The karoo

Ecological patterns and processes

Edited by **W. Richard J. Dean and Suzanne J. Milton**

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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 high-pressure (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

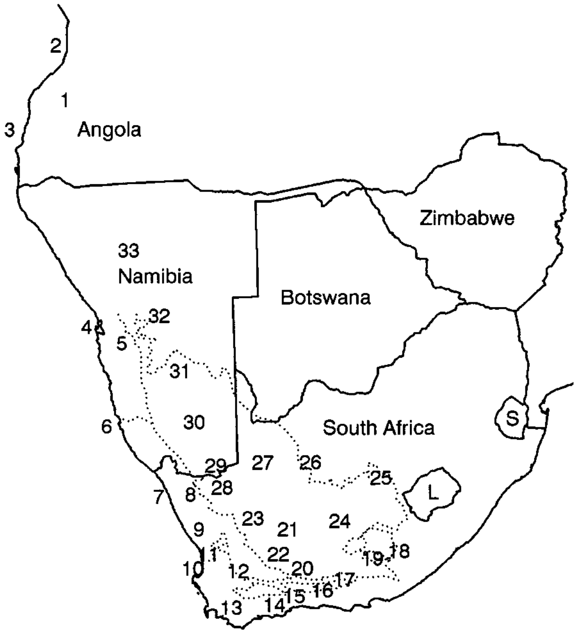


Figure 1.1(a) Map of southern Africa showing the localities of numbered weather stations from which climate data were obtained to generate the climate diagrams shown in Fig. 1.1(b) on p. 6. The boundary of the karoo sensu lato is shown as a dotted line. L = Lesotho, S = Swaziland

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 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).

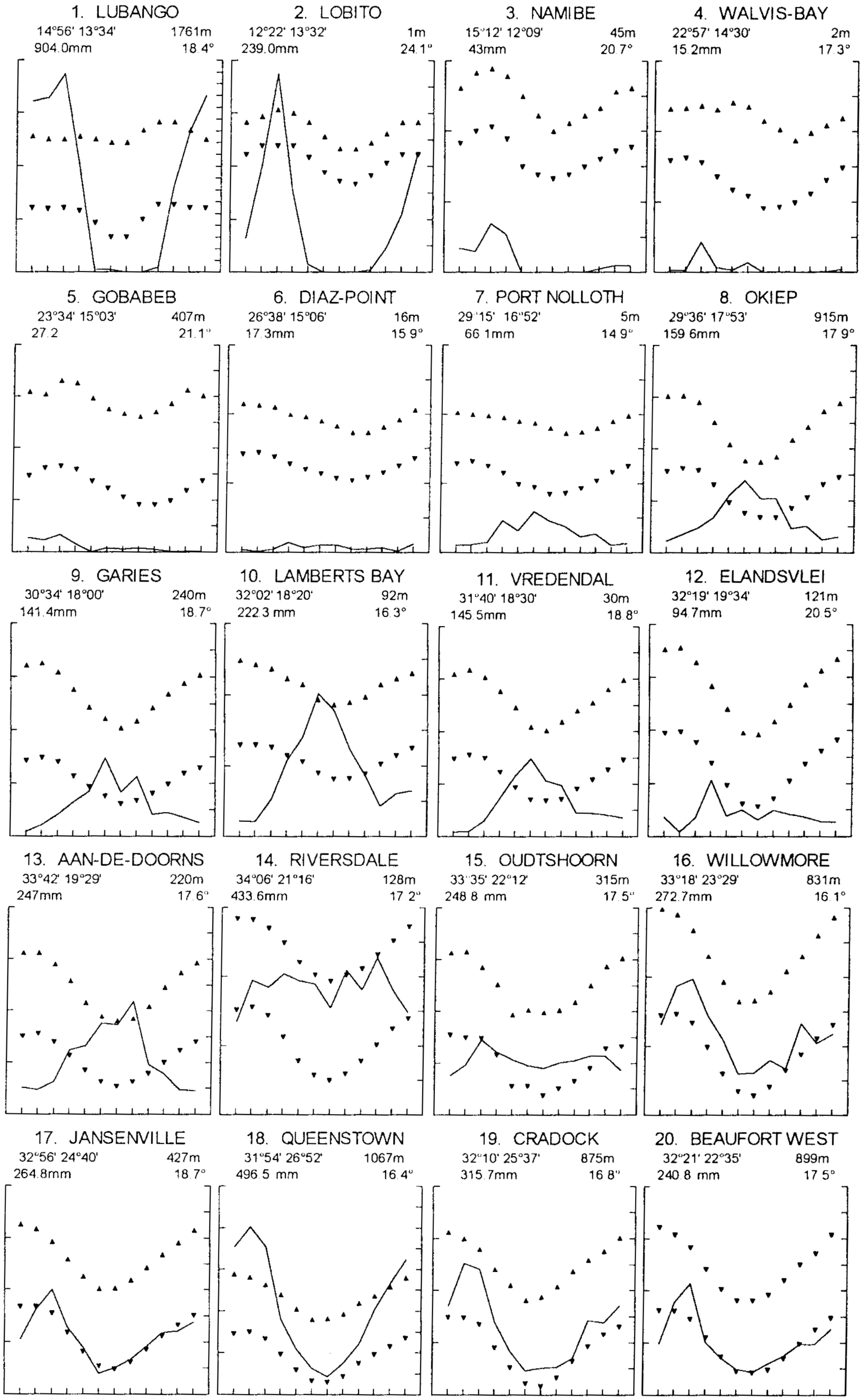
The potential amount of water that can be derived from a fog event, relative to the mean annual rainfall, is substantial. For Swakopmund, with 121 fog days per annum, the amount of water intercepted in 1958 was equivalent to 130 mm of rainfall. More than seven times the mean annual rainfall (Schulze 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


1. LUBANGO
14°56' 13°34' 1761m
904.0mm 18.4°
2. LOBITO
12°22' 13°32' 1m
239.0mm 24.1°
3. NAMIBE
15°12' 12°09' 45m
43mm 20.7°
4. WALVIS-BAY
22°57' 14°30' 2m
15.2mm 17.3°
5. GOBABEB
23°34' 15°03' 407m
27.2 21.1°
6. DIAZ-POINT
26°38' 15°06' 16m
17.3mm 15.9°
7. PORT NOLLOTH
29°15' 16°52' 5m
66.1mm 14.9°
8. OKIEP
29°36' 17°53' 915m
159.6mm 17.9°
9. GARIES
30°34' 18°00' 240m
141.4mm 18.7°
10. LAMBERTS BAY
32°02' 18°20' 92m
222.3 mm 16.3°
11. VREDENDAL
31°40' 18°30' 30m
145.5mm 18.8°
12. ELANDSVLEI
32°19' 19°34' 121m
94.7mm 20.5°
13. AAN-DE-DOORNS
33°42' 19°29' 220m
247mm 17.6°
14. RIVERSDALE
34°06' 21°16' 128m
433.6mm 17.2°
15. OUDTSHOORN
33°35' 22°12' 315m
248.8 mm 17.5°
16. WILLOWMORE
33°18' 23°29' 831m
272.7mm 16.1°
17. JANSENVILLE
32°56' 24°40' 427m
264.8mm 18.7°
18. QUEENSTOWN
31°54' 26°52' 1067m
496.5 mm 16.4°
19. CRADOCK
32°10' 25°37' 875m
315.7mm 16.8°
20. BEAUFORT WEST
32°21' 22°35' 899m
240.8 mm 17.5°

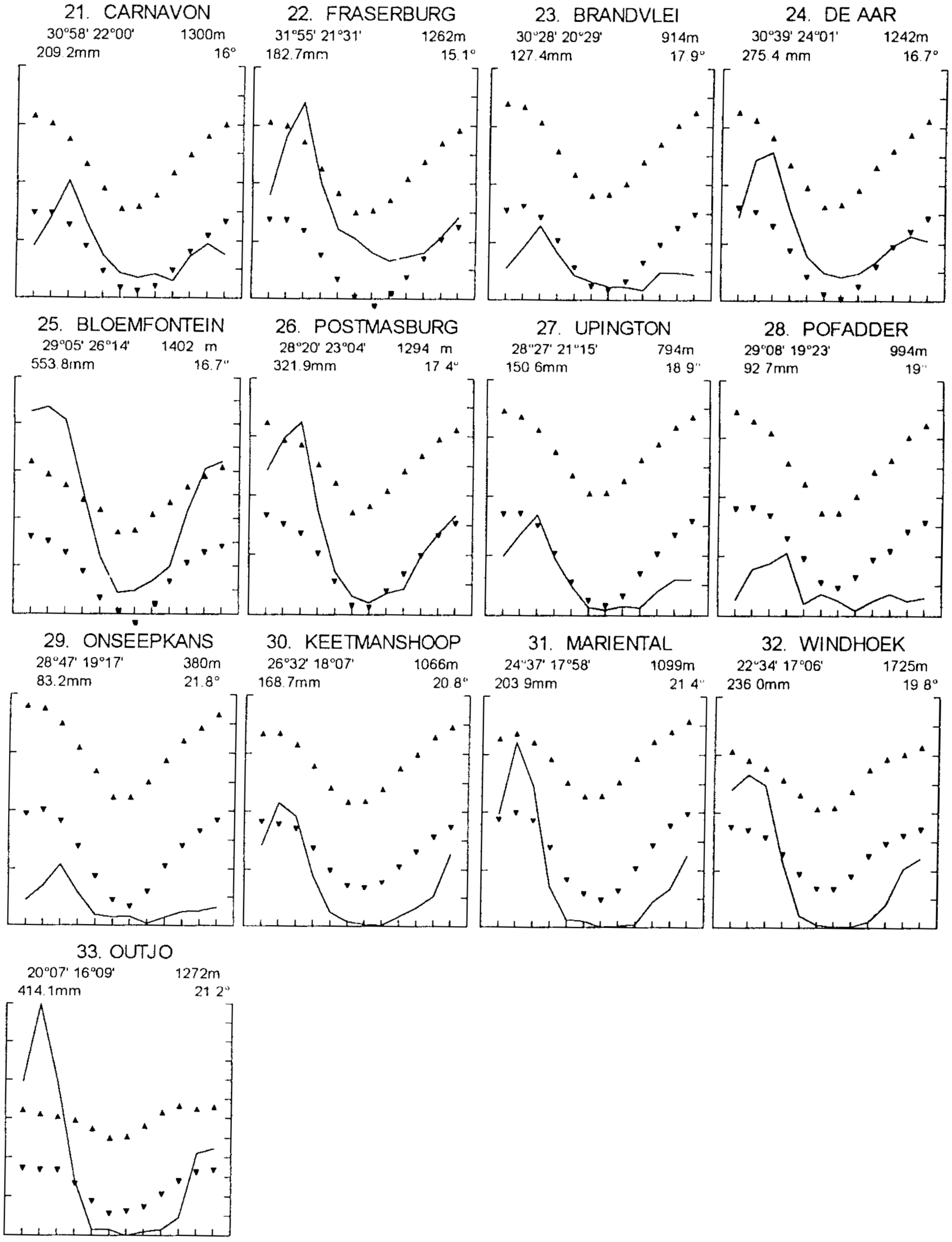


Figure 1.1(b) Climate diagrams for selected weather stations in the karoo and Namib Desert, and surrounding non-arid zone vegetation types. The title for each diagram contains the town name, co-ordinates, altitude (m), mean annual rainfall (mm) and mean annual temperature (°C). Points on each graph represent 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

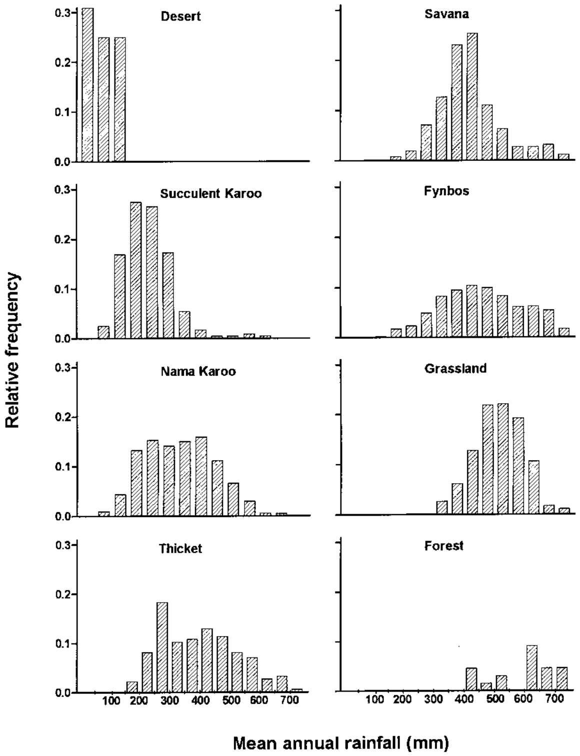


Figure 1.2 The relative frequency distribution of mean annual rainfall for rainfall stations in the arid zone of southern Africa in relation to surrounding biomes. The data used in this figure were obtained from the Computing Centre for Water Research (University of Natal) database for South Africa weather 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 dew-point 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^{-1} 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. Similarily, 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),

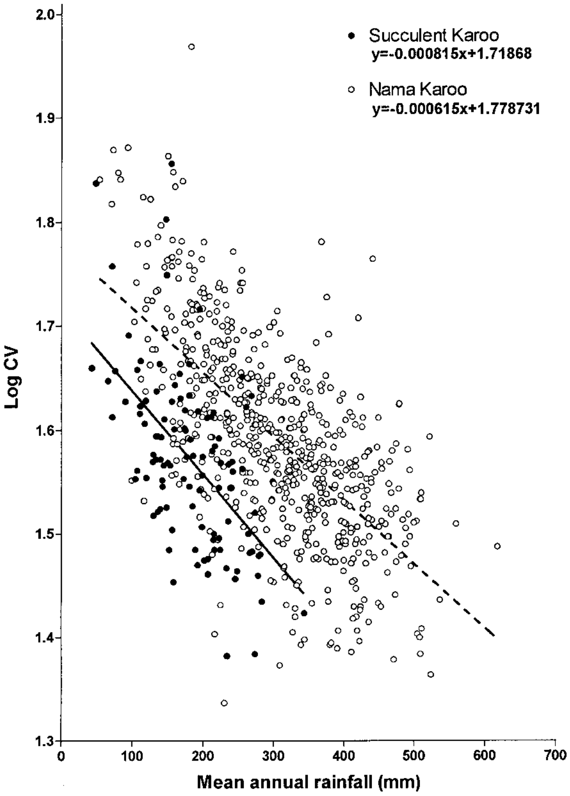


Figure 1.3 Co-efficient of variation (CV) of mean annual rainfall for the succulent karoo vs. Nama-karoo. Equations for the curves are $y = 0.0008148x + 1.71868$ and $y = 0.0006154x + 1.778731$, respectively. The slopes are not significantly different ($p = 0.1004$) but the intercepts are significantly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

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 subject to severe stress when summer heat waves persist for more than a week.

Coastal lows

Coastal lows, which have their highest frequency during the winter months, are associated with the generation of localized cyclonic vorticity as a result of the westward movement of air off the high plateau. They are initiated on the west coast, move southward to Cape Town, and thence eastward and north-eastward along the coast. Like cold fronts, they produce a substantial drop in temperature. However, they seldom result in precipitation other than orographic mist and fine drizzle, usually confined to the coastal margin. Thus, their influence on the climate of the karoo is largely restricted to the arid and semi-arid west and south coast regions (Namib Desert, Namaqualand and Little Karoo).

1.6.2. **Tropical disturbances**

Easterly waves and lows

Easterly waves and lows result from disturbances in the tropical easterly flow, at the junction of the inter-tropical convergence zone and the subtropical high-pressure belt. Moist air, sucked in from the north, is carried upwards by the diverging air mass, resulting in widespread and prolonged rains behind (to the east) the trough. These rains, whose regularity distinguishes abnormally wet years in the summer-rainfall region, have their highest frequency in mid-summer. Ahead of, and to the west of the trough (the region which includes much of the karoo) subsiding air masses ensure no rainfall, clear skies and hot conditions.

Subtropical lows

During summer, when the upper westerly waves are remote, low-pressure cells may develop in the upper troposphere. These conditions are usually associated with heavy rainfall in the central and eastern parts of the subcontinent.

1.6.3. **Temperate disturbances**

Westerly waves

Westerly waves are associated with disturbances in the westerly airstream. To the rear of the surface trough, cloud and precipitation occur in unstable air; ahead of the trough, stable air ensures clear, fine weather. These disturbances, which are rarely observed during winter, have their highest frequency in the spring and autumn months. Rainfall seldom extends inland of the Great Escarpment.

Cut-off lows

Cut-off lows, which have a profound influence on the climate of southern karroid regions, are a more intense form of the westerly trough. The depression starts as a trough in the upper westerlies and deepens, extending downwards to the surface. In doing so, the low is displaced northwards and 'cut-off' from the westerly current. These deep lows are a source of major divergence and account for many flood-producing rains in the southern karroid regions (e.g. the Laingsburg floods of 1981). Cut-off lows have their highest frequency during spring and autumn, but their overall occurrence is highly unpredictable.

Southerly meridional flow

When a deeply penetrating cold front (see *Cold fronts*) is followed by a well-developed high-pressure cell, a strong zonal pressure gradient develops between the two systems. These condition produce a trough in the upper atmosphere which overlies the convergence zone west of the surface trough or cold front. The resulting vertical motion produces rain, usually confined to the coastal seaboard west of Cape Agulhas. Thus, only parts of the Little Karoo are affected by these conditions, which have their highest frequency in the spring months. The southerly meridional flow is also associated with a sharp drop in temperatures over most of the subcontinent, as cold Antarctic air is advected inland.

Ridging anticyclones

When the South Atlantic High ridges around the subcontinent after the passage of a westerly wave in the upper atmosphere, widespread rains often fall in the eastern parts of the subcontinent. This rain results form the steep pressure gradients which advect moist, unstable air over the land. Orographic rain may be particularly intense. In the south-west, subsiding air associated with anticyclonic conditions brings clear, fine and hot weather, often accompanied by strong south-easters. This circulation type brings rainfall to the eastern part of the country throughout the summer months but with a slight tendency for maximum frequencies of occurrence in October and February.

West-coast troughs

Widespread rains over western South Africa occur with the coincident appearance of a surface trough on the west coast and an upper tropospheric westerly wave to the west of the continent. These conditions most frequently (albeit rarely) occur in early summer and autumn.

Cold fronts

Cold fronts are major disturbances in the westerly air stream that produce characteristic cold snaps. They occur together with westerly waves, depressions or cut-off lows, and should not be considered in isolation from these systems. However, they occur most frequently in winter, when the westerly belt penetrates furthest northwards. Ahead of the front, northerly winds associated with divergence and subsidence produce cloud-free conditions. At the rear of the front, conditions favourable for convection result in widespread rain, especially along the west and south-western coasts. Depending on the strength of the front, rain may be very widespread. Snow may fall on high-lying ground. Deep fronts penetrate well beyond the Cape Fold Belt and even the Great Escarpment. Post-frontal conditions are invariably cold and sometimes wet (in the east), especially if the front is followed by a well-developed high pressure cell (see *Ridging anticyclones*).

1.6.4. Other rain-producing systems

Thunderstorms

Much of the rainfall in the eastern, summer rainfall region is of convective origin. Thunder-storm activity is a complex phenomenon, being dependent on the diurnal heating cycle, synoptic conditions and regional and local effects. However, karroid regions, especially along the west coast, experience very few thunderstorms: fewer than 20 thunder days per year are experienced in the western Upper karoo (as opposed to 80 days on the eastern highveld).

Development of the continuous high-pressure cell

At the end of the summer rainfall season, towards the end of March, a single high-pressure cell (linking the South Atlantic and Indian anticyclones) develops over the subcontinent. This results in a northerly flow of moist air from the tropics over the western parts of southern Africa, including much of the karoo. The influx of moist air is largely responsible for the autumn rainfall maximum for these arid, western regions.

1.7. An ecological interpretation of the weather patterns of the karoo: the role of climate in understanding vegetation patterns

Previous analyses of the climate of southern Africa have failed to provide a convincing classification of the climate, i.e. one that provides an adequate and meaningful biogeographical subdivision of the subcontinent. In this section, we do not attempt a comprehensive reclassification of the subcontinents' climate, but instead present a new analysis of the climate of the karoo to stress the driving role that climate plays in determining landscape-scale vegetation patterns.

The availability of water is generally considered as the greatest limitation of plant growth and distribution (Woodward, 1987). There have been a number of classifications of southern Africa's climate, the most well known are probably those of Köppen, Holdridge and Thornthwaite. No attempt is made here to discuss these classifications further, as these have been adequately reviewed elsewhere (Schulze, 1947; Preston-Whyte, 1974; Schulze and McGee, 1978).

Other biogeographic climatic classifications of southern Africa include those of Jackson (1951), Preston-Whyte (1974) and Rutherford and Westfall (1986). In all cases, rainfall emerges as the primary driving variable. More importantly, though, the distinction between summer and winter rainfall maxima has emerged as the primary explanatory variable (Preston-Whyte, 1974; Rutherford and Westfall, 1986). The bulk of this chapter has been aimed at providing ecologist with a functional understanding of rainfall patterns in the karoo.

Consequently, the models produced attempt to summarize the range and variation in rainfall in a few meaningful indices. Such indices include the usual descriptive statistics of climate (e.g. mean annual rainfall, percentage winter rainfall, mean monthly temperature, etc.); climatic indices such as the summer aridity index (SAI) (Rutherford and Westfall, 1986) or Thornthwaite's climatic indices (Schulze, 1947; Schulze and McGee, 1978); and CV (Jackson 1951). These indices fail to integrate a number of important features of the regions' climate. These features are firstly, the lower, more variable rainfall expected in an arid zone (e.g. summer aridity index). Secondly, the three dimensions of the annual march of rainfall discussed earlier that arise as a result of the different weather systems influencing the regions' climate. Thirdly, the variability in occurrence and intensity of individual rainfall events. Consequently, the analyses fail to produce a climatic map of southern Africa that adequately explain plant biogeographic patterns. In the following sections, we have attempted to address these problems.

In addition to moisture, temperature needs to be considered. Temperature alone is not a significant factor in determining major regional vegetation patterns, although its indirect influence on water availability through its effects on, for instance, evapotranspiration rates is of primary importance (Schulze and McGee, 1978). On a meso- or micro-scale it does play a major part in determining plant patterns; this scale of variation will not be adressed here. Critical temperature indices therefore, like summer and winter maxima and minima (and associated frosts) or ranges are of more significance to plant distribution. The important distinction between temperature and rainfall patterns is that the annual march of temperature follows a relatively simple curve, readily tractable with these summary statistics.

1.7.1. The model

In our analyses, we have not attempted to provide a detailed classification of karoo climates, but have rather emphasized the intimate link between landscape vegetation patterns and climate. This classification differs significantly from previous efforts principally in the manner in which rainfall is incorporated into the analysis. Instead of using solely descriptive statistics (means or CV) or climatic indices (SAI), we use a novel approach of fitting the monthly rainfall data to a mathematical model to approximate the actual shape of the annual march of rainfall. Thus, it is possible to explicitly incorporate, in a relatively few values (model parameters), all three dimensions of the annual march of rainfall. What we fail to incorporate, however, is the variability between individual rainfall events, as this would require a considerably greater amount of time for collation of the raw data.

$$Y = k + (c1.\cos q_i + s1.\sin q_i) + (c2.\cos 2q_i + s2.\sin 2q_i) + (c3.\cos 3q_i + s3.\sin 3q_i)$$

Monthly rainfall and temperature data for all karoo weather stations (with both rainfall and temperature data) were extracted from the Computational Center for Water Research (CCWR). Additional data for Namibia and Angola were obtained from the South African Weather Bureau and Lebedev (1970). The monthly rainfall data for each station was fitted to Equation 1, where, y represents mean monthly rainfall; and, q_i the month expressed in degrees, such that January equals 15°, February 45°, March 75°, etc. Thus, for the ordination, rainfall was represented by the above seven parameters (k, $c1$, $s1$, $c2$, $s2$, $c3$, $s3$); plus, the amount of summer (September to March, **summer**) and winter (March to September, **winter**) rainfall; percentage winter rainfall (% **winter**); and, total annual rainfall (**avg rain**).

Temperature, on the other hand, is comparatively simple to model. Temperature does not show the same degree of plasticity as rainfall. Generally, it is easily represented by a simple sinusoidal curve. Thus, descriptive variables such as mean annual maximum (**avg max**) and minimum (**avg min**); and highest maximum (**max**) and lowest minimum (**min**) temperature, adequately describe the annual march of temperature. All these variables, except average annual temperature were used in the analysis.

The final data set with 100 weather stations and 15 climatic variables were subjected to correspondence analysis (CA). The eigenvalues and percentage variance explained for the first four axes of the ordination are presented in Table 1.1. The ordination of the first and second axis and first and third are presented in Figs. 1.4(a) and 1.4(b), respectively.

Table 1.1. *Eigenvalues and cumulative percentage variance explained for the first four axes of the correspondence analysis of the climate data for the karoo*

Axes	1	2	3	4	Total inertia
Eigenvalues	0.094	0.038	0.013	0.009	0.177
Cumulative percentage variance of climate data	53.4	75.2	82.7	88.0	

The first axis of the ordination is representative of seasonality of rainfall and explains most of the variance in the data. Percentage winter rainfall clearly separates the Succulent from the Nama-karoo. This axis also correlates well with the type of rainfall curve, where $c1$, $s1$ and $s2$ are indicative of summer maxima regimes; and, $c3$ and $s3$ with winter maxima. $c2$ represents bimodal rainfall curves and lies near the origin of the axis. Stations lying far from the first axis have less distinct rainfall curves tending towards aseasonal rainfall types. The second and third axes separate stations based on temperature. The results are discussed with regard to the vegetation types in the following section.

1.7.2. Discussion: vegetation–climate relationships

This analysis has shown a clear and effective separation of karoo climate stations that is consistent with a biome-level, and, to a lesser degree, vegetation type-level classification. In this section we discuss the relationships between vegetation and climate, with special emphasis on the weather systems presented in section 12.

Succulent karoo

At the biome scale, succulent karoo sites separate from the rest on the basis of low annual rainfall (Fig. 1.2), high percentage winter rain, high absolute and average minimum temperatures, and parameters from the non-linear regression model associated with strong winter peaks ($c3$ and $s3$) in the annual march of rainfall (Figs. 1.4(a) and 1.4(b)). Some of these associations have been described by many authors in the past (Werger, 1986; Rutherford and Westfall, 1986; see also Cowling and Hilton Taylor, this volume). However, little attempt has been made to explain these patterns in terms of the frequency and reliability of occurrence of the prevailing weather systems. This we do below.

The entire succulent karoo receives its rainfall from weather systems associated with disturbances in the westerly stream. The three western vegetation types of the Namaqualand–Namib Domain (Cowling and Hilton Taylor, this volume), namely strandveld, lowland and upland succulent karoo, receive the bulk of their rain from cold fronts during the winter months. Peak occur-

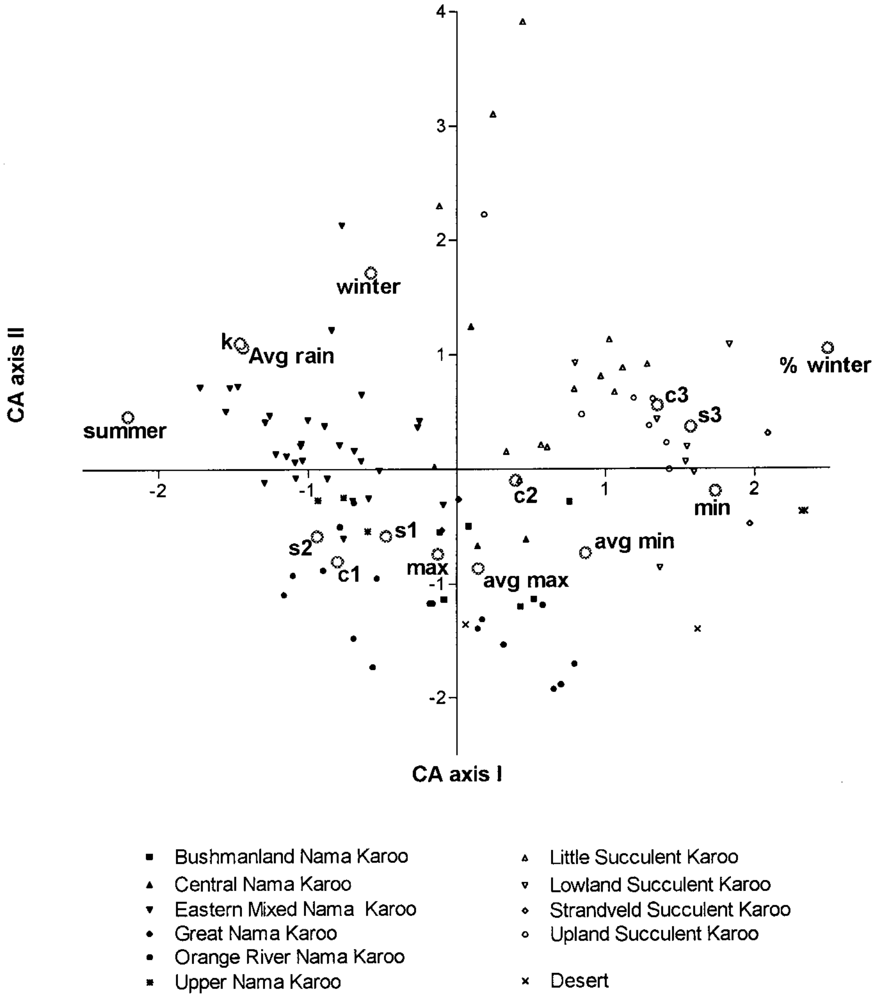


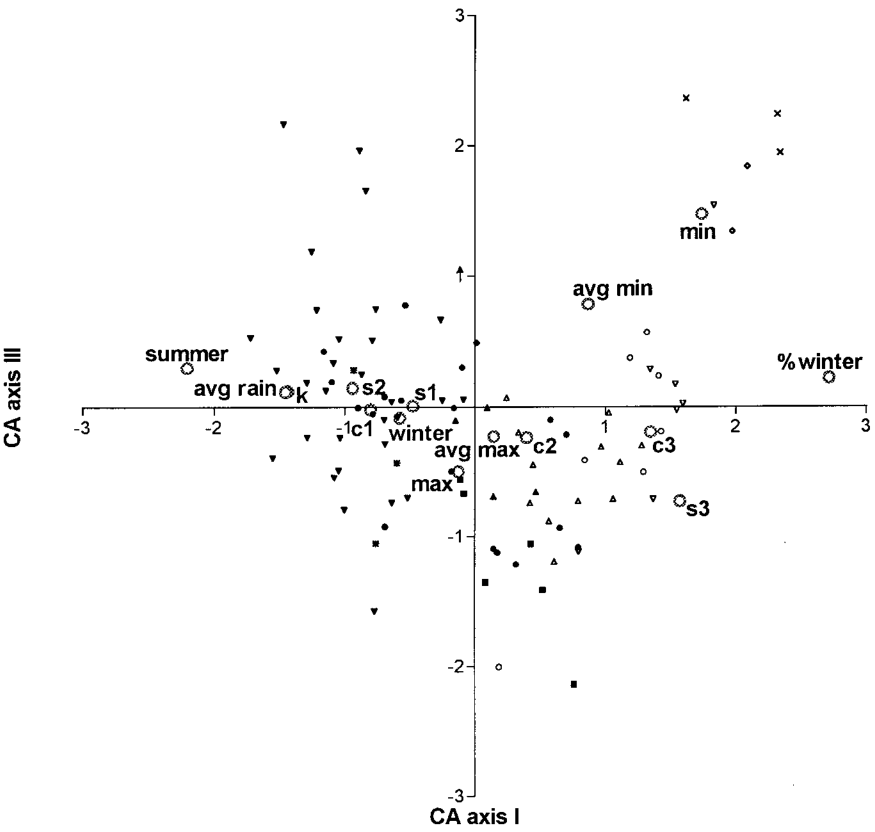
Figure 1.4(a) Ordination axes I and II of weather stations in the karoo. See text for explanation of climatic parameters

rence of fronts, and hence rainfall, is during the mid-winter months (Fig. 1.1(b)). In southern Africa, the equatorwards penetration of the westerly airstream is greatest among all continents (Preston-Whyte and Tyson, 1988); hence the high frequency and reliability of winter rainfall events in both a regional (Fig. 1.3) and global context (Esler et al., this volume).

The two strandveld succulent karoo stations were separated on the basis of highest percentage winter rain and highest minimum temperatures. These coastal sites receive almost no summer rain and are under the ameliorating influence of the Atlantic Ocean. The remaining sites show a clear trajectory in the multivariate graph, associated with increasing annual, summer, and winter rainfall. In geographical space this gradient moves in an easterly (lowland to upland succulent karoo) and south-easterly (Little Succulent Karoo) direction. The former areas receive more, albeit unpredictable warm season (mainly February-April) rainfall associated with west-coast troughs, thunderstorms and the autumnal northerly flow of moist, tropical air (see 1.6.4. *Development of the continuous high-pressure cell*). Higher altitudes result in a more pronounced continentality.

The Little Succulent Karoo covers a large tract of multivariate space. This is consistent with its location as transitional between winter and summer rainfall conditions. Some sites cluster near upland succulent karoo, others near central and eastern Nama-karoo in the south and south-eastern karoo regions, respectively (Figs. 1.4(a) and 1.4(b)). While the Little Karoo does receive a substantial proportion of its rain from winter, westerly fronts (Fig. 1.1(b)), most frontal rains fail to penetrate the barriers afforded by the Cape Fold Belt. The largest rainfall events in the Little Karoo are invariably associated with the less predictable cut-off lows, westerly waves, southern meridional flows, and ridging anticyclones. These systems generally have their highest frequency of occurrence in spring and autumn, thus explaining the bimodal peaks in the annual march of rainfall (Fig. 1.1(b)). This is also consistent

Figure 1.4(b) Ordination axes I and III of weather stations in the karoo. See text for explanation of climatic parameters. Symbols for stations correspond to those used in Fig. 1.4(a)



with the non-linear regression parameter which describes bimodal rainfall curves, c2, located in the centre of the ordination diagrams (Figs. 1.4(a) and 1.4(b)). The relatively strong association between Little Karoo sites and the amount of winter rainfall stems from our delineation of winter to include March and September, prime months for equinoctial rains associated with the weather systems mentioned above. Indeed, the proximity of total winter and summer rainfall in the ordination space (Fig. 1.4(a)) is a result of the inclusion of these months in delineating both seasons, and the fact that many karoo sites receive substantial equinoctial rain (Fig. 1.1(b)).

Nama-karoo

Nama-karoo sites are associated with higher maximum temperatures, bimodal (*c*2) or strongly seasonal (*c*1, *s*1) rains, and, for some areas at least, relatively high rainfall, especially during summer (see also Rutherford and Westfall, 1986).

The eastern mixed Nama-karoo, which grades into the grassland biome of the east-central plateau of South Africa, is largely distinguished on the basis of higher rainfall, especially during summer (Figs. 1.4(a) and 1.4(b)). This vegetation receives a great deal of its rainfall from tropical disturbances during the summer months. However, equinoctial rains associated with cut-off lows, etc. are also important, as are winter rains (and snowfalls) derived from occasional, deep cold fronts. Being centrally located, this vegetation type receives the fringe of all major weather systems in southern Africa.

The remaining Nama-karoo vegetation types are separated from eastern mixed Nama-karoo by stronger bimodality (central Nama-karoo), stronger seasonality (upper Nama-karoo), higher maximum temperatures (Orange River Nama-karoo), and higher maximum and higher minimum temperatures (Bushmanland Nama-karoo). With the exception of the central Nama-karoo sites which receive their rainfall from the same weather systems as the eastern mixed karoo, these more western Nama-karoo areas receive their largely autumnal rains (Figs. 1.4(a) and 1.4(b)) from west-coast troughs, thunderstorms and late-season influx of tropical air. The occurrence of these rainfall events is highly unpredictable. The combination of low and unpredictable rainfall, and extremely high summer temperatures, makes these some of the harshest environments in the karoo.

Desert

Rather than a biogeographically and climatically delineated region, the Namib Desert is a loosely defined geographical area (Jürgens, 1991; Cowling and Hilton Taylor, this volume). This is evident from the large range of multivariate space occupied by the four desert sites used in this analysis (Figs. 1.4(a) and 1.4(b)). Low-rainfall coastal sites in the central Namib (Luderitz and Walvis Bay) are closely clustered with strandveld succulent karoo, regarded by many (e.g. Jürgens 1991; Desmet, 1996) as a southern extension of the Namib Desert. Closely related to these two sites is Namibe in southern Angola. The fourth site, Lobito, at the most northern extremity of the Namib cannot be separated from Orange River Nama-karoo and can be regarded as having a similar climate (Fig. 1.1(b)).

In the context of the arid zone of southern Africa, the Namib is a special case, as the hyper-arid conditions that prevail are regarded as a palaeo feature (Ward et al., 1983). This is due to a permanent temperature inversion over cold Benguela current and adjacent landmass. As a result, warm air-currents from the east are blocked and the daily south-westerly sea breeze dominates, bringing cool, humid air (Walter, 1986). Thus, the core area of this climatic zone has remained stable in the face of the palaeo climatic fluctuations that affected other parts of the karoo. The consequences for the evolution of life forms unique to this system are discussed elsewhere (Cowling and Hilton-Taylor, this volume; Vernon, this volume).

1.8. Conclusions

Two-thirds of southern Africa have an arid to semi-arid climate, but the causes of this aridity are varied. Generally, aridity of the subcontinent is due to the presence of subtropical descending air (high-pressure cells), although the Namib Desert is a special exception. Higher rainfall regions in the karoo are due to the penetration of tropical systems (north-east) and regular penetration of westerly fronts and associated weather systems (south-west). The remainder of the region is located in a position that is marginal to these systems. Aridity is most pronounced along the west coast, but the succulent karoo has most reliable rainfall. Aridity is least pronounced to the north-east where the karoo grades into grasslands, and central areas have the least reliable rainfall and most extreme energy conditions. The great diversity of climatic determinants and associated patterns must play a pivotal role in the extremely varied patterns and processes associated with the biota of the karoo.