

Introductory paper

Namaqualand, South Africa – an overview of a unique winter-rainfall desert ecosystem

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Abstract

Namaqualand is a winter-rainfall desert of some 50 000 km², located in north-western South Africa. For a desert ecosystem, the region is characterized by a unique selective regime, namely highly predictable annual rainfall and a moderate temperature regime throughout the year. This selective regime is responsible for the unique plant ecological features of Namaqualand. These include: the dominance of communities by dwarf to low, shallow-rooted, short-lived and drought-sensitive leaf succulent shrubs; high abundance and diversity of geophytes; winter growth phenology; regular and spectacular spring flowering displays; rapid population turnover of perennials; weak competitive interactions; and high local and regional plant diversity. This paper provides a physiographical, biogeographical and ecological overview as background to this special issue. First, we outline the physiography and climate of Namaqualand, emphasizing unique components of its selective regime. Next we discuss the region's phytogeographical and floristic characteristics. Then we summarize what is known about plant form and function, focusing on growth form mix, phenology, carbon gain, water relations, and reproduction in vegetation dominated by leaf-succulent shrubs. Finally, we interpret Namaqualand's uniquely rich and dynamic plant communities in terms of plant functional processes. These plant ecological patterns and processes are discussed in terms of the predictions of a simple conceptual model for succulent-rich communities.

Introduction

Warm desert ecosystems (Evenari et al. 1986) occupy approximately 47% of the Earth's surface (Thomas & Singhvi 1993) and are coming under increasing pressure from human population growth, habitat degradation and other components of global change (Karrar & Stiles 1984, Stiles 1984; Ojima et al. 1994), especially in Africa (Ellis & Galvin 1994; Hulme 1996). Given the strong likelihood of an imminent and rapid escalation in temperatures globally, and the concomitant increase in climatic uncertainty, warm deserts may provide genetic stock essential for the survival of humankind in future decades. It is, therefore, important

to develop a predictive understanding of desert ecosystem structure and function at all levels of integration.

Over the past few decades, many volumes on desert ecology have appeared (e.g., Evenari et al. 1986; Polis 1991). None of these has identified South Africa's Namaqualand desert as exhibiting ecological features that are in any way unusual. However, when compared with other warm desert ecosystems of the world, Namaqualand has many unique biological features. Only relatively recently have these attracted the attention of researchers (Edwards & Werger 1981; Jürgens 1986; Cowling et al. 1994; 1998; Ihlenfeldt 1994; Esler et al. in press), despite a relatively long history of research in the region (see Milton et al. 1997, for a review).

The purpose of this special issue of *Plant Ecology* is to introduce some of the interesting plant ecological patterns and processes in Namaqualand to a wider audience of international scholars. This introductory paper provides the plant biogeographical and ecological context for the other contributions. We also present a model outlining key responses of plant individuals and communities to Namaqualand's unique selective regime (see also Esler et al. in press).

Physiography and climate

What is Namaqualand?

Namaqualand is formally defined as a magisterial district within the old Cape Province of South Africa. Here we define it (Figure 1) in physiographical and biogeographical terms as the strongly winter-rainfall part of southern Africa's Succulent Karoo biome (Rutherford & Westfall 1986; Milton et al. 1997). This zone is now recognized as the Namaqualand-Namib Domain of the Succulent Karoo floristic region (Jürgens 1991). We exclude from our concept those parts of the Namaqualand District east of the Great Escarpment (i.e., parts of the inselberg-studded sandy expanse known as Bushmanland which falls within the largely summer-rainfall Nama-karoo biome (Palmer & Hoffman 1997)). We also exclude the largely unexplored Sperregebied, the southern winter-rainfall portion of the Namib Desert between the Orange River and Luderitz in southern Namibia (Jürgens et al. 1997). Technically, this area falls within the Namaqualand-Namib Domain; however, almost no research has been conducted there. Following Le Roux & Schelpe (1988), we include the Knersvlakte or Vanrhynsdorp Centre in our concept of Namaqualand (Figure 1, see below). Thus, our delimitation encompasses an area that extends from the Olifants River and sandstone-capped Bokkeveld Mountains in the south and south-west (the northern boundary of the Fynbos biome), and includes all the area from the Atlantic coast to a line that runs from the vicinity of Loeriesfontein, along the inland margin of the escarpment, to the Orange River east of the border post at Vioolsdrift, and thence to its mouth at Alexander Bay – an area of approximately 50 000 km². By comparison, the winter-rainfall Mojave Desert encompasses about 124 000 km² (Rundel & Gibson 1996)

Geology and landscapes

The geology of Namaqualand is extremely complex (Meadows & Watkeys in press) The mountainous desert in the north-west – the Richtersveld (Figure 1, Table 1) – comprises a varied sequence of pre-Gondwanan rocks (ca. >2.5 billion years old) that were extensively intruded, at least a billion years ago, by granite and gneiss of the Namaqua Metamorphic Province. The escarpment zone to the south is almost entirely composed of the majestic bornhardts, nubbins and castle koppies derived from the erosion of these metamorphic rocks. This region is locally known as the Hardeveld. The highest peaks of this granitic landscape, and indeed, in all of Namaqualand, range between 1200 and 1700 m; these relatively moist and cool uplands are known as the Kamiesberg. The colluvial soils that form an apron at the base of the granite-gneiss outcrops are dotted with heuweltjies – mima-like mounds of biogenic origin (Lovegrove & Siegfried 1986, 1989; Dean & Milton in press). After this granitic intrusion, sedimentary rocks of the Gariep, Numees and Nama Formations were deposited between 900 and 500 million years ago in a rift basin that extended along much of the present west coast of Africa – the so-called Pan African Belt (Martin 1965). These rocks, which were violently folded and sheared during the assembly of Gondwanaland, are extensively exposed in the Richtersveld. They also form the wide floor of the palaeo-Orange River delta where weathering of quartz veins has deposited large expanses of white pebbles in an area known as the Knersvlakte (Schmiedel & Jürgens 1999). The Orange, southern Africa's largest river, now enters the sea several hundred kilometers to the north where it forms the border between Namibia and South Africa.

The level coastal plain (the Sandveld) consists of a complex sequence of marine and wind-blown sands ranging from weathered and fine-grained deposits of late Tertiary age to the recent white and calcareous sands of the coastal margin (Desmet 1996; Desmet & Cowling 1999). Most of this sandy landscape is underlain by hardpans of siliceous (dorbank) or calcareous (calcrete) material; outcrops of silcrete of Tertiary origin are also exposed in places (Partridge 1997).

Climate

Namaqualand is a relatively mild desert where extremes are tempered by its proximity to the cold, upwelled waters of the Benguela Current (Desmet & Cowling in press). Annual rainfall varies from about

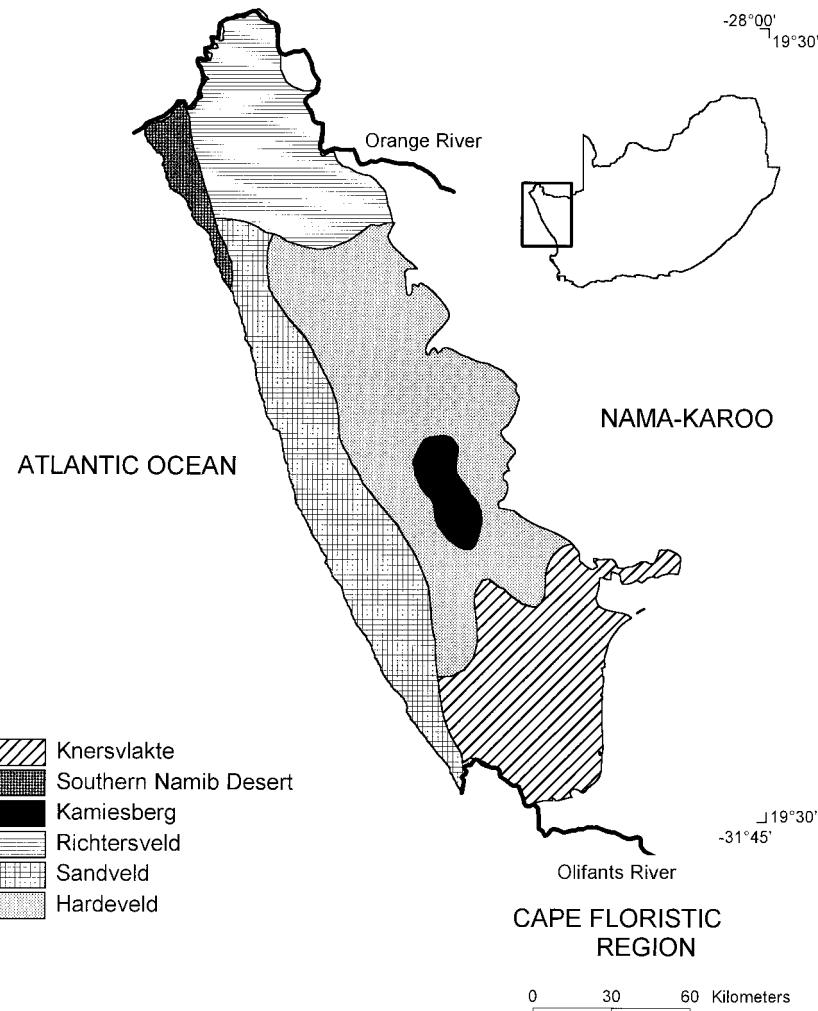


Figure 1. Location of Namaqualand showing delimitation of bioregions according to Hilton-Taylor (1996).

50 mm in the north-west to more than 400 mm in the Kamiesberg (Table 1). Most of the area, however, receives a winter rainfall of less than 150 mm per annum. Interestingly, this low rainfall is highly predictable (Hoffman & Cowling 1987) and prolonged droughts are very rare (Desmet & Cowling in press). The high rainfall reliability of Namaqualand, even relative to other winter-rainfall deserts of the world (Esler et al. in press), is a unique feature and underpins many of the biologically unusual patterns and processes of the region (Hoffman & Cowling 1987; Werger & Morris 1991; Cowling et al. 1994, 1998), including many of those described in this issue (Desmet & Cowling 1999; Esler & Rundel 1999; Jürgens et al. 1999; Rossa & von Willert 1999; Schmiedel & Jürgens 1999; Stock et al. 1999). Along the coastal margin and in

the escarpment foothills, the meager rainfall is supplemented by highly predictable coastal fog. Owing to high humidity and relatively cool nocturnal temperatures, copious dewfalls are widespread (Desmet & Cowling in press), even in the summer months (von Willert et al. 1992). Temperatures are relatively mild throughout the year, especially along the coast (Desmet 1996). Occasional frosts occur on upland peaks and the highest temperatures of about 40 °C are usually recorded in winter when hot, turbulent air, known as ‘berg winds’, descends coastward from the high-altitude plateau of southern Africa. These conditions, especially when they persist for several days, have a profound effect on plant life (von Willert et al. 1992; Rossa & von Willert 1999).

Table 1. Characteristics of bioregions in Namaqualand (after Hilton-Taylor 1996). ND = no data.

Bioregion	Area (km ²) ¹	Annual rainfall (mm)	Geology	No. endemic spp ²	Major vegetation types	
					Acocks (1953)	Low and Rebelo (1996)
Southern Namib Desert	1208	20–60	Recent-Tertiary sands; gravel plains; sheared and folded sediments of the Pan African Belt	ND	Strandveld; Succulent Karoo	Strandveld Succulent Karoo; Lowland Succulent Karoo
Richtersveld (Gariep Centre)	7235	30–300	Sheared and folded sediments of the Pan African Belt; granite-gneiss intrusions	336 ³	Namaqualand Broken Veld; Succulent Karoo; Western Mountain Karoo;	Lowland Succulent Karoo; Upland Succulent Karoo; North-western Mountain Renosterveld
Hardeveld (Namaqualand Rocky Hills)	19 229	100–200	Granite-gneiss of the Namaqualand Metamorphic Province	201	Succulent Karoo Namaqualand Broken Veld	Lowland Succulent Karoo; Upland Succulent Karoo; North-western Mountain Renosterveld
Kamiesberg	1211	200–400	Granite-gneiss of the Namaqualand Metamorphic Province	79	Namaqualand Broken Veld Mountain Renosterveld Fynbos	Upland Succulent Karoo; North-western Mountain Renosterveld; Mountain Fynbos
Sandveld	11 676	50–150	Recent-Tertiary sands	ND	Strandveld Succulent Karoo	Strandveld Succulent Karoo; Sandplain Fynbos
Knersvlakte (Vanrhynsdorp Centre)	9549	100–200	Pan African Belt sediments; Recent-Tertiary sands	138	Succulent Karoo; Strandveld	Lowland Succulent Karoo; Strandveld Succulent Karoo; Sandplain Fynbos

¹Excludes areas of bioregions (Gariep and Southern Namib Desert) in Namibia. ²Includes subspecific taxa. ³Includes Namibian portion of the bioregion.

Biogeography and flora

Biogeographical units and delimitation

The phytogeographical delimitation of southern Africa's arid lands is shrouded in controversy. Here we provide a brief overview of recent efforts to place Namaqualand in a coherent biogeographical context.

According to White (1976, 1983) and Werger (1978a), Namaqualand forms part of southern Africa's Karoo-Namib phytochorion, which, in turn, is part of the Palaeotropical Kingdom as opposed to the Cape Kingdom. Werger (1978b) did, however, emphasize the transitional nature of the region's flora, with strong Sudano-Zambezian (subtropical) affinities towards its northern and eastern boundaries, and strong Cape (temperate) affinities towards the southwest. Werger

(1978a) recognized four domains within the Karoo-Namib region (Namib, Namaland, Western Cape and Karoo). The Namib Domain includes the hyper-arid and arid Namib Desert, stretching from Alexander Bay at the mouth of the Orange River to 150 km south of Lobito in Angola. It thus includes the extreme northern part of Namaqualand as defined here. Werger's (1978b) Namaland Domain (erroneously labeled Namaqualand Domain in the map on p. 158) is centred on the elevated, shrub-covered plateau of Namaland in Namibia, but also includes the narrow escarpment zone inland of the Namib Domain, and, as a clearly defined sub-domain, the sandy flats of the southern Kalahari. The Western Cape Domain, which includes Namaqualand as we define it, corresponds to the predominantly winter-rainfall part of the Karoo-Namib

Region, in which leaf succulent shrubs predominate. The Karoo Domain comprises the extensive area of dwarf, grassy shrubland on the summer rainfall, inland plateau of South Africa.

Using distribution data for 1700 species, Jürgens (1991) developed a new phytogeographical subdivision of southern Africa's arid lands (Figure 2). Those aspects of his scheme that have implications for the phytogeography of Namaqualand are summarized below:

- The division of the Karoo-Namib Region into two phytochoria of equal rank, namely the Succulent Karoo Region (more-or-less coincident with Werger's (1978a) Western Cape Domain) and the Nama Karoo Region.

- The recognition that the Succulent Karoo Region forms part of a Greater Cape Floristic Region rather than part of the Paleotropical Kingdom, which includes his Nama Karoo Region (see Hilton-Taylor 1987; Desmet & Cowling 1999).

- The recognition of a new system of domains in both regions, delimited on the basis of the distribution of species from zonal vegetation complexes. The Namaqualand-Namib Domain (strongly winter rainfall) and the Southern Karoo Domain (non-seasonal rainfall) are recognized for the Succulent Karoo Region.

- The division of the Namib Desert (as a geographic entity) into two phytochoria: a south-central coastal portion as part of the Succulent Karoo (Namaqualand-Namib Domain); and a northern and inland zone as part of the Nama Karoo (Namib Subdomain of the Namaland Domain) (see also Robinson 1978).

The Namaqualand-Namib Domain has been further divided into a series of bioregions, some of which correspond to pronounced centres of endemism (Le Roux & Schelpe 1988; Hilton-Taylor 1996, Figure 1). Salient characteristics of these regions are summarized in Table 1.

Composition and characteristics of the flora

Like other floras of the Succulent Karoo Region (Cowling & Hilton-Taylor in press), the flora of Namaqualand is unusually rich and compositionally interesting (Tables 2 and 3). Preliminary data (vascular plants only) indicate 2750 species and infraspecific taxa, 648 genera and 107 families for the region. (A. Le Roux & C. Boucher unpubl. data). The tally for the taxonomically problematic Mesembryanthemaceae (Mesembryanthema, Aizoaceae *sensu* Bit-

Table 2. Number of species (including subspecies and varieties) in the largest 15 families in the Namaqualand flora. Unpublished data of A. le Roux.

Family	No. spp (% total)
Asteraceae	445 (16)
Mesembryanthemaceae ¹	348 (13)
Poaceae	157 (6)
Scrophulariaceae	140 (5)
Iridaceae	138 (5)
Fabaceae	131 (5)
Crassulaceae	113 (5)
Hyacinthaceae	97 (4)
Asclepiadaceae	85 (3)
Aizoaceae	80 (3)
Geraniaceae	56 (2)
Oxalidaceae	54 (2)
Sterculiaceae	47 (2)
Amaryllidaceae	41 (1)
Euphorbiaceae	40 (1)

¹Data for Mesembryanthemaceae are incomplete.

trich & Hartmann (1988)) is almost certainly incomplete. Overall endemism is unknown, but is generally higher than 50% for large genera of succulent shrubs and geophytes (Table 3, see also Cowling & Hilton-Taylor 1994; Hilton-Taylor 1996; Desmet & Cowling 1999).

Succulent Karoo floras, including that of Namaqualand (Table 2), are uniquely characterized among arid land floras by high numbers of Mesembryanthemaceae (a family largely endemic to southern Africa and overwhelmingly concentrated in the Succulent Karoo (Hartmann 1991)), and relatively high numbers of Iridaceae and Geraniaceae (Cowling & Hilton-Taylor in press; Desmet & Cowling 1999). The two last-mentioned families are well represented in all Cape Region floras, and the Mesembryanthemaceae rank highly in those from relatively xeric lowland and inland areas (Cowling & Holmes 1992). Succulents are extremely well represented in the Namaqualand flora and are associated with many of the larger families (Mesembryanthemaceae, Asteraceae, Crassulaceae, Geraniaceae, Euphorbiaceae and Asclepiadaceae) (Table 2). Indeed, Namaqualand probably harbours about 10% of the world's approximately 10 000 succulent species (Van Jaarsveld 1987). With about 480 species, the area is also home to an unusu-

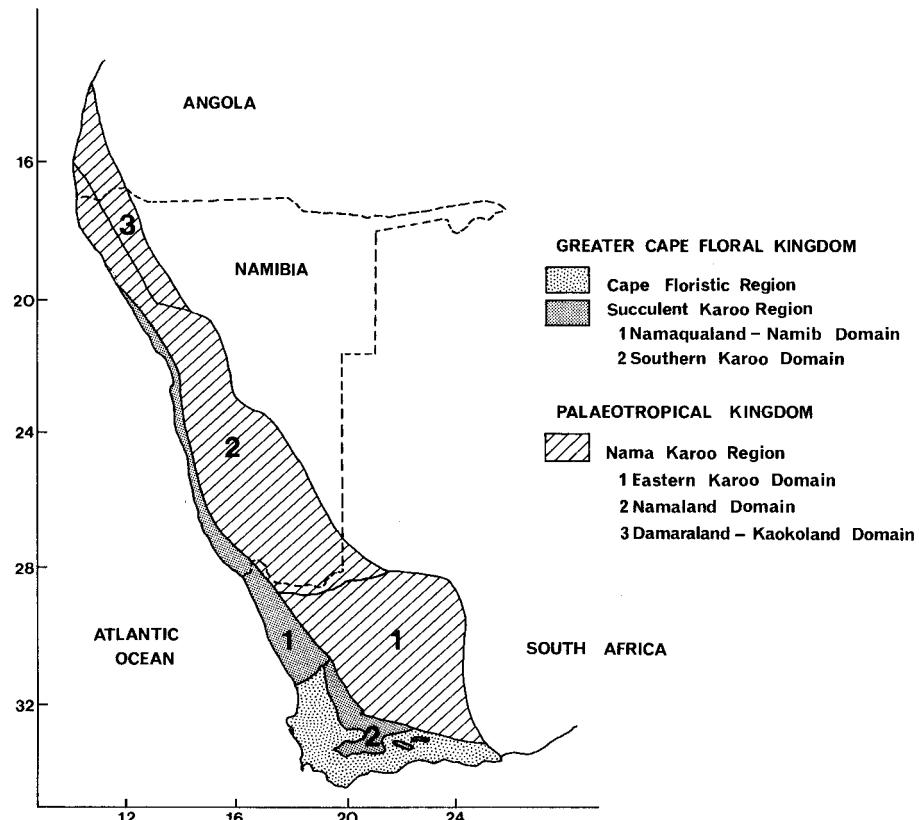


Figure 2. Phytogeographical map of south-western Africa. Redrawn from Jürgens (1991).

ally large number of geophytes (Cowling & Hilton-Taylor in press; Esler et al. 1999; Rossa & von Willert 1999).

The Namaqualand flora includes several unusually large genera for an arid land flora, including five with more than 50 taxa. These are *Crassula* (Crassulaceae), *Conophytum* and *Ruschia* (Mesembryanthemaceae), *Senecio* (Asteraceae), and *Oxalis* (Oxalidaceae) (Table 3). Most of these and other large genera are comprised mainly of either succulent shrubs or geophytes.

Vegetation and soils

There are limited data on the floristic delimitation of Namaqualand's vegetation types. The work by Acocks (1953) in defining veld types for the region, remains a standard text (Table 1, see Milton et al. 1997). Recently, Low & Rebelo (1996) produced a new assessment for the area, as part of a new vegetation map for southern Africa. Their spatial treatment, nested within the biome concept, is more detailed than Acocks although the accompanying memoir is

less richly worded. Our account, and accompanying map, follows their concepts (Figure 3, Table 1). The overview is very brief: we refer readers to Acocks (1953), Werger (1978b, 1986), Low & Rebelo (1996), Jürgens et al. (1997) and Milton et al. (1997) for details. Some finer-scale descriptive studies are also available. These have concentrated on vegetation of the coastal zone (Boucher & Le Roux 1993); the south-central Sandveld (Boucher & Le Roux 1989); the central Hardeveld (Le Roux 1984; Theron et al. 1993; Desmet & Cowling 1996), the South African portion of the Southern Namib Desert (Desmet 1996); the Southern Namib Desert and Richtersveld (Jürgens et al. 1997); and the quartz fields of the Vanrhynsdorp Centre (Schmiedel & Jürgens 1999).

The characteristic and most widespread vegetation of Namaqualand is Lowland Succulent Karoo (Figure 3). This is a dwarf succulent and species-rich shrubland dominated mainly by leaf-succulent members of the Mesembryanthemaceae and Crassulaceae. Compositional turnover along habitat and geographical gradients is extremely high (Werger 1983; Jürgens

Table 3. Number of species (including subspecies and varieties) and other information for the largest genera in the Namaqualand flora. Endemics include taxa with distributions extending into the winter-rainfall area of southern Namibia. Unpublished data of A. le Roux and C. Boucher. nd = no data.

Genus	Family	No. spp (% endemic)	Predominant growth form
<i>Crassula</i>	Crassulaceae	78 (49)	Dwarf succulent shrub/annual
<i>Conophytum</i>	Mesembryanthemaceae	55 (96)	Dwarf succulent shrub
<i>Senecio</i>	Asteraceae	55 (nd)	Perennial herb/ annual/ (succulent) dwarf shrub
<i>Oxalis</i>	Oxalidaceae	54 (72)	Geophyte
<i>Ruschia</i>	Mesembryanthemaceae	51 (nd)	Dwarf succulent shrub
<i>Hermannia</i>	Sterculiaceae	47 (nd)	Dwarf shrub
<i>Othonna</i>	Asteraceae	43 (nd)	Dwarf succulent shrub/geophyte
<i>Pelargonium</i>	Geraniaceae	42 (48)	(Succulent) shrub/geophyte
<i>Helichrysum</i>	Asteraceae	34 (nd)	Dwarf shrub
<i>Euphorbia</i>	Euphorbiaceae	32 (50)	Succulent shrub
<i>Lachenalia</i>	Hyacinthaceae	29 (79)	Geophyte
<i>Lotononis</i>	Fabaceae	29 (nd)	Perennial herb
<i>Helophilus</i>	Brassicaceae	26 (31)	Annual
<i>Arctotis</i>	Asteraceae	25 (16)	Dwarf shrub/herb/ annual
<i>Babiana</i>	Iridaceae	25 (88)	Geophyte
<i>Aloe</i>	Asphodelaceae	24 (nd)	Succulent shrub/tree
<i>Pteronia</i>	Asteraceae	24 (37)	Shrub/dwarf shrub
<i>Tylecodon</i>	Crassulaceae	24 (75)	Succulent dwarf shrub
<i>Osteospermum</i>	Asteraceae	23 (9)	Shrub/dwarf shrub/annual
<i>Felicia</i>	Asteraceae	22 (14)	Dwarf shrub/ annual
<i>Ornithogalum</i>	Hyacinthaceae	22 (nd)	Geophyte
<i>Thesium</i>	Santalaceae	22 (nd)	Dwarf shrub/shrub
<i>Wahlenbergia</i>	Campanulaceae	21 (52)	Annual/perennial herb

1986; Desmet & Cowling 1996, 1999). This vegetation type is generally found in low altitude (mostly <300 m) and low-rainfall (50–150 mm) sites on the inner margins of the coastal plain and lower slopes of the escarpment. It is associated with base-rich shallow sands and sandy loams, usually red to yellow in colour, and overlying bedrock (mostly granite

gneiss but also quartzite) and hardpans (calcrete and ‘dorbank’ – a reddish coloured hardpan cemented by silica) (Watkeys in press). A dwarf and endemic-rich form of Lowland Succulent Karoo is found on the edaphically extreme quartz fields (Schmiedel & Jürgens 1999).

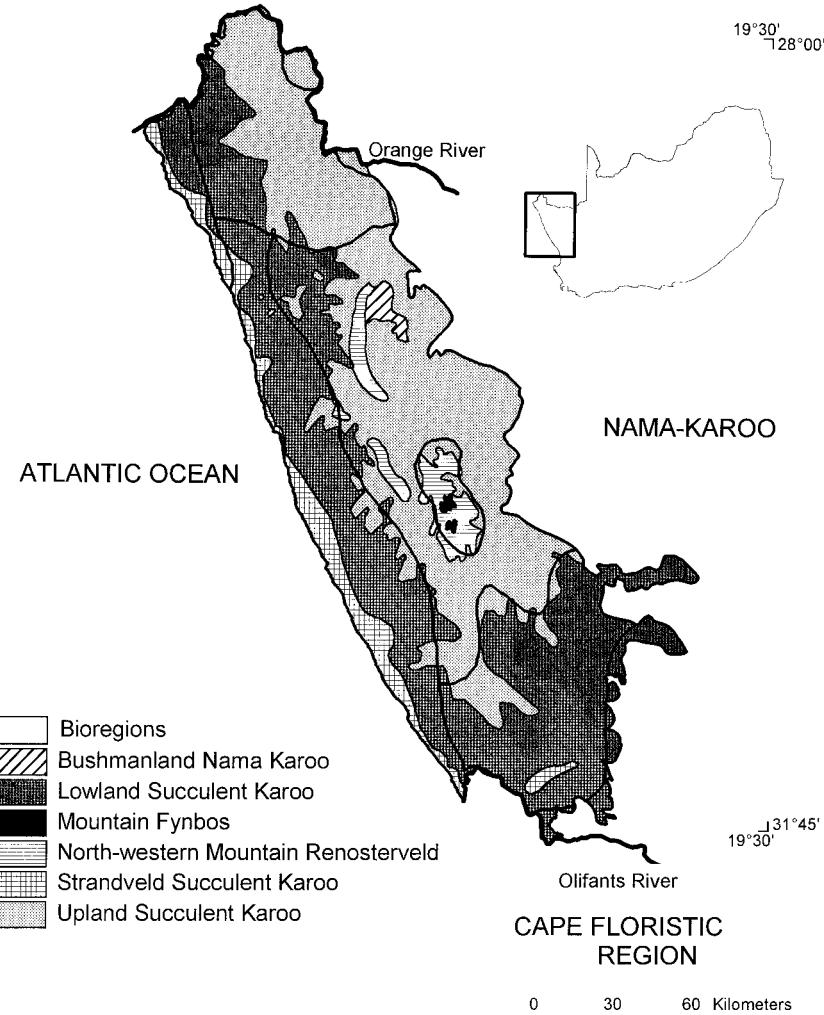


Figure 3. Vegetation types (according to Low & Rebelo 1996) of Namaqualand.

Upland Succulent Karoo is the typical vegetation of escarpment zone (Hardeveld) and higher mountains in the Richtersveld. Soils are generally similar to those of Lowland Succulent Karoo, although deeper, colluvial sands have accumulated at the base of granitic domes and some of the valleys between these. Owing to higher rainfall (up to 300 mm) and better soil development, many communities are more closed and have greater structural diversity than Lowland Succulent Karoo. While the dominants are still largely members of the Mesembryanthemaceae, succulent and deciduous Asteraceae are prominent. Geophytes, especially Iridaceae, are particularly common and old lands support brilliant displays of spring-flowering annuals. Trees are present in patches of evergreen, sclerophyllous thicket (dominated by species of *Diospy-*

ros, *Euclea* (Ebenaceae), *Ficus*, (Moraceae), *Pappea* (Sapindaceae), *Ozoroa* and *Rhus* (Anacardiaceae) as well as scattered individuals of arborescent aloes and the charismatic *Pachypodium namaquanum* (Wyley ex. Harv.) Welw. (Apocynaceae).

Strandveld Succulent Karoo occupies the sandy coastal plain throughout Namaqualand. Soils along the coastal margin are mainly grey, regic calcareous sands – these are recent deposits showing little evidence of pedogenesis (Watkeys in press). Moving inland, deep, yellow and red apedal sands predominate. These base-rich aeolian sands are derived from both coastal and inland sources. Boucher & Le Roux (1989) stratify Strandveld Succulent Karoo on the basis of vegetation height, which is largely a manifestation of depth of soil above the pervasive calcrete and dorbank hardpans.

Desmet (1996) provides a detailed phytosociological account of the Strandveld between Port Nolloth and Alexander Bay. Dominant species include leaf succulent Mesembryanthemaceae (especially *Ruschia* spp. and *Stoebaria utilis*), but there is a wide range of growth forms. These include evergreen and deciduous shrubs (up to 2 m) belonging to many genera, including *Eriocephalus*, *Osteospermum*, *Othonna*, *Pteronia* (Asteraceae), *Euclea* (Ebenaceae), *Hermannia* (Sterculiaceae), *Lebeckia* (Fabaceae), *Rhus* (Anacardiaceae), *Salvia* (Lamiaceae) and *Zygophyllum* (Zygophyllaceae). Grasslands of *Stipagrostis*, *Cladoraphis* and *Odyssea* cover large areas on finer-grained sands. Compositional turnover along soil depth gradients is substantial but the same is not true for the south-north moisture gradient (150–50 mm yr⁻¹) (P. G. Desmet & R. M. Cowling unpubl. data).

The three remaining vegetation types of Namaqualand are all northern satellites of the fynbos biome in the Namaqualand-Namib Domain. Extensive patches of North-western Mountain Renosterveld, a sclerophyllous shrubland associated with loamy, base-rich soils, occur in the Kamiesberg uplands (Figure 3, Adamson 1938) as well as the wetter parts (> 300 mm yr⁻¹) of the western escarpment zone, including the Richtersveld. Here dominant shrubs (1.5–2.5 m) are mainly evergreen members of the Asteraceae, including renosterbos (*Elytropappus rhinocerotis* (L.f.) Less.) and species of *Eriocephalus*, *Euryops*, *Helichrysum*, and *Pteronia*. Grasses (*Mermuella*, *Pentaschistis* and *Ehrharta*) are common in the understorey. The Kamiesberg is particularly rich in endemic geophytes (Hilton-Taylor 1996). Werger (1983) suggests that the rapid replacement of succulent shrubs by sclerophylls in these upland communities results from relatively frequent winter-night frosts when temperatures may drop to –6 to –8 °C. The higher peaks project above the fog zone and are, therefore, subject to much lower temperatures than the lowlands.

Although Adamson reported on the fynbos communities of the Kamiesberg as early as 1938, only recently has it been appreciated that fynbos is a widespread feature of the south-central Sandveld (Boucher & Le Roux 1989). In the Kamiesberg, fynbos elements are commonly associated with renosterveld, although some stands of pure fynbos (Mountain Fynbos *sensu* Low & Rebelo (1996)) are found on mesic, south-facing slopes. On the Sandveld, extensive tracts of restioid (Restionaceae) fynbos (dominated by *Willdenowia incurvata* (Thunb.) Linder on deep sands and *Thamnochortus bachmannii* Mast. on shallower

sands) are associated with landscapes of hummock dunes, derived from acid, aeolian sands. These communities are outliers of the Sandplain Fynbos of the Fynbos biome's west coast (P. G. Desmet & R. M. Cowling, unpubl. data).

Endemism and diversity

Endemism

In comparison to other arid lands, levels of species endemism are very high in the Succulent Karoo generally (Hilton-Taylor 1996), and especially in Namaqualand (see also Cowling & Hilton-Taylor 1994; Desmet & Cowling 1999). For example, the Succulent Karoo has three times as many endemics as the Sonoran Desert in one third of its area. The only other arid regions with similarly high levels of endemism are islands such as the drier parts of the Canary Archipelago (Shmida & Werger 1992), south-western Madagascar (WWF & IUCN 1994) and Socotra (WWF & IUCN 1994). Data on endemism in Namaqualand are available for some of the bioregions (Table 1) and a limited number of genera (Table 3); the final tally will probably range between 40 and 50%.

Highly range-restricted species in the north-western parts of Namaqualand are significantly over-represented in three families, namely the Mesembryanthemaceae, Crassulaceae and Asclepiadaceae (Cowling & Hilton-Taylor 1994; Desmet & Cowling 1999), all families of predominantly succulent species (Van Jaarsveld, 1987). Indeed, endemics are significantly over-represented among succulent (dwarf and low) shrubs and, to a lesser extent, geophytes, and under-represented among annuals, forbs, trees and non-succulent shrubs (Cowling & Hilton-Taylor 1994; Desmet & Cowling 1999; Schmiedel & Jürgens 1999). In terms of habitat preferences, locally-endemic Namaqualand species (especially dwarf succulent shrubs) are clustered in broken, rocky habitats rather than on sandy or loamy flats (Jürgens 1986; Van Jaarsveld 1987; Hammer 1993; Desmet & Cowling 1999), or on regionally unusual substrata such as quartzites and weathered quartz veins (Jürgens 1986; Schmiedel & Jürgens 1999). The vast majority of range-restricted species in Namaqualand are neoenemics: they are mostly members of large genera and have many close relatives, which are often species in different habitats within the same landscape, or geographic vicariants (Werger 1983; Hammer 1993; Cowling & Hilton-Taylor 1994; Ihlenfeldt 1994).

Diversity

Within-community or alpha diversity (Whittaker 1977) is very high in Namaqualand. A mean of 74 species has been recorded at the 0.1 ha scale, ranging from 30–40 species on the edaphically uniform Sandveld habitats, to 90–115 on the heterogeneous Hardeveld habitats (Cowling et al. 1989). These values are considerably higher than those recorded for North American deserts (Cowling et al. 1989) but comparable to those from the winter rainfall, semi-arid steppes and deserts of the Middle East (Aronson & Shmida 1992), where more than 100 species per site is not uncommon. However, a major difference between the two areas is that most species in the Namaqualand communities are dwarf evergreen leaf succulent shrubs (largely Mesembryanthemaceae) (Jürgens 1986; Cowling et al. 1994; Desmet 1996), whereas annuals predominate in the Middle East (Aronson & Shmida 1992).

Differentiation diversity – the compositional change along habitat gradients (beta diversity) and along geographical gradients (gamma diversity) – is largely the product of the evolution of habitat specialists and geographic vicariants (Cody 1986; Cowling et al. 1992). This aspect of diversity has been very poorly studied in Namaqualand as well as other arid lands of the world.

Despite the paucity of data, it is clear that differentiation diversity is unusually high in Namaqualand (see also Werger 1983; Desmet & Cowling 1999; Lombard et al. 1999; Todd & Hoffman 1999). Using Jürgens' (1986) data, Cowling et al. (1989) computed exceptional turnover along a gradient of increasing soil depth, spanning approximately 100 m of horizontal distance, in the Knersvlakte (see also Schmiedel & Jürgens 1999). Ihlenfeldt (1994) describes the extraordinary differentiation diversity within the genus *Argyroderma* (Mesembryanthemaceae) in the same area. What is especially remarkable is the fine-scale habitat (mainly edaphic) differentiation in an otherwise relatively homogeneous environment (Schmiedel & Jürgens 1999). Similar patterns are evident for many other genera of Mesembryanthemaceae (e.g., Hammer 1993), as well as geophytes (Goldblatt & Manning 1996).

These patterns suggest that in Namaqualand, explosive diversification within certain lineages has resulted in the fine-scale discrimination of habitats, and in the existence of many related species occurring in similar habitats separated by a few to tens of kilo-

meters (Hammer 1993; Ihlenfeldt 1994; Goldblatt & Manning 1996). As is the case in the species-rich fynbos vegetation to the south (Cowling et al. 1996), habitat specialization may be a consequence rather than a cause of diversification (Rosenzweig 1995).

Regional diversity refers to the richness of areas that encompass more than one community (10^1 – 10^6 km 2). At this scale, diversity is the product of the number of species within communities, the compositional change along environmental gradients (beta diversity), and the compositional change between equivalent environments along geographical gradients (Cowling et al. 1992). Any conditions that enhance the value of these diversity components will increase regional diversity.

Regional diversity in Namaqualand is extraordinarily high for an arid land (Cowling et al. 1998; Desmet & Cowling 1998). Von Willert et al. (1992) quote Norbert Jürgens' figure of 331 species in 1.3 km 2 at Numees, in the arid (ca. 70 mm yr $^{-1}$) Richtersveld mountains. A species-area curve for the Succulent Karoo, excluding the tally for Namaqualand (Cowling et al. 1998), predicts 2446 species for the region, some 300 fewer than the observed number. Generally, Succulent Karoo regions support 2.65 times more species than equivalent-sized areas of the summer-rainfall Nama-karoo, and 3.8 times more species than winter-rainfall desert areas in North America (Cowling et al. 1998). Given that the species-area relation for the Succulent Karoo underestimates regional diversity in Namaqualand (see above), these relative diversity differences are probably even higher.

In the Karoo-Namib Region generally (i.e., including sites from both the Succulent Karoo and Nama-Karoo), regional richness is best explained ($R^2 = 0.59$) by a measure of environmental heterogeneity (length of the rainfall gradient) and favourability (rainfall reliability as estimated by coefficient of variation of monthly rainfall averaged for the wettest three consecutive months) (Cowling et al. 1997). Thus, the most species-rich regions in the Karoo-Namib are those with long moisture gradients and predictable seasonal rainfall, such as would be found in the escarpment zone of the winter-rainfall Namaqualand-Namib Domain.

Plant form and function

This section of the paper, and the accompanying model (Figure 4), focuses on the succulent-rich com-

munities of Namaqualand, particularly Lowland Succulent Karoo, Upland Succulent Karoo and some of the shorter Strandveld vegetation types. Patterns and processes regarding plant form and function in renosterveld and fynbos vegetation are likely to be similar to those reported from the fynbos biome to the south. These are summarized in Cowling (1992).

Growth forms

Studies on the growth form mix of Namaqualand communities and floras indicate that the region's complement of structural-functional types is unique amongst the world's desert ecosystems. Dwarf (<0.5 m) succulent shrubs (chamaephytes), mainly members of the Mesembryanthemaceae, Crassulaceae and Asteraceae, are the dominant growth form in most Namaqualand communities (Jürgens 1986; Cowling et al. 1994; Schmiedel & Jürgens 1999). Such a dominance of leaf succulents contrasts sharply with other deserts, including winter-rainfall ones, where this growth form is rare (Esler & Rundel 1999). Other than in the Succulent Karoo, only in the drier, northern parts of the Canary Islands does one find assemblages relatively rich in leaf succulents (Jürgens 1986; Shmida & Werger 1992).

Most Namaqualand leaf succulents have extremely shallow (0.1–0.2 m) rooting systems (Esler et al. in press; Esler & Rundel 1999), even when growing in deep soils. A consequence of this unusual below-and above-ground morphology is that members of this growth form are vulnerable to drought-induced mortality after rare episodes of lower-than-average rainfall (Von Willert et al. 1985). Indeed, in contrast to many other desert ecosystems where the dominant perennial component is very long-lived, many of Namaqualand's leaf succulents have relatively short lifespans (5–10 years) (Jürgens et al. 1999; see also Stock et al. 1999).

A unique feature of Namaqualand's succulent flora is the presence of numerous minute (< 25 mm tall) and embedded succulent shrubs belonging to the Mesembryanthemaceae (e.g., *Argyroderma*, *Conophytum*, *Fenestraria*), Crassulaceae (*Crassula*, *Tylecodon*), Portulacaceae (*Anacampseros*) and Asphodelaceae (*Bulbine*, *Haworthia*) (Van Jaarsveld 1987; Hammer 1993; Midgley and Van der Heyden in press). The occurrence of such minute perennial growth forms is paradoxical in the context of a desert environment since their small storage organs offer little capacity to endure prolonged moisture stress. Many species grow

in shaded rock crevices where they are sheltered from excessive radiation and can exploit run off from rainfall, fog and dew (Van Jaarsveld 1987; Hammer 1993). However, a large number are associated with exposed sites, especially quartz fields (Schmiedel & Jürgens 1999). Members of the Mesembryanthemaceae are capable of recycling moisture from the previous season to newly developing leaf pairs: the withered leaves form a protective layer during the dry summer months (Von Willert et al. 1992). Other species have plant bodies which retract beneath the soil surface during the unfavourable months whereas minute *Tylecodon* spp. are strongly summer-deciduous (von Willert et al. 1992). Ultimately, the evolution of this intriguing growth form would only be possible in an environment characterized by low, but highly predictable inputs of moisture, thereby enabling plants to replenish moisture reserves on a regular basis. Indeed, there is good evidence that in southern Africa, succulence, especially the incidence of dwarf leaf succulent forms, is correlated with rainfall reliability and seasonality (winter rain) rather than annual totals (Werger & Morris 1991; Cowling et al. 1994).

Taller succulent shrubs and succulent trees are rare in the Namaqualand flora. Most of the shrubs are stem succulent *Euphorbia* spp. which are particularly common in the warmer and drier northern reaches, especially the Richtersveld. This area is also home to most of the region's small but charismatic tree succulent flora, namely *Aloe dichotoma* Masson, *A. pillansii* L. Guthrie, *A. ramosissima* Pillans (Asphodelaceae) and *Pachypodium namaquanum* (Apocynaceae).

Shrubs with drought-deciduous, orthophyllous leaves and aphyllous forms, which comprise the dominant perennial cover in other warm, winter-rainfall deserts (Esler et al. 1998), are relatively rare in Namaqualand, where the great majority of non-succulent woody species are evergreen (Cowling et al. 1994). Clearly, relative to evergreen succulence, the deciduous habit is not particularly advantageous in an environment characterized by reliable but low seasonal rainfall (Figure 4). Evergreen shrubs, most of which have sclerophyllous leaves (von Willert et al. 1992) include lineages endemic to the Karoo-Namib Region (e.g., *Pteronia* and other Asteraceae) as well as species of tropical affinity. The latter, a relatively small flora comprising species of *Euclea*, *Diospyros* (Ebenaceae), *Rhus*, *Ozoroa* (Anacardiaceae), *Ficus* (Moraceae) and *Schotia* (Fabaceae), are mainly restricted to water courses and run-on sites such as the base of large, granite domes. These tall shrubs

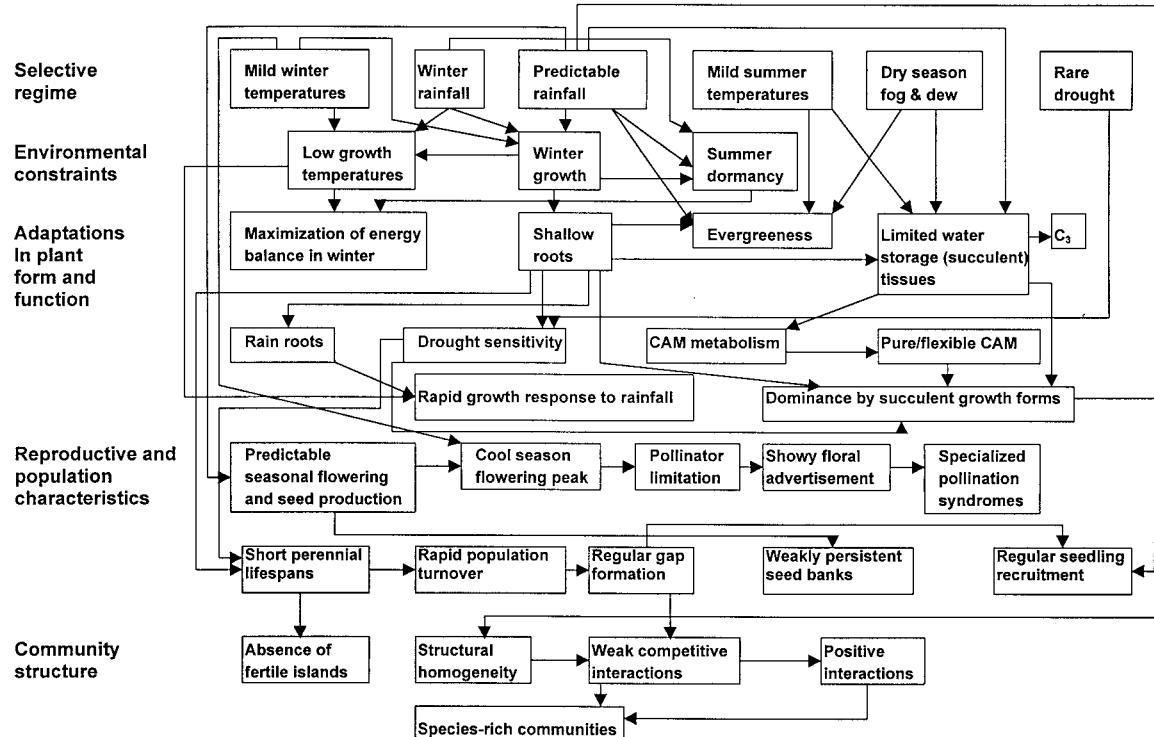


Figure 4. Model for explaining and predicting aspects of plant form and function, reproduction, population dynamics and community structure in Namaqualand's leaf succulent-dominated vegetation. Adapted from Esler et al. (in press).

and low trees, which are probably relicts of the Tertiary, summer-rainfall scrub forests that once dominated Namaqualand landscapes (Scott et al. 1997; Wand et al. 1999), are extremely long-lived, have vertebrate-dispersed propagules, and probably establish seedlings on rare occasions. This life history contrasts strongly with that exhibited by the short-lived and recruitment-dependent lifestyles of most other Namaqualand perennials (Cowling et al. 1994; Jürgens et al. 1999).

Another unique feature of Namaqualand's growth form mix is the high diversity and local abundance of geophytes (Cowling & Hilton-Taylor in press; Esler et al. in press). Namaqualand is home to about 480 species (17.5% of the flora) comprising about 100 genera in 19 families (A. le Roux & C. Boucher, unpubl. data). At a smaller spatial scale, petaloid monocot geophytes make up 16% of the flora (550 spp. in 150 km²) at Goegap Nature Reserve in the central Hardeveld (Van Rooyen et al. 1990), and nearly one third of the flora (280 spp. in 1.2 km²) at Nieuwoudtville on the Bokkeveld Escarpment of Namaqualand's eastern fringe (Manning & Goldblatt 1996a). The proportional representation of geophytes in other semi-arid, winter-

rainfall regions is much lower, e.g., Mojave Desert (1%) (Rundel 1996), Canary Islands (2.1%), south eastern Spain (4.3%) and mediterranean-climate Israel (4.8%) (Shmida & Werger 1992).

Namaqualand geophytes encompass a wide variety of leaf types, including species with large, broad leaves fully pressed against the soil surface (Esler et al. 1999; Rossa & von Willert 1999) as well as species with tightly-coiled and variously pleated leaves. Storage organ size varies from very large in many amaryllids (see Snijman 1984) to very small in *Oxalis*. However, the majority of species have small storage capacity; bulbs and corms of most geophytes are 1–3 cm in diameter. If geophytes are functionally interpreted as underground succulents, then their success in Namaqualand, like that of small-bodied aboveground succulents, may partly result from the region's reliable moisture regime.

Annuals, which are not especially conspicuous in undisturbed vegetation, are nevertheless an important component of the Namaqualand flora. They comprise about 330 species (12% of the total) in 85 genera and 24 families. In Goegab, they represent 28% of the flora (Van Rooyen et al. 1990). Generally, proportional rep-

resentation of annuals is much lower than in semi-arid, winter-rainfall regions of the Mediterranean Basin and the New World. Here annuals comprise 30–50% of floras (Shmida and Werger 1992; Rundel & Gibson 1996). Spectacular displays of spring-flowering annuals, especially on old fields, (Van Rooyen in press), are a popular tourist feature. The reliability of this display, which is marketed as an annual ecotourism event, is a function of the region's predictable rainfall regime. While much is known about the growth phenology and demography of Namaqualand annuals (Van Rooyen in press), very little is known about how these species interact competitively with other growth forms.

Climate and winter growth phenology

The selective regime in Namaqualand differs from other winter-rainfall deserts in two important respects: the predictability of rainfall between years and the mild winter and early spring temperatures (Esler & Rundel 1999). The only other desert region with a similarly climatic regime is the dry parts of the Canary Islands; interestingly, these areas also support a dwarf and predominantly leaf-succulent shrubland (Shmida & Werger 1992).

Rainfall reliability and mild winter temperatures combine to select for a winter growth phenology where both perennial and annual species begin vegetative development with autumn rains, and continue active growth to reproductive maturity during the winter months, well in advance of the comparable growth season in the winter rainfall deserts of North America (Esler & Rundel 1999). The significance of this selective environment has ramifications that extend from adaptations in plant form and function to aspects of population structure, demography, and community dynamics, as shown in Figure 4.

Carbon gain

Winter growth requires a number of ecophysiological traits (Figure 4). Since winter temperatures are relatively cool, significantly lower than those experienced during spring growth of winter-rainfall deserts in North America (Esler & Rundel 1999), one would predict relatively low temperature optima for net photosynthesis (Figure 4). Recent studies are showing exactly this, with optimum temperatures of 12–22 °C in Namaqualand geophytes (Rossa & von Willert 1998) and 22 °C for the stem succulent *Pachypodium namaquanum* (S. Wand unpubl. data). Temperature optima for species in winter rainfall deserts of North

America are typically 25–30 °C or more (Ehleringer 1985).

Additionally, it would be reasonable to expect adaptations among Namaqualand plants to maximize their solar energy balance during winter months when the solar angle is low and day length is short (Figure 4). Leaf orientation is one means of achieving increased irradiance on leaf surfaces, and such an adaptation has been demonstrated in the nodding northward orientation of leaf whorls in *Pachypodium namaquanum* in the Richtersveld (Rundel et al. 1995). Strategies to increase leaf temperatures might represent an alternative to low temperature optima for photosynthesis, and there are a number of studies underway to test this hypothesis. Flat-leaved geophytes could potentially utilize this strategy by tracking soil temperatures that exceed air temperatures in late afternoon (Esler et al. 1999). Although the orientation of leaf whorls of *P. namaquanum* allow this species to absorb about 60% more solar irradiance in mid-winter than would occur with a horizontal orientation (Rundel et al. 1995), leaf temperatures nevertheless track ambient air temperatures (P. W. Rundel et al. unpubl. data). However, meristem temperatures in the floral buds of this species are 4 °C above air temperatures at midday, allowing more rapid development than would otherwise occur.

Another feature to maximize radiation during the winter growing season is leaf windows – non-pigmented zones that enable the deep penetration of light to chlorophyllous tissue. Windowing is exclusively associated with succulent leaves that have low absorptance of PAR (Von Willert et al. 1992). Windows are most commonly found in embedded succulents, where light penetration is further restricted, but also on the large, cylindrical succulent and summer-deciduous leaves of shrubs and geophytes (von Willert et al. 1992, R. M. Cowling pers. obs.).

Crassulacean acid metabolism (CAM) is widespread among leaf succulent species in Namaqualand, particularly within the dominant Mesembryanthemaceae (Von Willert et al. 1992). Recent studies using carbon isotope analyses of leaf tissues have now provided a clearer picture of the relative importance of CAM among succulent-leaved species (Rundel et al. 1999). Complete reliance on CAM was found in species of *Aloe*, for long-lived Mesembryanthemaceae, and the majority of Crassulaceae. However, the great majority of Mesembryanthemaceae, and shrubby *Ceraria* (Portulacaceae) and *Senecio* (Asteraceae) all show a range of CAM flexibility.

ity. Leaf succulence and CAM are also not always correlated (Von Willert et al. 1992, Rundel et al. 1998). Succulent-leaved species of *Othonna* (Asteraceae), *Zygophyllum* (Zygophyllaceae), and *Pelargonium* (Geraniaceae) do not appear to utilize CAM.

The observed wide range of comparative water use efficiency present among Namaqualand species without CAM suggests multiple strategies of drought adaptation must occur (Rundel et al. 1999). While studies of comparative water use efficiency among North American desert perennials have suggested a correlation between longevity and increased water use efficiency, such a pattern does not appear to be present among species in the Richtersveld (Rundel et al. 1999).

Water relations

An implication of winter growth phenology is that species actively compete for water resources at the time that rainfall occurs. This is in sharp contrast to winter rainfall deserts in North America where 75% of the hydrologic year rainfall has already fallen before growth is initiated in the spring (Esler & Rundel 1999). Two common morphological characteristics of Namaqualand shrubs, shallow root systems and succulent leaf tissues, may well represent adaptations to compete for water uptake and to store water beyond immediate metabolic needs (Figure 4). Succulent leaf tissues provide an energetically efficient storage organ (Von Willert et al. 1992). It would not be surprising to find specialized 'rain roots', as have been described for succulents in North American deserts (Nobel & Sanderson 1984; Rundel & Nobel 1991), in many of the succulent-leaved shrubs of Namaqualand.

A strategy of shallow roots is reasonable so long as moisture from winter rains as well as fog and dew, is predictable (Figure 4). When prolonged periods of lower than average rainfall (i.e., droughts) do occur, however, even though they may be mild compared to droughts in other winter-rainfall deserts of the world, shallow root systems provide little buffering capacity and make Namaqualand plants sensitive to drought stress (Von Willert et al. 1985). The widespread dominance of shallow-rooted shrub species in Namaqualand (Esler & Rundel 1999) is entirely consistent with observations of episodic events of drought producing local patterns of shrub mortality and compositional change (Von Willert et al. 1985; Jürgens et al. 1999).

Reproduction

Reliable winter rain and fog- and dew-ameliorated summers potentially enable regular seed production and recruitment among Namaqualand's perennials (Figure 4). Ultimately, this may be the selective force responsible for the evolution of the short-lived lifestyles characteristic of the dominant succulent component. The implications for reproductive patterns and processes is that there is strong selection for individual species to maintain or increase their relative representation in the pool of propagules. To do this plants must compete for scarce pollinators during the winter and early spring flowering period (Struck 1994a). The result is a spectacular floral display of competitive advertising (Dafni & O'Toole 1994, Figure 4).

The sequence and occurrence of flowering is a relatively predictable event in Namaqualand communities, although the onset and abundance of floral displays may differ slightly from year to year, depending on weather conditions; generally, however, mass, multi-species displays occur from late winter to early spring (July–mid September) (Le Roux et al. 1989; Struck 1992, 1994a). While few species flower in the summer months, a pronounced peak occurs in autumn, outside of the normal winter-spring growth period. Most autumn-flowering species are geophytes (especially Amaryllidaceae) (Snijman 1984) and dwarf succulents in the Crassulaceae and Mesembryanthemaceae (Struck 1992, 1994a; Hammer 1993). Clearly, the production of flowers at this time must constitute a cost in terms of water economy but has the benefit of reduced competition for pollinators (Struck 1995). In addition, autumn flowering of species with fleshy, recalcitrant seed (as is the case of many Amaryllidaceae) ensures that germination coincides with the onset of the predictable rainy season (Snijman & Linder 1996).

Since obligate outcrossing (Jacobsen 1960; Snijman 1984; Goldblatt 1991) and insect-mediated pollination (Struck 1992, 1994b) predominate in the Namaqualand flora, and most plants rely on regular seedling recruitment for local persistence, attracting pollinators is of great ecological and evolutionary significance (Manning & Goldblatt 1996b; Johnson & Midgley 1997, Figure 4). Although conditions optimal for pollinator activity during the flowering season are not particularly common, no research has yet been done to test for pollinator limitation in Namaqualand. In the adjacent fynbos biome, where pollinator limitation is a widespread cause of low fruiting success –

especially among geophytes – specialized guilds have developed in order to ensure efficient pollen transfer (Johnson & Bond 1997). In Namaqualand, floral characteristics of many groups are clearly under strong pollinator-specific selection (e.g., oil collecting bees on *Diascia* spp.: Whitehead & Steiner (1985); long-tongued flies on species of Iridaceae and Geraniaceae: Manning & Goldblatt (1996b), Goldblatt et al. (1995); bee-flies on species of Asteraceae and Geraniaceae: Johnson & Midgley (1997), and many others). There has also been adaptive radiation of pollinator groups which are uncommon in the rest of the world and which show varying degrees of fidelity (e.g., monkey beetles: Picker & Midgley (1996) and bee-flies: Hesse (1938), Struck (1994a)). Generally, however, many of the endemic Namaqualand insect pollinators are generalists (Struck 1994b) that pollinate the predominant large, open flowers characteristic of the Mesembryanthemaceae (Hartman 1991; Ihlenfeldt 1994) and Asteraceae (Struck 1992, 1995). These open flowers present a showy advertisement to pollinators; perhaps the strategy of accommodating a generalist fauna is a means of overcoming limited pollinator activity. However, this does not solve the problem of pollination contamination. Clearly, more research is required on the pollination biology of the large, ‘daisy-like’ flowers that dominate Namaqualand’s floral displays.

Seed production both at a per plant and a landscape level is, not surprisingly, highly variable and depends on a wide variety of factors (Esler in press) including life-histories of individual plants. It is likely that the Mesembryanthemaceae do not maintain large seed banks (canopy or soil) except for annual species and those that occur in disturbed sites (cf., Esler & Cowling 1995 for data from the Southern Karoo). In addition, Mesembryanthemaceae tend to have very short-distance dispersal mechanisms. Most species in this family possess hydrochastic capsules (Hartmann 1991) that ensure that seeds are only released during rainfall events. Mesembryanthemaceae seeds can be dispersed up to 1.65 m away from the parent plant by raindrops (Lockyer 1932, Garside & Lockyer 1930), but secondary dispersal via sheet flow may increase this distance.

Most Namaqualand seeds are cued to germinate under cooler temperature regimes, indicating autumn/winter germination and seedling recruitment. Some recruitment of perennial species occurs almost every year (Esler in press, Jürgens et al. 1999).

Community structure dynamics

Succulent-dominated communities in Namaqualand are unique amongst those from arid lands in that the majority of the perennial component comprises relatively short-lived shrubs (Jürgens et al. 1999), most of which are functionally equivalent (Rundel et al. 1999) with limited water storage capacity and low drought resistance (Von Willert et al. 1992). The low overall growth form diversity of Namaqualand communities (Cowling et al. 1994) is unusual for desert vegetation which generally provides strong evidence for niche differentiation along axes of growth form complexity (Cody 1989). Unlike perennial shrubs in other arid lands, where recruitment events are highly episodic and populations comprise several discrete cohorts (Zedler 1981; Jordan & Nobel 1982), the age structure of Namaqualand succulents is uneven (Jürgens et al. 1999). Plants die and are replaced continuously, resulting in significant compositional change of the perennial component over decades-long periods (Von Willert et al. 1985; Jürgens et al. 1997; Jürgens et al. 1999). As expected, there is little inferential evidence for both inter- and intra-specific competition between succulent shrubs in these communities (Figure 4); indeed, in some communities, marked clumping or spatial aggregation exists across a wide range of spatial scales (Prentice & Werger 1987; Eccles et al. 1999). Furthermore, short shrub life-spans result in a poorly developed ‘fertile island effect’ – the plant-induced enrichment beneath the long-lived shrubs characteristic of North American and other desert ecosystems (Stock et al. 1999).

It appears, therefore, that community membership in Namaqualand is determined by a lottery process whereby functionally equivalent shrubs coexist in highly dynamic communities (Figure 4). Predictable winter rain, and fog-and dew-ameliorated summers provide conditions for regular recruitment. Occasional drought-induced mass mortality and inherent short lifespans continuously re-arrange emerging competitive hierarchies (Von Willert et al. 1985; Jürgens et al. 1999). The result is species-rich communities dominated by functionally equivalent shrubs (Cowling et al. 1994).

Conclusions

Namaqualand is a unique desert ecosystem that provides exceptional opportunities for the study of arid

ecosystems. In this paper we have presented a model (Figure 4, also see Esler et al. in press) which attempts to integrate these patterns and processes across different levels of organization. This model was developed by the authors as part of a research proposal to investigate plant form and function in Namaqualand. Of interest is the number of contributions to this issue that are consistent with the model predictions (e.g., the low temperature optima for photosynthesis (Rossa & von Wilpert 1999); the rapid population turnover of perennials (Jürgens et al. 1999); the weakly developed fertile island effect (Stock et al. 1999); and the weakly developed competitive interactions (Eccles et al. 1999)). Much more research is required to test and refine other aspects of the model.

Ultimately, we hope to develop a predictive understanding of the structure and function of Namaqualand ecosystems in order to provide insights for the wise management and use of the region's natural resources. These will include guidelines for designing reserve systems that are both representative of the region's enormous biodiversity, but will also retain this in the face of global change (Lombard et al. 1999; Cowling et al. in press), as well as appropriate range management and restoration protocols for overgrazed (Allsopp 1999; Todd & Hoffman 1999) and mined (Desmet 1996) areas. However, we also hope that this Special Issue will stimulate more fundamental ecological and evolutionary research in this unique desert ecosystem. Such research will improve our global understanding of the ecology of arid lands.

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