experience the greatest range in mean annual temperature (Werger, 1986);

The annual range of temperature shows a matching characteristic with the smallest ranges (<6 °C) along the west coast; and the greatest values (>16 °C) over the southern Kalahari and northern karoo, where the ameliorating effect of cloud is generally absent. High temperatures, low relative humidity and little to no cloud cover is characteristic of the karoo, especially the central areas. This results in large annual and daily ranges in temperature. This is a characteristic of arid climates generally (McGinnis, 1979). The exception is the west coast where there is an abundance of moisture in the air due to the predominately onshore sea breeze, relative humidity is high, and temperature is regulated by the cold Benguela current

The annual march of temperature in the region reflects both the coastal and continental patterns characteristic of the subcontinent. Coastal stations along the west coast generally show a lag of one month in maximum and minimum temperatures; thus, February and August are the two extremes. This is due to the lag in the heating and cooling of the ocean current, which exerts a strong regulating effect on these coastal climates. These coastal stations also show the temperature anomaly of recording their highest maximum temperatures in midwinter due to the sudden heating effect of warm berg winds blowing off the plateau this time of year (Schulze, 1965).

Mean daily minimum temperatures in the region are highest along the west coast and increase equatorwards with again the escarpment and high-lying areas of the plateau showing the coldest minimum temperatures (Schulze and McGee, 1978). In the karoo, the lowest mean minimum temperatures are found towards the centre of the subcontinent, and show the effect of both continentality and altitude (Werger, 1986). With the exception of the

## 10 P. G. Desmet and R. M. Cowling

coastal and northern subtropical Namib Desert, the entire karoo area falls within the line of 50% probability of receiving frosts during winter (Schulze, 1965). High-lying areas of the escarpment and central plateau are especially frostprone.

# 1.4. Cloud and light

At the regional scale, light is not considered limiting to plant growth in the karoo. Skies are normally clear and sunshine is abundant. Cloudiness is normally at a maximum during the morning hours in the winter rainfall areas, including parts of the central Namib (Schulze, 1965), but an afternoon maximum is normal for most of the summer rainfall area. During winter, cloudless conditions in the central karoo may persist for weeks on end.

The average annual duration of bright sunshine is more than 80% of the daylight hours in most of the region. Along the coast of Namibia, the average duration may drop below 50% in some places owing to fog and low cloud (see 1.2.1. *Fog*). Despite the abundance of light, energy for growth is limiting for many organisms growing during the cool winter months of the succulent karoo. Plant traits such as the northward curvature of the stem in *Pachypodium namaquanum* (Rundel et al., 1995), psammophily across a range of genera (Jürgens, 1996) and spiral-surfaced leaves in bulbous monocots, have been suggested as being adaptations to maximizing energy absorption by these winter growing plants (Midgley and Van Der Heyden, this volume).

# 1.5. Wind

The prevailing wind direction along the west coast is parallel to the coast, predominately from the southern quarter. Ecologically, these southerly sea breezes and the frequent warm, dry offshore berg winds play an important driving role in this arid coastal system (Desmet, 1996; Louw and Seely, 1982; Lancaster, 1989). In the western interior, winds in summer are mainly from the south-west and in winter from the north; in the eastern interior they are south-easterly and north-westerly, respectively. Mostly, these winds are dry. Dust devils and small whirlwinds are frequent in the interior in summer, but dust-storms are uncommon except in the coastal belt in winter due to berg winds. In the interior, winds are, for the most part, local in nature, such as valley winds due to local topographic relief (Schulze and McGee, 1978; Werger, 1986).

### 1.5.1. Berg winds

Berg winds are important features of coastal climates and are associated with large-scale pre-frontal divergence and dynamic warming of subsiding air moving offshore from the plateau (Preston-Whyte and Tyson, 1988). Berg winds may blow for several days or only a few hours, and are most common in late winter and early spring. They result in the anomaly of highest maximum temperatures being recorded in winter at many coastal stations. The strong offshore effect of berg winds on the west coast may produce significant dust plumes blowing over the coastal plain, and across the ocean on the west coast. The impact of berg winds on plants is discussed in Von Willert et al. (1992)

### 1.6. The weather systems of the karoo

Reference has already been made to the average atmospheric circulation patterns that determine the climate of southern Africa. In this section we explore some of the major deviations from these average conditions – events that influence the weather of the karoo. This account draws mainly on Preston-Whyte and Tyson (1988), while other sources include Heydorn and Tinley (1980), Schulze (1965) and Tyson (1987).

Throughout the year, the average circulation of the atmosphere over southern Africa is anticyclonic. This subtropical control is effected through the South Indian anticyclone, the continental high and the South Atlantic anticyclone. During winter, this continuous band of high pressure intensifies and moves northwards, while the upper level westerlies expand and displace the tropical easterlies equatorward. During summer, the continental high is displaced by low pressure conditions that arise in response to surface heating, and the oceanic anticyclones move southwards (about 6°), displacing the westerly airstream. Following Preston-Whyte and Tyson (1988), we recognize three categories of circulation patterns that influence the weather of the karoo: (1) fine-weather conditions, (2) tropical disturbances, and (3) temperate disturbances.

# 1.6.1. Fine-weather conditions

### Subtropical anticyclones

These conditions, associated with a strongly subsiding air mass, fine and clear conditions, and no rainfall, prevail over most of the interior plateau (including the bulk of the karoo) during the winter months. Anticyclonic conditions during summer are less common; however, when they prevail for extended periods they result in severe heat waves and desiccation. In the already arid karoo, ecosystems are