CHAPTER 1

INTRODUCTION

THE STRANDVELD SUCCULENT KAROO

The significance of the world's vast areas of arid land can only be appreciated when it is realized that over a quarter of the earth's land is either arid or semi-arid (Adams *et al.*, 1978; Cowling *et al.*, 1999). In these areas the sporadic rainfall is usually less than 400 mm per year (Gutterman, 1993) and evapotranspiration can be 15-20 times as much as the annual rainfall. Humidity in the soil and in the air is usually low, and extreme levels of temperature and radiation are common features in these areas (Adams *et al.*, 1978).

The arid and semi-arid rangelands of South Africa are extensive, covering approximately 33% (427 000 km^2) of the land surface (Cowling, 1986). These rangelands have been divided into distinct biomes based on climatic variables and life-form spectra, of which the Nama Karoo and Succulent Karoo Biomes (Low & Rebelo, 1998) comprise the largest part.

The Succulent Karoo Biome occupies 6.5% of South Africa's land surface (82 519 km^2) (Low & Rebelo, 1998) and is primarily determined by the presence of low, but predictable, winter rainfall (Jürgens, 1986; Hilton-Taylor & Le Roux, 1989; Desmet & Cowling, 1999) and relatively mild summers where drought is ameliorated by heavy dew and frequent fog (Cowling & Hilton-Taylor, 1999). The number of plant species, especially succulents, is very high (Esler, 1993; Cowling & Hilton-Taylor, 1999) and unparalleled elsewhere in the world for an arid area of this size (Low & Rebelo, 1998). The high levels of species diversity and endemism in the Succulent Karoo Biome can be attributed to a relatively few number of families, including the Mesembryanthemaceae, Crassulaceae, Euphorbiaceae and Asclepiadaceae (Esler, 1993; Cowling & Hilton-Taylor, 1999). The vegetation within this biome is a dwarf succulent shrubland (Hoffman & Cowling, 1987; Acocks, 1988; Cowling *et al.*, 1999) dominated by leaf succulents, although stem succulents and deciduous and evergreen dwarf shrubs are also common (Esler, 1993). Mass flowering displays of annuals (mainly Asteraceae) occur in spring, often on degraded or fallow lands. Grasses are rare, except in some sandy areas. This Biome is divided into four vegetation types (Low & Rebelo, 1998), namely the Strandveld Succulent Karoo, Upland Succulent Karoo, Lowland Succulent Karoo and Little Succulent Karoo (Figure 1.1). This thesis focuses on the seed bank dynamics of the Strandveld Succulent Karoo vegetation type.

The Strandveld Succulent Karoo covers approximately 3 817 km^2 (0.3% of South Africa's land surface) and comprises the vegetation of the sandy coastal plains on the West Coast of South Africa (Low & Rebelo, 1998). This vegetation type extends over a distance of more than 500 km from the Berg River Mouth in the south to Alexander Bay in the north. Rainfall is generally low and ranges from 300 mm in the south to less than 50 mm per annum at the mouth of the Orange River. Deep, calcareous, coastal Quaternary sands, generally poor in nutrients, dominate the area.

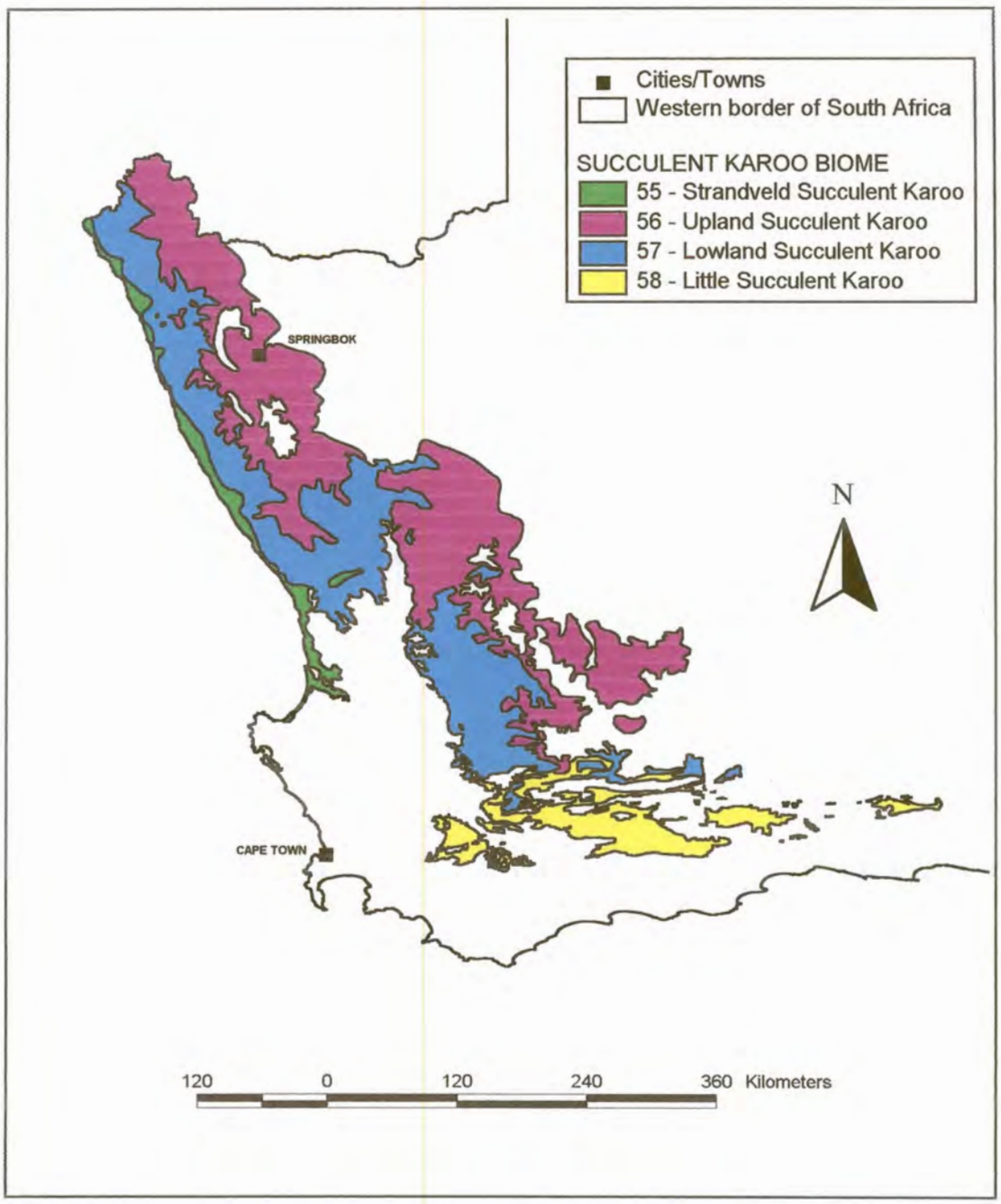

Figure 1.1. Vegetation types of the Succulent Karoo Biome (Low & Rebelo, 1998). Numbers preceding vegetation types indicate numbers allocated for each vegetation type by Low & Rebelo (1998).

The vegetation of the Strandveld Succulent Karoo is dominated by scattered, low shrubs and small trees such as *Salvia lanceolata* and *Nylandtia spinosa*, with succulent shrubs such as *Zygophyllum morgsana, Euphorbia mauritanica* and *Euphorbia burmannii* being common species. Geophytes, annuals and especially species of the Restionaceae become more dominant where this vegetation type is associated with Sand Plain Fynbos (type 68; Low & Rebelo, 1998). Large areas are subject to strip-mining for diamonds and heavy minerals. Very little agriculture takes place but some small stock farming does occur, and some cattle are kept in the river valleys. Tourism is probably a major potential source of revenue. Only 0.4% of this vegetation type currently has conservation status (Low & Rebelo, 1998).

THESIS RATIONALE

The revegetation of any drastically disturbed land, such as a surface mine, is probably the single best method of stabilising the soil. Vegetation is cheaper than any other form of soil stabilisation because of the continuous and long-term effect. It is also more efficient than any other method and more aesthetically pleasing. Finally revegetation can place the soil into continued economic production (Lyle, 1987).

Vegetation prevents or reduces soil erosion by providing a soil cover that intercepts raindrops and prevents them from dislodging soil particles and destroying soil structure. The plant roots bind soil particles together and prevent water from carrying soil downhill. Above-ground vegetation slows water runoff along the soil surface and enables more of the water to move into the soil for plant use. When this vegetation intercepts water flowing over the soil surface it also reduces the downhill movement of soil (Lyle, 1987).

Along the West Coast of South Africa, the sandy soils are rich in heavy minerals such as ilmenite, rutile and zircon, which are essential in the paint, ceramic and steel industries (Environmental Evaluation Unit, 1990). Mining activities in the area will destroy the topography, vegetation, animal life and chemical and physical characteristics of the soil. Mining companies, however, are compelled by law (Mining Rights Act No. 20 of 1967; Hoogervorst, 1990) to rehabilitate mined areas. The aim of the rehabilitation programme in this area is, firstly, to restore the land to a form and productivity in conformity with pre-mining land capabilities. Secondly, to restore the landscape to a form which is consistent with surrounding aesthetic values. Thirdly, to rehabilitate in such a way as to leave the maximum number of options open to future generations, and fourthly, to ensure that rehabilitation takes place continuously and is fully integrated with the mining operation (Environmental Evaluation Unit, 1990).

More specifically, the goal which has to be met is the revegetation of the area with no less than 60% (species diversity and abundance) of the original indigenous plant species as soon as possible after the mining of an area has been completed (Environmental Evaluation Unit, 1990). Three main methods are considered for the revegetation of the mined areas, *i.e.* topsoil replacement, as well as sowing and transplanting of selected species. The latter two methods are extremely labour intensive in that species have to be selected, seeds and/or bulbs have to be collected, treated and stored, and seedlings have to be nursed, prior to the period of sowing or transplanting. Since one of the aims of the rehabilitation programme is to restore the topography of the landscape, the replacement of topsoil during the final landscaping phase

may prove to be an important tool for achieving the revegetation goals. Replaced topsoil may contain reserves of viable seeds, the so-called seed bank, which represents the "memory" of previous conditions and is an important component of the potential of the community to respond to conditions in the present and future (Coffin & Lauenroth, 1989). The seeds present in the top layers of soil are potentially useful in restoration projects where establishment of plant cover is desired (Skoglund, 1992). Due to the high percentage of heavy minerals present in the uppermost soil layers, mining companies regard knowledge of the soil seed bank as vital for the planning of sound rehabilitation strategies.

Since the management of any system is based on an understanding of its dynamics (Esler, 1993), all factors which may influence inputs and outputs to the seed bank, should be considered prior to revegetation efforts in the Strandveld Succulent Karoo. Knowledge of the size and composition of the seed bank present prior to the start of mining activities, as well as the spatial and temporal distribution thereof, will be vital in assessing the suitability of the soil seed bank for revegetation purposes by means of topsoil replacement. Examination of the composition of the seed bank makes it possible to predict the initial composition of the post-recruitment vegetation. Knowledge of whether seeds are transient or persistent, the nature of germination cues, and the environmental conditions suitable for establishment are fundamental to successful vegetation management. Factors such as seed production, germination requirements, dormancy, viability, predation and seedling survival will give insight into the seed bank dynamics, not only concerning topsoil replacement, but also for the potential success following sowing and transplanting. Data on the pre-mining floristic composition and abundance of species in the aboveground vegetation can indicate the suitability of the seed bank as a potential source for revegetation. Once sea-water is used in the mining process, knowledge on seed production and seedling survival under saline soil conditions will also be essential.

The significance of recruitment from seeds stored in the soil was noted by Darwin (1859). However, the first detailed studies of seeds in the soil appear to be those of Putensen (1882 in Roberts, 1981) and Peter (1893 in Roberts, 1981). In recent years, interest in seed bank ecology has increased greatly (Fenner, 1985; Thompson *et al.*, 1996), and it has become well recognised that seed banks play a crucial role in the dynamics of plant populations and communities (Walck *et al.*, 1998). Seed bank studies are an important consideration in the development of a predictive understanding of plant community structure and function (Roberts, 1981; Leck *et al.*, 1989). In arid and semi-arid environments, where germination and recruitment are the critical stages in the life cycle of most plants, seed banks are thought to play a major role in population dynamics (Esler, 1993).

Seed banks have been the subject of numerous studies on grasslands, arable fields, woodlands, heathlands, dunes, marshes, forests and deserts (Bakker *et al.*, 1996). In the arid and semi-arid western regions of South Africa, seed bank studies include those of Van Rooyen & Grobbelaar (1982), Dean *et al.* (1991), Esler *et al.* (1992), Esler (1993) and De Villiers *et al.* (1994a). The role of the seed bank in restoration and revegetation studies, other than arable land, has been the subject of only few studies (Levassor *et al.*, 1990; Moll, 1992; Aerts *et al.*, 1995; Bakker *et al.*, 1996; Kotanen, 1996). This thesis represents a first attempt to incorporate seed bank dynamics data in the planning phase of the post-mining revegetation process in the Strandveld Succulent Karoo, South Africa.

Plants from arid and semi-arid environments have developed different strategies for coping with the climatic conditions of these areas. Annual plants complete their growth in a relatively short period and survive the dry season and drought in the form of seeds. This strategy is known as "drought-evading" and usually occurs in drought-sensitive species (Larcher, 1995). Another survival mechanism of plants in dry regions is drought-resistance, and species exhibiting this mechanism are either "desiccation-avoidant" or "desiccation-tolerant" (Larcher, 1995). The first type (desiccation-avoidant) is comprised of perennial plants where desiccation is delayed by mechanisms that enable the plant to maintain a favourable tissue water content as long as possible despite dryness of air and soil, for example, succulence. The second type (desiccation-tolerant) refers to the capacity of protoplasm to endure severe water loss, and is mostly found in woody perennial species (Adams *et al.*, 1978). For the most part, only the distinction between drought-evading and drought-resistant species was considered in this thesis.

The main objectives of this study were, firstly, to explain the seed bank dynamics of the Strandveld Succulent Karoo in terms of spatial and temporal variation in seed bank size and composition, and the main factors affecting the inputs and losses thereof. Secondly, to incorporate this knowledge in the formulation of suitable post-mining revegetation strategies at the management level.

The following goals were set out:

1) to determine the vegetation diversity of a selected mining area in the Strandveld Succulent Karoo, to serve as a pre-mining benchmark for rehabilitation;
2) to determine spatial and temporal variation in seed bank size and composition. These data will reflect the necessity of topsoil replacement as a means of revegetation and indicate appropriate revegetation strategies in time as well as in space;
3) to compare seed bank size and composition with that of the standing vegetation by means of density and phytosociological methods, as pre-mining seed bank patterns may determine initial post-mining vegetation patterns;
4) to determine the germination requirements, required dormancy-breaking treatments, endogenous germination patterns and viability of seeds of selected Strandveld Succulent Karoo plant species, and to use these data in addition to specific laboratory seed characteristics to construct a key, similar to that of Grime & Hillier (1981), to predict the seed bank type(s) characteristic of individual species and different species groups;
5) to determine the influence of seed production, pre- and post-dispersal seed predation and seed-borne fungi on seedling recruitment and survival of selected Strandveld Succulent Karoo species under field conditions. These data will quantify the inputs and some of the losses from the seed banks of individual plant species;
6) to determine whether shrub species to be transplanted will facilitate recruitment and seedling survival in the field, and
7) to determine seed production and seedling survival under saline soil conditions to indicate species suitable for achieving long-term revegetation goals.

The thesis is presented in the form of papers. These papers have been published / are to be submitted for publication in different scientific journals. In addition to the papers, a general introduction, a chapter on the study area, material and methods, a general conclusion and a comprehensive list of references are included.

CHAPTER 2

STUDY AREA, MATERIAL AND METHODS

The following is a description of the study area and a summary of the material and methods used in this study. For a more detailed description of the material and methods the reader is referred to the relevant chapters (3 – 15).

STUDY AREA

LOCATION

The study area covers approximately 9 400 ha and is situated in the vicinity of Brand-se-Baai (31°18'S, 17°54'E) on the Namaqualand coast, some 350 km north of Cape Town and about 80 km north-west of the nearest major town, Vredendal (Figure 2.1). Economic activities within the immediate area are restricted to diamond mining, dryland farming and kelp harvesting (Environmental Evaluation Unit, 1990). Brand-se-Baai has been used for many years as a traditional holiday and camping area by the local people.

CLIMATE

The climate of the study area is summarised in the climate diagram (Figure 2.2), which is based on data from the Council for Scientific and Industrial Research (1997). The study area lies in a transitional zone between the Namib Desert to the north and the Cape Mediterranean region to the south. The West Coast has a mediterranean-type climate with hot dry summers (November - January) and rain during the winter months (April - July). Rainfall increases from north to south with an average of 160 mm (measured over a period of four years) at the study area. Fog is a characteristic feature of the Namaqualand coastal climate, occurring throughout the year. These advective sea fog (*c.* 100 days per annum at the study area) and the heavy dew-falls supplement the low rainfall significantly. The average annual precipitation (rainfall + fog) at the study area was 282 mm for the period March 1993 to February 1997 (Figure 2.2).

The average annual temperature is 15.8°C (Figure 2.2) with a relatively small fluctuation due to the marine influence. The maximum average monthly temperature is 24.1°C in January (summer) and the minimum average monthly temperature is 7.5°C in July (winter). Frequent easterly berg winds, which blow from the interior, bring hot, dry conditions to the coast.

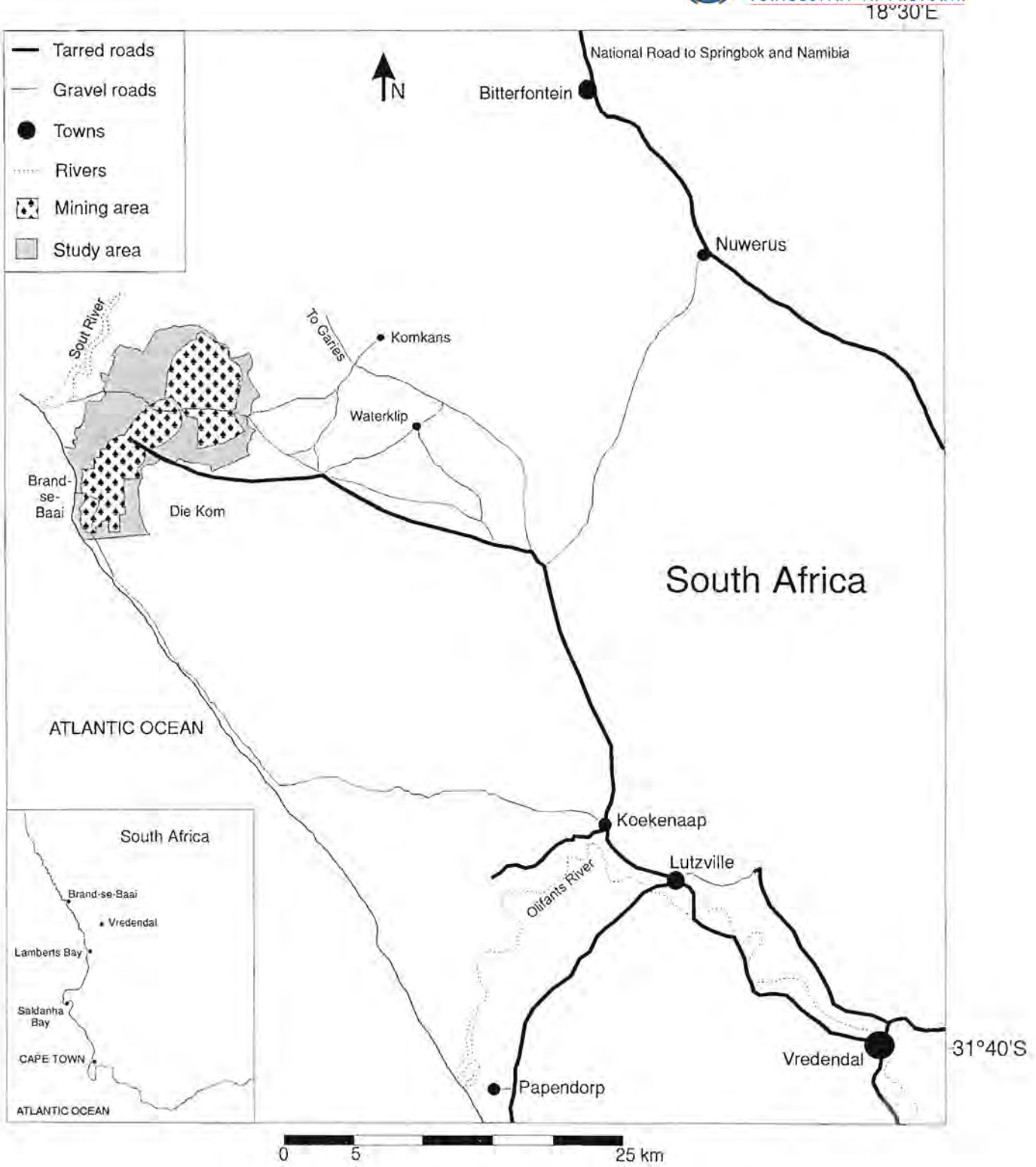

Figure 2.1. Location map of the Brand-se-Baai study area.

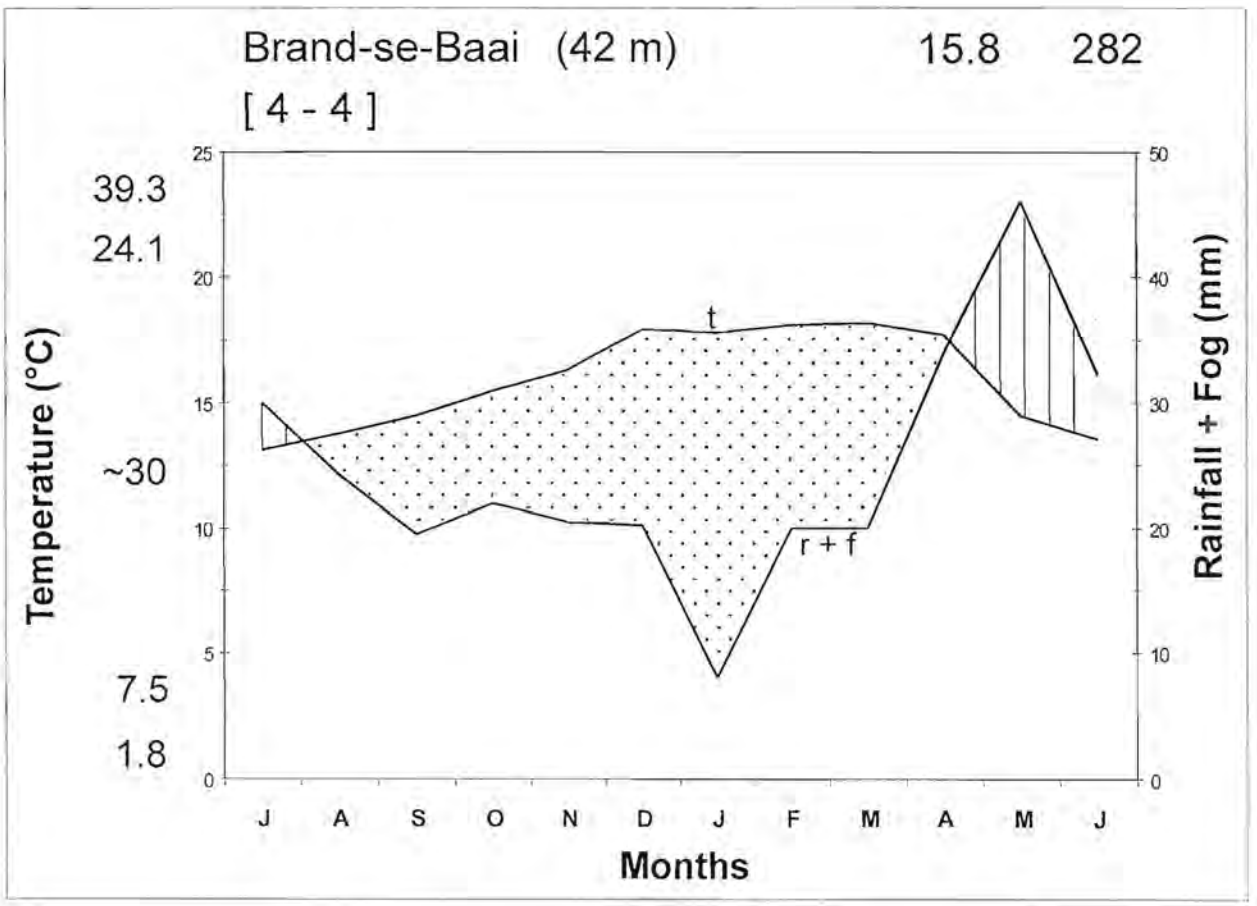

Figure 2.2. Climate diagram (following Walter & Lieth, 1960) of the Brand-se-Baai station for the period March 1993 - February 1997.

The wind regime along the Namaqualand coast is one of the strongest in the world. Washington (1990) reports that winds blow with the highest frequency from the south and south-south-east from September to March, with less frequent but strong winds blowing from the north and north-north-east during the months of June, July and August. Under northerly flow, daytime wind speeds at the coast may peak at 28.8 $km.h^{-1}$ increasing inland.

PHYSICAL ENVIRONMENT

The study area is bounded by a retrograding coastline, which trends north-north-west (Environmental Evaluation Unit, 1990). This orientation exposes the coastal land to the strong southerly winds prevailing in summer. The coast features wave-cut rocky platforms separated by a number of small, isolated beaches and a large primary dune belt *i.e.* Graauwduine, which is approximately five kilometers long and 500 m wide. Brand-se-Baai is one of many bays along this stretch of coast. In most places, the terrain rises steeply from the coast to the coastal plain. The undulating inland area is covered with vegetated sand dunes aligned roughly parallel to the prevailing wind direction *i.e.* north - south. Two prominent rounded hills, Graauwduin-se-kop (158 m above sea level) and Kalkbaken-se-kop (147 m above sea level) are landmarks in the area. A depression with a diameter of five to six kilometers, known as "Die Kom", is situated to the southeast of the study area (Figure 2.1). A steep-sided valley system, approximately 30 km long and 100 m deep follows the courses of the Goerap River and the Sout River estuary, on the northern boundary of the study area. The Salt River estuary is a severely degraded system which is being worked as a salt pan (Environmental Evaluation Unit, 1990).

The area is extremely dry with no visible surface water supply. The catchments of the Goerap River and Sout River, which flow episodically, are the only drainage systems near the study area. No groundwater was located in test boreholes in the study area (Environmental Evaluation Unit, 1990).

The study area is included in a geomorphological subdivision of the Namib Desert, and is referred to as the Namaqualand Sandy Namib. A thick overburden of marine and aeolian sediments overlie older basement rocks of the Namaqualand granite-gneiss suite, and metamorphosed Vanrhynsdorp Group rocks (Environmental Evaluation Unit, 1990).

Generally, the dunes along the coast are light coloured becoming progressively more red further away from the coast. The pale grey dune sands consist of unconsolidated quartz-rich material, whereas the red terrestrial deposits are derived from orange feldspathic sands. It is these terrestrial deposits which often display heavy mineral enrichment. Soils tend to be saline and alkaline, with a pH exceeding eight (Environmental Evaluation Unit, 1990).

Diamond mining used to be the main activity in the region. Heavy minerals presently being mined in the study area include: ilmenite, rutile, leucoxene, zircon and monazite (Environmental Evaluation Unit, 1990).

VEGETATION AND FAUNA

Boucher & Le Roux (1993) identified the littoral vegetation of the study area as Southern Namaqualand Strand Communities, which are sensitive to disturbance because they are subjected to heavy winds, salt spray and drift sands. It is therefore a naturally fragile ecosystem with a low resilience which is easily disturbed or destroyed. In terms of Acocks' classification (Acocks, 1988), the vegetation of the study area consists of Strandveld Proper (Veld Type 34b) with the Namaqualand Coast Belt Succulent Karoo (Veld Type 31a) in the north-eastern part.

According to Low & Rebelo (1998), the vegetation of the study area consists of Strandveld Succulent Karoo (55) and Lowland Succulent Karoo (57), both of which are classified under the Succulent Karoo Biome. The Strandveld Succulent Karoo (55) vegetation, containing many drought deciduous and succulent species, is associated with areas of calcareous sand. The vegetation varies in height according to the depth of the sand - the shortest vegetation growing on exposed calcrete and coastal rocks and the tallest being found in areas where deep calcareous sand occurs (Boucher & Le Roux, 1990). Small patches of Lowland Succulent Karoo (57) vegetation, characterised by a sparse cover of dwarf succulent-leaved shrubs which do not recover easily from disturbance, occur within the study area (Boucher & Le Roux, 1990). The poorly known Sand Plain Fynbos (68) occurs on the leached, acidic, low-nutrient sands in the area. This vegetation is characterised by the dominance of plants with small leaves and by members of the Restionaceae (Boucher & Le Roux, 1990).

The study area has a resident bird population of approximately 107 species, with a breeding population of about 52 species. Thirty-nine species of reptiles and amphibians, as well as 35 mammal species have been reported. No rare or threatened insect species have been recorded (Environmental Evaluation Unit, 1990).

MATERIAL AND METHODS

SPECIES USED IN THIS STUDY

All species names follow that of Arnold & De Wet (1999). For a complete list of taxa used and/or encountered in this study, the reader is referred to Appendix 1.

***Albuca exuviata* Bak.**

This species is a bulbous geophyte of the Hyacinthaceae with 2-4 leaves. The flowers are borne in a raceme, and are yellow, banded with green (Levyns, 1929). The perianth segments are free, the inner converging and folded over the tips. The fruit is a capsule, and produces flattened, black seeds. Flowering season is August to December (Thiselton-Dyer, 1904).

***Amellus tenuifolius* Burm.**

This dwarf shrub with small greyish leaves is a member of the Asteraceae and is found on sandy soils in Namaqualand. Inflorescences are solitary and consist of purple ray and yellow disc florets. Flowering occurs from October until December (Manning & Goldblatt, 1996).

***Arctotheca calendula* (L.) Levyns**

The Cape dandelion is an annual herb (up to 200 mm tall) of the Asteraceae with a basal rosette of leaves, roughly hairy above and felted below. The inflorescences appear from July until November. The ray florets are pale yellow and the disc florets black. This species is usually found in disturbed sites throughout Namaqualand as well as in the Western Cape (Van Rooyen *et al.*, 1999).

***Arctotis stoechadifolia* Berg.**

This perennial spreading herb of the Asteraceae grows up to 800 mm tall and has hairy stems. The hairy leaves are up to 100 mm long and lobed. The solitary yellow flowerheads (disc florets are black) are 40-60 mm in diameter. Flowers between September and October in sandy areas from Namaqualand to the Cape Peninsula (Manning & Goldblatt, 1996; Le Roux *et al.*, 1997).

***Ballota africana* (L.) Benth.**

Kattekruie is a member of the Lamiaceae and is found mainly along water courses and in the shelter of rocks or bushes. This species is an erect, greyish, aromatic, perennial herb with hairy, rounded leaves, growing up to 1.2 m tall. The pink to purple flowers appear in dense clusters above each leaf pair on the upper parts of branches. Flowers July to November. Early colonists used the plant for a number of ailments such as coughs, colds and sore throats (Van Rooyen *et al.*, 1999).

***Brassica tournefortii* Gouan**

An erect, rather slender annual of the Brassicaceae, up to 600 mm tall. The basal leaves are rosulate, petiolate and up to 250 mm long, while the upper leaves are much smaller. Flowers are pale yellow, sometimes tinged with mauve on fading, and the 5-7 petals *c.* 1.5 mm long. The siliqua, including the beak, is 30-50 mm long, 2-2.8 mm broad, linear-attenuate, and the valves bulged by the seeds, which are globose, brown, and about 1 mm in diameter. This species is a native of the maritime Mediterranean region and is common on sand-dunes and in disturbed places (Codd *et al.*, 1970).

***Cephalophyllum spongiosum* (L.Bol.) L.Bol.**

Volstruisvygie is a member of the Mesembryanthemaceae and is found in sandy soils along the coast of Namaqualand. This species is a spreading perennial (up to 300 mm tall) with succulent green leaves. The flowers are apricot, pink or red and 90 mm in diameter. The hygrochastic fruit capsules are 12 locular (Le Roux *et al.*, 1997).

***Chrysocoma longifolia* DC.**

This species is a member of the Asteraceae and is found on lower slopes and sandy flats from Namaqualand to Worcester. This shrub grows up to 1 m in height. The yellow flowerheads appear from November to December (Bond & Goldblatt, 1984).

***Conicosia elongata* (Haw.) N.E.Br.**

Varkiesknol is a perennial herb of the Mesembryanthemaceae with a succulent tuber and slender succulent leaves. The aerial parts of the plant die back in summer. White or cream coloured flowers are borne on short stalks during spring. This plant is found in sandy soils throughout Namaqualand (Le Roux *et al.*, 1997).

***Conicosia pugioniformis* (L.) N.E.Br.**

Snotwortel is a spreading perennial of the Mesembryanthemaceae with succulent leaves. Bright yellow flowers are borne on short stalks from September to October. This species is found in deep, sandy soils from Namaqualand to Bellville (Marshall & Mommsen, 1994; Manning & Goldblatt, 1996).

***Cotula thunbergii* Harv.**

This member of the Asteraceae is an annual herb with finely divided leaves. The flowerheads are yellow (Bond & Goldblatt, 1984).

***Cysticapnos cracca* (Cham. & Schlechtd.) Liden**

This species is a member of the Fumariaceae and is a soft climbing annual with divided leaves, often ending in tendrils. Flowers are pink with darker tips. The fruits are inflated and bladder-like (Bond & Goldblatt, 1984).

Didelta carnosa* (L.f.) Aiton var. *carnosa

Perdeblom is a dwarf shrub of the Asteraceae (up to 400 mm tall) with fleshy, slightly rolled under leaves. The flowerheads are solitary with yellow ray and disc florets. This species flowers July to December and after the flowers have withered the fruithead remains on the plant for a long time. It is found on coastal dunes and sandy flats from Namaqualand to Darling (Van Rooyen *et al.*, 1999). It is a highly palatable plant during winter as well as summer (Le Roux *et al.*, 1997).

***Dimorphotheca pluvialis* (L.) Moench.**

The Cape rain daisy is a member of the Asteraceae and is widespread in sandy soils from Namibia to Riversdal. This annual herb grows up to 400 mm tall and has lobed to toothed leaves. The ray florets are white above and purple on the reverse and the disc florets are yellow at the top (Van Rooyen *et al.*, 1999). The first flowers appear as early as mid-winter if the rains have been good, and continue until the end of spring (Marshall & Mommsen, 1994).

***Dimorphotheca tragus* (Ait.) T.Norl.**

Jakkalsbos is a member of the Asteraceae and grows up to 300 mm tall. This species is a perennial herb with sparsely toothed leaves. White or orange flowerheads with a diameter of 40 – 60 mm are borne on slender stalks. Found throughout Namaqualand (Le Roux *et al.*, 1997).

***Ehrharta calycina* J.E.Sm.**

Rooisaadgras is a member of the Poaceae and is found throughout the winter rainfall region. This species is a perennial, highly palatable grass with culms 300 to 700 mm tall. The inflorescence is a panicle with sprays of reddish-brown spikelets drooping from long stalks. Flowers from July to December, but usually in spring (Van Rooyen *et al.*, 1999).

***Eriocephalus africanus* L.**

Wild rosemary is a branched shrub of the Asteraceae, growing up to 1 m tall. This species has greyish-green aromatic leaves and small flowerheads with 2 to 3 conspicuous white ray florets. Fruits are covered with long

white hairs. Flowers from May to September throughout Namaqualand (Manning & Goldblatt, 1996; Le Roux *et al.*, 1997).

***Gazania leiopoda* (DC.) Rossl.**

This low growing perennial of the Asteraceae has divided leaves and large, deep yellow flowerheads borne on slender stalks; disc florets are black (Bond & Goldblatt, 1984).

***Grielum grandiflorum* (L.) Druce**

Platdoring is a member of the Neuradaceae and is found on coastal plains from Port Nolloth to the Cape Peninsula. This spreading perennial has grey-green, deeply incised leaves. The flowers are a glossy yellow and 30 – 50 mm in diameter. Flowers from August to October (Manning & Goldblatt, 1996; Le Roux *et al.*, 1997).

***Hebenstretia dentata* L.**

Vlagblom is an annual herb up to 300 mm tall and a member of the Selaginaceae. The leaves are narrow with minute hairs along the lower edges. The scented flowers are borne in spikes and are white with orange markings in the throat. Flowers July to October. This species is found on sandy flats and lower slopes from Namaqualand to the Cape Peninsula (Van Rooyen *et al.*, 1999).

***Hebenstretia repens* Jarosz**

This much-branched annual is up to 450 mm tall and a member of the Selaginaceae. The narrow leaves have a few teeth in the upper part. White, aromatic flowers are borne in spikes between July and November. This species is found on clay or sandy flats from Namaqualand to Bredasdorp (Manning & Goldblatt, 1996).

***Heliophila coronopifolia* L.**

Blue flax is an erect annual herb of the Brassicaceae, growing up to 600 mm tall, mostly with a single stem. This species has long, narrow leaves and pale to bright blue flowers with a white or yellow centre. Flowers between August and October. The fruits are long and narrow and constricted between the seeds. Plants are found in sandy or loamy soils from southern Namaqualand to the Cape Peninsula (Van Rooyen *et al.*, 1999).

***Hypertelis salsoloides* (Burch.) Adamson**

Haassuring is a member of the Aizoaceae and is widespread throughout the dry parts of South Africa and Namibia. This multi-stemmed perennial herb grows up to 250 mm tall. The leaves are cylindrical and succulent. The white or pink flowers are borne in small groups on long stalks during spring and summer (Le Roux *et al.*, 1997).

***Lebeckia multiflora* E.Mey.**

This species is a multi-stemmed shrub up to 1.5 m tall and a member of the Fabaceae. The leaves are trifoliate with hairy, narrowly-linear leaflets. The yellow flowers are borne in loose racemes. The pods are covered with small, silvery hairs. Plants are found on sandy soils from Namaqualand to the Cape Peninsula (Le Roux *et al.*, 1997).

***Nemesia bicornis* (L.) Pers.**

Kappieblommetjie is a member of the Scrophulariaceae and is found from Namaqualand to the Cape Peninsula. This annual herb grows up to 500 mm tall. The leaves are lance-shaped and toothed. The flowers are arranged in loose racemes. Each white or blue flower is 2-lipped, with the upper lip consisting of 4 lobes. The lower lip has two bulges and a straight spur. Flowers between July and October (Manning & Goldblatt, 1996).

***Othonna floribunda* Schltr.**

This branched shrublet of the Asteraceae grows up to 400-600 mm tall and has fleshy leaves. The orange or yellow flowerheads are borne between July and September (Bond & Goldblatt, 1984).

***Pharnaceum aurantium* (DC.) Druce**

This species is an erect shrublet between 100-800 mm tall and a member of the Aizoaceae. The small, white flowers are borne on slender stalks. Found in stony gravel between Nieuwoudtville and Worcester (Bond & Goldblatt, 1984).

***Pharnaceum exiguum* Adamson**

A delicate tufted annual up to 300 mm tall and a member of the Aizoaceae. The small green flowers appear in October. This species is found on sandy flats throughout Namaqualand (Bond & Goldblatt, 1984).

***Pharnaceum lanatum* Bartl.**

This species is an erect perennial up to 400 mm tall. It is a member of the Aizoaceae with woody stems and needle-like leaves. The small white flowers are borne on slender stalks and open late in the afternoon. Flowers from August to October and is found in sandy soils from Namaqualand to Caledon (Manning & Goldblatt, 1996).

***Polycarena pumila* (Benth.) Levyns**

This member of the Scrophulariaceae is a simple or branched annual up to 100 mm tall. The purple flowers appear between August and October. Found from Namaqualand to Riversdale (Bond & Goldblatt, 1984).

***Pteronia divaricata* (Berg.) Less.**

Geelknopbos is a member of the Asteraceae. This shrub grows up to 1 m tall and has broadly elliptic, velvety leaves. The flowerheads are a bright yellow and 40 mm in diameter. This species flowers from September to November and is found in sandy or rocky soils from Namibia to Hopefield (Manning & Goldblatt, 1996; Le Roux *et al.*, 1997).

***Ruschia bolusiae* Schwant.**

This stiff, robust shrublet of the Mesembryanthemaceae grows up to 120 mm tall and has succulent leaves. Pink flowers appear between May and September. Found in southern Namaqualand (Bond & Goldblatt, 1984).

***Salvia africana-lutea* L.**

Wild sage is a dense, grey shrub up to 2 m in height. It is a member of the Lamiaceae and is widespread on coastal dunes and in arid fynbos. The leaves are aromatic and covered with minute hairs. The 2-lipped flowers are golden to reddish-brown, arranged in racemes and appear from June to December (Manning & Goldblatt,

1996). The calyx remains on the plant, increasing slightly in size, after the flowers have faded (Burman *et al.*, 1985).

***Senecio arenarius* Thunb.**

Hongerblom, a member of the Asteraceae, is a branched annual up to 400 mm tall with basal leaves clasping the stem. The flowerheads are arranged in branched inflorescences, composed of magenta ray florets and yellow disc florets. This species flowers between July and October and is common on sandy flats from Namibia to the Cape Peninsula (Van Rooyen *et al.*, 1999).

***Senecio elegans* L.**

Wild cineraria, a member of the Asteraceae, is a branched annual up to 400 mm tall with deeply-incised leaves. The flowerheads are arranged in branched inflorescences, composed of magenta ray florets and yellow disc florets. This species flowers from September to November and is found on coastal plains from Namaqualand to the Eastern Cape (Manning & Goldblatt, 1996).

***Silene clandestina* Jacq.**

This species is a member of the Caryophyllaceae and is an erect annual up to 400 mm tall with white or cream coloured flowers. Flowers appear from August to November and open in the late afternoon. This species is introduced from Europe and found on sandy flats in southern Namaqualand (Bond & Goldblatt, 1984).

***Stoeberia* sp.**

This species is a member of the Mesembryanthemaceae. The plants are shrubby, tall and erect (up to 2.5 m in height) with succulent leaves, which are club-shaped, with slightly flattened upper surfaces and with a ridge along the bottom, but only towards the tip. The white flowers occur in much-branched clusters. There are no bracts on the flower stalks. Five to six triangular sepals are present, with short petals in more or less a single whorl and numerous filamentous staminodes and stamens. The fruit capsules have five or six locules, with valves remaining open. The valves are broad and bony in texture, valve wings are present and large closing bodies occur deep inside the seed cavities. The wind-dispersed seeds are pear-shaped with rough surfaces. Flowers during winter and spring (Smith *et al.*, 1998).

***Tetragonia microptera* Fenzl**

This species, a member of the Aizoaceae, is a prostrate annual with succulent stems and leaves. The leaves are broadly ovate and the greenish flowers are arranged in small groups of 2-5. Found on sandy flats and in disturbed areas (Le Roux *et al.*, 1997).

***Tetragonia virgata* Schltr.**

A sprawling, somewhat woody shrublet, 500 mm tall and a member of the Aizoaceae. This species has orange flowers and flowers during July. Found on sandy flats from Namaqualand to Clanwilliam (Bond & Goldblatt, 1984).

***Tripteris oppositifolia* (Ait.) T.Norl.**

Skaapbos, a member of the Asteraceae, is a rounded shrub up to 1 m tall with opposite, leathery leaves. The flowerheads are 40-50 mm in diameter and borne on short stalks. The ray florets are yellow to orange and the disc florets purple. The fruit is 3-winged with a transparent window in each of the 3 sides. This species flowers from July to October and is found in sandy soils from Namaqualand to Clanwilliam (Van Rooyen *et al.*, 1999).

***Ursinia anthemoides* (L.) Poir.**

Marigold is a member of the Asteraceae and is found in sandy soils from Namibia to Port Elizabeth. It is an annual herb with narrowly divided leaves, giving it a feathery appearance. Flowerheads are solitary and borne on long stalks, ray florets are yellow and the disc florets black. Achenes have a whorl of white scales. Flowers August to October (Manning & Goldblatt, 1996; Van Rooyen *et al.*, 1999).

***Ursinia speciosa* DC.**

This annual herb of the Asteraceae is up to 400 mm tall with deeply-incised leaves. The flowerheads are solitary and borne on long stalks. The ray florets are yellow or white and the disc florets, yellow. This species is found throughout Namaqualand up to Malmesbury (Le Roux *et al.*, 1997).

***Vanzijlia annulata* (Berger) L.Bol.**

This prostrate shrublet, a member of the Mesembryanthemaceae, is up to 120 mm tall. The plants have numerous short shoots forming compact clumps at the centre and also several long shoots which may be trailing or climbing into other shrubs. The leaves on short shoots and the first pair of the long shoots consist of long sheaths with only short free tips, forming a body during the dry season. Leaf pairs on long shoots have basal sheaths less than half their lengths. Flowers are solitary at the end of long shoots, the white petals thin and spreading. The apically pink and purple filamentous staminodes elongate while the flower opens and closes over several days, eventually drooping with age. Fruit capsules have 10 locules and are long-stalked; they possess valve wings, covering membranes with distal closing bulges, and large, white closing bodies. Flowers appear between July and September (Bond & Goldblatt, 1984; Smith *et al.*, 1998).

***Wahlenbergia paniculata* (Thunb.) A.DC.**

This slender annual herb with small hairy leaves is a member of the Campanulaceae. The flowers are blue and arranged in loose racemes. Flowering from September to November. This species is found in sandy soils from Piketberg to Worcester (Manning & Goldblatt, 1996).

***Zygophyllum morgsana* L.**

Skilpadbos, a member of the Zygophyllaceae, is found throughout Namaqualand and in arid areas of Namibia. It is a multi-stemmed shrub up to 1.5 m tall. The leathery leaves are divided into 2 oval leaflets. The flowers are yellow and are borne in pairs at the ends of branches. Flowers from June to November. The fruit has four, large membrane-like wings (Marshall & Mommsen, 1994; Manning & Goldblatt, 1996).

VEGETATION DIVERSITY

The study area was stratified into relatively homogeneous physiographic-physiognomic units on 1:50 000 aerial photographs. A total of 128 sample plots, each with an area of 100 m^2, was randomly located within these stratification units. In each sample plot, all plant species were recorded and the cover-abundance of each species estimated according to the Braun-Blanquet cover-abundance scale (Mueller-Dombois & Ellenberg, 1974). Average height and average canopy cover were estimated for the woody and herbaceous layers in each plot. Environmental data included soil colour, distance from the sea (salt spray & fog intensity), aspect, slope, sand depth and disturbance (grazing & trampling).

The first classification of the vegetation, based on the total floristic data set, was obtained by the application of the TWINSPAN classification algorithm (Hill, 1979a) in the TURBOVEG (Henneken, 1996a) computer program. Further refinement of the classification was achieved by Braun-Blanquet (Zürich-Montpellier) procedures. The final result of the classification procedure was a differential or phytosociological table. The DECORANA ordination algorithm (Hill, 1979b) was applied to the floristic data to detect possible gradients in and between plant communities and to detect possible habitat gradients associated with vegetation gradients (Bezuidenhout, 1995).

These methods are described in more detail in Chapter 3.

SPATIAL AND TEMPORAL VARIATION IN SEED BANK SIZE AND COMPOSITION

Ten soil sample locations were randomly selected within each of six vegetation units. At each of the 60 sampling locations, 15 soil samples were taken linearly over a total distance of 28 meters. Each sample consisted of a soil core with a diameter of 65 mm taken to a depth of 100 mm, totalling a volume of approximately 246 cm^3. The germinable seed content was estimated by means of the seedling emergence method, conducted at the University of Pretoria, some 1 200 km north-east of the study area. Sampling was done four times a year (once every season) for a total period of two years.

For each of six sampling seasons and the 60 sampling localities, three subsamples of 100 cm^3 were stored dry in paper bags under ambient conditions at the University of Pretoria. During the following autumn, the germinable seed density and composition in each of the subsamples was determined in the same manner as described above.

The Presence Coefficient of Sorensen and the Abundance Coefficient of Motyka *et al.* (Mueller-Dombois & Ellenberg, 1974) were used to determine the similarity in soil seed bank size and composition between samples examined directly after sampling and those examined at the peak season for germination.

For detailed descriptions of these methods, the reader is referred to Chapters 4 and 5.

SEED BANK VS. STANDING VEGETATION PHYTOSOSIOLOGY

A vegetation survey of the study area (De Villiers *et al.*, 1999a; Chapter 3) resulted in the identification of six main plant communities. Seed bank sample plots were randomly located within each of five of these communities, and totalled 60 plots for the study site. These five communities are situated within the western mining area, which is being mined first. The sixth community predominantly constitutes the eastern mining area, and was not sampled. The seed bank emergence method was used for determining seed bank size and composition.

Seed bank abundance data obtained during the eight sampling seasons were lumped. These abundance values for each species (individuals m^{-2}) from each plot were transformed to a scale of 1 – 9, for classification purposes with the TURBOVEG (Hennekens, 1996a) and MEGATAB (Hennekens, 1996b) computer programs. Using the Zürich-Montpellier (Braun-Blanquet) approach (Mueller-Dombois & Ellenberg, 1974), the species and relevés in the matrix were assembled to produce a phytosociological table for the seed bank (Werger, 1974). Canonical Correspondence Analysis (CCA) was applied to the seed bank data with the computer program CANOCO version 3.15 (Ter Braak, 1997), to detect possible gradients in and between seed bank units and to detect possible habitat gradients associated with seed bank gradients.

Similarity in species composition between the seed bank and the standing vegetation was determined by means of Sorensens' Presence Coefficient (Mueller-Dombois & Ellenberg, 1974).

These methods are described thoroughly in Chapter 6.

SEED BANK VS. STANDING VEGETATION DENSITY

Within each of six vegetation units, two sites were randomly selected using 1:50 000 aerial photographs. At each site, both the density and species composition of the standing vegetation and the soil seed bank (seedling emergence method) were determined. To determine species' density in the standing vegetation, an area of 10 m x 10 m at each site was divided into 100 quadrants measuring 1 m^2 each. Within each quadrant the number of individuals of all perennial and annual plant species (excluding grass species) were recorded. For grass species (Poaceae), percentage cover was estimated in each quadrant.

To compare species composition and density in the vegetation with that in the seed bank, data were ordinated by Principal Component Analysis (PCA) with the computer program CANOCO version 3.15 (Ter Braak, 1997). Before the analysis, the vegetation and seed bank density values for each species (individuals m^{-2}) from each plot were transformed to scores on a 1-9 abundance scale.

For both vegetation and soil seed bank, the density of individual m^{-2}, percentage frequency as well as the mean number of taxa per community were calculated. Similarity in species composition between the standing vegetation and the soil seed bank was determined by means of Sorensen's index of similarity

(Mueller-Dombois & Ellenberg, 1974). Spatial distribution of the soil seed bank was determined by calculating the variance/mean ratio (Odum, 1971).

The values and indices determined and calculated are explained in Chapter 7.

GERMINATION REQUIREMENTS

Mature diaspores (seeds) of 28 plant species (31 seed types) were collected from natural populations at the study site. Collected seeds were air-dried at room temperature for a period of two weeks, whereafter seeds were stored in brown paper bags under ambient conditions for 28 weeks.

Seeds were germinated in Petri dishes, containing two layers of filter paper. Germination tests were conducted in germination cabinets and each treatment consisted of five replicates of 50 seeds for each species. Germination tests were conducted in the light and dark at six constant temperatures (7°C; 12°C; 17°C; 22°C; 27°C and 32°C) and one alternating temperature regime (12°C/22°C; 12h/12h). Petri dishes of the dark treatments were placed in cardboard boxes and sealed with aluminium foil to eliminate light. Petri dishes were examined every second day and germinated seeds counted and removed. Dark replicates were examined under a green safety light. Germination tests were continued for a period of 30 days. The optimal temperature for germination of a specific species was calculated as the average value of all temperatures, weighted for the percentage germination at each temperature (Olff *et al.*, 1994).

A Canonical Correspondence Analysis (CCA) ordination (Ter Braak, 1997) was performed on the germination data, using both species and environmental (temperature & light) parameters.

These methods are described in more detail in Chapter 8.

DORMANCY-BREAKING TREATMENTS

Collected seeds of 27 local plant species were air-dried at *c.* 20°C for a period of two weeks (henceforth referred to as fresh seeds) before dormancy-breaking experiments commenced. Seeds were germinated in Petri dishes containing two layers of filter paper. Germination tests were conducted in germination cabinets and radicle protrusion was the germination criterion.

After-ripening

To determine the requirement for an after-ripening period, freshly collected seeds of 26 species were divided into three sets. The first set was used to determine the germination percentage of fresh seeds (stored for 2

weeks at *c.* 20°C). The second and third sets were stored dry in paper bags at ambient temperatures at the University of Pretoria, for either six weeks or 28 weeks respectively, before conducting germination tests.

Germination tests were conducted in the light (under constant fluorescent light with a photosynthetic photon flux density of 9.3 µmol m^{-2} s^{-1}) at a constant temperature of 17°C.

Endogenous germination pattern

Collected seeds of seven species were stored dry in paper bags at a constant temperature of 20°C. For each species, germination in five replicates of 20 seeds each was investigated at a two-weekly interval for a period of 40 weeks, whereafter sampling occurred at a four-weekly interval for 48 weeks. Germination tests were conducted at a constant temperature of 17°C, under constant fluorescent light with a photosynthetic photon flux density of 9.3 µmol m^{-2} s^{-1}. Petri dishes were opened weekly for a period of four weeks, and germinated seeds counted and removed. To establish whether an endogenous germination pattern was present, 6^{th} order polynomial functions (Microsoft® Excel 97 SR-1, 1985-1997, Microsoft Corporation) were fitted to the data, as these yielded higher R^2 values than did functions of lower orders.

Alternative dormancy-breaking treatments

Seeds of ten species were stored dry in paper bags at ambient temperatures at the University of Pretoria for periods of 15 – 26 weeks, before conducting dormancy-breaking treatments. Untreated seeds were used as a control. Five main dormancy-breaking treatments were applied:

1) Seeds were scarified mechanically by pricking the seed coat or by scarifying with sandpaper, whereafter they were germinated directly or leached in distilled water for four hours.
2) Chemical scarification entailed the submergence of the seeds in 98% sulphuric acid for periods of 0.5, 1, 2, 4, 8, 16, 32 or 64 minutes. After the period of submergence, seeds were rinsed with distilled water for five minutes.
3) In hydration/dehydration treatments, seeds were submerged in 50 cm^3 distilled water for periods of 1, 2, 4, 8 or 16 hours. The water containing the submerged seeds was disturbed as little as possible. After hydration, seeds were air-dried at room temperature for 24 hours.
4) Seeds of the heat and/or cold pre-treatments were stored dry for one week at constant temperatures of 45°C or 5°C respectively. The seeds of the heat+cold treatment were stored dry for one week at a temperature of 45°C, followed by a one week dry storage period at 5°C. The seeds of the cold+heat treatment were stored dry for one week at a temperature of 5°C, followed by a dry storage period of one week at 45°C.
5) In the "leaching' experiment, seeds were submerged in 50 cm^3 distilled water for periods of 1, 2, 4, 8 or 16 hours. The water containing the submerged seeds was stirred every 30 minutes, and was replaced with fresh distilled water every 60 minutes.

Germination tests were conducted at optimum temperature and light conditions for the germination of seeds of each species (Chapter 8).

These treatments are described more thoroughly in Chapter 9.

RELATIVE HUMIDITY AND VIABILITY

Seeds of six species, collected during spring 1994 at the study site, were air-dried at room temperature (*c.* 20°C) for a period of two weeks, whereafter they were sealed in glass dessicators containing saturated solutions to obtain a specific relative humidity (RH) within the dessicator. The following solutions were used to obtain the required relative humidities at 20°C (Winston & Bates, 1960; Copeland & McDonald, 1995): NaOH for a low RH (7%), $K_2CO_3.H_2O$ for an intermediate RH (43%), and either NaCl or KNO_3 for a high RH of 75% or 93% respectively.

After four weeks, 30 replicates of 50 seeds each were hermetically sealed in aluminium foil bags. After eight weeks of storage at 20°C, half of these replicates were buried in the field at Brand-se-Baai, under 50 mm of soil, while the other half remained at a constant temperature of 20°C in the laboratory. Seeds stored dry (ambient RH) in paper bags at 20°C for either 6 or 30 months were used respectively as an initial control and a control treatment.

After 27 months of storage or burial (autumn), five replicates of each treatment and species were germinated. Germination tests were conducted in germination cabinets at a constant temperature of 17°C, under constant fluorescent light with a photosynthetic photon flux density of 9.3 µmol m^{-2} s^{-1}, with the exception of *Conicosia pugioniformis* and *Gazania leiopoda*, of which the seeds were germinated in darkness. These conditions were found to be near optimum for the germination of the different species (Chapter 8).

For more details on these methods, the reader is referred to Chapter 10.

SEED BANK CLASSIFICATION

The key of Grime & Hillier (1981) was used as a template for determining numerous laboratory characteristics of collected seeds.

Mature seeds of 37 local plant species (41 seed types) were used in this study. Both fresh seeds (air-dried for two weeks) and seeds stored dry at 20° for one month after the initial air-drying period of two weeks, were used in the germination experiments.

Mean dispersule length was determined by measuring the length of 100 dispersules for each species. Small dispersules were measured under a stereo microscope. Mean seed mass was determined by weighing 100

seeds collectively on a Mettler AT100 balance. Abscission of seeds from the mother plant, scarification requirement and dispersal type were inferred from seed morphological characteristics. The lowest temperature for 50% germination (T_L) was determined from data on stored seeds of these species, germinated at various temperatures (Chapter 8).

These methods are described in more detail in Chapter 11.

SEED PRODUCTION, PREDATION, FUNGI AND SEEDLING RECRUITMENT

Seed production and pre-dispersal seed predation

The seed production of six perennial shrub species was estimated by counting 1) the number of seeds produced by each of 10 flowers or inflorescences per plant, 2) the number of flowers or inflorescences per reproductive shoot, and 3) the number of reproductive shoots per plant. Ten plants of each species were investigated. Pre-dispersal seed predation in five of these species was determined by the exclusion of insects and vertebrates from one randomly chosen reproductive shoot on each of the ten plants, by bagging it with nylon fabric (mesh size < 0.25 mm) immediately after flowering and treatment with insecticide. After three months (summer 1994), the yield (total number of seeds) of bagged flowers/inflorescences were compared with those of random samples of unbagged flowers/inflorescences located on the same plant.

The fruits of *Tetragonia microptera* do not disperse easily after maturation and seed production was determined by counting the total number of fruits produced by each of 10 randomly selected plants. Seed production under laboratory conditions, of three species, was reported by De Villiers *et al.* (1999b).

For the determination of pre-dispersal seed predation in five species, ten replicates of 100 mature seeds each were harvested randomly within a population of each species. These seeds were inspected under a dissection microscope for signs of insect attack.

Data were analysed with linear and logarithmic regression analyses (Microsoft® Excel 97 SR-1, 1985-1997, Microsoft Corporation) to confirm possible correlation between seed production and pre-dispersal seed predation or the number of seeds entering the seed pool.

Post-dispersal seed predation

During spring 1994, 1 dm^3 plastic containers were buried randomly within a 10 m x 10 m area, with the top edges of the pots protruding 5 mm above soil level. Each container was refilled with soil from the specific burial position. Seeds of the five species investigated, present in the soil, were removed from the replaced soil by means of a 1 mm mesh sieve. For each species, a total of 50 harvested intact seeds were spread evenly on top of the replaced soil in each of the 10 replicates per treatment. A 5 mm layer of soil was spread

over the seeds to prevent secondary seed dispersal by wind. The soil level within each container corresponded to the soil level adjacent to each buried container. To exclude predators, containers were covered with fine mesh plastic cloth (1 mm). Drainage holes at the bottom of the containers were not covered to exclude soil fauna. Containers of the non-exclosure treatment were left uncovered. After nine months of burial in the field (winter 1995), each of the containers was retrieved and emerged seedlings of the sown species recorded and removed. Seeds still present in the soil were removed by means of a 1 mm mesh sieve and considered apparently viable when an intact seed resisted slight pressure applied by a set of forceps.

Seed-borne fungi

Seeds of the five species examined were surface-disinfected by pre-treating for one minute in a 1% available chlorine solution of sodium hypochlorite (NaOCl) (Copeland & McDonald, 1995). The surface-disinfected seeds were individually rinsed in distilled water and placed on sterile potato dextrose supplemented agar in 90 mm Petri dishes (Copeland & McDonald, 1995; Maude, 1996). Twenty replicates of 20 seeds each were plated.

After plating, batches of ten Petri dishes each were sealed in plastic bags to which approximately 5 ml of distilled water was added. Petri dished were incubated in the dark, at a constant temperature of 25°C for two weeks. At the end of the incubation period, Petri dishes possibly containing fungal colonies were placed under near-ultraviolet light at 25°C to encourage the development of fruiting bodies (Limonard, 1968; Maude, 1996). After two weeks, the seed-borne fungi were identified under a light-microscope.

Seedling recruitment

Prior to the start of the rainy season, treatments similar to those used to determine post-dispersal seed predation were set out for each of four species. After three months of burial in the field, the mesh covering each container was removed and the number of emerged seedlings recorded. After an additional three months, the number of remaining plants were recorded.

For detailed descriptions of these methods, please see Chapter 12.

SEEDLING SURVIVAL UNDERNEATH AND BETWEEN SHRUBS

Eight localities, each dominated by different perennial shrub (P) or annual (A) plant species, were selected at the study site. In localities dominated by perennial species, a 1 m x 0.5 m metal frame was randomly placed either directly under the canopy or in open areas between shrubs of the dominant species. Ten replicates were used for each micro-site (under or between dominant shrubs) and species. In localities dominated by

annual species, ten randomly placed replicates were used in total. The position of each frame was marked semi-permanently with 150 mm long plastic pegs. Within each frame, all seedlings were identified and counted.

After three months, the surveys were repeated. Seedlings that emerged after the initial winter count were incorporated in the recount. These methods are described thoroughly in Chapter 13.

SALINITY AND SEED PRODUCTION

Seeds of four species, collected at the study site, were sown in 1 dm^3 pots containing fine sand and irrigated daily with tap water, under free-draining conditions, for a period of two weeks. Thereafter the plants were irrigated daily under free draining conditions, with solutions having a sodium chloride (NaCl) concentration of either 1%, 2% or 3%. Distilled water was used as a control. The chemicals of half strength Arnon and Hoagland's nutrient solution (Hewitt, 1952) were added to all dilutions. Salts, that might have accumulated in the soil, were leached from the soil by giving each pot 500 cm^3 distilled water twice a week, before the saline solution was applied. One plant was grown per pot and ten replicates of each treatment were used for each of the four species. Fruits and mature seeds were harvested and counted before dispersal.

The treatments are described in more detail in Chapter 14.

SALINITY, SEEDLING EMERGENCE AND SURVIVAL

Achenes of three species were sown in 8 dm^3 trays, containing fine sand, and irrigated daily under free-draining conditions with 2 dm^3 solution depending on the treatment. In the emergence experiment, solutions with salinities of 1%, 2% or 3% NaCl were applied from the start. In the seedling survival experiment, seeds in the trays were irrigated with distilled water for four weeks, whereafter the salinity of the solutions applied was raised gradually (0.5% NaCl per day) until the correct salinity was reached *i.e.* 1%, 2% or 3% NaCl. Distilled water was used as a control. Half strength Arnon and Hoagland's nutrient solution (Hewitt, 1952) was added to all dilutions. Salts, that might have accumulated in the soil, were leached from the soil by giving each tray 2 dm^3 distilled water twice a week, before applying the saline solution.

Trays were placed in a Phytotron green house, and maintained at a constant temperature of 20°C. Each tray contained 20 seeds/seedlings and five replicates of each salinity treatment were used for each of the experiments and three species. The number of emerged and surviving seedlings was noted weekly.

More detail on these methods is presented in Chapter 15.

STATISTICAL TREATMENT OF DATA

Where applicable, the least significant difference (LSD) one-way analysis of variance (ANOVA) and/or LSD multi-factor ANOVA were used to test for a statistical significant difference at $P \leq 0.05$. The LSD multiple range test was applied to data where $P \leq 0.05$. Data were analysed with the use of the Statgraphics 5.0 (1989, STSC, Inc., U.S.A.) computer program.

CHAPTER 3

VEGETATION DIVERSITY OF THE BRAND-SE-BAAI COASTAL DUNE AREA, WEST COAST, SOUTH AFRICA: A PRE-MINING BENCHMARK SURVEY FOR REHABILITATION

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ABSTRACT

Prior to the mining of heavy minerals, the vegetation diversity of the Brand-se-Baai coastal area was investigated to serve as a benchmark for the future rehabilitation of the area. The vegetation was surveyed using the Braun-Blanquet procedure to classify the different plant communities. Six plant communities, some of which include several variants, were identified, described and mapped. A revegetation goal of 30%, rather than 60%, of the number of plant species present prior to mining are recommended.

Key words: Braun-Blanquet, coastal dune, mining, phytosociology, plant communities, rehabilitation, revegetation, vegetation classification.

INTRODUCTION

Along the West Coast of South Africa, the sandy soils are rich in heavy minerals such as ilmenite, rutile and zircon, which are essential in the paint, ceramic and steel industries (Environmental Evaluation Unit, 1990). Mining activities in the area and the eventual use of sea-water in the extraction process will destroy the topography, vegetation, animal life and chemical and physical characteristics of the soil. Mining companies are, however, compelled by law (Mining Rights Act No. 20 of 1967, Hoogervorst, 1990) to rehabilitate mined areas. The aim of the rehabilitation programme along the west coast of South Africa (Environmental Evaluation Unit, 1990) is to restore the mined area as close as possible to its pre-mining natural condition. The requirement that has to be met is the revegetation of the area with no less than 60% of the original indigenous plant species as soon as possible after mining has been completed (Environmental Evaluation Unit, 1990). A pre-mining vegetation survey is a prerequisite to compile a databank on the floristic and plant community diversity of the area. These data can also be used for selecting suitable species for the revegetation process.

Apart from Boucher & Le Roux's (1981) classification of South African west coast strand vegetation, Acocks' (1988) description of the veld types of South Africa and Low & Rebelo's (1996) description of the South African

vegetation, little is known about the vegetation of the area. The aim of this study was to classify, describe and map the vegetation of the Brand-se-Baai area prior to mining, to serve as an inventory of the representative plant communities.

STUDY AREA

Location

The study area covers approximately 9 400 ha and is situated in the vicinity of Brand-se-Baai (31°18'S, 17°54'E) on the Namaqualand coast, some 350 km north of Cape Town and about 80 km northwest of the nearest major town, Vredendal (Figure 3.1). Economic activities within the immediate area are restricted to diamond mining, dryland farming and kelp harvesting (Environmental Evaluation Unit, 1990). Brand-se-Baai has been used for many years as a traditional holiday and camping area by the local people.

Climate

The climate of the study area is summarised in the climate diagram (Figure 3.2), which is based on data from the Council for Scientific and Industrial Research (1997). The study area lies in a transitional zone between the Namib Desert to the north and the Cape Mediterranean region to the south. The west coast has a mediterranean-type climate with hot dry summers (November - January) and rain during the winter months (April - July). Rainfall increases from north to south with an average of 160 mm (measured over a period of four years) at the study area. Fog is a characteristic feature of the Namaqualand coastal climate, occurring throughout the year. These advective sea fog (±100 days per annum at the study area) and the heavy dew-falls supplement the low rainfall significantly. The average annual precipitation (rainfall + fog) at the study area was 282 mm for the period March 1993 to February 1997 (Figure 3.2).

The average annual temperature is 15.8°C (Figure 3.2) with a relatively small fluctuation due to the marine influence. The maximum average monthly temperature is 24.1°C in January (summer) and the minimum average monthly temperature is 7.5°C in July (winter). Frequent easterly berg winds, which blow from the interior, bring hot, dry conditions to the coast.

The wind regime along the Namaqualand coast is one of the strongest in the world. Washington (1990) reports that the highest frequency of winds blows from the south and south-south-east from September to March, with less frequent but strong winds blowing from the north and north-north-east during the months of June, July and August. Under northerly flow, daytime wind speeds at the coast may peak at 28.8 $km.h^{-1}$ increasing inland.

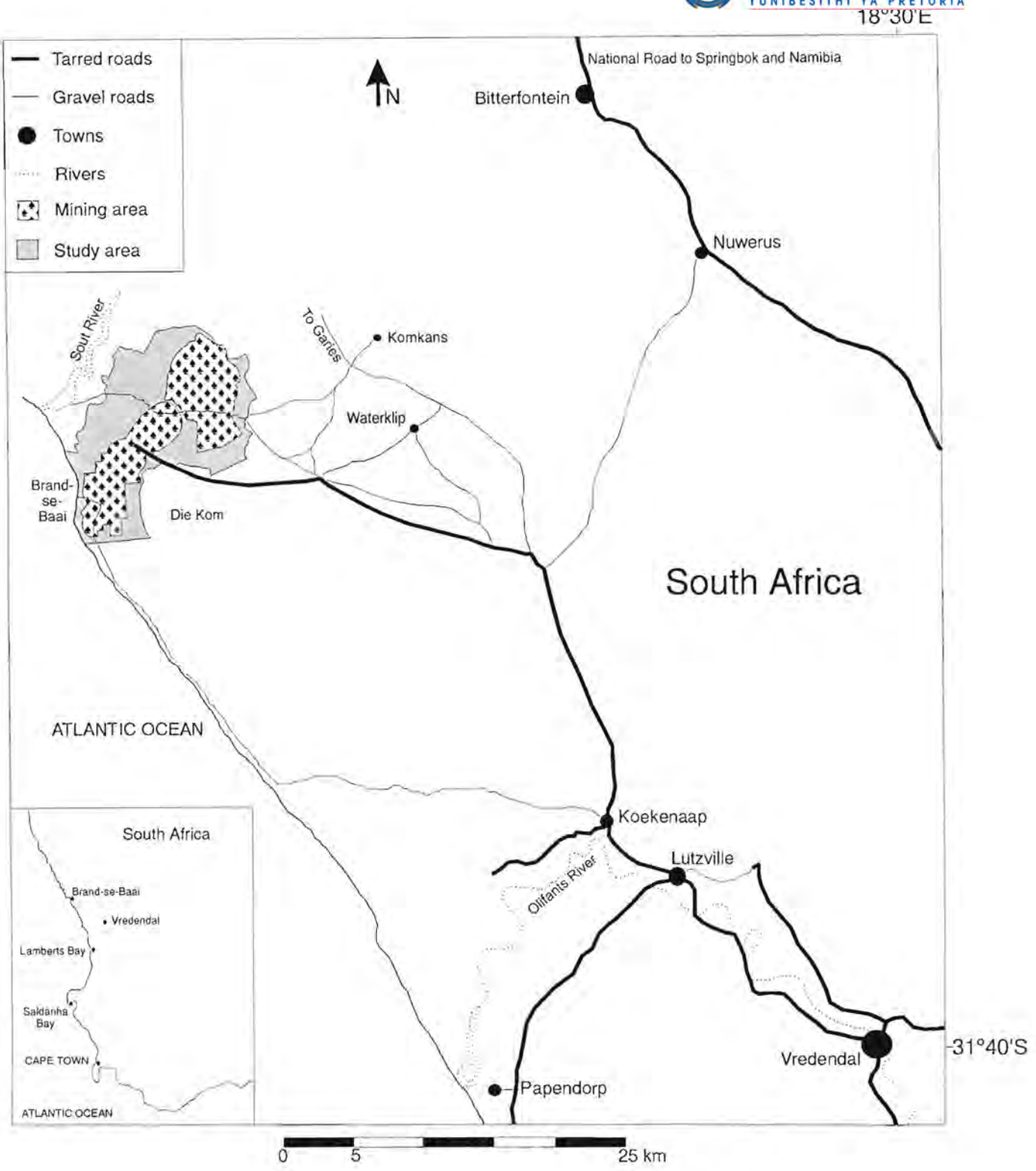

Figure 3.1. Location map of the mining area at Brand-se-Baai.

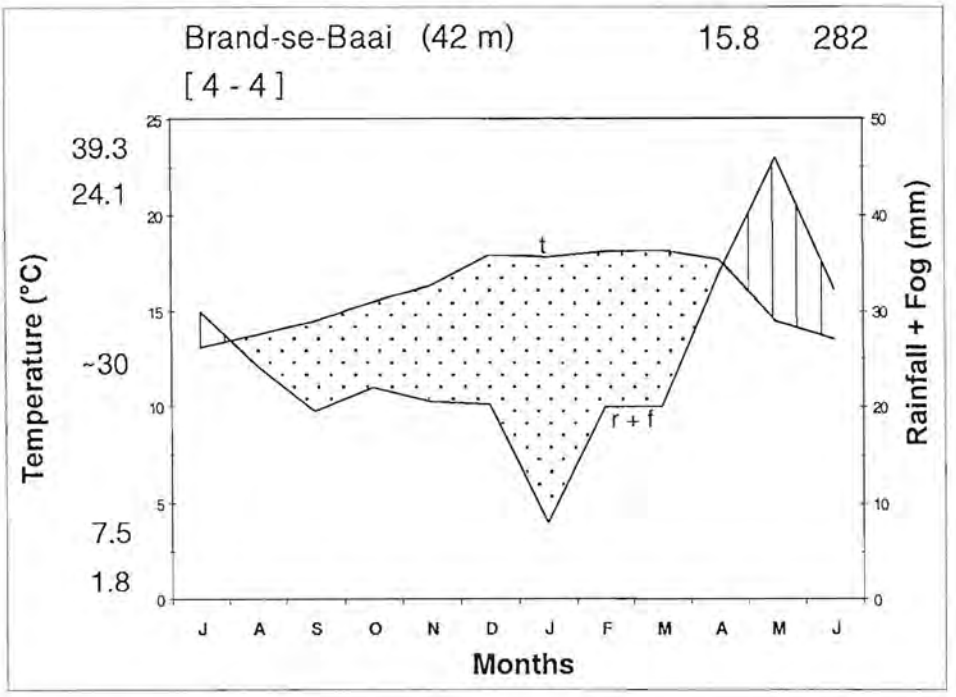

Figure 3.2. Climate diagram of the Brand-se-Baai station for the period March 1993 - February 1997 (following Walter & Lieth, 1960).

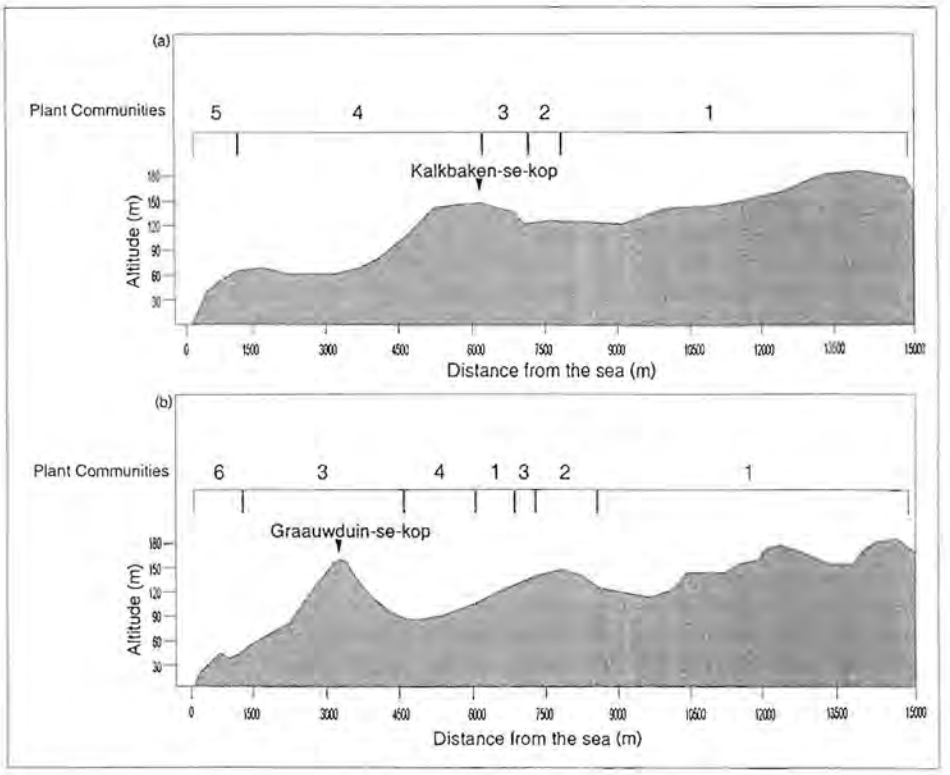

Figure 3.3. A simplified sketch of two gradients through the landscape, indicating the topographical positions of the plant communities.

Physical environment

The study area is bounded by a retrograding coastline, which trends north-north-west (Environmental Evaluation Unit, 1990). This orientation exposes the coastal land to the strong southerly winds prevailing in summer. The coast features wave-cut rocky platforms separated by a number of small, isolated beaches and a large primary dune belt *i.e.* Graauwduine, which is approximately five kilometers long and 500 m in width (Figure 3.3b). Brand-se-Baai is one of many bays along this stretch of coast. The terrain rises steeply in most places from the coast to the coastal plain (Figure 3.3).

The undulating inland area is covered with vegetated sand dunes aligned roughly parallel to the prevailing wind direction *i.e.* north - south. Two prominent rounded hills, Graauwduin-se-kop (158 m above sea level) and Kalkbaken-se-kop (147 m above sea level) are landmarks in the area (Figure 3.3a & b). A depression with a diameter of five to six kilometers, known as "Die Kom", is situated to the southeast of the study area (Figure 3.1). A steep-sided valley system, approximately 30 km long and 100 m deep follows the courses of the Goerap River and the Sout River estuary, on the northern boundary of the study area. The Salt River estuary is a severely degraded system which is being worked as a salt pan (Environmental Evaluation Unit, 1990).

The area is extremely dry with no visible surface water supplies. The catchments of the Goerap River and Sout River, which flow episodically, is the only drainage systems near the study area. No groundwater was located in test boreholes in the study area (Environmental Evaluation Unit, 1990).

The study area is included in a geomorphological subdivision of the Namib Desert, and is referred to as the Namaqualand Sandy Namib. A thick overburden of marine and aeolian sediments overlie older basement rocks of the Namaqualand granite-gneiss suite, and metamorphosed Vanrhynsdorp Group rocks (Environmental Evaluation Unit, 1990).

Generally, the dunes along the coast are light coloured becoming progressively more red further away from the coast. The pale grey dune sands consist of unconsolidated quartz-rich material, whereas the red terrestrial deposits are derived from orange feldspathic sands. It is these terrestrial deposits which often display heavy mineral enrichment. Soils tend to be saline and alkaline, with a pH exceeding eight (Environmental Evaluation Unit, 1990).

Diamond mining used to be the main activity in the region. Heavy minerals presently being mined in the study area include: ilmenite, rutile, leucoxene, zircon and monazite (Environmental Evaluation Unit, 1990).

Vegetation and Fauna

Boucher & Le Roux (1993) identified the littoral vegetation of the study area as Southern Namaqualand Strand Communities, which are sensitive to disturbance because they are subjected to heavy winds, salt spray and drift sands. It is therefore a naturally fragile ecosystem with a low resilience which is easily disturbed or destroyed.

In terms of Acocks' classification (1988), the vegetation of the study area consists of Strandveld Proper (Veld Type 34b) with the Namaqualand Coast Belt Succulent Karoo (Veld Type 31a) in the north-eastern part.

According to Low & Rebelo (1996), the vegetation of the study area consists of Strandveld Succulent Karoo (55) and Lowland Succulent Karoo (57), both of which are classified under the Succulent Karoo Biome. The Strandveld Succulent Karoo (55) vegetation, containing many drought deciduous and succulent species, is associated with areas of calcareous sand. The vegetation varies in height according to the depth of the sand - the shortest vegetation growing on exposed calcrete and coastal rocks and the tallest being found in areas where deep calcareous sand occurs (Boucher & Le Roux, 1990). Small patches of Lowland Succulent Karoo (57) vegetation, characterised by a sparse cover of dwarf succulent-leaved shrubs which do not recover easily from disturbance, occur within the study area (Boucher & Le Roux, 1990). The poorly known Sand Plain Fynbos (68) occurs on the leached, acidic, low-nutrient sands in the area. This vegetation is characterised by the dominance of plants with small leaves and by members of the Restionaceae (Boucher & Le Roux, 1990).

The study area has a resident bird population of approximately 107 species, with a breeding population of about 52 species. Thirty-nine species of reptiles and amphibians, as well as 35 mammal species have been reported. No rare or threatened insect species have been recorded (Environmental Evaluation Unit, 1990).

METHODS

The stratification of the study area into relatively homogeneous physiographic-physiognomic units was done on 1:50 000 aerial photographs. A total of 128 sample plots were randomly located within these stratification units to ensure that all major variations in the vegetation were sampled. Plot size was fixed at 100 m^2 (10 m x 10 m) as determined by Le Roux (1984). Fieldwork was done in August and September of 1992, 1993 and 1994. In each sample plot all plant species were recorded and the cover-abundance of each species estimated according to the Braun-Blanquet cover-abundance scale (Mueller-Dombois & Ellenberg, 1974). The plant names conform to those of Arnold & De Wet (1993). In cases where plant species were unidentifiable, the species were named according to the collection number (Table 3.1). Average height and average canopy cover were estimated for the woody and herbaceous layers in each plot. Environmental data include soil colour, distance from the sea (salt spray & fog intensity), aspect, slope, sand depth and disturbance (grazing & trampling).

Table 3.1. A phytosociological table of the vegetation prior to mining at Brand-se-Baai (values according to the Turboveg scale)

Community Number	1				2		3	4			5	6
	1.1	1.2	1.3	1.4	2.1	2.2		4.1	4.2	4.3		
Relevé Number	4 5 6 6 4 9 7 1 6 4	6 6 4 4 5 6 4 6 2 5 7 8 8 3 5 4	5 5 6 6 2 1 0 8	5 5 5 4 8 5 0 3 4 8 7 6	1 1 1 1 1 2 2 2 2 2 3 7 4 5 6	1 1 1 1 1 1 1 1 0 0 0 1 2 2 2 2 3 6 8 8 9 0 1 2 8 3	1 1 1 1 1 1 1 1 2 1 2 2 1 3 2 2 2 3 3 3 3 3 3 5 2 4 5 1 1 1 1 8 0 1 3 1 4 2 4 2 3 1 6 9 0 1 2 4 5 6 9 0 3 5 4 5 6 8 5 0 7	1 9 1 9 1 9 1 0 1 1 8 8 8 8 9 1 7 8 9 6 2 8 2 9 0 4 7 0 9 9	1 1 1 1 1 1 2 8 9 8 9 C 0 1 0 0 0 9 2 8 7 8 5 6 6 8 4 1 4 3 3 5 7 7 7 0 9 5	1 3 1 1 1 1 3 1 2 8 8 8 1 7 7 8 1 5 1 0 2 3 8 3 5 6 4 8 7 1 2 3 2 0	4 5 7 7 3 4 7 7 4 7 2 9 1 4 9 1 2 3 0 5	7 7 7 6 7 8
Species Group A												
Ruschia tumidula	3 1 1	1 1 1 1 1	2 1 1	1 1 1 1								
Leysera gnaphalodes	1 1	1 1 1	1 1 1	1 1 1			1					
Galenia africana	1 1 1 1	1	1 2 1	1 1 1	1	1 1	3 1 1		1 1	1		
Pharnaceum lanatum	1 1 1 1	1 1 1 1	1	1 1 1 1 1			1	1 1 1 1 1 1		1 1 1 1 1 1 1	1 1	
Pteronia spp.	5 1	1	1	1 1 1								
Geophyte spp.	1	1 1		1 1			1	1		1		
Species Group B												
Lapeirousia spp.	1 1 1 1 1	1	1	1		1 1		1	1 1	1		
Sarcocaulon sp.	1 1 1 1	1					1					
Species Group C												
Scirpoides dioecus		1 5 3 5 3 1 3										
Gymnodiscus capillaris		1 1 1 1 1										
Stoebe nervigera	1	5 8 1										
Tripteris sinuata		1 1 1										
Monilaria chrysoleuca		3 1										
Wahlenbergia sonderi		1 1 1					1 1 1					
Species Group D												
Chenopodium opulifolium		1 1	1 1 1	1						1		
Hermannia cuneifolia			1 1	1					1			
Species Group E												
Ferraria densepunctulata				1 1 1			1					
Crassula dichotoma				1 1 1								
Species Group F												
Arctotis sp. (RDV220)					1 1 1 1	1 1 1 1 1 1 1	1 1 1	1	1 1 1 1 1		1	
Coelanthum semiquinquefidum					1 1 1 1	1 1 1 1 1 1	1 1		1			
Lebeckia lotonoides					1 1 1 1	1 1 1 1 1	1 1 3		1 1	1		
Asparagus fasciculatus					1 1 1	1 1 1 1 1 1	1 1	1	1	1 1		
Gethyllis sp.					1	1 1 1 1 1	1 1					
Gloveria integrifolia					1 1	1 1		1		1		
Species Group G												
Felicia merxmuelleri	1	1 1		1 1 1 1 1	1 1 1 1 1	1 1				1		
Diascia sp.	1 1			1 1 1 1		1 1 1						
Nemesia ligulata	1 1			1 1 1	1	1		1 1				
Species Group H												
Sonderina tenuis		1				1 1	1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1	1 1 1	1	1 1 1 1		1
Ballota africana							1 1 1 1 1 1 1 1 1 1 1 1 1 1			1		
Pentaschistis patula	1 1	1	5 5 1	1 1			1 1 1 1 1 1 1 1 1 1	1	1	1 1 1 1 1		
Solanum guineense	1			1 1	1	1	1 1 1 1 1 1 1 1 1 1 1		1	1 1 1		
Bromus pectinatus				1 1 1 1			6 1 3 1 1 1 1 1 1 1	1 1	1 1	1 3 1 1 1 1		
Lessertia benguellensis						1 1 1	1 1 1 1 1 1 1 1 1 1 1		1 1			
Tetragonia pillansii							1 1 1 1 1 1 1					
Melianthus minor			1	1			1 1 1 1 1 1 1		1			
Chrysanthemoides monilifera							1 1 1 1 1 1					
Emex australis							1 1 3 1		1			
Species Group I												
Dimorphotheca pluvialis					1 1 1	1 1 1 1 1	3 1 1 1 1 1 1 1 1 1 3 3 3 3 1		1 1	1		
Grielum humifusum					1 1	1 1 1 1 1	1 1 1 1 1 1 1		1 1 1 1 1	1		
Tetragonia microptera					1	1 1 1	1 1 1 1 1		1	1 1		

Table 3.1. (Continued)

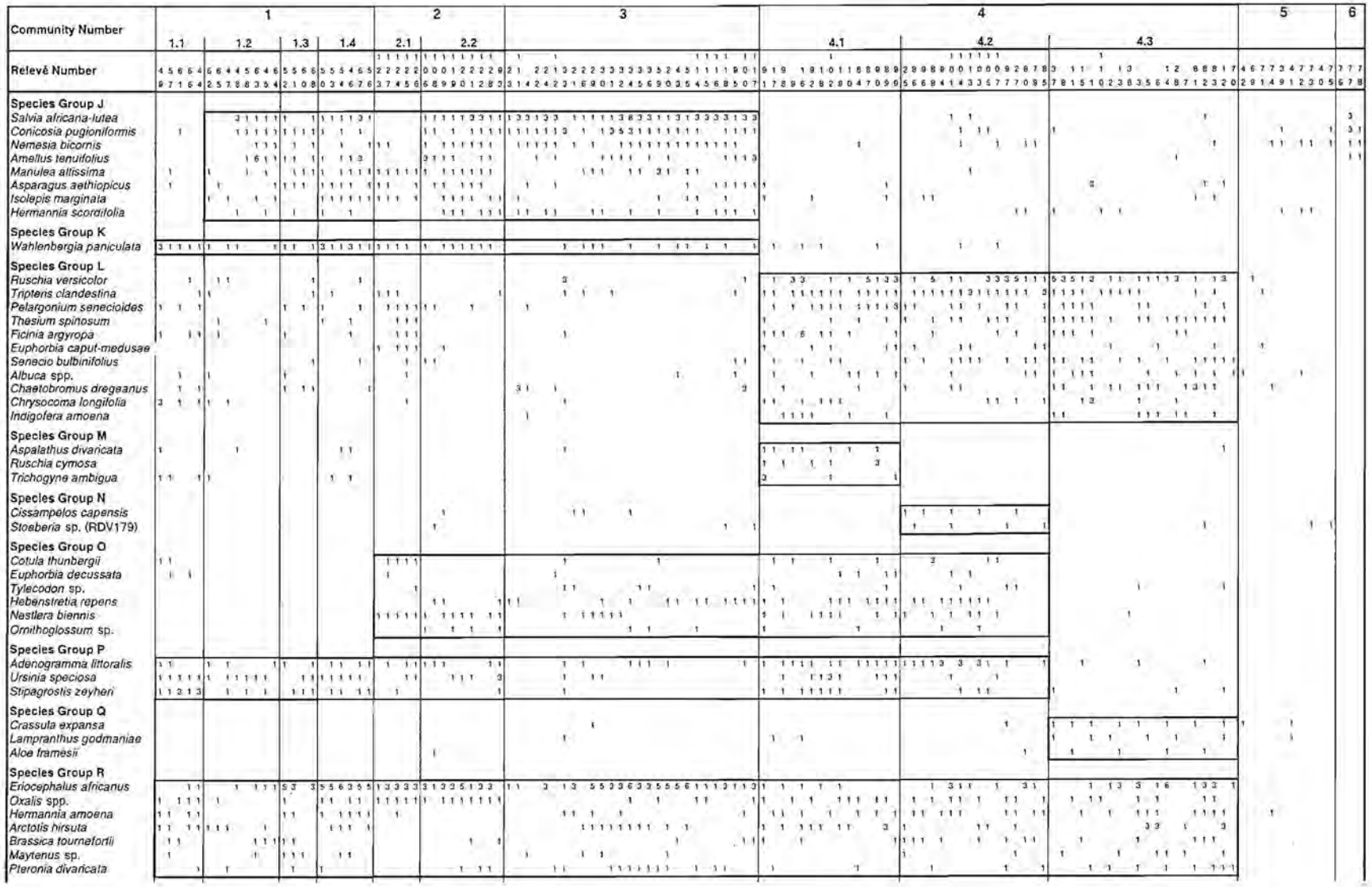

Table 3.1. (Continued)

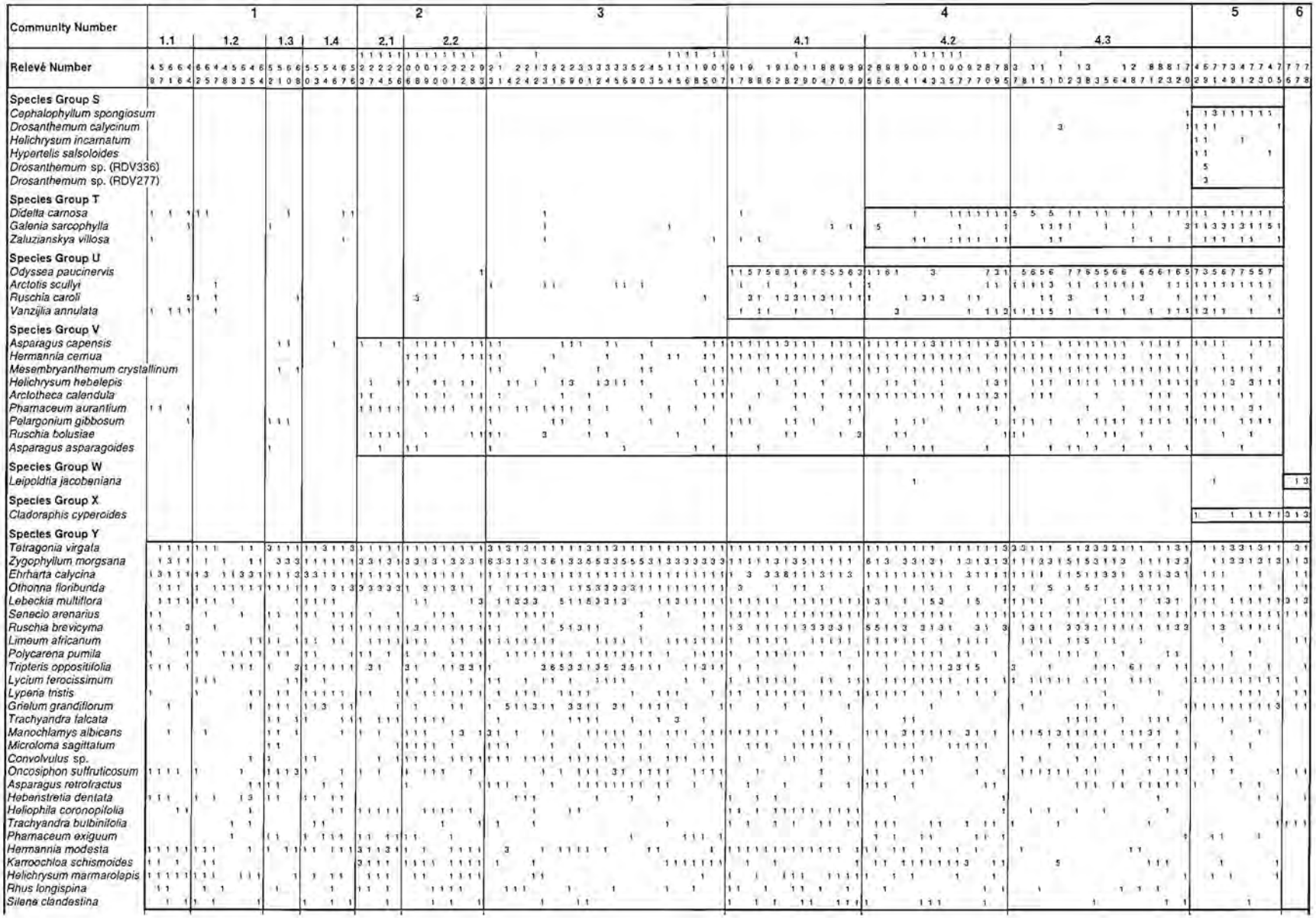

Table 3.1. (Continued)

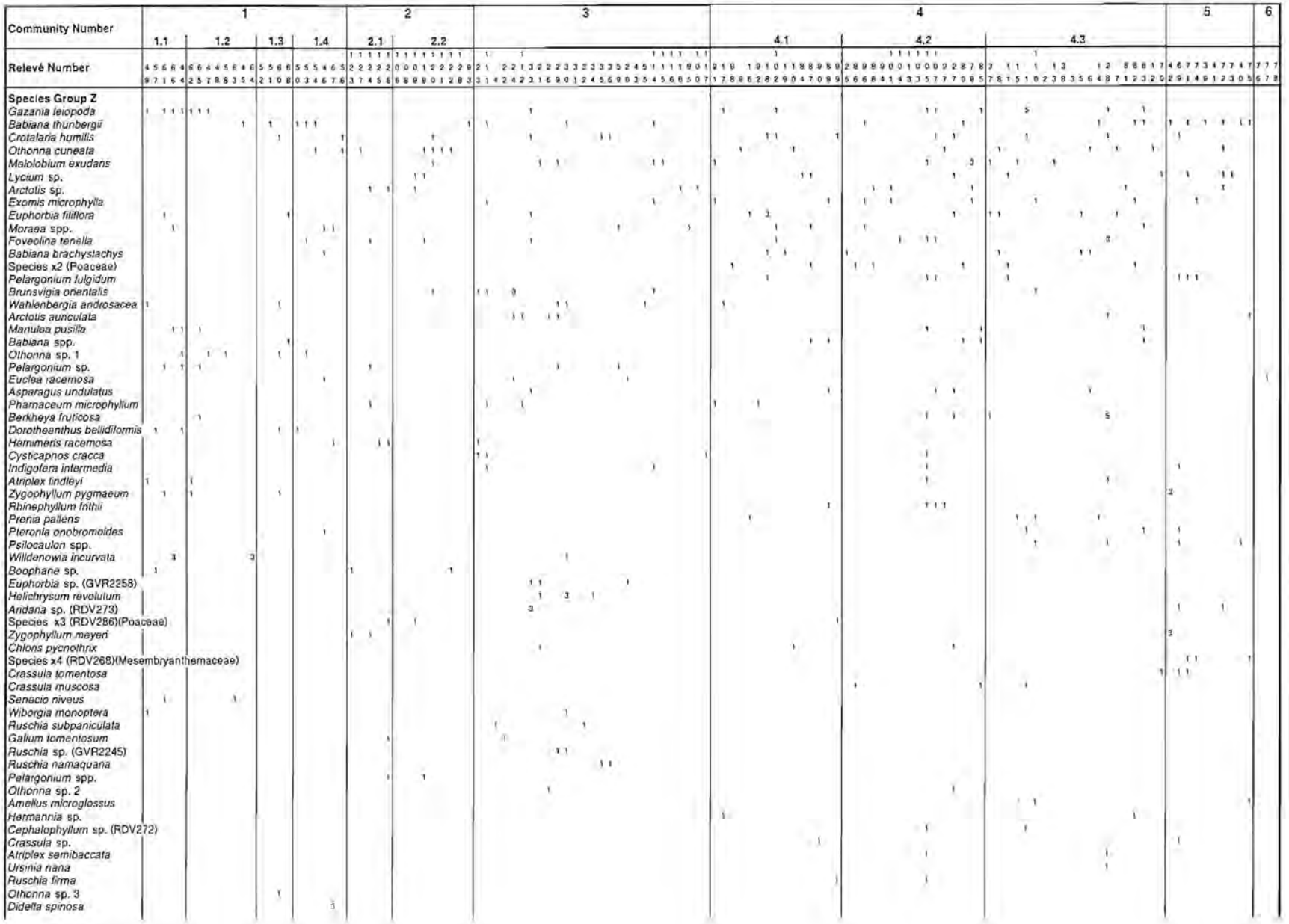

Table 3.1. (Continued)

Community Number	1				2		3	4			5	6
	1.1	1.2	1.3	1.4	2.1	2.2		4.1	4.2	4.3		
Relevé Number	4 5 6 6 4 9 7 1 6 4	6 6 4 4 5 6 4 6 2 5 7 8 8 3 5 4	5 5 6 6 2 1 0 8	5 5 5 4 6 5 0 3 4 6 7 6	1 1 1 1 1 2 2 2 2 2 3 7 4 5 6	1 1 1 1 1 1 1 1 1 0 0 0 1 2 2 2 2 9 6 8 9 9 0 1 2 8 3	1 1 1 1 1 1 1 2 1 2 2 1 3 2 2 2 3 3 3 3 3 5 2 4 5 1 1 1 1 9 0 1 3 1 4 2 4 2 3 1 6 9 0 1 2 4 5 6 9 0 3 5 4 5 6 8 5 0 7	1 9 1 9 1 9 1 0 1 1 8 8 9 8 9 1 7 8 9 6 2 8 2 9 0 4 7 0 9 9	1 1 1 1 1 1 2 8 9 8 9 0 0 1 0 0 0 9 2 8 7 8 5 6 8 8 4 1 4 3 3 5 7 7 7 0 9 5	1 3 1 1 1 1 3 1 2 6 8 8 1 7 7 8 1 5 1 0 2 3 8 3 5 6 4 8 7 1 2 3 2 0	4 6 7 7 3 4 7 7 4 7 2 9 1 4 9 1 2 3 0 5	7 7 7 6 7 8
Species Group Z continued												
Ferraria divaricata		1										
Wiborgia obcordata		5										
Berkheya spinosa	1											
Dimorphotheca sinuata			1									
Senecio cardaminifolius		1										
Clutia alaternoides		1										
Psammotropha quadrangularis	1											
Ruschia lecta							1					
Manulea cinerea												1
Viscum capense						1						
Dimorphotheca nudicaulis					1							
Helichrysum kraussii										1		
Haemanthus amarylloides										1		
Sphalmanthus sp. (RDV270)											1	
Annesorhiza macrocarpa									1			
Oxalis pardalis									1			
Bulbine sp.										1		
Pteronia ovalifolia										1		
Othonna sp. 4										1		
Pteronia paniculata									1			
Conicosia elongata									1			
Limonium perigrinum								1				
Cynanchum africanum									1			
Crassula spp.											1	
Lachenalia spp.		1 1 1		1		1 1	1 1	1	1 1 1 1			
Hirpicium alienatum		1 1			1	1			1			
Felicia dregei					1 1 1							
Ferraria spp.							1 1 1 1		1 1	1		

The first classification of the vegetation, based on the total floristic data set, was obtained by the application of the TWINSPAN classification algorithm (Hill, 1979a). Further refinement of the classification was achieved by Braun-Blanquet (Zürich-Montpellier) procedures - successive rearrangement of rows (species) and columns (relevés) in a matrix are continued until a clear pattern of mutually discriminant noda of species-relevé groups is obtained (Werger, 1974; Bredenkamp & Bezuidenhout, 1995). This phytosociological or Braun-Blanquet approach is based on the floristic composition of a plant community, and diagnostic species are used to organize communities into a hierarchical classification (Whittaker, 1980). The final result of the classification procedure is a differential table (Table 3.1) and the identified plant communities are mapped in Figure 3.4. The cover-abundance scale in the phytosociological table was converted to a percentage scale for the TURBOVEG (Hennekens, 1996a) and MEGATAB (Hennekens, 1996b) computer programs.

In the description of the communities, the growth forms of the species are indicated between brackets, *i.e.* shrub (S), dwarf shrub (DS), ephemeral (E), grass (Gr), sedge (Sg) and geophyte (G).

The DECORANA ordination algorithm (Hill, 1979b) was applied to the floristic data to detect possible gradients in and between plant communities and to detect possible habitat gradients associated with vegetation gradients (Figure 3.5)(Bezuidenhout, 1995).

RESULTS

Six plant communities or associations are recognised, some of which are divided into variants (Table 3.1, Figure 3.4). The hierarchical classification of these vegetation units is summarised as follows:

1. *Ruschia tumidula - Tetragonia virgata* Tall Shrub Strandveld
   - 1.1. *Stipagrostis zeyheri - Lapeirousia* spp. Variant
   - 1.2. *Scirpoides dioecus - Stoebe nervigera* Variant
   - 1.3. *Pentaschistis patula - Chenopodium opulifolium* Variant
   - 1.4. *Eriocephalus africanus - Ferraria densepunctulata* Variant
2. *Eriocephalus africanus - Asparagus fasciculatus* Tall Shrub Strandveld
   - 2.1. *Othonna floribunda - Lebeckia lotonoides* Variant
   - 2.2. *Zygophyllum morgsana - Coelanthum semiquinquefidum* Variant
3. *Salvia africana-lutea - Ballota africana* Tall Shrub Strandveld
4. *Ruschia versicolor - Odyssea paucinervis* Dwarf Shrub Strandveld
   - 4.1. *Ruschia caroli - Aspalathus divaricata* Variant
   - 4.2. *Tripteris oppositifolia - Cissampelos capensis* Variant
   - 4.3. *Ehrharta calycina - Crassula expansa* Variant
5. *Cephalophyllum spongiosum - Odyssea paucinervis* Coastal Strandveld
6. *Cladoraphis cyperoides - Lebeckia multiflora* Coastal Strandveld

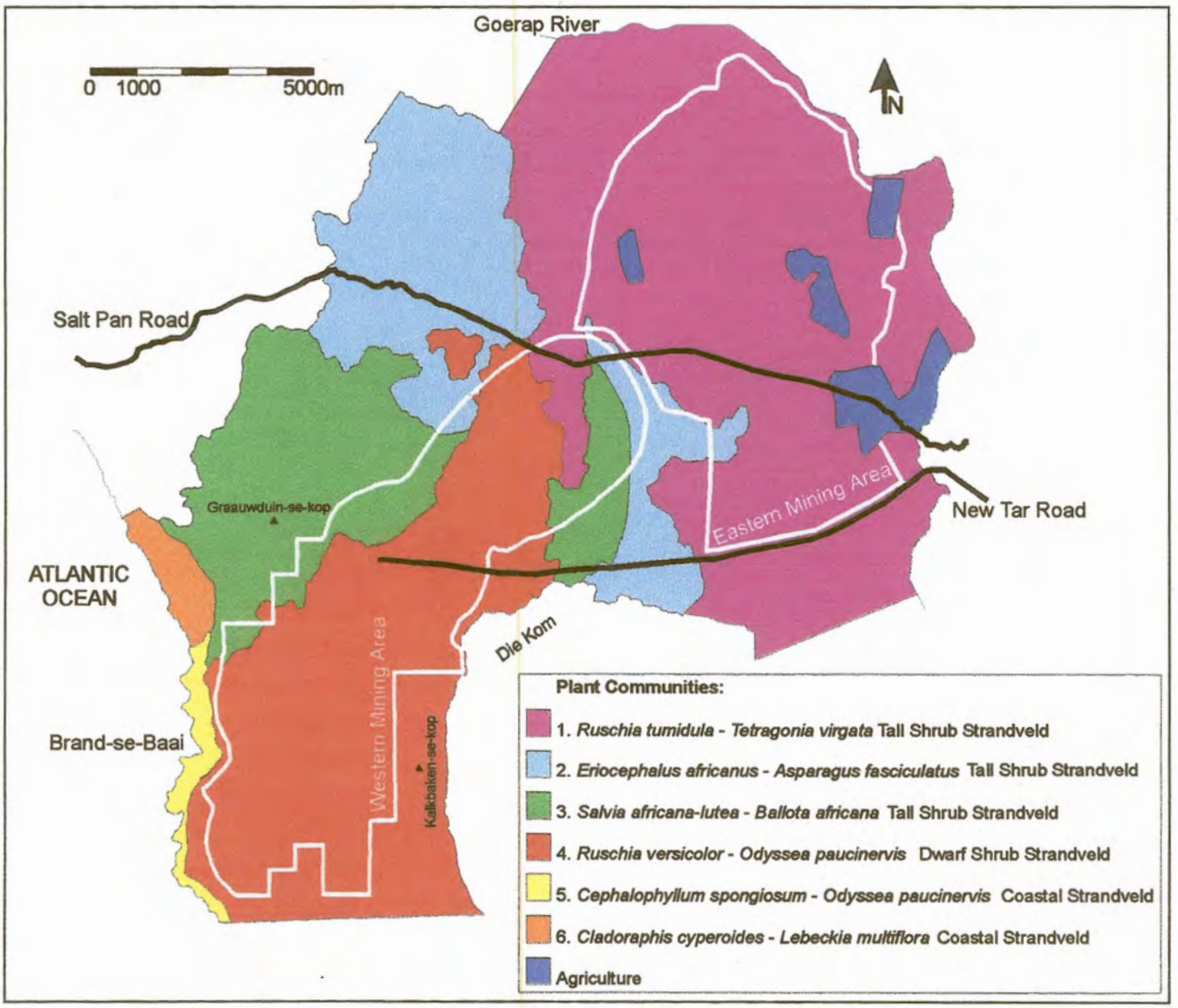

Figure 3.4. Vegetation map of the study area.

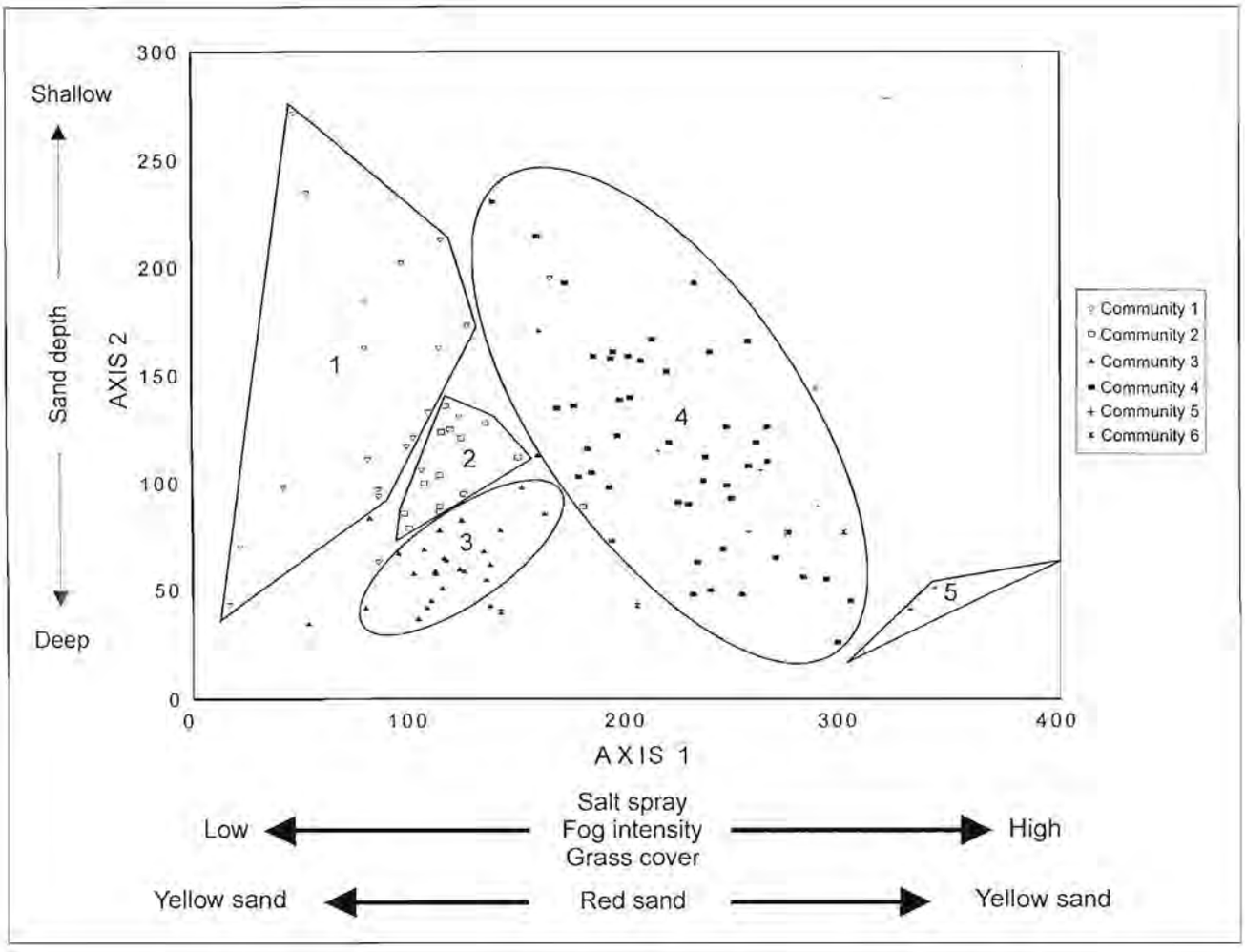

Figure 3.5. The relative positions of the plant communities (numbers refer to text) along the first and second axes of a floristic ordination by means of DECORANA (Eigenvalues: Axis 1 = 0.466, Axis 2 = 0.306).

As a whole, the vegetation of the study area is characterised by species of Species Group Y (Table 3.1). The most prominent species which occur in almost all the communities are the shrubs *Tetragonia virgata*, *Zygophyllum morgsana*, *Othonna floribunda* and *Lebeckia multiflora*, the grass *Ehrharta calycina* and the ephemerals *Senecio arenarius* and *Tripteris clandestina*. These species (Species Group Y, Table 3.1) will therefore not be repeatedly mentioned in the description of the communities. The six communities identified can be grouped into two major units, on account of the presence or absence of the perennial creeping grass *Odyssea paucinervis* (Species Group U). Communities 4 and 5 are dominated by *Odyssea paucinervis* (Species Group U), while this species is absent from communities 1, 2, 3 and 6. In communities 1 to 3 the shrubs *Eriocephalus africanus* (Species Group R) and *Tripteris oppositifolia* (Species Group Y) are prominent. The spiky grass *Cladoraphis cyperoides* (Species Group X) is dominant in community 6. The average canopy cover for both the shrub and herbaceous strata, as well as the total number of plant species recorded within each community and variant, are summarised in Table 3.2.

Description of the plant communities (Tables 3.1 & 3.2 and Figure 3.4)

1. *Ruschia tumidula - Tetragonia virgata* Tall Shrub Strandveld

This community is situated the furthest inland (Figure 3.4), and consequently it receives the least amount of fog and salt spray and is the driest of the communities in the study area. Agricultural fields within this community are mainly restricted to the Goerap River which flows episodically. The area mainly consists of small dune systems which give rise to the four variants. A large part of this community, which is found on yellow sand, is destined to be destroyed by the mining activities. This community is characterised by Species Group A (Table 3.1) and the diagnostic species are *Ruschia tumidula* (S), *Galenia africana* (S), *Leysera gnaphalodes* (DS), *Pharnaceum lanatum* (DS), *Oncosiphon suffruticosum* (E) and several *Pteronia* species.

1.1. *Stipagrostis zeyheri - Lapeirousia* spp. Variant

This variant is found in the dune valleys in the eastern part of the study area. Diagnostic species for this variant (Species Group B) are *Lapeirousia* spp. (G) and *Sarcocaulon* sp. (DS) (Table 3.1). The absence of species from Species Group J also characterises this variant. Other abundant species include *Wahlenbergia paniculata* (E)(Species Group K), *Stipagrostis zeyheri* (GR)(Species Group P) and *Hermannia modesta* (DS)(Species Group Y).

1.2. *Scirpoides dioecus - Stoebe nervigera* Variant

This variant is found on small dunes and the diagnostic species (Species Group C) include *Scirpoides dioecus* (Sg), *Tripteris sinuata* (S), *Stoebe nervigera* (DS), *Monilaria chrysoleuca* (DS), *Gymnodiscus capillaris* (E) and *Wahlenbergia sonderi* (E)(Table 3.1). Other conspicuous species are *Salvia africana-lutea* (S), *Amellus tenuifolius* (S), the succulent *Conicosia pugioniformis* (DS)(Species Group J) and *Ursinia speciosa* (E)(Species Group P). The presence of species such as *Stoebe nervigera* and *Willdenowia incurvata* (Species Group Z) indicates the relation of this variant with the Sand Plain Fynbos described by Boucher & Le Roux (1990) and Low & Rebelo (1996). The sandy soil supporting Sand Plain Fynbos is leached, acidic and has a lower nutrient

Table 3.2. The average canopy cover and total number of plant species recorded, for the six plant communities and their variants

Plant community / variant	Canopy cover (%)		Total number of plant species recorded
	Shrub stratum	Herbaceous stratum	
1. *Ruschia tumidula* - *Tetragonia virgata* Tall Shrub Strandveld	22.2	8.0	132
1.1. *Stipagrostis zeyheri* - *Lapeirousia* spp. Variant	17.0	8.0	83
1.2. *Scirpoides dioecus* - *Stoebe nervigera* Variant	16.9	3.6	92
1.3. *Pentaschistis patula* - *Chenopodium opulifolium* Variant	26.3	11.3	75
1.4. *Eriocephalus africanus* - *Ferraria densepunctulata* Variant	30.8	11.7	87
2. *Eriocephalus africanus* - *Asparagus fasciculatus* Tall Shrub Strandveld	14.7	4.9	109
2.1. *Othonna floribunda* - *Lebeckia lotonoides* Variant	13.8	5.2	80
2.2. *Zygophyllum morgsana* - *Coalanthum semiquinquefidum* Variant	15.2	4.8	92
3. *Salvia africana-lutea* - *Ballota africana* Tall Shrub Strandveld	26.0	6.0	140
4. *Ruschia versicolor* - *Odyssea paucinervis* Dwarf Shrub Strandveld	16.8	15.5	171
4.1. *Ruschia caroli* - *Aspalathus divaricata* Variant	16.8	17.3	111
4.2. *Tripteris oppositifolia* - *Cissampelos capensis* Variant	16.9	8.5	136
4.3. *Ehrharta calycina* - *Crassula expansa* Variant	19.5	19.7	135
5. *Cephalophyllum spongiosum* - *Odyssea paucinervis* Coastal Strandveld	13.0	26.0	83
6. *Cladoraphis cyperoides* - *Lebeckia multiflora* Coastal Strandveld	4.0	4.3	23

status than that supporting the other vegetation types in the area. Sand Plain Fynbos is sensitive to overgrazing which enhances wind erosion.

1.3. *Pentaschistis patula - Chenopodium opulifolium* Variant

This variant is found in disturbed areas of the *Ruschia tumidula - Tetragonia virgata* Tall Shrub Strandveld. *Hermannia cuneifolia* (S) and the annual *Chenopodium opulifolium* are the only diagnostic species for this variant (Species Group D, Table 3.1). Conspicuous shrubs include *Ruschia tumidula* (S), *Galenia africana* (S)(Species Group A), *Conicosia pugioniformis* (DS)(Species Group J) and *Eriocephalus africanus* (S)(Species Group R). *Oncosiphon suffruticosum* (E)(Species Group A) and *Pentaschistis patula* (Gr)(Species Group H) are abundant within the herbaceous stratum of this variant. *Chenopodium opulifolium* mainly occurs in areas disturbed by man, while *Oncosiphon suffruticosum* (Species Group A) is known to occur in areas where heavy grazing has resulted in a lower vegetation cover (Boucher & Le Roux, 1990).

1.4. *Eriocephalus africanus - Ferraria densepunctulata* Variant

Diagnostic species for this variant, constituting the largest portion of Community 2 (Figure 3.4), are *Ferraria densepunctulata* (G) and *Crassula dichotoma* (E)(Species Group E, Table 3.1). The shrub stratum has an average canopy cover of 30.8% (Table 3.2), which is the highest value for all the communities and variants. Conspicuous species include *Pharnaceum lanatum* (DS)(Species Group A), *Felicia merxmuelleri* (E)(Species Group G), *Salvia africana-lutea* (S), *Asparagus aethiopicus* (S), *Amellus tenuifolius* (S), *Manulea altissima* (E)(Species Group J), *Eriocephalus africanus* (S) and *Hermannia amoena* (DS)(Species Group R). Small patches of Lowland Succulent Karoo vegetation occur within this variant (Boucher & Le Roux, 1990).

2. *Eriocephalus africanus - Asparagus fasciculatus* Tall Shrub Strandveld

Found on small dune systems, this community seems to represent a transition between communities 1 and 3 (Figure 3.4, Table 3.1). Both fog and salt spray intensity are less than that of the communities closer to the coast. Only a small part of this community, found on yellowish sandy soil, is included in the area to be mined. This community is differentiated by the diagnostic species of Species Group F (Table 3.1). Conspicuous shrubs within this community include *Asparagus aethiopicus* (S)(Species Group J), *Nestlera biennis* (DS)(Species Group O), *Eriocephalus africanus* (S)(Species Group R), *Asparagus capensis* (S) and *Pharnaceum aurantium* (DS)(Species Group V). Abundant species included in the herbaceous stratum are *Manulea altissima* (E)(Species Group J) and *Oxalis* spp. (G)(Species Group R).

2.1. *Othonna floribunda - Lebeckia lotonoides* Variant

This variant is situated in the dune valleys and the species dominating are of a smaller stature than those on the dunes. Although there are no diagnostic species for this variant, the presence of species from Species Groups F and G are characteristic (Table 3.1). Conspicuous species include *Euphorbia caput-medusae* (DS), *Pelargonium senecioides* (E)(Species Group L), *Nestlera biennis* (DS), *Cotula thunbergii* (E)(Species Group O), *Eriocephalus africanus* (S), *Oxalis* spp. (G)(Species Group R), *Ruschia bolusiae* (S) and *Pharnaceum aurantium*

(DS)(Species Group V). The relationship between this variant and the *Eriocephalus africanus - Ferraria densepunctulata* Variant (1.4) is indicated by Species Group G.

2.2. *Zygophyllum morgsana - Coelanthum semiquinquefidum* Variant

The vegetation of this variant, located on small dunes, is taller than that of the *Othonna floribunda - Lebeckia lotonoides* Variant, mainly because of the greater sand depth on the dunes (Figure 3.4). This variant has no diagnostic species, but is differentiated by the presence of species from Species Group F, together with the absence of species from Species Group G (Table 3.1). The presence of species such as *Salvia africana-lutea* (S), *Amellus tenuifolius* (S), *Conicosia pugioniformis* (DS), *Hermannia scordifolia* (DS)(Species Group J), *Ornithoglossum* sp. (G)(Species Group O) and *Hermannia cernua* (DS)(Species Group V), as well as the absence of *Thesium spinosum* (DS), *Ficinia argyropa* (DS), *Euphorbia caput-medusae* (DS), *Tripteris clandestina* (E)(Species Group L) and *Cotula thunbergii* (E)(Species Group O), distinguish this variant from the *Othonna floribunda - Lebeckia lotonoides* Variant (2.1).

3. *Salvia africana-lutea - Ballota africana* Tall Shrub Strandveld

This community, associated with a loose yellow sand, is found mainly on Graauwduin, stretching east-west, and a smaller dune to the east (Figures 3.3 & 3.4). The latter can still be considered as part of the Graauwduin dune belt. The vegetation of this community is taller than that of the surrounding communities, mainly because of the deep sand on which it occurs. About 40% of this community will eventually be destroyed by the mining process. Species Group H indicates the species which differentiate this community from the others (Table 3.1). Abundant and conspicuous species in this community include *Dimorphotheca pluvialis* (E)(Species Group I), *Salvia africana-lutea* (S), *Conicosia pugioniformis* (DS), *Nemesia bicornis* (E)(Species Group J), *Eriocephalus africanus* (S)(Species Group R) and *Helichrysum hebelepis* (S)(Species Group V). The relationship between this community and community 2 is indicated by Species Group I.

4. *Ruschia versicolor - Odyssea paucinervis* Dwarf Shrub Strandveld

This community is found in the southern part of the study area and covers the largest part of the western area to be mined (Figure 3.4). The soil varies from compact dark-red sand in the west to loose yellowish sand in the east. The dark-red sand contains most of the heavy minerals to be mined. The diagnostic species of this community are listed in Species Group L (Table 3.1). The most conspicuous shrubs within this community include *Ruschia caroli* (Species Group U) and *Asparagus capensis* (Species Group V). The dominant grass species of the herbaceous stratum is *Odyssea paucinervis* (Gr), while other conspicuous herbaceous species are restricted to Species Group Y. According to Gibbs Russell *et al.* (1990), *Odyssea paucinervis* is commonly found on brackish or saline soil in or near water, and is eaten by livestock because of salty deposits on the leaves.

Compared to to the other communities, the *Ruschia versicolor - Odyssea paucinervis* Dwarf Shrub Strandveld has more succulent species belonging to the family Aizoaceae, as partly indicated by species from Species

Groups L, M, N and Q (Table 3.1). A total of 171 plant species were recorded within this community, which is the highest value for all the communities and variants (Table 3.2).

4.1. *Ruschia caroli - Aspalathus divaricata* Variant

This variant is located in the central part of the *Ruschia versicolor - Odyssea paucinervis* Dwarf Shrub Strandveld community, and is found on dark-red sandy soil. Most of this variant is included in the area to be mined (Figure 3.4). The diagnostic species are *Aspalathus divaricata* (DS), *Ruschia cymosa* (DS) and *Trichogyne ambiqua* (DS) (Species Group M, Table 3.1). The shrub stratum of this variant includes the following conspicuous species: *Ruschia versicolor* (S)(Species Group L), *Ruschia caroli* (S)(Species Group U), *Asparagus capensis* (S) and *Hermannia cernua* (DS)(Species Group V). Conspicuous species of the herbaceous stratum include *Adenogramma littoralis* (E), *Ursinia speciosa* (E)(Species Group P) and *Odyssea paucinervis* (Gr)(Species Group U).

4.2. *Tripteris oppositifolia - Cissampelos capensis* Variant

Situated in the eastern part of the *Ruschia versicolor - Odyssea paucinervis* Dwarf Shrub Strandveld community (Figure 3.4), this variant is found on yellowish sandy soils, has the tallest vegetation of the three variants, and has visible signs of extensive overutilization by livestock. Most of it is included in the area to be mined.

The diagnostic species of this variant include *Stoeberia* sp. (S) and *Cissampelos capensis* (DS) (Species Group N, Table 3.1). Conspicuous shrub species include *Ruschia versicolor* (S)(Species Group L), *Asparagus capensis* (S) and *Hermannia cernua* (DS)(Species Group V), while conspicuous species of the herbaceous layer are *Tripteris clandestina* (E)(Species Group L), *Adenogramma littoralis* (E)(Species Group P) and *Arctotheca calendula* (E)(Species Group V). The relationship of this variant with communities 2 and 3, as well as with variant 4.1 is indicated by Species Group O. If community 1 is also included in the relationship, then Species Group P acts as indicator.

4.3. *Ehrharta calycina - Crassula expansa* Variant

Located in the southern part of the study area, this variant is found on compact reddish sand, including the large dune called "Kalkbaken-se-kop" (147m), which is situated west of "Die Kom" (Figure 3.4). The area to be mined does not include much of this variant. This variant, characterised by Species Group Q (Table 3.1), has the shortest vegetation of the three variants within the Dwarf Strandveld community, and small patches of Sand Plain Fynbos (Boucher & Le Roux, 1990) occur to the south of "Kalkbaken-se-kop". The diagnostic species include *Ruschia* sp. 1 (S), *Aloe framesii* (S) and *Crassula expansa* (E) (Species Group Q, Table 3.1). The absence of Species Groups P and X also characterise this variant. The relationship of this variant with communities 1, 2, 3 and variants 4.1 and 4.2 is indicated by Species Group R. Conspicuous shrubs include *Ruschia versicolor* (S)(Species Group L), *Eriocephalus africanus* (S)(Species Group R), *Arctotis scullyi* (DS), *Vanzijlia annulata* (DS)(Species Group U), *Asparagus capensis* (S), *Helichrysum hebelepis* (S) and *Hermannia cernua* (DS)(Species Group V). Abundant species of the herbaceous stratum include *Didelta carnosa* (E)(Species Group T) and *Odyssea paucinervis* (Gr)(Species Group U). The hemicryptophyte *Gazania leiopoda*

(Species Group Z) as well as *Karroochloa schismoides* (Gr)(Species Group Y) are very abundant at certain sites.

5. *Cephalophyllum spongiosum - Odyssea paucinervis* Coastal Strandveld

This community is found on yellowish sand, in a narrow strip along the coast and will not directly be affected by the mining activities (Figure 3.4). Species Group S is diagnostic for this mainly succulent community and include *Cephalophyllum spongiosum* (DS), *Drosanthemum calycinum* (DS), *Helichrysum incarnatum* (DS), *Hypertelis salsoloides* (DS) and two other *Drosanthemum* species (DS) (Table 3.1). Conspicuous shrubs are restricted to Species Group Y, while the conspicuous dwarf shrubs include *Galenia sarcophylla* (Species Group T), *Arctotis scullyi, Vanzijlia annulata* (Species Group U), *Pharnaceum aurantium* (Species Group V) and *Cladoraphis cyperoides* (Sg) (Species Group X, Table 3.1). The herbaceous stratum has an average canopy cover of 26.0% (Table 3.2), which is the highest value for all the plant communities and variants. Conspicuous species of this stratum include *Didelta carnosa* (E)(Species Group T), *Odyssea paucinervis* (Gr)(Species Group U) and *Mesembryanthemum crystallinum* (E)(Species Group V). In this community, the average canopy cover (Table 3.2) of the herbaceous stratum (26.0%) is also higher than that of the shrub stratum (13.0%), mainly because of the abundance of *Odyssea paucinervis*. Both community 4 and 5 are dominated by *Odyssea paucinervis*, and this relationship is indicated by Species Group U. The relationship of this community with communities 2, 3 and 4 is indicated by Species Group V.

6. *Cladoraphis cyperoides - Lebeckia multiflora* Coastal Strandveld

This community is found in a narrow strip along the northern coast of the study area (Figure 3.4), predominantly on white sand dunes. Boucher & Le Roux (1990) called this a White Dune Strandveld community type, which is often associated with river estuaries and disturbance here easily leads to dune movement. The only diagnostic species for this community is *Leipoldtia jacobeniana*, a member of the Mesembryanthemaceae (Species Group W)(Table 3.1). The relationship of this community with community 5 is indicated by Species Group X, which only contains one conspicuous dwarf shrub, namely *Cladoraphis cyperoides*. This spiky grass is one of the first dominant colonisers of the loose sand blown up from the beach (Boucher & Le Roux, 1990). The dominant species are restricted to Species Group Y. A total of 23 plant species were recorded within this community (Table 3.2), which is the lowest for all the communities and variants.

Ordination

The position of the plant communities on the ordination diagram, along the first and second axes of the scatter diagram, is given in Figure 3.5. Gradients occur along the first and second axes which could be related to the grass cover, soil colour, salt spray, sand depth and fog intensity. Community 4 occurs on red sand while the other communities are restricted to yellowish sand. Communities situated closer to the coast, have the highest grass cover, as well as the highest salt spray and fog intensity. The position of the different plant communities

along gradients from the sea, eastwards, is illustrated in Figure 3.3. Communities 1 and 2 are furthest away from the sea, while communities 5 and 6 are close to the sea.

DISCUSSION

Species restricted to a particular community (*i.e.* those belonging to the diagnostic Species Groups A, B, C, D, E, F, H, L, M, N, Q, S and W)(Table 3.1) have narrow ecological amplitudes and are correlated with particular environmental factors. These species would be the most difficult to re-establish after the mining operation and are therefore not recommended for use in the initial revegetation program.

On the other hand, species belonging to Species Group Y (Table 3.1) occurred throughout the entire area and are adapted to varying environmental conditions. With the exception of the narrow coastal zone (which is not to be mined), species belonging to Species Group R (Table 3.1), also occurred throughout the mining area. Many of these species (Species Groups R and Y) are perennials with high cover-abundance values and are typical of the strandveld vegetation as a whole. Revegetating with these species should largely restore the former appearance and structure of the vegetation.

If, however, only the area of the eastern ore body is considered, Species Groups I, J and K (Table 3.1), which contain the species common to communities 1, 2 and 3, can provide many species which should be useful in the revegetation program. Similarly, if only the area of the western ore body is considered, Species Groups T and U, which contain species common to communities 4 and 5, can provide many useful species. These groups includes many succulent species belonging to the Aizoaceae, which is typical of the low strandveld vegetation. Other groups which contain species which are fairly widespread are Species Groups O, P and V (Table 3.1). These species will be beneficial in the revegetation process.

A total number of 230 plant species were recorded in the 128 sampling plots. The rehabilitation program for this area states that 60% of the total number of species present prior to mining, should be reintroduced (Environmental Evaluation Unit, 1990). If only the 230 species from this investigation are taken into consideration, then 168 plant species should be reintroduced to the area. However, the percentage of plant species occuring in Species Groups I, J, K, O, P, R, V and Y only amounts to 28.3% (65 species) of the total number of species encountered in this study. The revegetation goal of 60% thus seems unrealistic, and a more obtainable goal would be 30% of the plant species present prior to mining.

CONCLUSIONS

The description of the plant communities, together with the vegetation map, can serve as a basis in the final formulation of the rehabilitation plan for the area to be mined. An understanding of the pre-mining plant

communities and their associated habitats is of fundamental importance for divising sound rehabilitation, management and conservation strategies.

The aim of the rehabilitation programme in this area is to revegetate the area with indigenous species, as soon as possible after mining has been completed (Environmental Evaluation Unit, 1990). It is recommended that the rehabilitation programme concentrates on the perennial species, as these species will help to stabilize the mined sand during the windy, dry and hot summer months. The life history strategy of annuals is such that they are able to colonize open or disturbed habitats easily, provided the habitat is suitable and seeds can be disseminated from the surrounding vegetation. The usefulness of annual species in the revegetation programme is, however, restricted to the wet and cool winter months.

The ultimate goal of revegetation of this area is to obtain a homogeneous vegetation cover which contains plant species from all the pre-mining communities of the mined area. The floristic classification of the vegetation at the Brand-se-Baai area can serve as a bench-mark, to indicate species with which the greatest success should be achieved in the rehabilitation of the area after mining has been completed. It should be possible to revegetate the entire area with species belonging to Species Groups R and Y, which contain 15.2% of the total number of 230 plant species encountered during this study (Table 3.1). If only the eastern mining area is considered, preference should also be given to species belonging to Species Groups I, J and K (5.2%)(Table 3.1). If the western mining area is considered, preference should be given to species belonging to Species Groups T and U (3.0%), while the establishment of the grass species *Odyssea paucinervis* should be a priority. Species Groups O, P and V (7.8%) also contain species which are abundant. A more realistic revegetation goal will be 30% of the total number of plant species present prior to mining, rather than the 60% suggested by the initial rehabilitation plan.

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CHAPTER 4

SPATIAL AND TEMPORAL PATTERNS IN THE SOIL SEED BANK OF THE STRANDVELD SUCCULENT KAROO, SOUTH AFRICA: I. SEED BANK SIZE

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ABSTRACT

The mining of heavy minerals along the West Coast of South Africa will destroy all the standing vegetation. The upper soil layers contain much of the minerals to be mined, rendering topsoil replacement a less favourable option for revegetation. These upper soil layers, however, also contain the seed bank, which may be essential for the revegetation of the area, as it is a vast pool of genetic material already adapted to the prevailing environmental conditions. Seed bank size was determined seasonally for six vegetation units in the Strandveld Succulent Karoo by means of the seedling emergence method. A mean emerged seedling density of 2 725 m^{-2} was recorded at the study site. Annual species dominated the soil seed bank in terms of numbers of individuals. Temporal variation in the seed bank was significantly higher than spatial variation. Mean emerged seedling densities ranged from 1 612 to 3 276 m^{-2} between vegetation units, and from 838 to 7 772 m^{-2} between seasons. Due to the large seed bank, topsoil replacement will be essential for the revegetation of mined areas. During topsoil replacement, spatial variation in the soil seed bank will not affect the density of the resulting vegetation. Transplanting of selected species should start during winter and be completed at the end of the rainy season. Areas where topsoil replacement and sowing have been completed should not be irrigated until the start of the rainy season. Seedling survival of perennials may benefit from irrigation during the following dry seasons.

Key words: Mining; revegetation; seed bank size; seedling emergence; spatial variation; temporal variation; topsoil replacement

INTRODUCTION

The term "seed bank" is a short and convenient one which has been widely adopted to denote the reserves of viable seeds present in the soil and on its surface (Roberts, 1981; Leck *et al.*, 1989; Manchester & Sparks, 1998). The term "seed" is used in the broad sense to describe both true seeds and fruits, but not spores, or propagules which are produced vegetatively.

The soil seed bank is composed of: (1) a transient component, made up mostly of seeds at the soil surface which are capable of immediate germination, and few of which remain viable for more than a year, and (2) a persistent component consisting of seeds which may remain viable for several years (Graham & Hutchings, 1988).

The number of viable seeds of each species buried in the soil, at any given time, will depend on the balance of gains and losses. The gain in seed numbers by a species results largely from the amount of seed shed in the field, which is affected by the plants' abundance and seed production, and the proportion of seeds which become buried in the soil. The losses are due largely to death, predation and germination. Both gains and losses are affected by current and previous environmental and management factors and how these interact with the species present (Howe & Chancellor, 1983).

Numerous studies have reported on the spatial and temporal variation in soil seed banks (Bigwood & Inouye, 1988; Granström, 1988; Henderson *et al.*, 1988; Matlack & Good, 1990; Kalisz, 1991; Willems & Huijsmans, 1994; Albrecht & Forster, 1996; Bertiller, 1998; Milberg & Andersson, 1998). Studies on the horizontal distribution of seeds in soil have been neglected, perhaps because of methodological difficulties. Yet, this aspect is important for seedling recruitment pattern and vegetation structure following a major disturbance in the ecosystem (Kjellsson, 1992).

Seed numbers present in the soil are determined either by placing the soil samples under conditions suitable for seed germination, or by using physical methods to separate seeds from the soil particles based on differences in size and/or density (Roberts, 1981). Direct counting of extracted seeds determines total seed numbers in soil, but quantitative information on viability must be established subsequently (Leck *et al.*, 1989). The seedling emergence method gives information on seed viability and seasonality of germination as well as the species composition of the seed bank (Manchester & Sparks, 1998). For most restoration and creation projects, a precise estimate of seed density for a particular species in the seed bank is not needed. An estimate of the relative abundance of species, determined by the emergence method, is usually sufficient (Van der Valk *et al.*, 1992).

Various studies have reported on the estimation of the size of the seed bank by means of the emergence method (Chippindale & Milton, 1934; Feast & Roberts, 1973; Baskin & Baskin, 1978; Howe & Chancellor, 1983; Graham & Hutchings, 1988; Granström, 1988; Poiani & Johnson, 1988; Coffin & Lauenroth, 1989; Levassor *et al.*, 1990; Barberi *et al.*, 1998; Jones, 1998). Soil seed banks of natural vegetation (Archibold, 1981; Matlack & Good, 1990; Badger & Ungar, 1994), as well as on the importance of the soil seed bank in the revegetation of disturbed areas other than in agriculture (Van der Valk *et al.*, 1992; Milberg & Persson, 1994; Kotanen, 1996), have been the subject of numerous studies in recent years. In most regions of South Africa, however, soil seed banks have been a neglected area of study. Seed bank studies in the arid areas of South Africa include those of Van Rooyen & Grobbelaar (1982), Dean *et al.* (1991), Esler *et al.* (1992), Esler (1993) and De Villiers *et al.* (1994).

Ecologists and evolutionary biologists have become increasingly aware of the role that seed banks can play in maintaining ecological (species) and genetic diversity in populations and communities (Gross, 1990). For the applied biologist in particular, the aspect of greatest significance is the role of the seed bank in determining the future vegetation, especially after natural or deliberate perturbation (Roberts, 1981). The seed bank of a plant community represents the "memory" of previous conditions and it is an important measure of the potential of the community to respond to conditions in the present and future (Coffin & Lauenroth, 1989; Van der Valk *et al.*, 1992). For the population dynamics and persistence of species, the

soil seed bank plays a crucial role (Harper, 1977), and for the rational management of diversity and abundance, knowledge of the seed bank is literally vital (Berge & Hestmark, 1997).

The mining of heavy minerals along the arid West Coast of South Africa will destroy all the standing vegetation in the mined areas. The aim of the rehabilitation program (Environmental Evaluation Unit, 1990) is to obtain a state as close as possible to the state in which the area was before mining activity started, as soon as possible after the mining of an area has been completed. Topsoil replacement as well as seeding and/or transplanting of selected species are considered as viable means for the revegetation of the area (Environmental Evaluation Unit, 1990). Because of the high percentage of heavy minerals in the upper soil layers, seeding rather than topsoil replacement is favoured by the mining company. Prior knowledge about the size and composition of the soil seed bank, as well as its distribution in space and time, will therefore be essential in determining appropriate revegetation strategies.

This paper is the first of two concerning the consequences of spatial and temporal patterns in the soil seed bank of the Strandveld Succulent Karoo on revegetation strategies, and deals mainly with the size of the germinable soil seed bank. The second paper deals with seed bank composition (Chapter 5).

MATERIAL AND METHODS

The study area covers approximately 9 400 ha and is situated in the vicinity of Brand-se-Baai (31°18'S, 17°54'E) on the Cape West Coast, South Africa, some 350 km north of Cape Town and about 80 km northwest of the nearest major town, Vredendal (Figure 4.1).

The climate of the study area is summarised in the climate diagram (Figure 4.2), which is based on data from the Council for Scientific and Industrial Research (1997). The West Coast has a mediterranean-type climate with hot dry summers (November - January) and rain during the winter months (April - July). Rainfall increases from north to south with an average of 160 mm per annum (measured over a period of four years) at the study area. Fog is a characteristic feature of the Namaqualand coastal climate, occurring throughout the year. This advective sea fog (*c.* 100 days per annum at the study area) and the heavy dew-falls supplement the low rainfall significantly. The average annual precipitation (rainfall + fog) at the study area is 282 mm (Figure 4.2).

The average annual temperature is 15.8°C (Figure 4.2) with a relatively small annual fluctuation due to the marine influence. The maximum average monthly temperature is 24.1°C in January (summer) and the minimum average monthly temperature is 7.5°C in July (winter). Frequent easterly berg winds, which blow from the interior, bring hot, dry conditions to the coast.

According to Low & Rebelo (1998), the vegetation of the study area consists mainly of Strandveld Succulent Karoo, which is classified under the Succulent Karoo Biome. The Strandveld Succulent Karoo vegetation, containing many drought deciduous and succulent species, is associated with areas of calcareous sand. Boucher & Le Roux (1993) identified the littoral vegetation of the study area as Southern Namaqualand Strand Communities, which are sensitive to disturbance because they are subjected to heavy winds, salt spray and drift

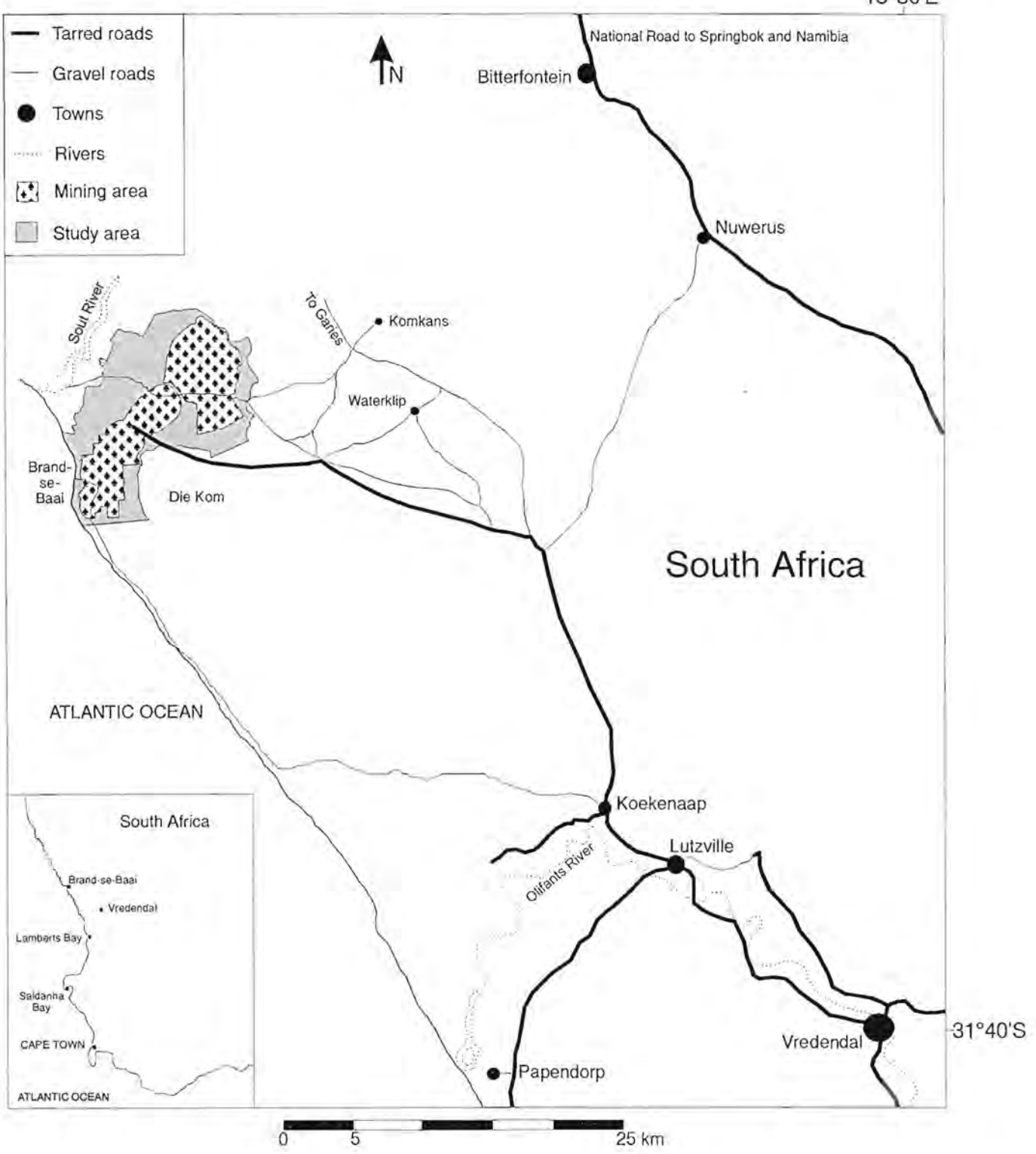

Figure 4.1. Location map of the Brand-se-Baai study area.

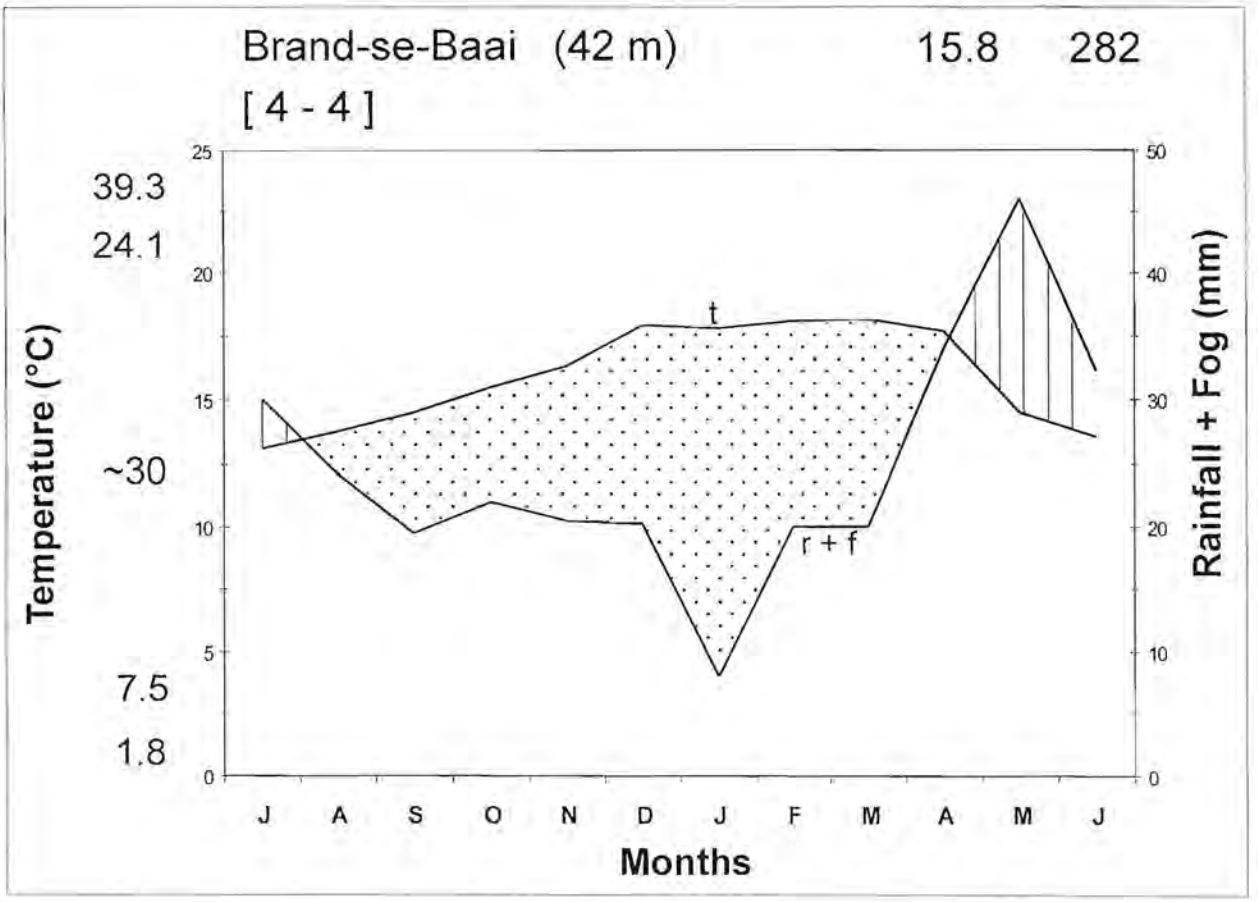

Figure 4.2. Climate diagram (following Walter & Lieth, 1960) of the Brand-se-Baai station for the period March 1993 – February 1997.

sands. It is therefore a naturally fragile ecosystem with a low resilience, which is easily disturbed or destroyed. The vegetation varies in height according to the depth of the sand - the shortest vegetation growing on exposed calcrete and coastal rocks and the tallest being found in areas with deep calcareous sand (Boucher & Le Roux, 1990).

A vegetation survey of the study area (De Villiers *et al.*, 1999) revealed six plant communities for the area to be mined at Brand-se-Baai. These six main communities have been classified as follows (Figure 4.3)(Vegetation units sampled for seed bank estimates are indicated in brackets):

1. *Ruschia tumidula - Tetragonia virgata* Tall Shrub Strandveld
   - 1.1 *Stipagrostis zeyheri - Lapeirousia* spp. Variant
   - 1.2 *Scirpoides dioecus - Stoebe nervigera* Variant
   - 1.3 *Pentaschistis patula - Chenopodium opulifolium* Variant
   - 1.4 *Eriocephalus africanus - Ferraria densepunctulata* Variant
2. *Eriocephalus africanus - Asparagus fasciculatus* Tall Shrub Strandveld **(Unit 6)**
   - 2.1 *Othonna floribunda - Lebeckia lotonoides* Variant
   - 2.2 *Zygophyllum morgsana - Coelanthum semiquinquefidum* Variant
3. *Salvia africana-lutea - Ballota africana* Tall Shrub Strandveld **(Unit 5)**
4. *Ruschia versicolor - Odyssea paucinervis* Dwarf Shrub Strandveld
   - 4.1 *Ruschia caroli - Aspalathus divaricata* Variant **(Unit 3)**
   - 4.2 *Tripteris oppositifolia - Cissampelos capensis* Variant **(Unit 4)**
   - 4.3 *Ehrharta calycina - Crassula expansa* Variant **(Unit 2)**
5. *Cephalophyllum spongiosum - Odyssea paucinervis* Coastal Strandveld **(Unit 1)**
6. *Cladoraphis cyperoides - Lebeckia multiflora* Coastal Strandveld **(Unit 1)**

Ten soil sample locations were randomly selected within each of five of these plant communities (Communities 2 - 6), situated in the western mining area, which is being mined first. Community 1 almost solely constitutes the eastern mining area, and was not sampled. The two variants of Community 2 were not sampled individually, while the three variants of community 4 were sampled individually. Since the coastal Communities 5 and 6 are not included in the area to be mined, these communities were sampled as a single vegetation unit.

At each of the 60 sampling locations, 15 soil samples were taken linearly at 2 m intervals. Each sample consisted of a soil core with a diameter of 65 mm taken to a depth of 100 mm, totaling a volume of approximately 246 cm^3. The soil samples were stored dry in cloth soil sampling bags at ambient temperatures for approximately one week, before the germinable seed content was estimated. Starting in June 1993 (winter), sampling was done four times a year, *i.e.* once every season over a period of two years (until March 1995, autumn).

From each of the 900 samples per season, a subsample of 100 cm^3 was spread evenly on top of sterile sand in a 1 dm^3 pot and placed under ambient conditions at the University of Pretoria, some 1 200 km north-east of the study area. Samples were watered daily and emerged seedlings were marked with wooden

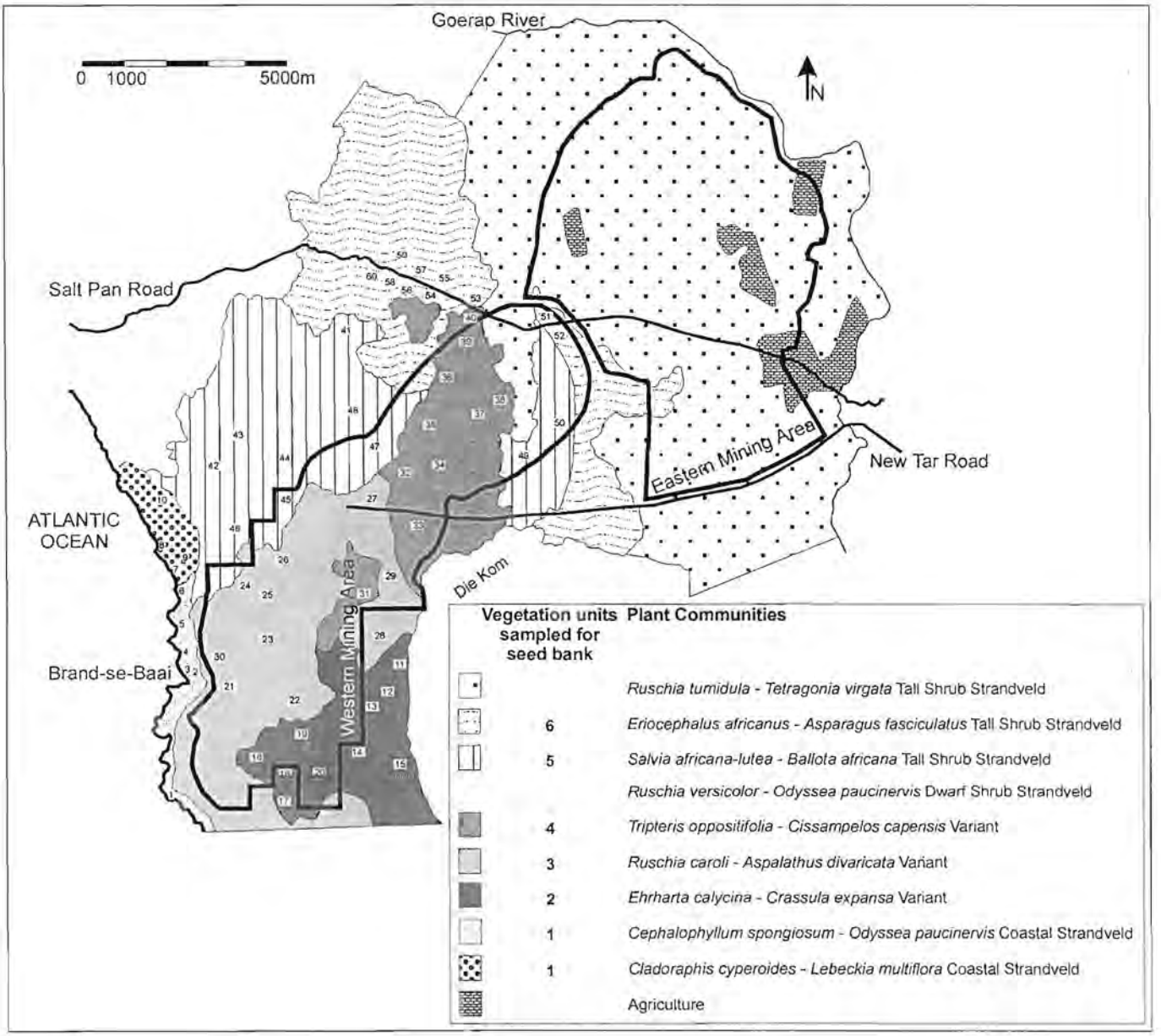

Figure 4.3. Vegetation map of the study area and corresponding vegetation sample units, indicating 60 seed bank sampling points.

toothpicks. Half strength Arnon and Hoagland's complete nutrient solution (Hewitt, 1952) was applied fortnightly. Examination of the samples continued for a period of six months, as recommended by Thompson (1993), whereafter the number of emerged seedlings (toothpicks) were counted. Identified seedlings were categorized as either perennial or annual species.

For each of six sampling seasons (with exception of the first and last sampling season) and the 60 sampling localities, three subsamples of 100 cm^3 were stored dry in paper bags under ambient conditions at the University of Pretoria. During the following autumn, which is considered as the peak season for the germination of most Strandveld Succulent Karoo plant species in the field (Chapter 8), the germinable seed density in each of the 1 080 subsamples was determined in the same manner as described above.

The Abundance Coefficient of Motyka *et al.* (IS_{MO}) (Mueller-Dombois & Ellenberg, 1974) was used to determine the similarity in soil seed bank size between samples examined directly after sampling and those examined at the peak season for germination:

$$IS_{MO} = \frac{2Mw}{MA + MB} \times 100$$

where Mw refers to the sum of the smaller quantitative values of the species common to two plots, MA is the sum of the quantitative values of all species in one of the two plots, and MB is the sum of the quantitative values of all species in the other plot.

Results were analyzed using the least significant difference (LSD) one-way and multi-factor analysis of variance (ANOVA) and LSD multiple range test of the Statgraphics 5.0 computer program (1989, STSC, Inc., U.S.A.), to test for significant differences at $P \leq 0.05$.

RESULTS AND DISCUSSION

The soil seed bank of the Strandveld Succulent Karoo yielded a mean of 2 725 emerged seedlings m^{-2} for samples collected in six vegetation units and in eight sampling seasons (Table 4.1a). This value is comparable with seed bank densities reported for the northwestern Northern Cape Province, South Africa, *i.e.* 100 – 4 000 seeds m^{-2} (Dean *et al.*, 1991), but is somewhat lower than the soil seed densities reported for the annual-rich Upland Succulent Karoo in Namaqualand, which ranged from 5 000 to 41 000 seeds m^{-2} (Van Rooyen & Grobbelaar, 1982). The seed bank estimates in this study were considerably higher than that reported for the southern Succulent Karoo (17 – 426 seeds m^{-2}) (Esler *et al.*, 1992). Reichman (1984) reported seed densities ranging from 4 000 to 15 000 seeds m^{-2} in the Sonoran desert. The size of the seed bank of the Strandveld Succulent Karoo compares well with seed bank densities in shrub steppe desert communities of the North American Great Basin which ranged from 45 to 3 940 seeds m^{-2}, depending on the micro-habitat (Parmenter & MacMahon, 1983). Seed densities in desert soils have previously been shown to be highly variable in time as well as space (Van Rooyen & Grobbelaar, 1982; Reichman, 1984; Esler *et al.*, 1992; Esler, 1993).

Table 4.1a. Mean number of emerged seedlings m^{-2} of different plant types, for samples taken in six vegetation units. Between vegetation units, the mean for 1 200 samples were calculated (seasonal data were lumped). Within a plant type, values followed by the same letter are not significantly different at $P \leq 0.05$. Within the mean for the study area, values followed by the same letter are not significantly different at $P \leq 0.05$

Plant type	VEGETATION UNIT						Significance level ($P \leq 0.05$)	Mean for study area
	1	2	3	4	5	6		
Perennials	225.0	253.8	170.0	221.6	187.8	115.9	0.0888	195.7 x
Annuals	742.6	1767.8	1870.2	1717.1	1826.2	1056.5	0.0545	1496.7 z
Unidentified	644.5 a	842.5 ab	1060.7 bc	1155.4 bc	1262.0 c	1232.4 c	0.0015	1032.9 y
All species	1612.1 a	2864.0 b	3100.9 b	3094.1 b	3276.0 b	2404.8 ab	0.0464	2725.3

Table 4.1b. Mean number of emerged seedlings m^{-2} of different plant types, for samples taken in different seasons. Between seasons, the mean for 900 samples were calculated (vegetation unit data were lumped). Within a plant type, values followed by the same letter are not significantly different at $P \leq 0.05$

Plant type	SEASON								Significance level ($P \leq 0.05$)
	Winter'93	Spring'93	Summer'93	Autumn'94	Winter'94	Spring'94	Summer'94	Autumn'95	
Perennials	23.7 a	42.9 a	146.6 a	562.8 c	146.6 b	50.8 a	47.4 a	544.7 c	0.0000
Annuals	216.5 a	500.8 ab	1072.6 ab	4933.0 d	1283.4 b	394.7 a	306.8 a	3266.1 c	0.0000
Unidentified	730.8 bc	335.0 a	852.6 c	2275.9 f	1389.5 d	421.8 ab	483.8 ab	1774.0 e	0.0000
All species	971.0 a	878.6 a	2071.8 b	7771.7 d	2819.5 b	867.3 a	838.0 a	5584.9 c	0.0000

Seedlings of annual species (1 497 seedlings m^{-2}) were significantly more abundant than perennial (196 seedlings m^{-2}) and unidentified (1 033 seedlings m^{-2}) species (Table 4.1a). Various authors have reported on the dominance of annual species in seed banks (Coffin & Lauenroth, 1989; Bertiller, 1998). In the Karoo, South Africa, soil seed densities of annual species were also found to be significantly higher than that of perennial species (Van Rooyen & Grobbelaar, 1982; Dean *et al.*, 1991).

Spatial distribution

Expression of spatial and temporal distribution depends on the scale of sampling. In this study, spatial distribution was expressed on a vegetation unit scale, and temporal distribution on a seasonal scale.

A 2-fold variation in spatial distribution between vegetation units was observed (Table 4.1a). The maximum mean number of emerged seedlings were recorded in vegetation unit 5, for samples collected and examined in autumn 1994 (9 575 m^{-2}) (Figure 4.4). The minimum mean number of emerged seedlings were recorded in vegetation unit 3, for samples collected and examined in spring 1994 (596 m^{-2}) (Figure 4.4).

Vegetation unit 1 yielded the lowest mean number of emerged seedlings (1 612 m^{-2}) irrespective of sampling season, which was mainly due to low densities of annual and unidentified species, compared to the other vegetation units (Table 4.1a). The vegetation of this unit is located nearest to the ocean (Figure 4.3) and occurs mainly on sand dunes exposed to salt spray, fog and prevailing winds.

The *Eriocephalus africanus* - *Asparagus fasciculatus* Tall Shrub Strandveld (Vegetation unit 6) yielded relatively low mean numbers of emerged seedlings during autumn (Figure 4.4). This unit is located furthest away from the ocean (Figure 4.3) and generally receives less fog that contributes to the annual precipitation (De Villiers *et al.*, 1999), than the other vegetation units at the study site.

In general, the mean number of emerged seedlings did not differ significantly between vegetation units 2, 3, 4 and 5 within a single sampling season (Figure 4.4) or when sampling season data were lumped (Table 4.1a). Emerged seedling densities of perennial and annual species did not differ significantly between vegetation units (Table 4.1a).

According to the multi-factor analysis of variance (Table 4.2), mean emerged seedling densities, for all plant types, did not differ significantly between vegetation units. The multi-factor ANOVA confirmed low spatial variation in soil seed bank size of the Strandveld Succulent Karoo on vegetation unit level. Under homogeneous soil and management conditions, the soil seed content has been reported to vary spatially to a factor of ten and more (Albrecht & Forster, 1996). Differences in seed bank spatial variability between this study and that reported in several other seed bank studies, may also be due to the scale of sampling (Manchester & Sparks, 1998). Low spatial variability in the size of the seed bank has been reported for other vegetation types (Coffin & Lauenroth, 1989).

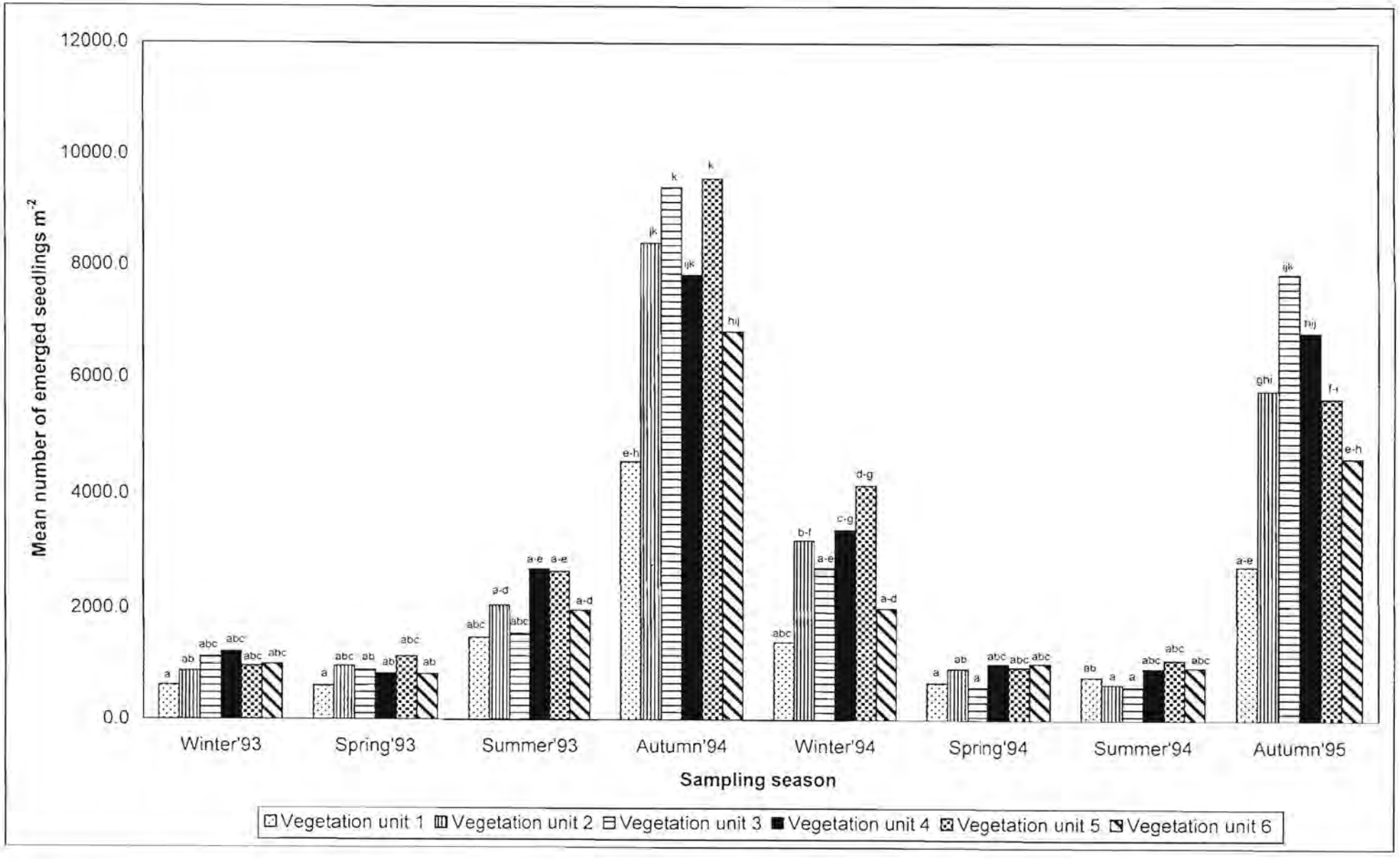

Figure 4.4. Mean number of emerged seedlings for samples collected in different vegetation units and seasons. Bars with the same letter are not significantly different at $P \leq 0.05$.

Table 4.2. Multi-factor analysis of variance ($P \leq 0.05$) for the mean number of emerged seedlings in samples taken in different vegetation units and seasons

Plant type	Between vegetation units		Between seasons	
	F-ratio	Significance level ($P \leq 0.05$)	F-ratio	Significance level ($P \leq 0.05$)
Perennials	0.311	0.9036	22.795	0.0000
Annuals	0.549	0.7383	28.865	0.0000
Unidentified	0.714	0.6167	13.192	0.0000
All species	0.421	0.8318	40.519	0.0000

Table 4.3. Abundance coefficient of similarity (Motyka *et al.* in Mueller-Dombois & Ellenberg, 1974) for species emerged, between samples examined directly after sampling and samples stored and examined at the peak season for germination (autumn)

Source of variation		Abundance Coefficient of Similarity (%) (Motyka *et al.* in Mueller-Dombois & Ellenberg, 1974)		
		Perennials	**Annuals**	**All species**
Between vegetation units	1	46.7	67.4	62.9
	2	45.5	58.0	56.4
	3	27.5	68.7	63.9
	4	13.2	54.7	49.6
	5	24.7	52.3	48.8
	6	20.0	58.6	52.9
Between seasons	Spring '93	22.9	51.2	48.2
	Summer '93	31.9	43.8	42.2
	Autumn '94	50.7	84.9	80.5
	Winter '94	16.1	59.9	52.9
	Spring '94	10.1	36.4	32.0
	Summer '94	8.2	13.4	12.8
Total		33.9	63.3	59.3

On a microtopographical scale, a 98-fold variation in seedling density was estimated for a single location in the Strandveld Succulent Karoo, compared to a 197-fold variation reported for the Upland Succulent Karoo (Van Rooyen, 1999). It appears that the seeds are very patchily distributed in the soil of the Succulent Karoo (Chapter 5; Esler, 1993; Van Rooyen, 1999).

Temporal distribution

The mean number of seedlings emerging from soil collected and examined in different seasons varied up to 9-fold (Table 4.1b), with the majority of seedlings being recorded in autumn (2 761 – 9 575 m^{-2}) (Figure 4.4). A 24-fold, 23-fold and 7-fold variation in seedling density between seasons were observed for perennial, annual and unidentified species respectively. All plant types yielded significantly higher numbers of emerged seedlings during autumn than during other sampling seasons, irrespective of vegetation unit (Table 4.1b). Sampling during autumn occurred before the onset of the rainfall season. By this time, seeds of many species should have completed their period of after-ripening (Chapter 9) and be in a state of conditional or non-dormancy (Baskin & Baskin, 1998). Another factor contributing to the high number of emerged seedlings recorded during autumn was the favourable environmental conditions for germination (Chapter 8). Most local species germinate naturally at this time of the year, providing sufficient rainfall.

In general, winter sampling yielded significantly less emerged seedlings (616 – 4 162 m^{-2}) than autumn sampling in all vegetation units and years (Figure 4.4; Table 4.1b). Viable seeds that did not germinate under favourable environmental conditions in the field during autumn, either had not after-ripened yet, or had entered secondary dormancy (Baskin & Baskin, 1998). In winter rainfall areas, sampling of the soil seed bank during winter (after the peak time for germination in autumn and before seed dispersal in spring) usually gives a good estimate of the size and composition of the persistent seed bank. This is, provided that estimation by means of the emergence method incorporates conditions favourable for the germination of as many species as possible and estimation continues for as long as possible (Simpson *et al.*, 1989). A long-term persistent seed bank is the only seed bank type likely to contribute to the regeneration of destroyed or degraded vegetation units (Thompson, 1993).

As in the case of winter sampling, the mean number of emerged seedlings from samples collected in spring (596 – 1 150 m^{-2}), were significantly lower than that of sampling during autumn (Figure 4.4; Table 4.1b). During spring sampling, many species have not completed production and dispersal of seeds. This, as well as seed dormancy and unfavourable environmental conditions for germination were probably responsible for the low numbers of emerged seedlings recorded during spring sampling and examination.

The mean number of emerged seedlings recorded from samples collected in summer (609 – 2 693 m^{-2}) was also significantly less than that recorded during autumn (Figure 4.4; Table 4.1b). During summer, most plants have completed production and release of seeds, and a large seed bank would have been expected. The low numbers of emerged seedlings recorded during summer were probably due to seed dormancy and unfavourable conditions for germination, e.g. high temperature.

When samples were stored and examined during the following autumn (Figures 4.5a & 4.5b), the size of the soil seed bank of summer and winter collected samples was not significantly different from that collected during autumn. These high seed densities recorded in the seed bank during winter sampling indicate the predominance of species with persistent seed bank strategies.

According to the multi-factor ANOVA (Table 4.2), mean emerged seedling densities, for all plant types, differed significantly between seasons. The soil seed bank of the Strandveld Succulent Karoo therefore showed high temporal variation on seasonal level. Such seasonal variation in soil seed bank densities has been reported elsewhere (Chippendale & Milton, 1934; Reichman, 1984; Coffin & Lauenroth, 1989; Esler, 1993; Malo *et al.*, 1995; Milberg & Andersson, 1998; Waick *et al.*, 1998) and may be the result of seasonal inputs of seeds (Graham & Hutchings, 1988). As noted in this study, the spatial pattern of soil seed density is often not as pronounced as that of the temporal pattern (Coffin & Lauenroth, 1989). Populations that experience more temporal variation in the soil seed bank are predicted to have lower germination fractions and a higher fraction of their seeds in between-year seed banks than populations that experience less temporal variation (Pake & Venable, 1996).

Examination time

The abundance coefficient of similarity (Motyka *et al.* in Mueller-Dombois & Ellenberg, 1974) between seed bank samples examined directly after sampling and at the peak time for germination, are presented in Table 4.3. Vegetation unit 5 yielded the lowest similarity in species abundance, for all species (48.8%) as well as for annual species (52.3%), between examination times. For perennial species, vegetation unit 4 yielded the lowest (13.2%) and vegetation unit 1 the highest (46.7%) similarity between examination times. Vegetation unit 3 yielded the highest similarity, for all species (63.9%) as well as for annual species (68.7%), between examination times.

When examination of samples commenced in the same season as sample collection, the highest degree of spatial variation in seed bank size between vegetation units occurred during the autumn sampling season (Figure 4.5a). Variation in seed bank size between vegetation unit 1 and vegetation units 2, 3, 4, 5 and 6 increased when samples collected during summer 1994 were examined during the following autumn (Figures 4.5a & 4.5b). This may be due to increases in emerged seedling numbers as a result of favourable conditions for germination during autumn examination.

With the exception of vegetation unit 1, the mean number of emerged seedlings from samples collected during summer 1994 increased significantly when samples were stored and examined during the following autumn (Figures 4.5a & 4.5b). This was the only season when examination time significantly influenced emerged seedling density. Unfortunately, the summer 1993 sampling period did not yield similar results. Various reasons for this difference in seed numbers between similar seasons may be evident, e.g. low seed production, clustered seed bank distribution, sampling method and seed characteristics such as dormancy, germination requirements and fractional germination. For annual plants, fractional germination (*i.e.* between-year seed banks) provides a variance reducing mechanism (Pake & Venable, 1996). Delayed germination of

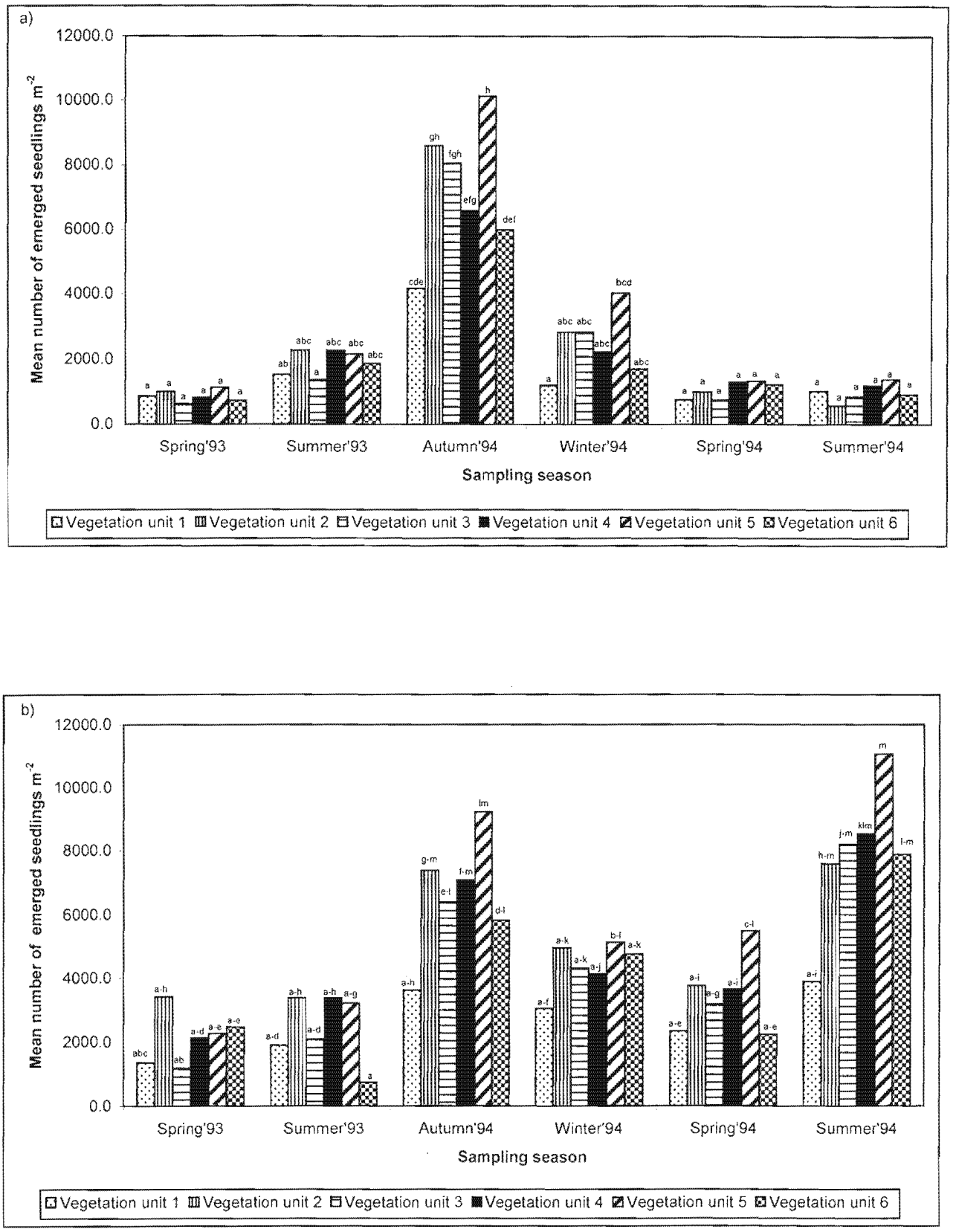

Figure 4.5. Mean number of emerged seedlings of samples collected in different vegetation units and seasons, and examined a) directly after sampling and b) at the peak time for field germination (autumn). Bars with the same letter are not significantly different at $P \leq 0.05$.

a fraction of a plant's progeny buffers it from the consequences of near or complete reproductive failure in unfavourable years. It also reduces variance by lowering success in favourable years, when greater fitness would have resulted from germination.

For all plant types, autumn 1994 sampling yielded the highest similarity in species abundance, between seed bank samples examined directly after sampling and at the peak time for germination (Table 4.3). Summer 1994 sampling yielded lowest similarity between examination times, which stresses the significant increase in mean number of emerged seedling when samples were examined during autumn (Figures 4.5a & 4.5b).

Revegetation

Because annual species dominated the soil seed bank of the Strandveld Succulent Karoo in terms of numbers of individuals, topsoil replacement as a means of revegetation will yield mainly annuals. Although annuals will contribute to post-mining vegetation efforts, and are essential in the initial sand stabilizing phase of rehabilitation, these species are of less importance to long-term revegetation goals than perennial species. The latter species dominate the pre-mining standing vegetation in terms of abundance and species richness (Chapters 3, 6 & 7). Sowing and transplanting of selected perennial species should therefore be considered for achieving long-term revegetation goals.

During topsoil replacement at the study site, the low spatial variation between vegetation units will not affect the density of the resulting vegetation. High spatial variation expected on a microtopographical scale will not affect post-mining vegetation density due to the lumping of topsoil during the mining process. Possible differences in seed bank species richness and composition between vegetation units will be important in achieving proposed revegetation goals (Chapter 5).

Topsoil collection and replacement during the period of highest soil seed density, *i.e.* summer and autumn, will ensure the largest possible reserve of genetic diversity (Baskin & Baskin, 1978; Vavrek *et al.*, 1991) in post-mining restored areas. During summer and autumn, the soil seed bank will contain species with transient seed banks and those that accumulate persistent seed banks. The presence of a large persistent seed bank (*c.* 1 894 seeds m^{-2} recorded during two winter seasons; Table 4.1b) ensures the continuation of the population at a given site, even if seeds are not produced every year, and it increases the size, and thus the genetic diversity and stability, of the effective breeding population (Silvertown & Lovett-Doust, 1995). Utilization of the persistent seed bank by means of topsoil replacement will therefore be essential for successful revegetation of the study area.

The period between collection and replacement of topsoil should also be as short as possible, because the stockpiling of soils before they are used in restoration can negatively influence recruitment in at least two ways. Short-lived viable seeds may be lost if the soil is held too long, and environmental conditions, particularly temperatures, in the stockpiled soil may be so unfavourable that seeds are killed (Van der Valk *et al.*, 1992). Several reports on stockpiled topsoil have referred to the low organic matter content of such soils as a result of high rates of mineralization (Williamson & Johnson, 1990).

During autumn, the size of the germinable soil seed bank should be largest and chances for seedling survival greatest. This is also the period when environmental conditions are favourable for the germination of most species at the study site (Chapter 8). Irrigation of areas where topsoil replacement and sowing have been completed should only commence in autumn. Mechanisms to preserve replaced topsoil and/or sown seeds, such as hydromulch or sand-binding techniques, should be applied during the period prior to irrigation. Transplanting of selected species should take place during winter and be completed at the end of the rainy season. Irrigation during the following dry seasons will benefit the survival of perennial plants. Environmental conditions (soil moisture and temperature) can greatly influence recruitment from the seed bank, and the success or failure of a project can depend as much on environmental conditions as on the size and composition of the seed bank.

CONCLUSIONS

The soil seed bank of the Strandveld Succulent Karoo yielded a mean of 2 725 emerged seedlings m^{-2}, and was dominated in terms of numbers by annual species. Topsoil replacement in post-mining areas of the Strandveld Succulent Karoo will yield mainly annual species, while selected perennial species will have to be sown or transplanted during revegetation efforts.

At the scales used, the spatial pattern of soil seed density was not as pronounced as that of the temporal pattern. At vegetation unit level, spatial variation in soil seed density was low. Spatial variation in the soil seed bank will not affect the density of vegetation resulting from topsoil replacement.

Seasonal variation in seed bank size was high at the study site. Samples collected during autumn and summer did not differ significantly from each other in size, and include both the transient and persistent fractions of the soil seed bank. However, when these samples were examined directly after sampling, there was a significant difference in seed bank size, which was probably due to unfavourable environmental conditions for germination during summer. When samples were examined directly after sampling, the highest mean number of emerged seedlings occurred in samples collected during autumn. Winter sampling indicated the presence of a large persistent seed bank at the study site.

The relatively large size of the soil seed bank in the Strandveld Succulent Karoo indicates that topsoil replacement can meaningfully contribute to the revegetation of mined areas. Although annual species dominate the seed bank, the potential contribution of perennial seed bank species should not be underestimated in revegetation efforts and will be addressed in Chapter 5.

The ultimate goal that was stipulated in the original revegetation plan was to revegetate the area with indigenous plant species in an attempt to return the area to a state as close as possible to its original state (Grindley & Barbour, 1990). More specifically, revegetation should aim to leave the area with sufficient indigenous species to prevent erosion, to be able to sustain itself and to hasten the return to a complete natural cover with as great a species diversity as possible. To evaluate the success with which topsoil

replacement will aid in achieving these goals, a comparison between the seed bank and standing vegetation will also be essential.

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CHAPTER 5

SPATIAL AND TEMPORAL PATTERNS IN THE SOIL SEED BANK OF THE STRANDVELD SUCCULENT KAROO, SOUTH AFRICA: II. SEED BANK COMPOSITION

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ABSTRACT

Topsoil replacement, sowing and transplanting of selected species are viewed as possible means for the revegetation of post-mining areas in the Strandveld Succulent Karoo, South Africa. However, the upper soil layers contain a high percentage of the heavy minerals to be mined, rendering topsoil replacement a less favourable method for revegetation from the mining company's point of view. The upper soil layers also contain the seed bank, which may be essential for revegetation purposes. Seed bank composition was determined seasonally for six vegetation units at Brand-se-Baai using the seedling emergence method. A total of 109 species were recorded from samples collected at the study site. In terms of species richness, the soil seed bank was not dominated by any specific plant type, *i.e.* perennials or annuals. Temporal variation in soil seed bank species richness was more pronounced than spatial variation. Total species richness at the study site ranged from 55 to 65 species between vegetation units and from 30 to 78 species between seasons. Due to the relatively high species richness of both perennial and annual species in the soil seed bank, topsoil replacement will be essential for the revegetation of mined areas in the Strandveld Succulent Karoo. During topsoil replacement, spatial variation in the soil seed bank will not affect the species richness of the resulting vegetation. To sustain as high as possible species richness, areas where topsoil replacement and sowing have been completed should not be irrigated until the start of the rainy season.

Key words: Mining; revegetation; seed bank composition; seedling emergence; spatial variation; species richness; temporal variation; topsoil replacement

INTRODUCTION

The composition of the seed bank is notoriously variable both in space and time (Lavorel *et al.*, 1993). Spatial and temporal variation in soil seed banks has been the subject of numerous studies (Bigwood & Inouye, 1988; Granström, 1988; Henderson *et al.*, 1988; Matlack & Good, 1990; Kalisz, 1991; Willems & Huijsmans, 1994; Albrecht & Forster, 1996; Bertiller, 1998; Milberg & Andersson, 1998). Studies on the horizontal distribution of seeds in soil have been neglected, perhaps because of methodological difficulties. Yet, this aspect is important for seedling recruitment pattern and vegetation structure following a major disturbance in the ecosystem (Kjellsson, 1992). The importance of a seed bank is species dependent and varies among plant communities (Badger & Ungar, 1994). For this reason, species composition has been included in most seed bank studies (Henderson *et al.*, 1988; Levassor *et al.*, 1990; Kjellsson, 1992; Milberg

& Persson, 1994; Aerts *et al.*, 1995; Dutoit & Alard, 1995; Albrecht & Forster, 1996; Aziz & Khan, 1996; Kirkham & Kent, 1997; Lunt, 1997), including those in the arid areas of South Africa (Van Rooyen & Grobbelaar, 1982; Dean *et al.*, 1991; Esler, 1993; De Villiers *et al.*, 1994).

Seed bank studies are an important consideration in the development of a predictive understanding of plant community structure and function (Roberts, 1981; Leck *et al.*, 1989; Esler, 1993). In arid and semi-arid environments, where germination and recruitment are the critical stages in the life cycle of most plants, seed banks are thought to play a major role in population dynamics. Seed bank studies in arid environments have been concentrated mainly in areas with an abundance of annuals (Van Rooyen & Grobbelaar, 1982; Reichman, 1984; Coffin & Lauenroth, 1989), and indicated that seed banks in these areas are often persistent and large (Von Willert *et al.*, 1992) with annual species as the main contributors. Knowledge of seed banks of perennial species in arid environments is very poor (Leck *et al.*, 1989; Esler, 1993).

For most restoration and creation projects, a precise estimate of seed density for a particular species in the seed bank is not needed. An estimate of the relative abundance of species, determined by the emergence method, is usually sufficient (Van der Valk *et al.*, 1992). Even a list of species present in the seed bank is enough to establish which desirable and undesirable species are present or absent. The seedling emergence method gives information on seed viability and seasonality of germination as well as the species composition of the seed bank (Manchester & Sparks, 1998).

Topsoil replacement as well as seeding and/or transplanting of selected species are considered as viable means for the revegetation of mined areas in the Strandveld Succulent Karoo, South Africa (Environmental Evaluation Unit, 1990). Due to the high percentage of heavy minerals present in the upper soil layers, topsoil replacement is not favoured by the mining company. The initial revegetation goal stated that vegetation of post-mining areas should conform as close as possible to pre-mining vegetation. This goal includes both species richness and abundance. The standing vegetation prior to mining is dominated by perennial species, while annual species predominated the seed bank in terms of number of individuals (Chapter 4). Knowledge about the composition of the soil seed bank, as well as its distribution in space and time, will therefore indicate the suitability of topsoil replacement in achieving the proposed revegetation goals. The formulation of appropriate revegetation strategies is dependent on detailed information on the seed bank of species that are dominant in the vegetation. This information would also aid in the understanding of the processes involved in the dynamics of the system.

This paper is the second of two concerned with the consequences of spatial and temporal variation in the soil seed bank of the Strandveld Succulent Karoo on revegetation strategies, and deals mainly with the species richness and composition of the germinable soil seed bank. The first paper focused on seed bank size (Chapter 4).

MATERIAL AND METHODS

The study area is situated in the vicinity of Brand-se-Baai (31°18'S, 17°54'E) on the Cape West Coast, South Africa, and covers approximately 9 400 ha (De Villiers *et al.*, 1999). Rainfall occurs mainly during the winter months with an average of 160 mm. The average annual temperature measured at the study site is 15.8°C (Chapter 4). The vegetation at Brand-se-Baai consists mainly of Strandveld Succulent Karoo (Low & Rebelo, 1998), which contain many drought deciduous and succulent species. This vegetation type contain plant species which are sensitive to disturbance because they are subjected to heavy winds, salt spray and drift sands Boucher & Le Roux, 1993). It is therefore a naturally fragile ecosystem with a low resilience, which is easily disturbed or destroyed.

Collection, treatment and examination (emergence method) of seed bank soil samples, as well as statistical treatment of data, were identical to that described in the paper dealing with seed bank size (Chapter 4).

The presence coefficient of Sorensen (IS_s) (Mueller-Dombois & Ellenberg, 1974) were used to determine the similarity in soil seed bank composition of samples examined directly after sampling and those examined at the peak season for germination:

$$IS_s = \frac{2c}{A+B} \times 100$$

where, in this study, c is the number of species common to two examination times, A is the total number of species recorded directly after sampling, and B is the total number of species recorded at the peak time for germination.

RESULTS AND DISCUSSION

The perennial and annual species, which emerged from samples collected in different vegetation units and seasons in the Strandveld Succulent Karoo, and their abundance's are presented in Tables 5.1a and 5.1b respectively. Abundance's of unidentified species are also presented in Table 5.1b. The grass *Ehrharta calycina* was the perennial with the highest overall density (Table 5.1a), while the grass *Karroochloa schismoides* was the annual that yielded the highest overall number of emerged seedlings (Table 5.1b).

A total of 109 species were recorded in the soil seed bank of the study site (Tables 5.1a & 5.1b; Table 5.2). This value is markedly lower than the 230 species recorded in the standing vegetation at the study site (De Villiers *et al.*, 1999). Low correspondence between standing vegetation and soil seed banks has been reported by numerous authors (Roberts, 1981; Milberg & Persson, 1994; Berge & Hestmark, 1997; Breck & Jenkins, 1997; Lunt, 1997).

Table 5.1a. Mean number of emerged seedlings m^{-2} of perennial species, for samples taken in six vegetation units during different seasons. Between vegetation units, the mean for 1 200 samples were calculated (season data were lumped). Between seasons, the mean for 900 samples were calculated (vegetation unit data were lumped)

Species	VEGETATION UNIT						SEASON							
	1	2	3	4	5	6	Winter'93	Spring'93	Summer'93	Autumn'94	Winter'94	Spring'94	Summer'94	Autumn'95
Amellus tenuifolius	0.8	0.8	0.8	3.4	9.3	0.0	0.0	2.3	0.0	0.0	1.1	0.0	0.0	16.9
Arctotis spp.	3.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	4.5
Atriplex semibaccata	0.0	3.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	4.5	0.0	0.0	0.0
Ballota africana	0.0	0.0	0.0	0.0	1.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.3
Cephalophyllum spongiosum	4.2	0.0	0.0	0.0	0.0	0.0	0.0	1.1	0.0	4.5	0.0	0.0	0.0	0.0
Chaetobromus dregeanus	2.5	0.8	0.0	2.5	0.8	0.0	1.1	5.6	0.0	0.0	0.0	2.3	0.0	0.0
Chrysocoma longilolia	0.0	0.0	0.0	2.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	3.4
Conicosia pugioniformis	2.5	0.0	5.1	4.2	3.4	0.0	0.0	0.0	1.1	4.5	4.5	2.3	0.0	7.9
Crassula muscosa	0.8	0.8	0.0	1.7	0.0	0.0	0.0	0.0	2.3	1.1	1.1	0.0	0.0	0.0
Drosanthemum calycinum	3.4	0.0	0.0	7.6	0.0	1.7	2.3	0.0	3.4	10.2	0.0	0.0	1.1	0.0
Ehrharta calycina	80.4	157.3	67.7	66.8	65.1	21.1	0.0	3.4	63.2	240.2	50.8	21.4	6.8	225.6
Eriocephalus africanus	0.0	0.0	0.0	12.7	1.7	3.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	23.7
Euphorbia spp.	0.0	0.0	0.0	0.0	0.8	0.0	0.0	0.0	1.1	0.0	0.0	0.0	0.0	0.0
Exomis microphylla	0.0	0.0	0.8	0.0	0.0	0.0	0.0	1.1	0.0	0.0	0.0	0.0	0.0	0.0
Galenia africana	0.0	0.0	0.0	1.7	0.0	0.8	0.0	1.1	0.0	1.1	0.0	0.0	0.0	1.1
Galenia sarcophylla	5.1	6.8	0.8	0.8	3.4	0.8	0.0	4.5	7.9	4.5	2.3	1.1	1.1	2.3
Gazania leiopoda	0.0	10.2	2.5	1.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	19.2
Geophyte spp.	11.0	9.3	23.7	24.5	22.0	22.8	0.0	1.1	4.5	72.2	4.5	2.3	2.3	64.3
Grielum grandiflorum	5.9	0.0	0.0	0.0	3.4	3.4	1.1	1.1	0.0	9.0	1.1	1.1	0.0	3.4
Helichrysum incarnatum	0.8	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.1	0.0	0.0	0.0	0.0
Hermannia spp.	7.6	2.5	6.8	3.4	0.8	1.7	0.0	2.3	10.2	9.0	1.1	0.0	3.4	4.5
Hirpicium alienatum	0.8	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.1	0.0	0.0	0.0	0.0	0.0
Hypertelis salsoloides	18.6	21.1	0.0	7.6	0.8	3.4	3.4	1.1	4.5	47.4	1.1	0.0	6.8	4.5
Lampranthus godmaniae	0.8	0.0	0.0	0.0	0.0	0.8	0.0	0.0	1.1	0.0	0.0	0.0	0.0	1.1
Lampranthus lanatus	0.0	0.0	0.0	0.8	0.0	0.0	0.0	0.0	0.0	1.1	0.0	0.0	0.0	0.0
Lebeckia lotonoides	0.8	0.0	0.0	0.0	0.0	4.2	0.0	0.0	0.0	4.5	0.0	0.0	0.0	2.3
Lebeckia multiflora	1.7	0.0	0.0	0.0	0.8	0.0	0.0	0.0	0.0	2.3	0.0	0.0	0.0	1.1
Leipoldtia jacobeniana	1.7	0.0	0.0	0.0	0.0	0.0	1.1	0.0	0.0	0.0	1.1	0.0	0.0	0.0
Leysera gnaphalodes	0.0	0.8	0.8	0.0	0.0	3.4	0.0	2.3	2.3	1.1	0.0	0.0	0.0	1.1
Manochlamys albicans	2.5	3.4	9.3	4.2	10.2	3.4	6.8	0.0	3.4	14.7	3.4	1.1	0.0	14.7
Mesembryanthemaceae	29.6	5.1	4.2	16.1	16.1	1.7	0.0	4.5	11.3	49.6	11.3	1.1	0.0	19.2
Microloma sagittatum	0.0	0.0	0.0	0.8	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.1
Nestlera biennis	0.8	0.0	5.1	16.1	5.1	18.6	0.0	2.3	0.0	2.3	6.8	5.6	11.3	32.7
Odyssea paucinervis	5.9	0.8	0.0	0.0	1.7	0.0	0.0	0.0	1.1	2.3	2.3	1.1	0.0	4.5
Othonna floribunda	0.8	0.0	0.0	2.5	2.5	2.5	1.1	0.0	1.1	3.4	2.3	0.0	1.1	2.3
Pharnaceum aurantium	6.8	5.9	0.0	3.4	0.0	0.0	0.0	0.0	0.0	3.4	0.0	0.0	0.0	18.0
Pharnaceum lanatum	0.0	0.0	0.0	0.0	0.0	1.7	0.0	0.0	0.0	0.0	0.0	2.3	0.0	0.0
Psilocaulon spp.	0.0	0.0	0.0	0.0	2.5	0.0	0.0	0.0	1.1	0.0	0.0	0.0	1.1	1.1
Pteronia onobromoides	0.0	0.0	0.0	0.0	0.8	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.1	0.0
Rhus longispina	0.0	0.0	0.0	1.7	0.0	0.0	0.0	0.0	2.3	0.0	0.0	0.0	0.0	0.0
Ruschia bolusiae	0.8	0.0	2.5	6.8	1.7	1.7	1.1	0.0	5.6	4.5	3.4	0.0	0.0	3.4
Ruschia brevicyma	5.1	6.8	4.2	2.5	0.0	5.1	2.3	5.6	10.2	0.0	10.2	3.4	0.0	0.0
Ruschia caroli	0.0	0.8	4.2	8.5	0.0	0.8	0.0	0.0	0.0	15.8	3.4	0.0	0.0	0.0
Ruschia cymosa	0.0	0.0	2.5	0.0	0.0	0.0	0.0	0.0	1.1	1.1	1.1	0.0	0.0	0.0
Ruschia extensa	1.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.3	0.0	0.0	0.0	0.0
Ruschia namaquana	0.0	0.0	0.8	0.0	0.0	0.0	0.0	0.0	0.0	1.1	0.0	0.0	0.0	0.0
Ruschia sp.	0.8	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.1	0.0	0.0	0.0	0.0
Ruschia subpaniculata	0.0	0.0	1.7	0.0	0.0	0.0	0.0	0.0	0.0	1.1	0.0	1.1	0.0	0.0
Ruschia tecta	0.0	0.8	2.5	0.0	0.0	0.0	0.0	0.0	0.0	3.4	0.0	0.0	0.0	1.1
Ruschia tumidula	0.0	0.0	4.2	0.0	6.8	0.0	0.0	0.0	0.0	9.0	5.6	0.0	0.0	0.0
Ruschia versicolor	0.0	2.5	1.7	1.7	0.0	0.0	1.1	0.0	1.1	3.4	2.3	0.0	0.0	0.0
Stipagrostis zeyheri	0.8	0.8	1.7	0.8	0.0	0.0	0.0	0.0	2.3	0.0	0.0	2.3	1.1	0.0
Stoeberia spp.	5.1	0.0	0.0	0.0	0.8	0.0	0.0	1.1	0.0	5.6	0.0	0.0	0.0	1.1
Tetragonia virgata	5.1	6.8	11.0	13.5	23.7	6.8	2.3	2.3	3.4	16.9	14.7	2.3	3.4	44.0
Tripteris oppositifolia	0.0	0.0	0.8	0.8	0.0	0.8	0.0	0.0	0.0	0.0	0.0	0.0	2.3	1.1
Vanzijlia annulata	5.1	2.5	0.8	0.0	0.0	0.8	0.0	0.0	0.0	3.4	4.5	0.0	0.0	4.5
Zygophyllum morgsana	0.8	3.4	1.7	0.0	0.0	2.5	0.0	0.0	0.0	2.3	2.3	0.0	1.1	5.6
Zygophyllum pygmaeum	0.0	0.0	0.0	0.0	1.7	0.8	0.0	0.0	0.0	0.0	0.0	0.0	3.4	0.0
Total for perennials	**225.0**	**253.8**	**170.0**	**221.6**	**187.8**	**115.9**	**23.7**	**42.9**	**146.6**	**562.8**	**146.6**	**50.8**	**47.4**	**544.7**

Table 5.1b. Mean number of emerged seedlings m^{-2} of annual species, for samples taken in six vegetation types during different seascns. Between vegetation types, the mean for 1 200 samples were calculated (season data were lumped). Between seasons, the mean for 900 samples were calculated (vegetation unit data were lumped)

Species	VEGETATION UNIT						SEASON							
	1	2	3	4	5	6	Winter'93	Spring'93	Summer'93	Autumn'94	Winter'94	Spring'94	Summer'94	Autumn'95
Adenogramma littoralis	0.0	82.0	79.5	300.3	93.0	11.8	5.6	13.5	13.5	291.0	132.0	21.4	9.0	269.5
Amellus microglossus	0.0	4.2	0.0	0.8	329.0	0.0	0.0	4.5	0.0	116.2	0.0	16.9	30.5	277.4
Arctotheca calendula	0.8	1.7	0.0	1.7	1.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	3.4	4.5
Arctotis adpressa	0.0	0.0	0.0	0.0	0.8	4.2	0.0	0.0	0.0	0.0	1.1	0.0	0.0	5.6
Brassica tournefortii	0.0	2.5	3.4	0.0	0.0	0.0	0.0	0.0	0.0	1.1	1.1	0.0	0.0	5.6
Bromus pectinatus	2.5	1.7	0.0	0.0	78.7	2.5	0.0	1.1	0.0	45.1	32.7	29.3	3.4	2.3
Cardamine hirsuta	8.5	2.5	5.9	0.8	0.0	0.0	0.0	15.8	7.9	0.0	0.0	0.0	0.0	0.0
Chenopodium opulifolium	0.0	0.8	0.8	4.2	66.8	1.7	0.0	4.5	32.7	6.8	0.0	10.2	2.3	42.9
Cotula thunbergii	1.7	2.5	5.1	7.6	0.8	20.3	2.3	6.8	2.3	11.3	0.0	4.5	5.6	18.0
Crassula expansa	21.1	255.4	130.3	43.1	14.4	58.4	51.9	74.4	64.3	76.7	100.4	56.4	42.9	230.1
Crassula umbellata	0.8	111.6	9.3	6.8	18.6	299.4	4.5	19.2	14.7	342.9	37.2	9.0	1.1	166.9
Crotalaria humilis	0.0	0.0	0.0	1.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.1	1.1
Cysticapnos cracca	0.0	0.0	0.0	0.0	0.8	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.1
Diascia spp.	0.0	0.0	0.0	0.0	0.0	0.8	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.1
Didelta carnosa	0.0	5.9	0.8	0.8	0.0	0.0	1.1	0.0	0.0	0.0	0.0	0.0	3.4	5.6
Dimorphotheca pluvialis	0.0	3.4	1.7	0.8	36.4	2.5	3.4	3.4	0.0	4.5	1.1	1.1	0.0	46.2
Ehrharta brevifolia	0.8	0.0	0.0	0.0	0.0	0.0	1.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Felicia merxmuelleri	0.0	0.8	0.8	0.8	1.7	11.0	0.0	1.1	6.8	3.4	0.0	0.0	0.0	9.0
Ficinia argyropa	6.8	5.9	14.4	7.6	8.5	11.0	3.4	18.0	5.6	0.0	7.9	6.8	30.5	0.0
Foveolina tenella	0.0	0.0	0.0	7.6	0.0	0.0	1.1	2.3	0.0	0.0	0.0	1.1	1.1	4.5
Frankenia pulverulenta	4.2	0.0	0.0	0.0	0.0	0.0	4.5	1.1	0.0	0.0	0.0	0.0	0.0	0.0
Gymnodiscus capillaris	0.0	0.8	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.1
Hebenstretia dentata	0.0	7.6	8.5	5.9	8.5	0.0	0.0	0.0	0.0	15.8	2.3	0.0	0.0	22.6
Hebenstretia repens	0.0	5.1	0.0	3.4	1.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	13.5
Helichrysum marmarolepis	66.0	47.4	93.9	48.2	63.4	23.7	9.0	33.8	66.5	101.5	95.9	44.0	49.6	56.4
Heliophila coronopifolia	0.0	1.7	0.0	3.4	4.2	0.8	0.0	0.0	1.1	4.5	0.0	0.0	3.4	4.5
Isolepis marginata	0.8	5.1	3.4	12.7	4.2	12.7	0.0	6.8	3.4	5.6	11.3	10.2	1.1	13.5
Karroochloa schismoides	55.8	447.5	1192.7	754.5	839.9	431.4	1.1	194.0	762.4	2256.7	518.8	120.7	54.1	1054.5
Lessertia benguellensis	0.0	0.0	0.0	0.8	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.1	0.0
Lyperia triste	0.8	0.8	0.8	0.0	0.0	0.0	0.0	0.0	1.1	1.1	0.0	0.0	0.0	1.1
Manulea altissima	1.7	0.8	1.7	3.4	6.8	46.5	16.9	3.4	4.5	6.8	20.3	1.1	5.6	22.6
Manulea pusilla	0.0	34.7	0.0	15.2	0.0	0.0	6.8	5.6	5.6	19.2	2.3	1.1	0.0	25.9
Mesembryanthemum crystalinum	77.0	17.8	17.8	16.9	6.8	0.8	7.9	0.0	3.4	93.6	41.7	2.3	2.3	31.6
Nemesia bicornis	0.8	0.8	0.0	0.0	2.5	2.5	0.0	0.0	0.0	3.4	0.0	0.0	0.0	5.6
Nemesia ligulata	0.0	0.0	0.0	0.0	0.0	0.8	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.1
Ocimum canum	0.0	0.0	1.7	0.0	0.0	0.8	0.0	0.0	0.0	2.3	0.0	0.0	0.0	1.1
Oncosiphon suffruticosum	205.5	203.9	87.1	99.8	148.9	47.4	65.4	38.3	49.6	480.4	113.9	32.7	10.2	266.2
Pelargonium senecioides	0.0	0.0	0.8	7.6	0.0	0.0	0.0	0.0	1.1	5.6	1.1	0.0	0.0	3.4
Pentaschistis patula	14.4	281.7	47.4	217.4	11.8	10.2	1.1	39.5	1.1	541.3	16.9	0.0	24.8	152.3
Pharnaceum exiguum	5.9	16.1	29.6	36.4	0.8	11.8	0.0	0.0	0.0	55.3	3.4	2.3	1.1	72.2
Polycarena pumila	0.0	23.7	8.5	21.1	9.3	9.3	18.0	4.5	3.4	14.7	2.3	3.4	7.9	41.7
Portulaca quadrifida	0.0	0.0	0.8	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.1	0.0	0.0
Senecio arenarius	186.1	123.5	82.9	33.0	48.2	10.2	11.3	9.0	15.8	277.4	110.5	10.2	3.4	207.5
Silene clandestina	0.0	18.6	13.5	5.9	4.2	3.4	0.0	0.0	1.1	41.7	0.0	0.0	0.0	18.0
Sonderina tenuis	0.0	0.0	0.0	0.0	1.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.3
Tetragonia microptera	0.0	0.0	0.0	0.8	10.2	0.0	0.0	0.0	1.1	0.0	0.0	0.0	0.0	13.5
Tripteris clandestina	0.0	4.2	0.8	0.0	0.0	1.7	0.0	0.0	1.1	2.3	0.0	0.0	1.1	4.5
Ursinia speciosa	0.0	0.0	2.5	5.9	0.0	6.8	0.0	0.0	0.0	4.5	0.0	0.0	0.0	15.8
Wahlenbergia androsacea	0.0	5.1	0.8	0.8	0.0	0.8	0.0	0.0	0.0	0.0	0.0	1.1	0.0	9.0
Wahlenbergia paniculata	0.0	2.5	13.5	16.1	1.7	11.8	0.0	0.0	0.0	0.0	2.3	5.6	2.3	50.8
Zaluzianskya villosa	80.4	37.2	11.0	22.8	0.0	0.0	0.0	0.0	2.3	102.6	27.1	2.3	4.5	63.2
Total for annuals	742.6	1767.8	1870.2	1717.1	1826.2	1056.5	216.5	500.8	1072.6	4933.0	1283.4	394.7	306.8	3266.1
Unidentified	644.5	842.5	1060.7	1155.4	1262.0	1232.4	730.8	335.0	852.6	2275.9	1389.5	421.8	483.8	1774.0
TOTAL FOR ALL SPECIES	1612.1	2864.0	3100.9	3094.1	3276.0	2404.8	971.0	878.6	2071.8	7771.7	2819.5	867.3	838.0	5584.9

Table 5.2. Total number and frequencies (%) of species that emerged from samples taken in different vegetation units and seasons

Plant type	Vegetation unit	Season								Total for all seasons	Total for area	Frequency (%)
		Winter'93	Spring'93	Summer'93	Autumn'94	Winter'94	Spring'94	Summer'94	Autumn'95			
Perennials	1	5	9	13	19	9	5	2	10	33	58	12.4
	2	1	3	7	10	10	5	1	13	24		
	3	3	6	6	14	11	3	3	10	27		
	4	3	4	2	17	8	6	5	17	29		
	5	3	4	6	11	8	2	8	13	25		
	6	3	4	5	10	3	3	7	15	26		
Total for all vegetation units		11	17	23	37	25	14	15	34			
Annuals	1	6	10	9	9	8	7	11	9	22	51	42.0
	2	7	11	11	19	14	12	11	24	36		
	3	9	11	9	17	9	12	10	20	32		
	4	8	12	11	17	15	15	18	26	36		
	5	8	13	10	17	11	9	10	20	31		
	6	6	11	9	18	9	9	8	24	29		
Total for all vegetation units		19	22	26	30	23	25	27	44			
All species	1	11	19	22	28	17	12	13	19	55	109	67.9
	2	8	14	18	29	24	17	12	37	60		
	3	12	17	15	31	20	15	13	30	59		
	4	11	16	13	34	23	21	23	43	65		
	5	11	17	16	28	19	11	18	33	56		
	6	9	15	14	28	12	12	15	39	55		
Total for all vegetation units		30	39	49	67	48	39	42	78			

Seed bank species richness ranged from 8 to 43 species (Table 5.2), for all species recorded in different vegetation units and seasons. In the southern Succulent Karoo, soil seed bank species richness ranged between 10 and 27 species, depending on season and microhabitat (Esler, 1993). Seed bank species richness of the Upland Succulent Karoo in Namaqualand ranged from 25 to 41 species between sites (Van Rooyen & Grobbelaar, 1982). Factors such as the scale of sampling, sampling sizes, seasonality, population and community type and seed characteristics, will influence the estimated composition and size of soil seed banks (Howe & Chancellor, 1983; Granström, 1988; Gross, 1990; Willems & Huijsmans, 1994; Albrecht & Forster, 1996; Berge & Hestmark, 1997; Manchester & Sparks, 1998).

Of the 109 species recorded in the soil seed bank (Table 5.2), 58 species were perennials and 51 species were annuals. Although annual species dominated the soil seed bank in terms of seed numbers (emerged seedling numbers) (Tables 5.1a & 5.1b; Chapter 4), perennial species predominated the soil seed bank in terms of species richness on a regional scale (Table 5.2).

The species composition of a seed bank reflects the differing strategies of past and present components of the vegetation, and great diversity is apparent (Roberts, 1981). These strategies are also linked to the life-histories of the individual species (Esler, 1999). At one extreme are short-lived species, which most commonly spread the risk of germination through space and time. These species commonly produce large numbers of seeds, many of which are capable of remaining viable for long periods when buried; these are often the major contributors to seed banks. At the other are species in which regeneration is entirely or mainly clonal, or that produce seeds which all germinate rapidly, retain viability for only a short period, or are subject to severe predation. These species either do not occur in seed banks or are represented for only a limited part of the year by seeds present at or near the soil surface. Many large-seeded, non-succulent perennials belong to this category.

On a microtopographical scale, the soil seed bank of the study area tended to be clustered, as many soil samples (32.1%) yielded no emerged seedlings (Table 5.2), leading to data that were skewed and kurtotic, similar to that reported in other studies (Benoit *et al.*, 1989; Pake & Venable, 1996). Seeds often are shed close to the parent plant, which leads to strong departures from randomness in the seed distribution of populations on and in the soil. The occurrence frequencies of perennial and annual species were 12.4% and 42.0% respectively (Table 5.2). The most abundant species often have a normal distribution, while the less abundant ones usually have an aggregated distribution (Benoit *et al.*, 1989).

Spatial distribution

In this study, spatial distribution was expressed on a vegetation unit scale, and temporal distribution on a seasonal scale. Between vegetation units, the total number of species recorded from soil samples varied between 55 (units 1 & 6) and 65 (unit 4) (Table 5.2). The highest number of species were recorded in vegetation unit 4 during autumn 1995 (43 species), while the lowest number of species were recorded in vegetation unit 2 during winter 1993 (8 species). For perennial species, total species richness ranged between 24 in vegetation unit 2 and 33 in vegetation unit 1 (Table 5.2). The total number of annual species

varied between 22 in vegetation unit 1 and 36 in vegetation units 2 and 4. With the exception of vegetation unit 1, species richness of annuals in the seed bank was higher than perennial species' richness (Table 5.2). Similar results have been reported for the Upland Strandveld Succulent Karoo in Namaqualand (Van Rooyen & Grobbelaar, 1982), where annual species dominated the soil seed bank in terms of seed numbers and species richness.

Perennial species that occurred in all vegetation units (Table 5.1a) included the grass species *Ehrharta calycina*, the dwarf shrub *Galenia sarcophylla*, and the shrubs *Manochlamys albicans* and *Tetragonia virgata*. Annual species (Table 5.1b) that were recorded in all vegetation units were *Cotula thunbergii, Crassula expansa, Ficinia argyropa, Helichrysum marmarolepis, Isolepis marginata, Manulea altissima, Mesembryanthemum crystallinum, Oncosiphon suffruticosum, Pharnaceum exiguum, Senecio arenarius*, and the annual grass species *Karroochloa schismoides* and *Pentaschistis patula*.

According to Sorensen's presence coefficient (Table 5.3), similarity in total species composition between vegetation units at the study site ranged between 54% and 78%. Annual species generally yielded a higher similarity in species composition between vegetation units than perennial species. Considering all species, vegetation units 2 and 3 yielded the highest similarity in species composition (Table 5.3).

In general, spatial variation in seed bank total species richness was low (1-fold; Table 5.2). On a microtopographical scale, a 2-fold variation in seed bank species richness has been reported for the southern Succulent Karoo (Esler, 1993), and low spatial variability in the composition of the seed bank has been reported for other vegetation types (Coffin & Lauenroth, 1989).

Temporal distribution

Between seasons, autumn sampling yielded the highest species richness in soil samples, for all species (Table 5.2). The total number of species recorded varied between 30 (winter 1993) and 78 (autumn 1995). With the exception of autumn and winter 1994, species richness of annuals (19 – 44 species) was higher than the species richness of perennials (11 – 37 species) (Table 5.2).

The seedlings of only one perennial species, *i.e. Tetragonia virgata*, were recorded during all sampling seasons (Table 5.1a), while annual species that occurred during all seasons (Table 5.1b) included *Adenogramma littoralis, Helichrysum marmarolepis, Karroochloa schismoides, Manulea altissima, Oncosiphon suffruticosum, Polycarena pumila* and *Senecio arenarius*. Although seeds of these species germinated and emerged during all seasons, highest seedling densities were recorded during autumn sampling (Tables 5.1a & 5.1b). The ability of seeds of these species to germinate over a wide range of temperatures may cause a faster rate of depletion of the seed bank of these species, when occasional out of season rainfall occurs. The annual species probably compensate by forming large soil seed banks (Table 5.1b) with fractional germination, while perennial species persist in the standing vegetation.

Table 5.3. Sorensen's index of similarity (presence coefficient)(Mueller-Dombois & Ellenberg, 1974) in species composition for perennial, annual and the total number of species, in samples collected from different vegetation units

Plant type	Vegetation unit	1	2	3	4	5
Perennials	2	59.6				
	3	46.7	70.6			
	4	58.1	67.9	60.7		
	5	58.6	49.0	46.2	55.6	
	6	61.0	52.0	60.4	61.8	54.9
Annuals	2	65.5				
	3	63.0	82.4			
	4	55.2	80.6	79.4		
	5	60.4	77.6	66.7	77.6	
	6	54.9	76.9	75.4	70.8	80.0
All species	2	62.6				
	3	54.4	77.3			
	4	56.7	75.2	71.0		
	5	59.5	65.5	57.4	67.8	
	6	58.2	66.1	68.4	66.7	68.5

Table 5.4. Sorensen's index of similarity (presence coefficient)(Mueller-Dombois & Ellenberg, 1974) in species richness for perennial, annual and the total number of species, in samples collected in different seasons

Plant type	Season	Winter'93	Spring'93	Summer'93	Autumn'94	Winter'94	Spring'94	Summer'94
Perennials	Spring'93	35.7						
	Summer'93	47.1	45.0					
	Autumn'94	33.3	48.1	53.3				
	Winter'94	50.0	52.4	62.5	67.7			
	Spring'94	40.0	58.1	48.6	39.2	51.3		
	Summer'94	30.8	43.8	52.6	38.5	45.0	41.4	
	Autumn'95	26.7	51.0	49.1	67.6	57.6	37.5	44.9
Annuals	Spring'93	78.0						
	Summer'93	62.2	70.8					
	Autumn'94	53.1	65.4	78.6				
	Winter'94	61.9	62.2	65.3	75.5			
	Spring'94	63.6	72.3	62.7	69.1	79.2		
	Summer'94	60.9	65.3	64.2	70.2	68.0	76.9	
	Autumn'95	47.6	54.5	65.7	81.2	65.7	66.7	70.4
All species	Spring'93	60.9						
	Summer'93	55.7	59.1					
	Autumn'94	43.3	56.6	65.5				
	Winter'94	56.4	57.5	63.9	71.3			
	Spring'94	55.1	66.7	56.8	54.7	66.7		
	Summer'94	50.0	56.8	59.3	55.0	57.8	64.2	
	Autumn'95	39.3	53.0	58.3	74.5	61.9	54.7	60.0

According to Sorensen's presence coefficient (Table 5.4), similarity in total species composition between seasons at the study site varied between 39% and 75%. Annual species generally yielded a higher similarity in species composition between seasons than perennial species. For all species, autumn 1994 and autumn 1995 yielded the highest similarity in species composition.

Temporal variation in species richness of the germinable fraction of the seed bank was relatively high (3-fold), more pronounced than spatial variation at a vegetation unit scale (1-fold), and reflect the life-history strategies of the component species (Esler, 1999). In the desert grasslands of New Mexico, a decrease in seed bank species richness for annuals and an increase in species richness for perennials, through the annual vegetation cycle has been reported (Henderson *et al.*, 1988). High seasonal variation in soil seed bank species composition has been reported (Grubb, 1977; Thompson & Grime, 1979; Schenkeveld & Verklaar, 1984; Grubb, 1988; Esler, 1993) and may be the result of species specific seasonal inputs of seeds (Graham & Hutchings, 1988) as well as dispersal mechanisms. Other studies reported on the lack of a clear seasonal trend in seed bank composition (Graham & Hutchings, 1988; Lavorel *et al.*, 1993). Populations that experience more temporal variation in the soil seed bank are predicted to have lower germination fractions and a higher fraction of their seeds in between-year seed banks than populations that experience less temporal variation (Pake & Venable, 1996).

Examination time

When 1 080 subsamples were examined directly after sampling and at the peak time for germination (autumn), the soil seed bank of the Strandveld Succulent Karoo yielded a combined total species richness of 92 species (Table 5.5). Of these, 51 species were common to both examination times. Examination of the seed bank at the peak time for germination (82 species) yielded a higher species richness than examination directly after sampling (61 species). Annual species' richness was higher than that of perennial species when subsamples were either examined directly after sampling or at the peak time for germination (Table 5.5). However, the combined total species richness of two examination times was similar for annual and perennial species, *i.e.* 46 species each. These results differ from that obtained when all 7 200 samples were considered, and are due to differences in sample size.

In all vegetation units and plant types, the number of species recorded at the peak time for germination (autumn) was equal or higher than that recorded directly after sampling (Table 5.5). Also, the number of annual species recorded was higher than the number of perennial species recorded. This was true for the number of species recorded directly after sampling, for the number of species recorded at the peak time for germination, as well as for the number of species common to both examination times. The multi-factor ANOVA (Table 5.6) indicated that vegetation unit, examination time and plant type significantly influenced species richness. At vegetation unit level, similarity in total species composition between examination times ranged between 54% and 78% (Table 5.7). Similarity in annual species' composition (56% - 77%) between examination times was higher than perennial species' composition (40% - 64%), per vegetation unit.

Table 5.5. Total number of perennial and annual species that occurred in samples collected in different vegetation units and seasons, and examined directly after sampling (ss) and at the peak time for germination (pg)

Plant type	Experimental time	Vegetation unit						Season						Total for all vegetation units and seasons
		1	2	3	4	5	6	Spring'93	Summer'93	Autumn'94	Winter'94	Spring'94	Summer'94	
Perennials	Sampling season	9	10	10	13	8	7	7	11	16	10	9	5	27
	Peak time for germination	16	10	12	13	15	16	10	6	21	15	12	18	38
	Total of ss & pg	18 (7)*	16 (4)	15 (7)	20 (6)	17 (6)	17 (6)	14 (3)	14 (3)	25 (12)	20 (6)	18 (3)	19 (4)	46 (19)
Annuals	Sampling season	10	16	18	19	21	16	14	14	22	17	17	17	34
	Peak time for germination	19	21	21	28	28	23	20	17	27	29	26	35	44
	Total of ss & pg	20 (9)	24 (13)	26 (14)	29 (18)	31 (18)	28 (11)	23 (11)	24 (7)	31 (18)	31 (15)	27 (16)	37 (15)	46 (32)
All species	Sampling season	19	26	28	32	29	23	21	25	38	27	26	22	61
	Peak time for germination	35	31	33	41	43	39	30	23	48	44	38	53	82
	Total of ss & pg	38 (16)	40 (17)	41 (21)	49 (24)	48 (24)	45 (17)	37 (14)	38 (10)	56 (30)	51 (21)	45 (19)	56 (19)	92 (51)

* Number of species common to ss and pg

Table 5.6. Multi-factor ANOVA for the total number of emerged species from samples taken in different vegetation units and seasons. Samples were examined directly after sampling and at the peak time for germination

	Source of variation	F-ratio	Significance
Between vegetation units	**Main effects**		
	Vegetation unit (Vu)	5.351	0.0119
	Examination time (Et)	45.492	0.0001
	Plant type (Pt)	99.445	0.0000
	2-Factor interactions		
	Vu x Et	0.583	0.7132
	Vu x Pt	3.081	0.0452
	Et x Pt	14.258	0.0012
Between seasons	**Main effects**		
	Sampling season (Ss)	9.346	0.0016
	Examination time (Et)	14.936	0.0031
	Plant type (Pt)	32.651	0.0000
	2-Factor interactions		
	Ss x Et	3.944	0.0309
	Ss x Pt	2.361	0.0958
	Et x Pt	4.681	0.0367

Table 5.7. Index of similarity (presence coefficient)(Mueller-Dombois & Ellenberg, 1974) for species emerged, between samples examined directly after sampling and samples stored and examined at the peak season for germination (autumn)

Source of variation		Presence Coefficient (%) (Sorensen in Mueller-Dombois & Ellenberg, 1974)		
		Perennials	Annuals	All species
Between vegetation units	1	56.0	62.1	59.3
	2	40.0	70.3	59.6
	3	63.7	71.8	68.9
	4	46.2	76.6	65.8
	5	52.2	73.5	77.4
	6	52.2	56.4	54.8
Between seasons	Spring '93	35.3	64.7	54.9
	Summer '93	35.3	45.2	41.7
	Autumn '94	64.9	73.5	69.8
	Winter '94	48.0	65.2	59.2
	Spring '94	28.6	74.4	59.4
	Summer '94	34.8	57.7	50.7
Total		58.5	82.1	71.3

With exception of the summer 1993 sampling season, the number of species recorded at the peak time for germination were higher than that recorded directly after sampling, for all seasons and plant types (Table 5.5). Also, the number of annual species recorded per season was higher than the number of perennial species recorded. This was true for the number of species recorded directly after sampling, for the number of species recorded at the peak time for germination, for the total number of species recorded at both examination times, as well as for the number of species common to both examination times. Samples collected during summer 1994 and examined during the following autumn yielded a total species richness of 53 species, which was still lower than the species richness recorded in samples collected and examined during autumn 1995 (78 species) (Table 5.2). Samples collected during winter and examined during the following autumn yielded a persistent seed bank with a species richness of 51 species (Table 5.5).

The multi-factor ANOVA (Table 5.6) indicated that sampling season, examination time and plant type significantly influenced species richness between seasons, for samples examined directly after sampling and at the peak time for germination. Between seasons, similarity in total species composition between examination times ranged from 41% in summer 1993 to 70% in autumn 1994 (Table 5.7). Similarity in annual species' composition (45% - 75%) between examination times was higher than perennial species' composition (28% - 65%), per season.

Revegetation

Revegetation efforts at the study site by means of topsoil replacement may yield at least as many perennial species as annual species. The density of perennials will, however, be much lower than that of annuals (Tables 5.1a & 5.1b). Because the standing vegetation at the study site is dominated in terms of composition by perennial species (De Villiers *et al.*, 1999), the return of these species on mined areas will be most important for achieving revegetational goals. Topsoil replacement will not only return large numbers of annual plants, but will also significantly increase the post-mining perennial species' richness.

During topsoil replacement at the study site, spatial variation in seed bank species richness will not greatly affect the composition of the resulting vegetation. Mining of heavy minerals at the study site commences in a specific sequence, and topsoil is replaced directly to the adjacent preceded mined area (Environmental Evaluation Unit, 1990). Consequently, after revegetation by means of topsoil replacement, post-mining vegetation unit boundaries may show little deviation from pre-mining vegetation unit boundaries. The effectiveness of topsoil replacement for the restoration of a specific vegetation unit will therefore depend mainly on the size and composition of the seed bank of that unit.

Seedling recruitment during the period of highest soil seed density and species richness, *i.e.* summer and autumn, will ensure the largest possible reserve of genetic diversity (Baskin & Baskin, 1978; Vavrek *et al.*, 1991) in post-mining restored areas. During summer and autumn, the soil seed bank will contain species that accumulate transient, and species that accumulate persistent seed banks. Replacement of the persistent seed bank by means of topsoil replacement will be essential for successful revegetation of the study area. A long-lived soil seed bank may act as a reserve of genetic variability for a population (Vavrek

et al., 1991), and is an important repository for the total plant species richness of a habitat. Quite often soil seed banks contain species or genotypes not found in the standing vegetation (Chapters 6 & 7).

Because topsoil replacement and sowing will continue throughout the year, recruitment during the dry summer months should be restricted. For this reason, irrigation of areas where topsoil replacement and sowing have been completed should only commence at the start of the rainy season. Seed losses from replaced topsoil due to wind erosion during the dry season should be controlled by means of wind barriers and sand-binding techniques.

CONCLUSIONS

The soil seed bank of the Strandveld Succulent Karoo yielded 109 species, and was not dominated in terms of species richness by any specific plant type. On a regional scale, perennial species predominated with the use of a large sample size (7 200 samples), while annual species predominated with the use of smaller sample sizes (1 080). Annual species predominated on a vegetation unit scale. Topsoil replacement in post-mining areas of the Strandveld Succulent Karoo will significantly contribute to increased species richness of both perennials and annuals, but annual species will dominate in terms of abundance and occurrence frequency. Selected perennials will have to be sown or transplanted during revegetation efforts, as a means of increasing species diversity.

Spatial variation in soil seed bank species richness was not as pronounced as temporal variation. Both spatial and seasonal variation in seed bank composition was of intermediate magnitude, and clear trends was not distinguishable. Samples collected during summer and autumn yielded highest total species richness, and include both the transient and persistent fractions of the soil seed bank. Winter sampling indicated that *c.* ½ of the total soil seed bank species richness at the study site constituted of species that accumulate persistent seed banks.

The relatively high species richness of both perennial and annual species in the soil seed bank indicates that topsoil replacement will be essential for the revegetation of mined areas in the Strandveld Succulent Karoo. Also, species present in the soil seed bank may be absent from the standing vegetation, and *vice versa*. For this reason, comparison between the soil seed bank and the standing vegetation will be essential for the formulation of sound revegetation strategies.

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