SEED BANK DYNAMICS OF THE STRANDVELD SUCCULENT KAROO

by

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PHILOSOPHIAE DOCTOR

in the Faculty of Natural, Agricultural and Information Sciences
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TO MY PARENTS, FAMILY AND FRIENDS

"I took in February three table-spoonfuls of mud from three different points, beneath water, on the edge of a little pond; this mud when dry weighed only 6¾ ounces; I kept it covered up in my study for six months, pulling up and counting each plant as it grew; the plants were of many kinds, and were altogether 537 in number; and yet the viscid mud was all contained in a breakfast cup" (Darwin, 1859).

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ABSTRACT

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The seed bank dynamics of the Strandveld Succulent Karoo was described in terms of spatial and temporal variation in seed bank size and composition. Factors affecting inputs and outputs, such as seed production, predation, dispersal, dormancy, germination, seed-borne fungi and environmental conditions, were investigated. This information was incorporated in the development of suitable post-mining revegetation strategies at a management level.

Phytosociological benchmark studies on the pre-mining standing vegetation and seed bank indicated that a realistic revegetation goal will be to return 30% of the total number of plant species recorded. The revegetation program should concentrate on perennial species, as these dominate the pre-mining standing vegetation. Perennial shrub species exhibited transient seed bank strategies, while perennial herb species exhibited both transient and persistent strategies. Seed banks of annual species were of a persistent nature and large in comparison with annual inputs and losses. Since annual species predominated the soil seed bank, topsoil replacement as well as sowing and transplanting of selected perennial species will be essential for the rehabilitation of the area.

Spatial variation in seed bank size and composition, at community level, was not as pronounced as temporal variation. The general dissimilarity between the seed bank and its associated vegetation was manifested in species composition, plant/seed densities and frequencies.

Taking seed bank dynamics into account, mining authorities should achieve great success in revegetating mined areas. Furthermore, knowledge obtained from this seed bank study will aid plant ecologists in gaining a better understanding of the processes contributing to reproductive strategies and plant population and community dynamics in the Strandveld Succulent Karoo.

UITTREKSEL

SAADBANKDINAMIKA VAN DIE STRANDVELD SUKKULENTE KAROO

deur

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Die saadbankdinamika van die Strandveld Sukkulente Karoo is beskryf in terme van ruimtelike en temporele variasie in saadbankgrootte en -samestelling. Faktore wat toevoegings en verliese beinvloed, byvoorbeeld saadproduksie, predasie, saadverspreiding, dormansie, ontkieming, saadswamme en omgewingstoestande, is ondersoek. Hierdie inligting is op bestuursvlak geïnkorporeer in die ontwikkeling van geskikte plantegroeihervestiging strategieë vir gebruik in rehabilitasie van gemynde areas.

Fitososiologiese studies van die staande plantegroei en die saadbank het aangetoon dat 'n hervestigingsdoelwit van 30% van die totale aantal spesies aangeteken, realisties sal wees. Die hervestigingsprogram moet konsentreer op meerjarige spesies, aangesien dié spesies die oorspronklike staande plantegroei domineer. Meerjarige struikspesies het kortstondige, en meerjarige kruidspesies het beide kortstondige en blywende saadbankstrategieë getoon. Die saadbank van eenjarige spesies was blywend en groot in vergelyking met jaarlikse toevoegings en verliese. Aangesien eenjarige spesies die saadbank oorheers, sal die terugplaas van bogrond sowel as die saai en oorplant van geselekteerde meerjarige spesies, noodsaaklik wees vir die rehabilitasie van die gebied.

Op gemeenskapsvlak was ruimtelike variasie in die grootte en samestelling van die saadbank nie so opvallend soos variasie in tyd nie. Die algemene onooreenkomstigheid tussen die saadbank en geassosieerde staande plantegroei is bevestig deur spesiesamestelling, plant/saad digthede en frekwensies.

Mynbou-instansies behoort groot sukses te behaal in die hervestiging van plantegroei op gemynde areas, indien hulle die saadbankdinamika in ag neem. Die kennis ingewin deur hierdie saadbankstudie sal plantekoloë help om die prosesse wat bydra tot voortplantingstrategieë asook plantpopulasie- en gemeenskapsdinamika van die Strandveld Sukkulente Karoo beter te verstaan.

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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.

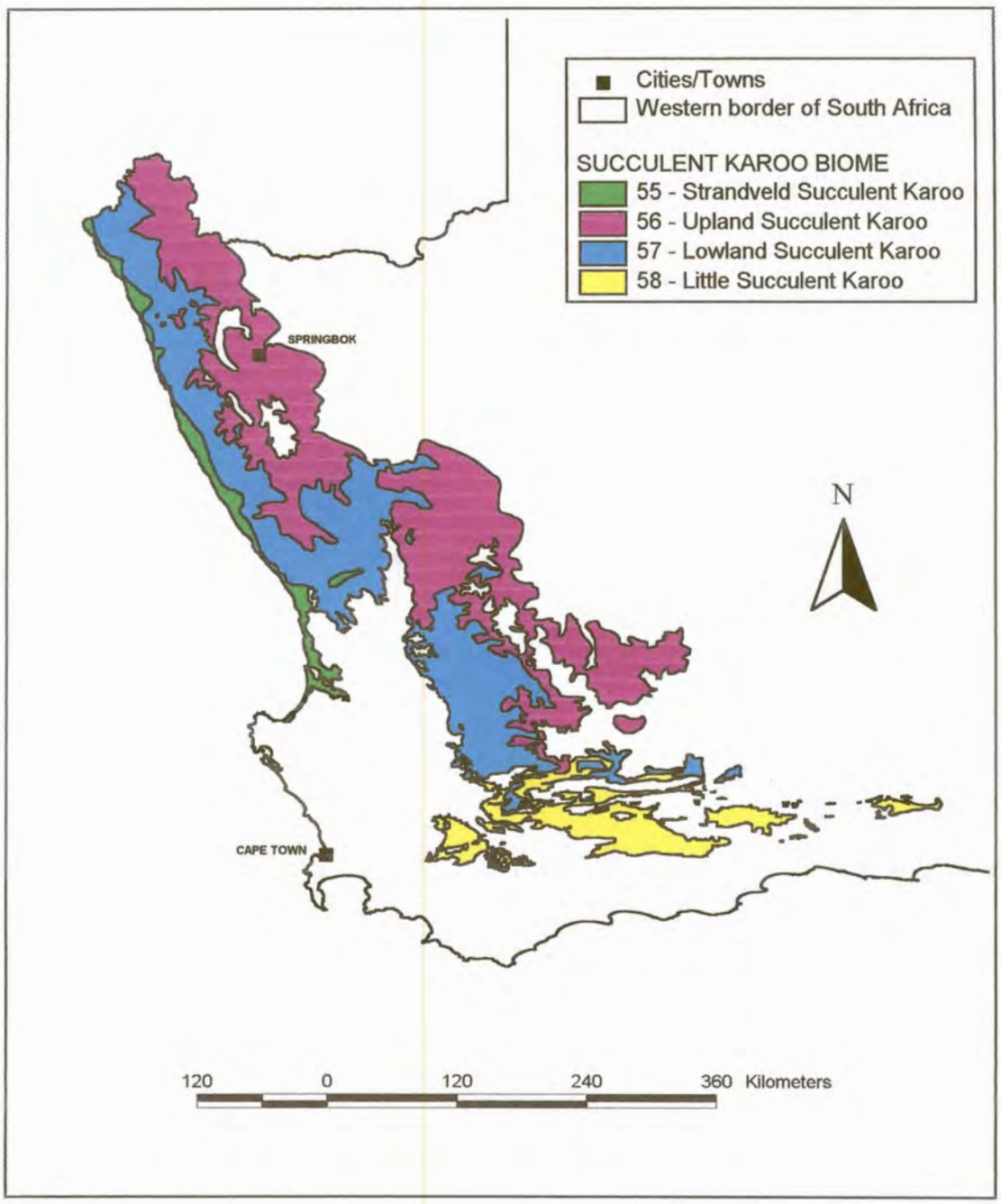

Figure 1.1. Vegetation types of the Succulent Karoo Biome (Low & Rebelo, 1998). Numbers preceding vegetation types indicate numbers allocated for each vegetation type by Low & Rebelo (1998).

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.

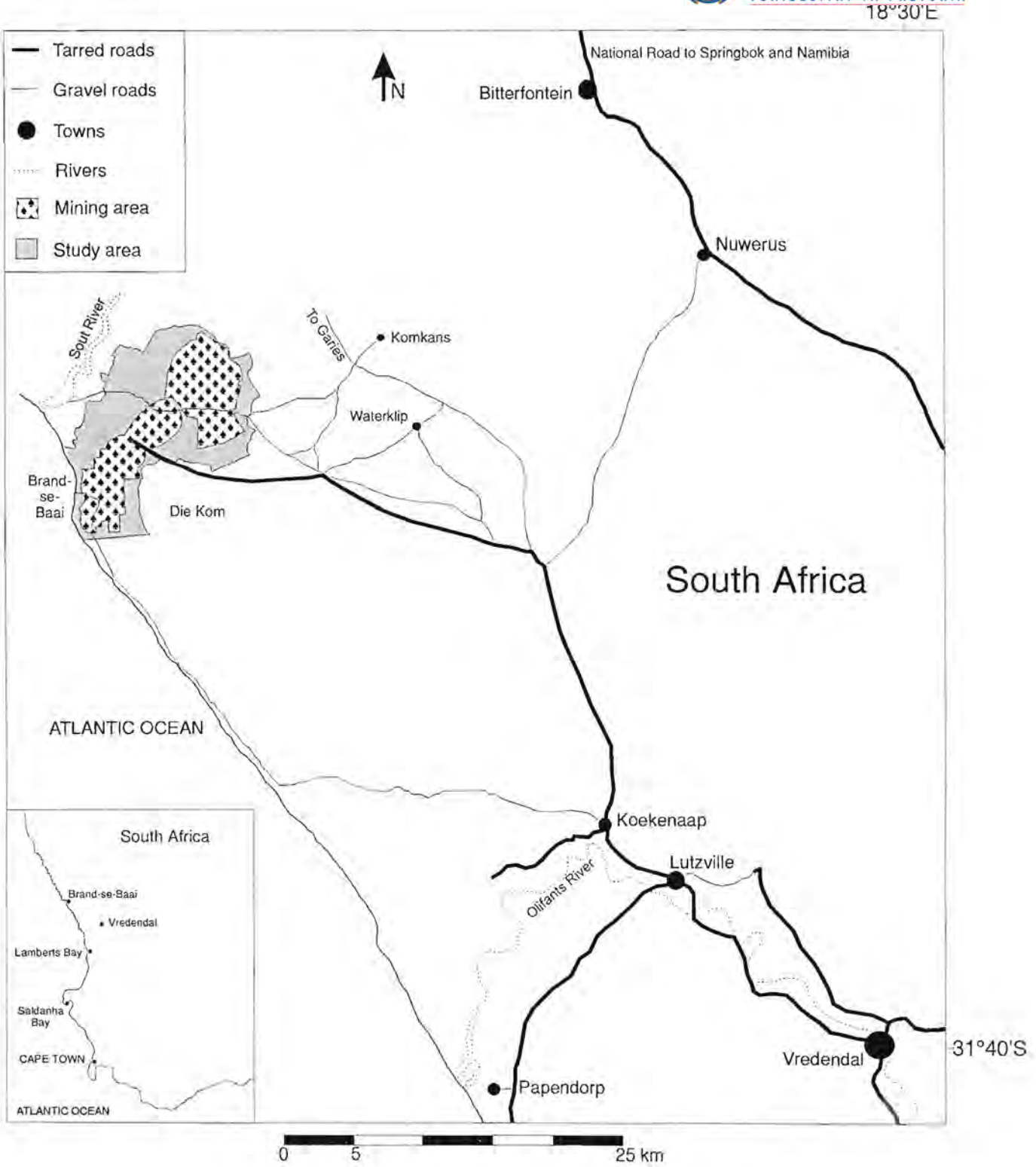

Figure 2.1. Location map of the Brand-se-Baai study area.

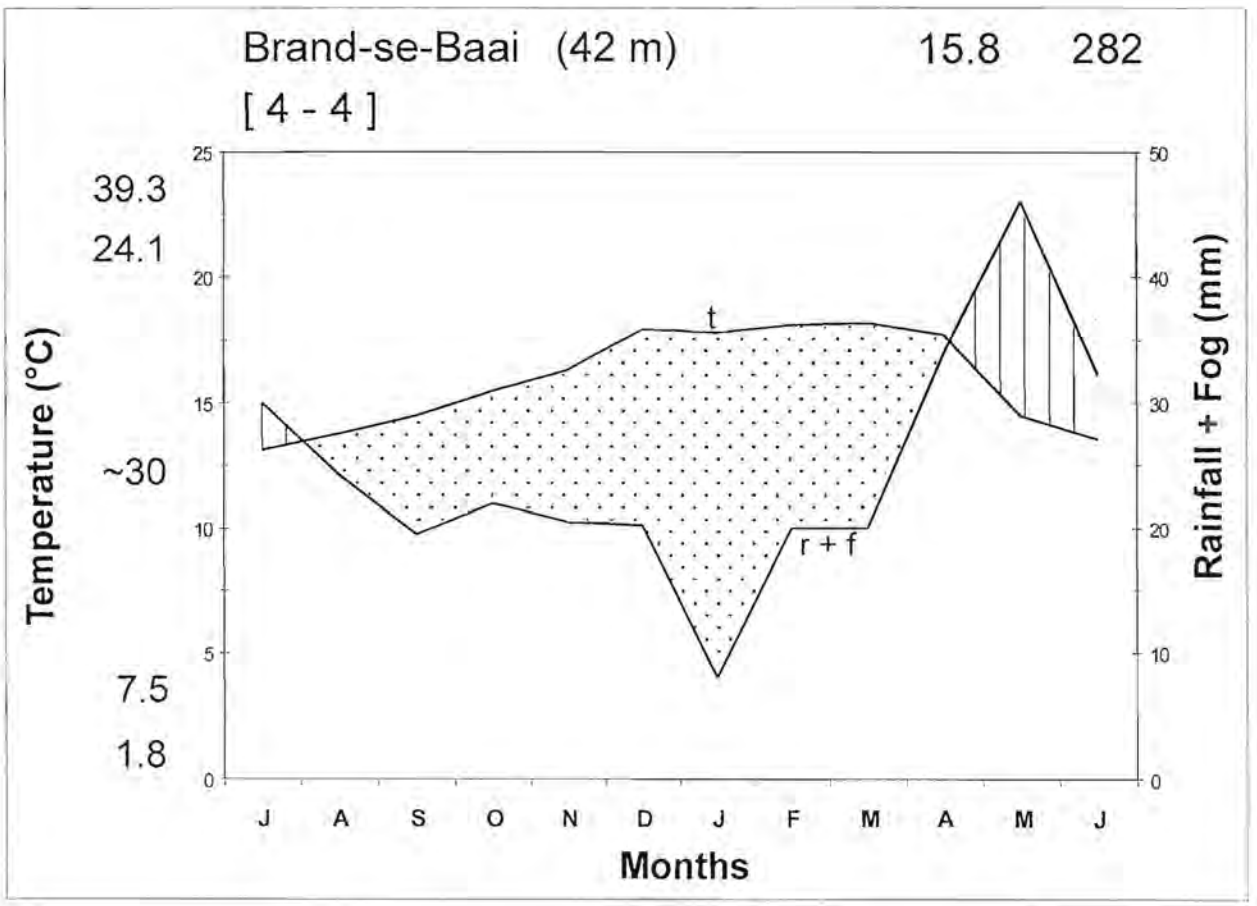

Figure 2.2. Climate diagram (following Walter & Lieth, 1960) of the Brand-se-Baai station for the period March 1993 - February 1997.

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.

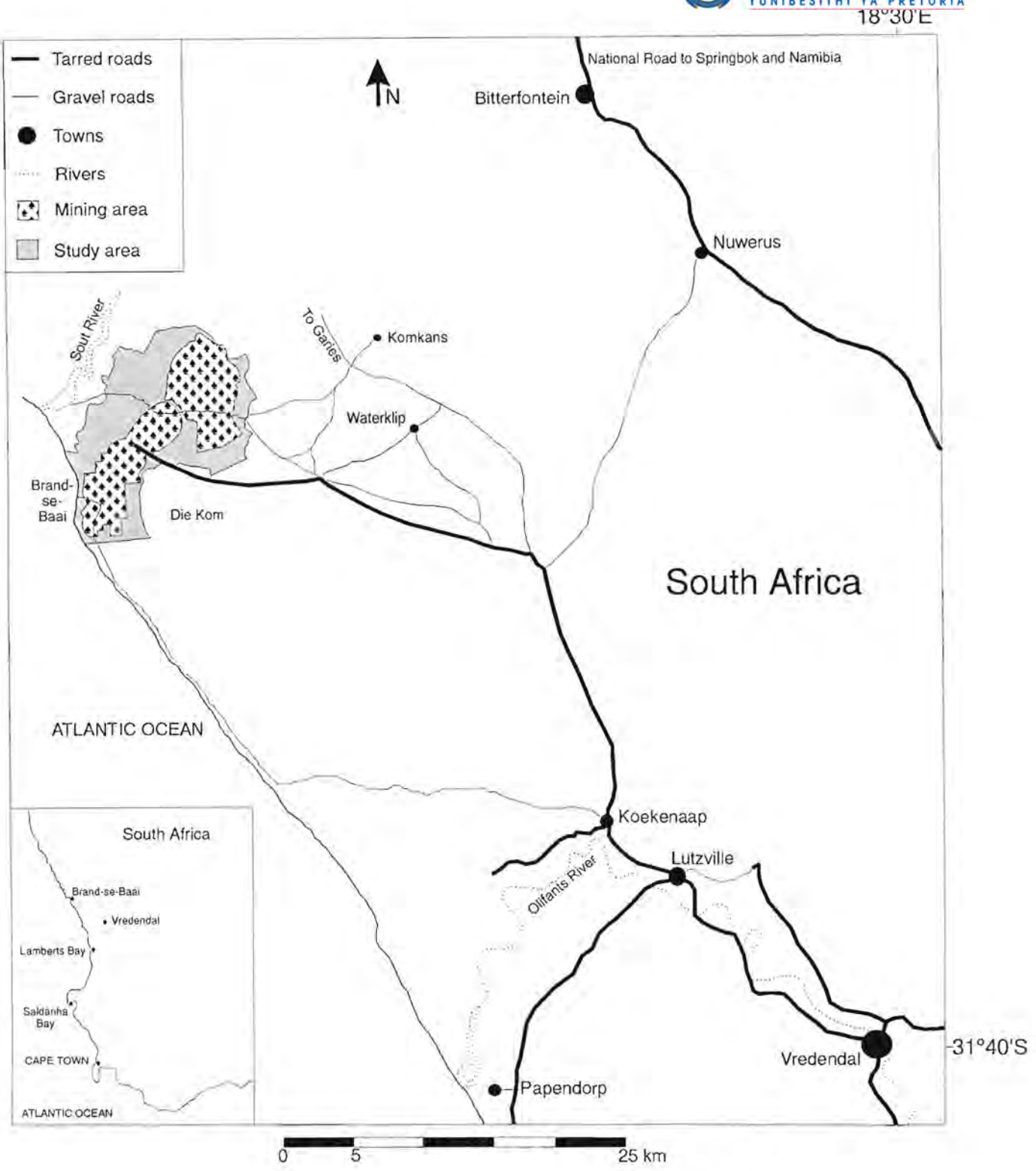

Figure 3.1. Location map of the mining area at Brand-se-Baai.

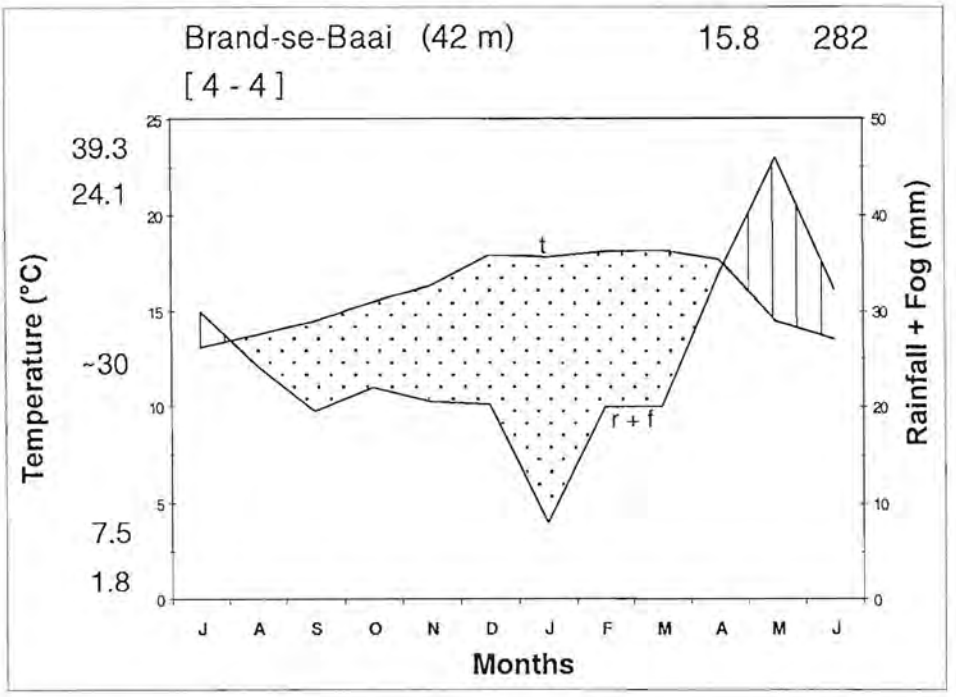

Figure 3.2. Climate diagram of the Brand-se-Baai station for the period March 1993 - February 1997 (following Walter & Lieth, 1960).

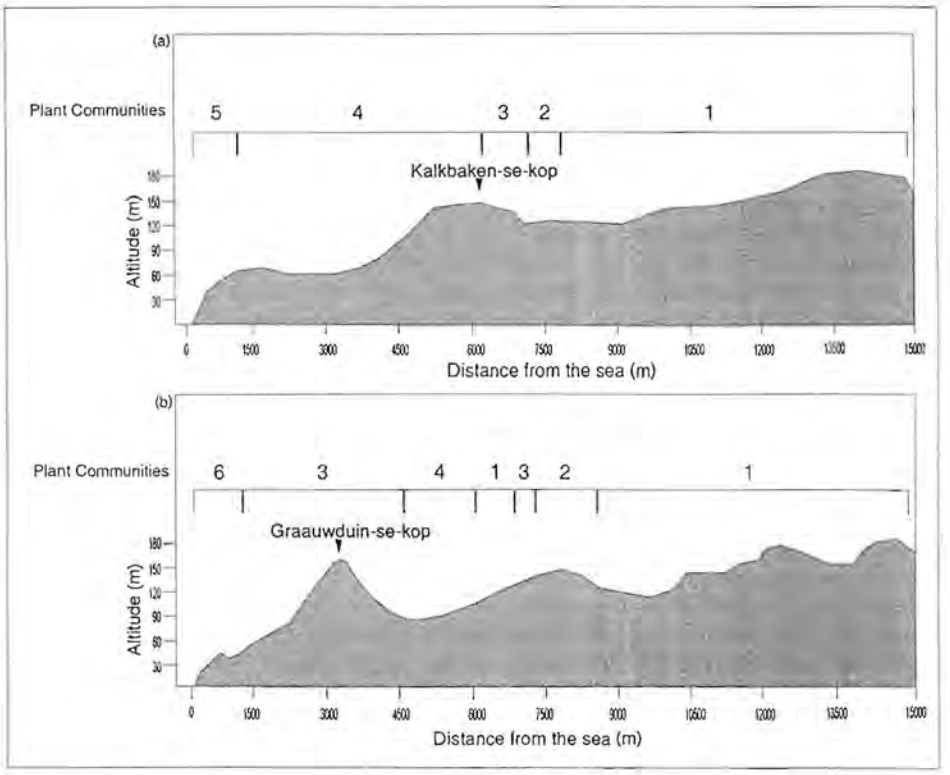

Figure 3.3. A simplified sketch of two gradients through the landscape, indicating the topographical positions of the plant communities.

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 1 / 0 0 0 1 2 2 2 2 9 / 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 8 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			1		
Galenia africana	1 1 1 1	1	1 2 1	1 1 1	1	1 1	3 1 1		1 1	1		
Phamaceum 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	
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		1			
Lebeckia lotonoides					1 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 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		1
Ballota africana							1 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 1		
Solanum guineense	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			
Tetragonia pillansii							1 1 1 1 1 1 1					
Melianthus minor			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)

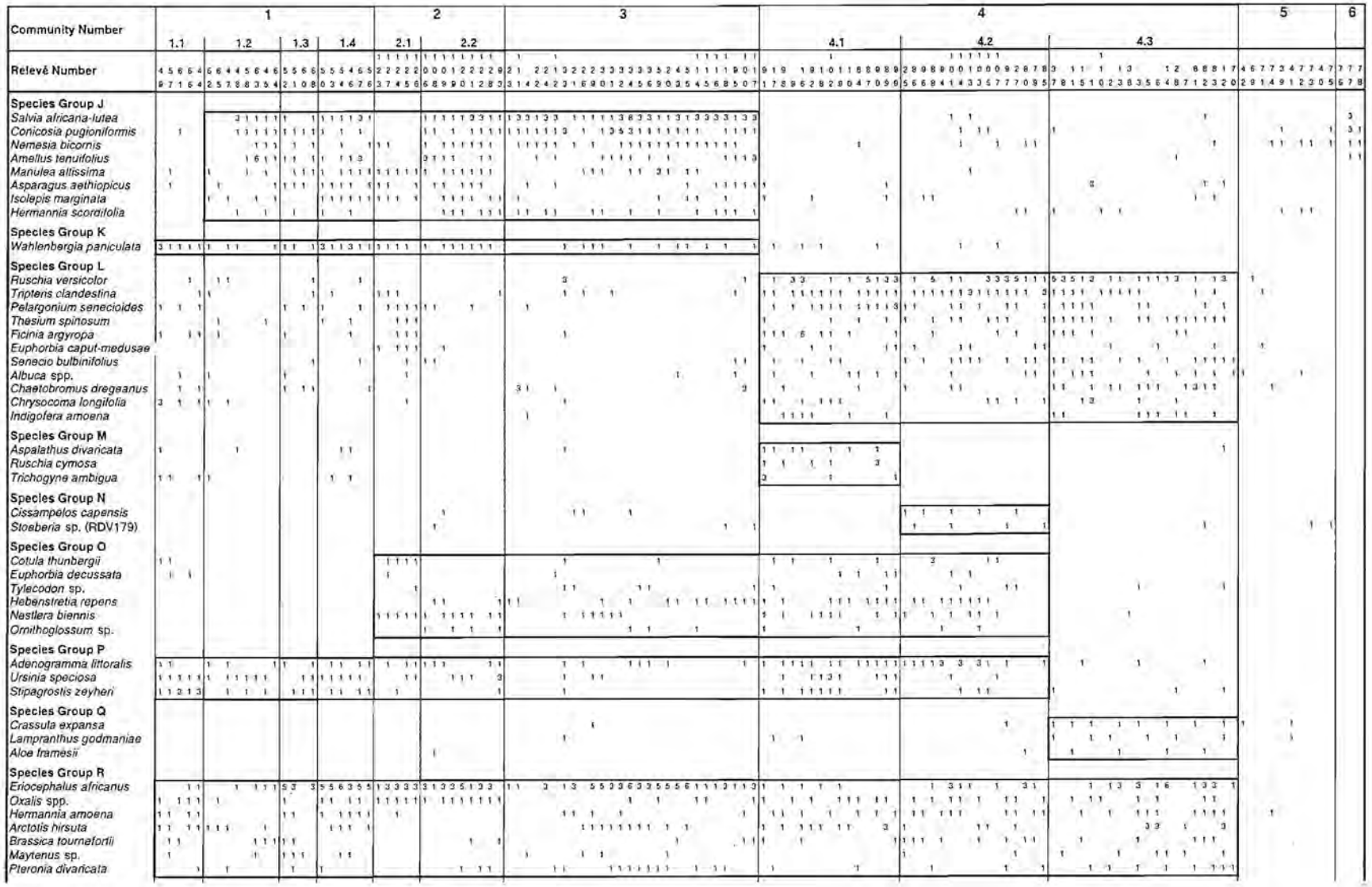

Table 3.1. (Continued)

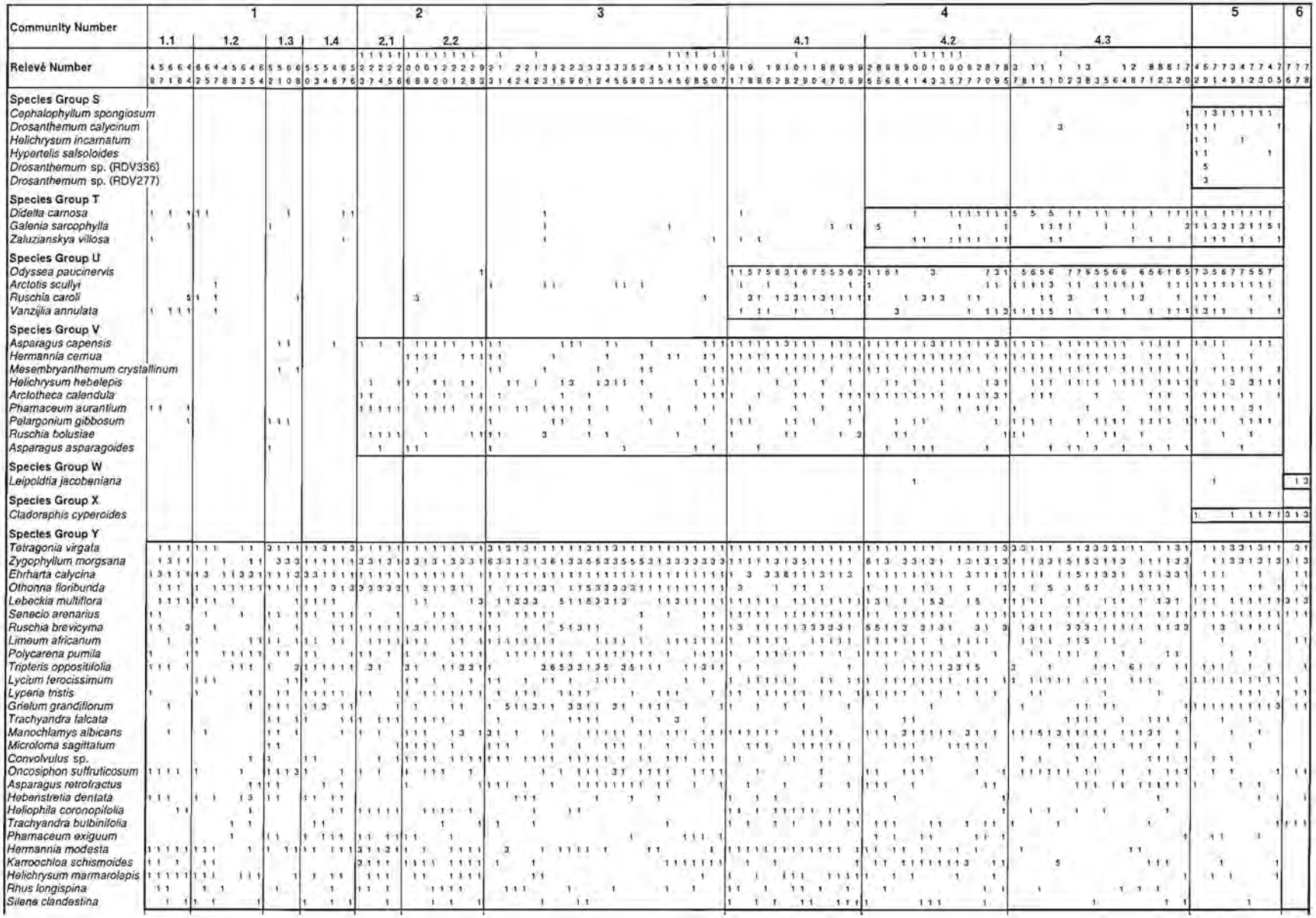

Table 3.1. (Continued)

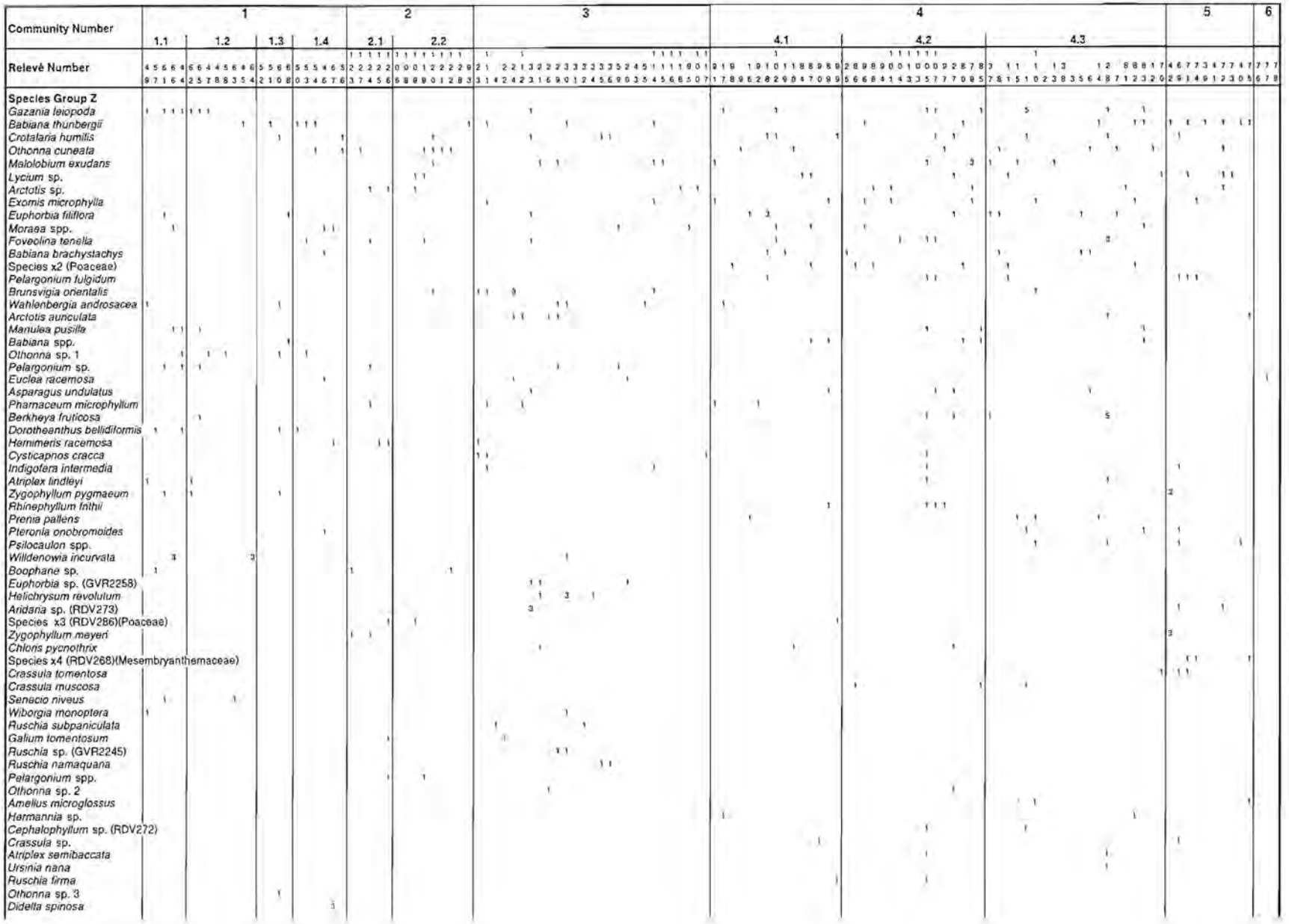

Table 3.1. (Continued)

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	49 57 61 66 44	62 65 47 48 58 63 45 64	52 51 60 68	50 53 54 46 67 56	123 127 124 125 126	106 108 109 119 120 121 122 128 93	23 11 4 22 24 12 33 21 26 29 30 31 32 34 35 36 39 30 53 25 44 55 116 118 115 90 107	91 17 98 9 16 92 18 2 19 10 14 17 80 89 99	25 96 98 88 94 101 104 113 103 105 107 97 22 80 77 85	37 8 11 15 1 110 2 13 8 3 5 6 14 28 7 61 82 83 12 70	42 69 71 74 39 41 72 73 40 75	76 77 78
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 amaryllioides										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

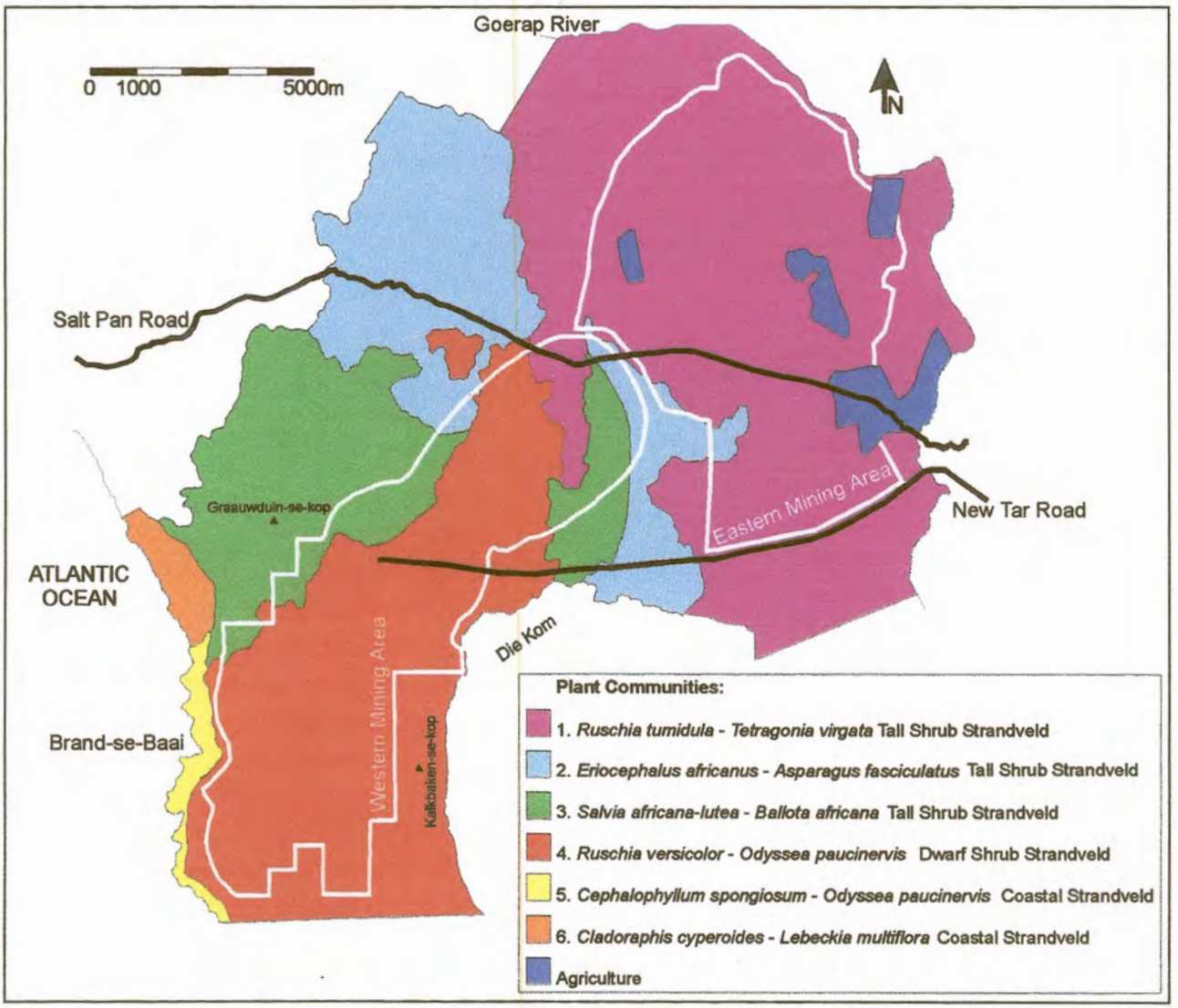

Figure 3.4. Vegetation map of the study area.

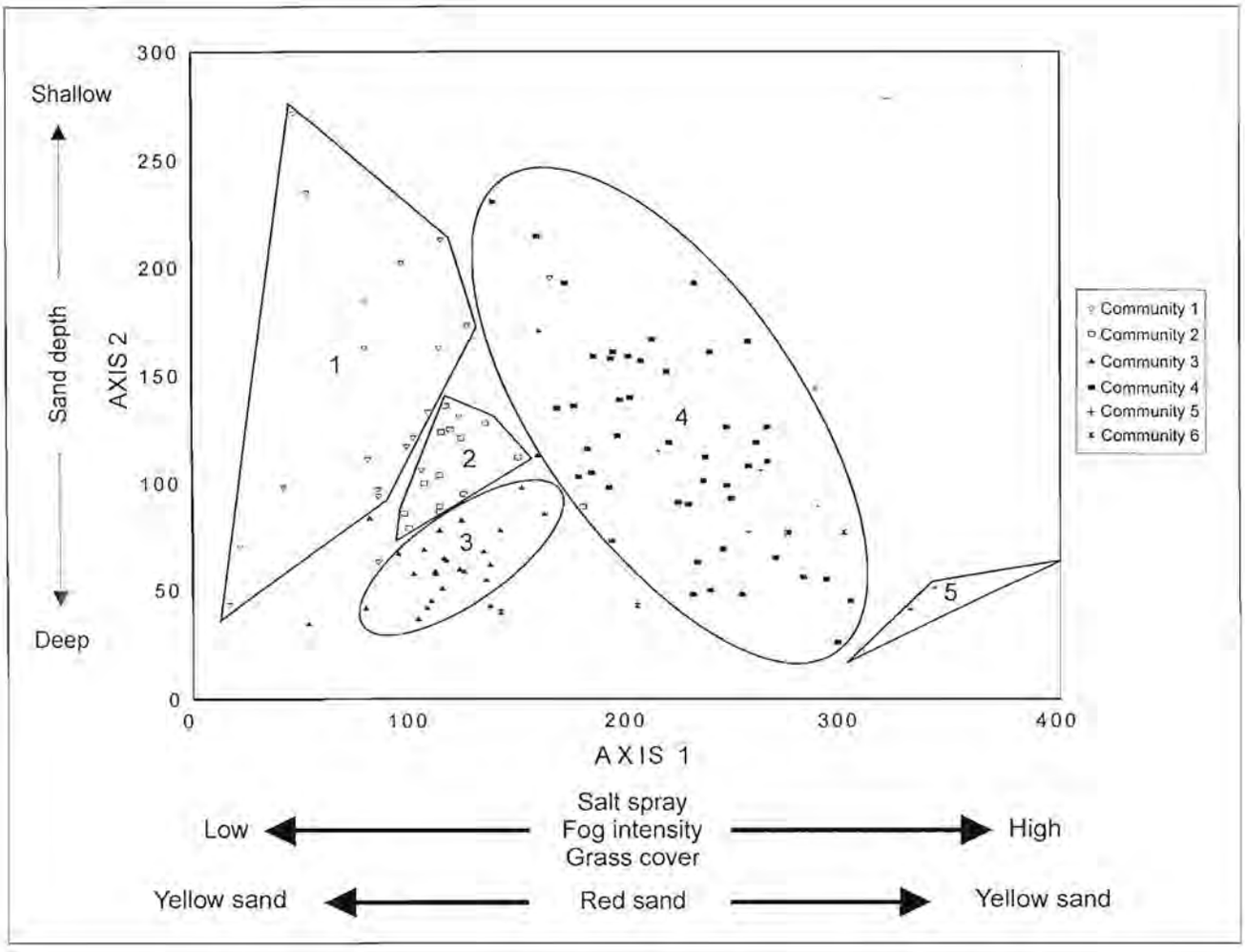

Figure 3.5. The relative positions of the plant communities (numbers refer to text) along the first and second axes of a floristic ordination by means of DECORANA (Eigenvalues: Axis 1 = 0.466, Axis 2 = 0.306).

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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REFERENCES

ACOCKS, J.P.H. 1988. Veld types of South Africa. 3rd ed. *Memoirs of the botanical Survey of South Africa*, **57**: 1-146.

ARNOLD, T.H. & DE WET, B.C. 1993. Plants of southern Africa: names and distribution. *Memoirs of the botanical Survey of South Africa*, **62**: 1-825.

BEZUIDENHOUT, H. 1995. An ecological study of the major vegetation communities of the Vaalbos National Park, Northern Cape. 2. The Graspan-Holpan section. *Koedoe*, **38**: 65-83.

BOUCHER, C. & LE ROUX, A. 1993. Dry coastal ecosystems of the South African West Coast. In: Goodall, D.W. & Van der Maarel, E. (eds). *Ecosystems of the World. Volume 2B. Dry Coastal Ecosystems*. Elsevier, Amsterdam. pp. 75-88.

BOUCHER, C. & LE ROUX, A. 1990. Heavy mineral sand mining project assessment vegetation report. In: Environmental Evaluation Unit. *Anglo American Corporation: West Coast heavy mineral sands project - Supplementary Report.* Unpublished report. University of Cape Town, Cape Town. Section A5.

BREDENKAMP G.J. & BEZUIDENHOUT, H. 1995. A proposed procedure for the analysis of large phytosociological data sets in the classification of South African grasslands. *Koedoe*, **38**: 33-39.

COUNCIL FOR SCIENTIFIC AND INDUSTRIAL RESEARCH. 1997. Prints of climate statistics of the Brand-se-Baai Station from March 1993 up to February 1997. Pretoria.

ENVIRONMENTAL EVALUATION UNIT. 1990. *Anglo American Corporation: West Coast heavy mineral sands project.* Unpublished report. University of Cape Town, Cape Town.

GIBBS RUSSELL, G.E., WATSON, L., KOEKEMOER, M., SMOOK, L., BARKER, N.P., ANDERSON, H.M. & DALLWITZ, M.J. 1990. Grasses of southern Africa. *Memoirs of the botanical Survey of South Africa*, **58**: 1-437.

HENNEKEN, S. 1996a. *TURBOVEG – software package for input, processing, and presentation of phytosociological data.* IBN-DLO, University of Lancaster, Lancaster.

HENNEKEN, S. 1996b. *MEGATAB - a visual editor for phytosociological tables.* Giesen & Geurts, Ulft.

HILL, M.O. 1979a. *TWINSPAN - A Fortran program for arranging multivariate data in an ordered two-way table by classification of the individuals and attributes.* Cornell University, New York.

HILL, M.O. 1979b. *DECORANA - A Fortran program for detrended correspondence analysis and reciprocal averaging.* Cornell University, New York.

HOOGERVORST, A. 1990. Legislation identification & authorities' consultation study. In: Environmental Evaluation Unit. *Anglo American Corporation: West Coast heavy mineral sands project - Supplementary Report.* Unpublished report. University of Cape Town, Cape Town. Section C7.

LE ROUX, A. 1984. 'n Fitososiologiese studie van die Hester Malan-natuurreservaat. M.Sc. dissertation, University of Pretoria, Pretoria.

LOW, A.B. & REBELO, A. 1996. *Vegetation of South Africa, Lesotho and Swaziland.* Department of Environmental Affairs & Tourism, Pretoria.

MUELLER-DOMBOIS, D. & ELLENBERG, H. 1974. *Aims and methods of vegetation ecology.* Wiley, New York.

WALTER, H. & LIETH, H. 1960. *Klimadiagramm - Weltatlas.* Fischer, Jena.

WASHINGTON, R. 1990. Report on predicted wind patterns and sediment transfer at Brand-se-Baai on the West Cape coast. In: Environmental Evaluation Unit. *Anglo American Corporation: West coast heavy mineral sands project - Supplementary Report.* Unpublished report. University of Cape Town, Cape Town. Section B4.

WERGER, M.J.A. 1974. On concepts and techniques applied in the Zürich-Montpellier method of vegetation survey. *Bothalia*, **11**: 309-323.

WHITTAKER, R.H. 1980. *Classification of plant communities.* Dr. W. Junk bv Publishers, The Hague.

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

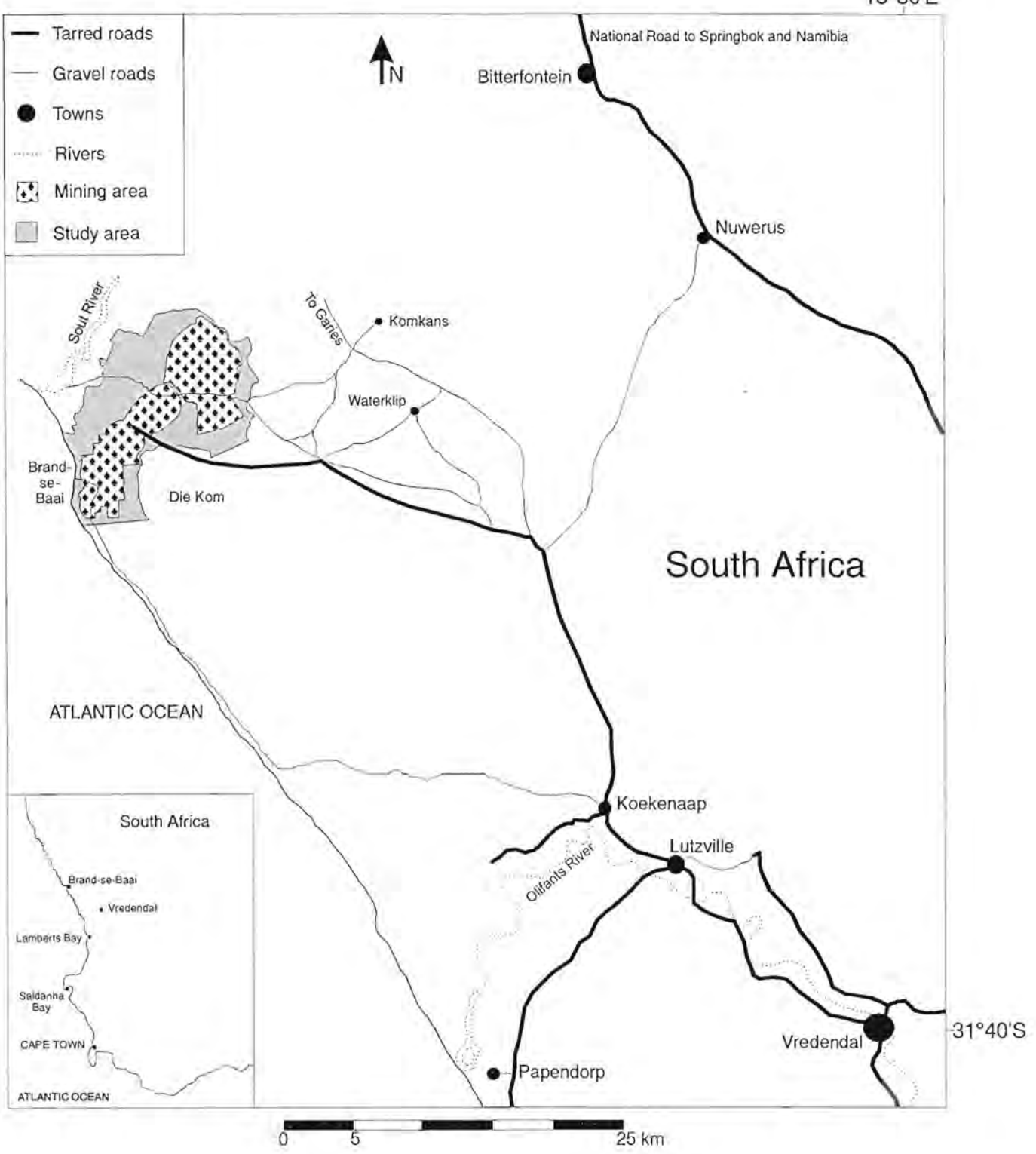

Figure 4.1. Location map of the Brand-se-Baai study area.

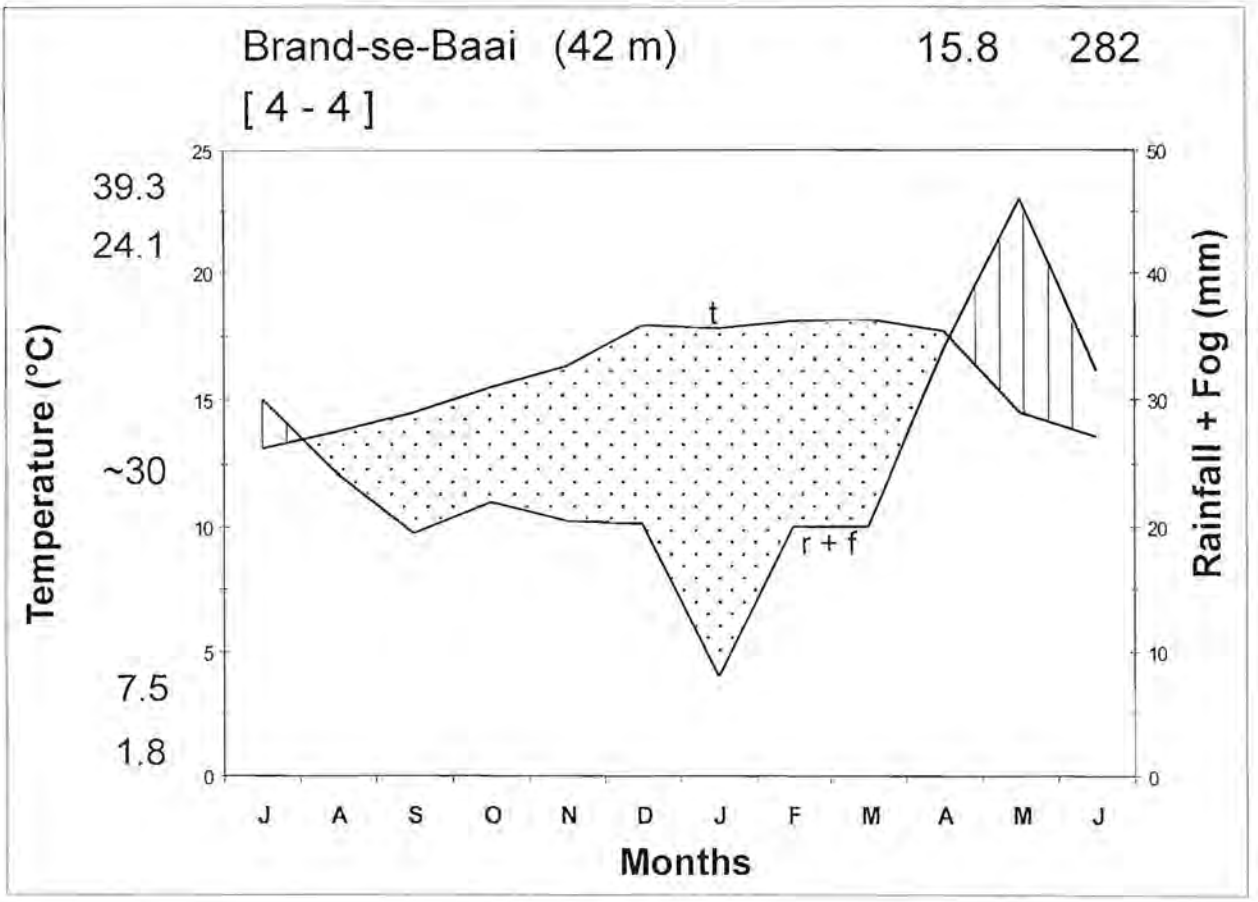

Figure 4.2. Climate diagram (following Walter & Lieth, 1960) of the Brand-se-Baai station for the period March 1993 – February 1997.

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

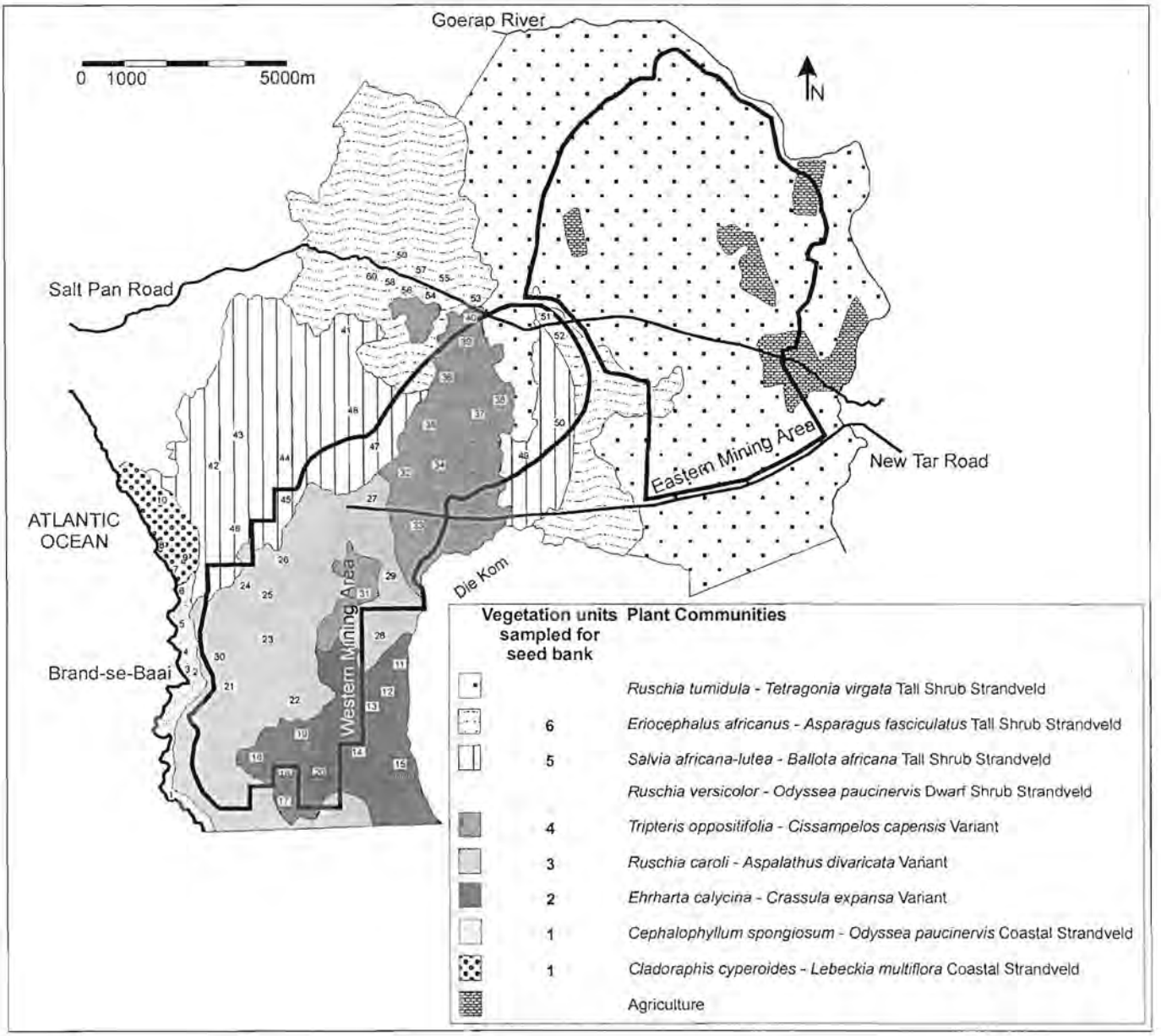

Figure 4.3. Vegetation map of the study area and corresponding vegetation sample units, indicating 60 seed bank sampling points.

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).

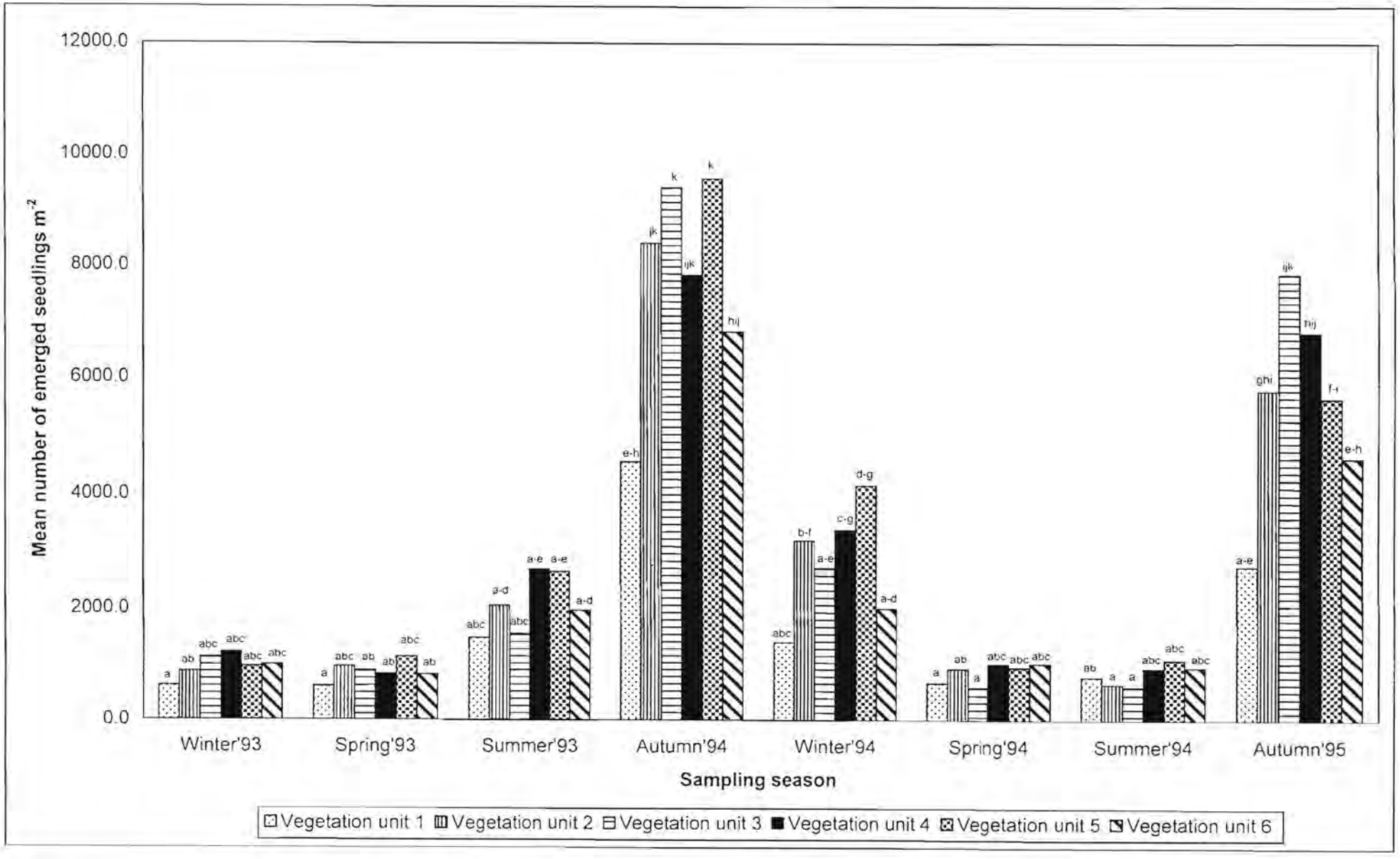

Figure 4.4. Mean number of emerged seedlings for samples collected in different vegetation units and seasons. Bars with the same letter are not significantly different at $P \leq 0.05$.

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

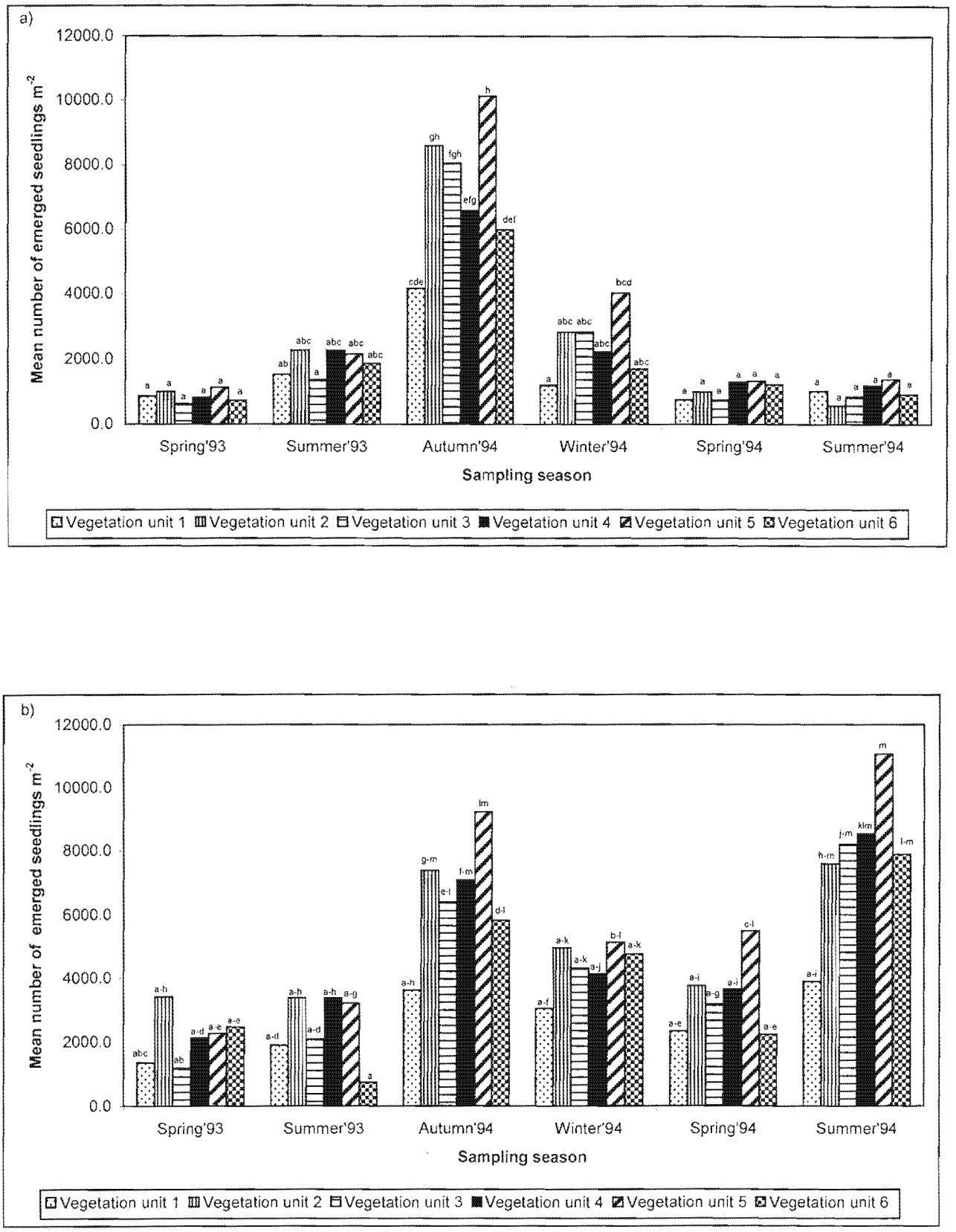

Figure 4.5. Mean number of emerged seedlings of samples collected in different vegetation units and seasons, and examined a) directly after sampling and b) at the peak time for field germination (autumn). Bars with the same letter are not significantly different at $P \leq 0.05$.

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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REFERENCES

ALBRECHT, H. & FORSTER, E.-M. 1996. The weed seed bank of soils in a landscape segment in southern Bavaria – I. Seed content, species composition and spatial variability. *Vegetatio*, **125**: 1-10.

ARCHIBOLD, O.W. 1981. Buried viable propagules in native prairie and adjacent agricultural sites in central Saskatchewan. *Canadian Journal of Botany*, **59**: 701-706.

BADGER, K.S. & UNGAR, I.A. 1994. Seed bank dynamics in an inland salt marsh, with special emphasis on the halophyte *Hordeum jubatum* L.. *International Journal of Plant Science*, **155**: 66-72.

BARBERI, P., MACCHIA, M. & BONARI, E. 1998. Comparison between the seed extraction and seedling emergence methods for weed seedbank evaluation. *Aspects of Applied Biology*, **51**: 9-14.

BASKIN, C.C. & BASKIIN J.M. 1998. *Seeds: Ecology, biogeography, and evolution of dormancy and germination.* Academic Press, New York.

BASKIN, J.M. & BASKIN, C.C. 1978. The seed bank in a population of an endemic plant species and its ecological significance. *Biological Conservation*, **14**: 125-130.

BERGE, G. & HESTMARK, G. 1997. Composition of seed banks of roadsides, stream verges and agricultural fields in southern Norway. *Annales Botanici Fennici*, **34**: 77-90.

BERTILLER, M.B. 1998. Spatial patterns of the germinable soil seed bank in northern Patagonia. *Seed Science Research*, **8**: 39-45.

BIGWOOD, D.W. & INOUYE, D.W. 1988. Spatial pattern analysis of seed banks: an improved method and optimized sampling. *Ecology*, **69**: 497-507.

BOUCHER, C. & LE ROUX, A. 1990. Heavy mineral sand mining project assessment vegetation report. In: Anglo American Corporation. *West Coast heavy mineral sands project - Supplementary Report.* Unpublished report. University of Cape Town, Cape Town. Section A5.

BOUCHER, C. & LE ROUX, A. 1993. Dry coastal ecosystems of the South African West Coast. In: Goodall, D.W. & Van der Maarel, E. (eds). *Ecosystems of the World. Volume 2B. Dry Coastal Ecosystems.* Elsevier, Amsterdam. pp. 75-88.

CHIPPINDALE, H.G. & MILTON, W.E.J. 1934. On the viable seeds present in the soil beneath pastures. *Journal of Ecology*, **22**: 508-531.

COFFIN, D.P. & LAUENROTH, W.K. 1989. Spatial and temporal variation in the seed bank of a semiarid grassland. *American Journal of Botany*, **76**: 53-58.

COUNCIL FOR SCIENTIFIC AND INDUSTRIAL RESEARCH. 1997. Prints of climate statistics of the Brand-se-Baai Station from March 1993 up to February 1997. Pretoria.

DEAN, M.R.J., MILTON, S.J., WATKEYS, M.K. & HOCKEY, P.A.R. 1991. Distribution, habitat preference and conservation status of the Red Lark *Certhilauda burra* in Cape Province, South Africa. *Biological Conservation*, **58**: 257-274.

DE VILLIERS, A.J., VAN ROOYEN, M.W. & THERON, G.K. 1994. Comparison of two methods for estimating the size of the viable seed bank of two plant communities in the Strandveld of the West Coast, South Africa. *South African Journal of Botany*, **60**: 81-84.

DE VILLIERS, A.J., VAN ROOYEN, M.W., THERON, G.K. & VAN ROOYEN, N. 1999. Vegetation diversity of the Brand-se-Baai coastal dune area, West Coast, South Africa: A pre-mining benchmark survey for rehabilitation. *Land Degradation & Development*, **10**: 207-224.

ENVIRONMENTAL EVALUATION UNIT. 1990. *Anglo American Corporation: West Coast heavy mineral sands project.* Unpublished report. University of Cape Town, Cape Town.

ESLER, K.J. 1993. Vegetation patterns and plant reproductive processes in the Succulent Karoo. Ph.D. thesis, University of Cape Town, Cape Town.

ESLER,K.J., COWLING, R.N. & IVEY, P. 1992. Seed biology of three species of Mesembryanthema in the southern Succulent Karoo. *South African Journal of Botany*, **58**: 343-348.

FEAST, P.M. & ROBERTS, H.A. 1973. Note on the estimation of viable weed seeds in soil samples. *Weed Research*, **13**: 110-113.

GRAHAM, D.J. & HUTCHINGS, M.J. 1988. Estimation of the seed bank of a chalk grassland ley established on former arable land. *Journal of Applied Ecology*, **25**: 241-252.

GRANSTRöM, A. 1988. Seed banks at six open and afforested heathland sites in southern Sweden. *Journal of Applied Ecology*, **25**: 297-306.

GRINDLEY, S. & BARBOUR, B. 1990. Conceptual rehabilitation plan. In: Anglo American Corporation. *West Coast heavy mineral sands project - Supplementary Report.* Unpublished report. University of Cape Town, Cape Town. Section A6.

GROSS, K.L. 1990. A comparison of methods for estimating seed numbers in the soil. *Journal of Ecology*, **78**: 1079-1093.

HARPER, J.L. 1977. *Population biology of plants.* Academic Press, London.

HENDERSON, C.B., PETERSEN, K.E. & REDAK, R.A. 1988. Spatial and temporal patterns in the seed bank and vegetation of a desert grassland community. *Journal of Ecology*, **76**: 717-728.

HEWITT, E.J. 1952. *Sand and water culture methods used in the study of plant nutrition.* Farnham Royal, Bucks, Commonwealth Agricultural Bureau.

HOWE, C.D. & CHANCELLOR, R.J. 1983. Factors affecting the viable seed content of soils beneath lowland pastures. *Journal of Applied Ecology*, **20**: 915-922.

JONES, N.E. 1998. The number of soil cores required to accurately estimate the seed bank on arable land. *Aspects of Applied Biology*, **51**: 1-8.

KALISZ, S. 1991. Experimental determination of seed bank age structure in the winter annual *Collinsia verna*. *Ecology*, **72**: 575-585.

KJELLSSON, G. 1992. Seed banks in Danish deciduous forests: species composition, seed influx and distribution pattern in soil. *Ecography*, **15**: 86-100.

KOTANEN, P.M. 1996. Revegetation following soil disturbance in a California meadow: the role of propagule supply. *Oecologia*, **108**: 652-662.

LECK, M.A., PARKER, V.T. & SIMPSON, R.L. 1989. *Ecology of soil seed banks.* Academic Press, London.

LEVASSOR, C., ORTEGA, M. & PECO, B. 1990. Seed bank dynamics of Mediterranean pastures subjected to mechanical disturbance. *Journal of Vegetation Science*, **1**: 339-344.

LOW, A.B. & REBELO, A. 1998. *Vegetation of South Africa, Lesotho and Swaziland.* Department of Environmental Affairs & Tourism, Pretoria.

MALO, J.E., JIMÉNEZ, B. & SUáREZ, F. 1995. Seed bank build-up in small disturbances in a Mediterranean pasture: the contribution of endozoochorous dispersal by rabbits. *Ecography*, **18**: 73-82.

MANCHESTER, S.J. & SPARKS, T.H. 1998. Determining the seed bank of former flood meadow fields. *Aspects of Applied Biology*, **51**: 15-22.

MATLACK, G.R. & GOOD, R.E. 1990. Spatial heterogeneity in the soil seed bank of a mature coastal plain forest. *Bulletin of the Torrey Botanical Club*, **117**: 143-152.

MILBERG, P. & ANDERSSON, L. 1998. Dormancy dynamics in buried weed seeds. *Aspects of Applied Biology*, **51**: 153-158.

MILBERG, P. & PERSSON, T.S. 1994. Soil seed bank and species recruitment in road verge grassland vegetation. *Annales Botanici Fennici*, **31**: 155-162.

MUELLER-DOMBOIS, D. & ELLENBERG, H. 1974. *Aims and methods of vegetation ecology.* Wiley, New York.

PAKE, C.E. & VENABLE, D.L. 1996. Seed banks in desert annuals: implications for persistence and coexistence in variable environments. *Ecology*, **77**: 1427-1435.

PARMENTER, R.R. & MACMAHON, J.A. 1983. Factors determining the abundance and distribution of rodents in a shrub-steppe ecosystem: the role of shrubs. *Oecologia*, **59**: 145-156.

POIANI, K.A. & JOHNSON, W.C. 1988. Evaluation of the emergence method in estimating seed bank composition of prairie wetlands. *Aquatic Botany*, **32**: 91-97.

REICHMAN, O.J. 1984. Spatial and temporal variation of seed distributions in Sonoran desert soils. *Journal of Biogeography*, **11**: 1-11.

ROBERTS, H.A. 1981. Seed banks in soils. *Advances in Applied Biology*, **6**: 1-55.

SILVERTOWN, J.W. & LOVETT-DOUST, J.L. 1995. *Introduction to plant population biology.* Blackwell Science Ltd., Oxford.

SIMPSON, R.L., LECK, M.A. & PARKER, V.T. 1989. Seed bank: General concepts and methodological issues. In: Leck, M.A., Parker, V.T. & Simpson, R.L. (eds). *Ecology of soil seed banks.* Academic Press, London. pp. 257-281.

THOMPSON, K. 1993. Persistence in soil. In: Hendry, G.A.F & Grime, J.P. (eds). *Methods in comparative plant ecology.* Chapman and Hall, London. pp. 199-202.

VAN DER VALK, A.G., PEDERSON, R.L. & DAVIS, C.B. 1992. Restoration and creation of freshwater wetlands using seed banks. *Wetlands Ecology and Management*, **1**: 191-197.

VAN ROOYEN, M.W. 1999. Functional aspects of short-lived plants. In: Dean, W.R.J. & Milton, S.J. (eds). *The Karoo – Ecological patterns and processes.* Cambridge University Press, Cambridge. pp. 105-122.

VAN ROOYEN, M.W. & GROBBELAAR, N. 1982. Saadbevolkings in die grond van die Hester Malan-natuurreservaat in die Namakwalandse Gebrokeveld. *South African Journal of Botany*, **1**: 41-50.

VAVREK, M.C., McGRAW, J.B. & BENNINGTON, C.C. 1991. Ecological genetic variation in seed banks. III. Phenotypic and genetic differences between young and old seed populations of *Carex bigelowii*. *Journal of Ecology*, **79**: 645-662.

WALCK, J.L., BASKIN, J.M. & BASKIN, C.C. 1998. A comparative study of the seed germination biology of a narrow endemic and two geographically-widespread species of *Solidago* (Asteraceae). 6. Seed bank. *Seed Science Research*, **8**: 65-74.

WALTER, H. & LIETH, H. 1960. *Klimadiagramm - Weltatlas.* Fischer, Jena.

WILLEMS, J.H. & HUIJSMANS, K.G.A. 1994. Vertical seed dispersal by earthworms: a quantitative approach. *Ecography*, **17**: 124-130.

WILLIAMSON, J.C. & JOHNSON, D.B. 1990. Mineralisation of organic matter in topsoils subjected to stockpiling and restoration at opencast coal sites. *Plant and Soil*, **128**: 241-247.

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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REFERENCES

AERTS,R., HUISZOON, A., VAN OOSTRUM, J.H.A., VAN DE VIJVER, C.A.D.M. & WILLEMS, J.H. 1995. The potential for heathland restoration on formerly arable land at a site in Drenthe, The Netherlands. *Journal of Applied Ecology*, **32**: 827-835.

ALBRECHT, H. & FORSTER, E.-M. 1996. The weed seed bank of soils in a landscape segment in southern Bavaria – I. Seed content, species composition and spatial variability. *Vegetatio*, **125**: 1-10.

AZIZ, S. & KHAN, M.A. 1996. Seed bank dynamics of a semi-arid coastal shrub community in Pakistan. *Journal of Arid Environments*, **34**: 81-87.

BADGER, K.S. & UNGAR, I.A. 1994. Seed bank dynamics in an inland salt marsh, with special emphasis on the halophyte *Hordeum jubatum* L.. *International Journal of Plant Science*, **155**: 66-72.

BASKIN, J.M. & BASKIN, C.C. 1978. The seed bank in a population of an endemic plant species and its ecological significance. *Biological Conservation*, **14**: 125-130.

BENOIT, D.L., KENKEL, N.C. & CAVERS, P.B. 1989. Factors influencing the precision of soil seed bank estimates. *Canadian Journal of Botany*, **67**: 2833-2840.

BERGE, G. & HESTMARK, G. 1997. Composition of seed banks of roadsides, stream verges and agricultural fields in southern Norway. *Annales Botanici Fennici*, **34**: 77-90.

BERTILLER, M.B. 1998. Spatial patterns of the germinable soil seed bank in northern Patagonia. *Seed Science Research*, **8**: 39-45.

BIGWOOD, D.W. & INOUYE, D.W. 1988. Spatial pattern analysis of seed banks: an improved method and optimized sampling. *Ecology*, **69**: 497-507.

BOUCHER, C. & LE ROUX, A. 1993. Dry coastal ecosystems of the South African west coast. In: Goodall, D.W. & Van der Maarel, E. (eds). *Ecosystems of the World. Volume 2B. Dry Coastal Ecosystems: Africa, America, Asia and Oceania*. Elsevier, Amsterdam. pp. 75-88.

BRECK, S.W & JENKINS, S.H. 1997. Use of an ecotone to test the effects of soil and desert rodents on the distribution of Indian ricegrass. *Ecography*, **20**: 253-263.

COFFIN, D.P. & LAUENROTH, W.K. 1989. Spatial and temporal variation in the seed bank of a semiarid grassland. *American Journal of Botany*, **76**: 53-58.

DEAN, M.R.J., MILTON, S.J., WATKEYS, M.K. & HOCKEY, P.A.R. 1991. Distribution, habitat preference and conservation status of the Red Lark *Certhilauda burra* in Cape Province, South Africa. *Biological Conservation*, **58**: 257-274.

DE VILLIERS, A.J., VAN ROOYEN, M.W. & THERON, G.K. 1994. Comparison of two methods for estimating the size of the viable seed bank of two plant communities in the Strandveld of the west coast, South Africa. *South African Journal of Botany*, **60**: 81-84.

DE VILLIERS, A.J., VAN ROOYEN, M.W., THERON, G.K. & VAN ROOYEN, N. 1999. Vegetation diversity of the Brand-se-Baai coastal dune area, West Coast, South Africa: A pre-mining benchmark survey for rehabilitation. *Land Degradation & Development*, **10**: 207-224.

DUTOIT, T. & ALARD, D. 1995. Permanent seed banks in chalk grassland under various management regimes: their role in the restoration of species-rich plant communities. *Biodiversity and Conservation*, **4**: 939-950.

ENVIRONMENTAL EVALUATION UNIT. 1990. *Anglo American Corporation: West Coast heavy mineral sands project*. Unpublished report. University of Cape Town, Cape Town.

ESLER, K.J. 1993. Vegetation patterns and plant reproductive processes in the Succulent Karoo. Ph.D. thesis, University of Cape Town, Cape Town.

ESLER, K.J. 1999. Plant reproductive ecology. In: Dean, W.R.J. & Milton, S.J. (eds). *The Karoo – Ecological patterns and processes*. Cambridge University Press, Cambridge. pp. 123-144.

GRAHAM, D.J. & HUTCHINGS, M.J. 1988. Estimation of the seed bank of a chalk grassland ley established on former arable land. *Journal of Applied Ecology*, **25**: 241-252.

GRANSTRöM, A. 1988. Seed banks at six open and afforested heathland sites in southern Sweden. *Journal of Applied Ecology*, **25**: 297-306.

GROSS, K.L. 1990. A comparison of methods for estimating seed numbers in the soil. *Journal of Ecology*, **78**: 1079-1093.

GRUBB, P.J. 1977. The maintenance of species richness in species-rich communities: the importance of the regeneration niche. *Biological Reviews*, **52**: 107-145.

GRUBB, P.J. 1988. The uncoupling of disturbance and recruitment, two kinds of seed banks, and persistence of plant populations at the regional and local scales. *Annales Zoologici Fennici*, **25**: 23-36.

HENDERSON, C.B., PETERSEN, K.E. & REDAK, R.A. 1988. Spatial and temporal patterns in the seed bank and vegetation of a desert grassland community. *Journal of Ecology*, **76**: 717-728.

HOWE, C.D. & CHANCELLOR, R.J. 1983. Factors affecting the viable seed content of soils beneath lowland pastures. *Journal of Applied Ecology*, **20**: 915-922.

KALISZ, S. 1991. Experimental determination of seed bank age structure in the winter annual *Collinsia verna*. *Ecology*, **72**: 575-585.

KIRKHAM, F.W. & KENT, M. 1997. Soil seed bank composition in relation to the standing vegetation in fertilized and unfertilized hay meadows on a Somerset peat moor. *Journal of Applied Ecology*, **34**: 889-902.

KJELLSSON, G. 1992. Seed banks in Danish deciduous forests: species composition, seed influx and distribution pattern in soil. *Ecography*, **15**: 86-100.

LAVOREL, S., DEBUSSCHE, M., LEBRETON, J-D. & LEPART, J. 1993. Seasonal patterns in the seed bank of Mediterranean old-fields. *Oikos*, **67**: 114-128.

LECK, M.A., PARKER, V.T. & SIMPSON, R.L. 1989. *Ecology of soil seed banks*. Academic Press, London.

LEVASSOR, C., ORTEGA, M. & PECO, B. 1990. Seed bank dynamics of Mediterranean pastures subjected to mechanical disturbance. *Journal of Vegetation Science*, **1**: 339-344.

LOW, A.B. & REBELO, A. 1998. *Vegetation of South Africa, Lesotho and Swaziland*. Department of Environmental Affairs & Tourism, Pretoria.

LUNT, I.D. 1997. Germinable soil seed banks of anthropogenic native grasslands and grassy forest remnants in temperate south-eastern Australia. *Plant Ecology*, **130**: 21-34.

MANCHESTER, S.J. & SPARKS, T.H. 1998. Determining the seed bank of former flood meadow fields. *Aspects of Applied Biology*, **51**: 15-22.

MATLACK, G.R. & GOOD, R.E. 1990. Spatial heterogeneity in the soil seed bank of a mature coastal plain forest. *Bulletin of the Torrey Botanical Club*, **117**: 143-152.

MILBERG, P. & ANDERSSON, L. 1998. Dormancy dynamics in buried weed seeds. *Aspects of Applied Biology*, **51**: 153-158.

MILBERG, P. & PERSSON, T.S. 1994. Soil seed bank and species recruitment in road verge grassland vegetation. *Annales Botanici Fennici*, **31**: 155-162.

MUELLER-DOMBOIS, D. & ELLENBERG, H. 1974. *Aims and methods of vegetation ecology*. Wiley, New York.

PAKE, C.E. & VENABLE, D.L. 1996. Seed banks in desert annuals: implications for persistence and coexistence in variable environments. *Ecology*, **77**: 1427-1435.

REICHMAN, O.J. 1984. Spatial and temporal variation of seed distributions in Sonoran desert soils. *Journal of Biogeography*, **11**: 1-11.

ROBERTS, H.A. 1981. Seed banks in soils. *Advances in Applied Biology*, **6**: 1-55.

SCHENKEVELD, A.J. & VERKLAAR, H.J. 1984. The ecology of short-lived forbs in chalk grasslands: distribution of germinative seeds and its significance for seedling emergence. *Journal of Biogeography*, **11**: 251-260.

THOMPSON, K. & GRIME, J.P. 1979. Seasonal variation in the seed banks of herbaceous species in ten contrasting habitats. *Journal of Ecology*, **67**: 893-921.

VAN DER VALK, A.G., PEDERSON, R.L. & DAVIS, C.B. 1992. Restoration and creation of freshwater wetlands using seed banks. *Wetlands Ecology and Management*, **1**: 191-197.

VAN ROOYEN, M.W. & GROBBELAAR, N. 1982. Saadbevolkings in die grond van die Hester Malan-natuurreservaat in die Namakwalandse Gebrokeveld. *South African Journal of Botany*, **1**: 41-50.

VAVREK, M.C., McGRAW, J.B. & BENNINGTON, C.C. 1991. Ecological genetic variation in seed banks. III. Phenotypic and genetic differences between young and old seed populations of *Carex bigelowii*. *Journal of Ecology*, **79**: 645-662.

VON WILLERT, D.J., ELLER, B.M., WERGER, M.J.A., BRINCKMANN, E. & IHLENFELDT, H.D. 1992. *Life strategies of succulents in deserts: with special reference to the Namib desert.* Cambridge University Press, Cambridge.

WILLEMS, J.H. & HUIJSMANS, K.G.A. 1994. Vertical seed dispersal by earthworms: a quantitative approach. *Ecography*, **17**: 124-130.

CHAPTER 6

SEED BANK PHYTOSOCIOLOGY OF THE STRANDVELD SUCCULENT KAROO, SOUTH AFRICA: A PRE-MINING BENCHMARK SURVEY FOR REHABILITATION

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ABSTRACT

Prior to the mining of heavy minerals, the seed bank of the Strandveld Succulent Karoo was investigated to serve as a benchmark for the future rehabilitation of the area. Seed bank composition and species' abundance were determined with the seedling emergence method. By using the Braun-Blanquet method, five main vegetation units were identified in concordance with results obtained for the standing vegetation. A total of 108 species were recorded in the seed bank, which represents *c.* 50% of the species recorded in the standing vegetation of the total study area. Seven annual species (3%) were unique to the soil seed bank. On community level, similarity in species composition between the standing vegetation and the soil seed bank ranged between 39.2% and 48.8%, with a similarity of 54.3% for the total study area. Annual and perennial species' similarity in species composition between the standing vegetation and the seed bank totalled 74.8% and 43.1% respectively. Post-mining topsoil replacement as well as seeding and transplanting of selected local species will be essential to revegetate this area.

Key words: Braun-Blanquet; mining; phytosociology; revegetation; seed bank; Sorensens' Index; standing vegetation

INTRODUCTION

Mining activities along the West Coast of South Africa 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 specific requirement that has to be met is the revegetation of the area with indigenous plant species, to obtain a vegetation cover that conforms to the pre-mining vegetation as soon as possible after mining has been completed (Environmental Evaluation Unit, 1990). To restore the mined area as close as possible to its pre-mining natural condition, a pre-mining vegetation survey can serve as a benchmark to measure the success of the rehabilitation process. A complete description of the plant communities must also include the buried viable seeds, because they are as much part of the species composition as is the aboveground components (Major & Pyott, 1966; Fenner, 1985; Thompson, 1992).

The soil seed bank of most plant communities represents a vast pool of regenerative potential (Henderson *et al.*, 1988) as well as a 'memory' of previous conditions (Coffin & Lauenroth, 1989). 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; Coffin & Lauenroth, 1989).

The aim of this study was to compare the floristic composition of the soil seed bank with that of the standing vegetation of the Brand-se-Baai area prior to mining. If the species composition of the seed bank is used as a predictor of future standing vegetation composition, this comparison will indicate the suitability or shortcomings of topsoil replacement as a means of revegetation. It will also aid in the selection of species, which will have to be sown and/or transplanted.

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 arid West Coast, South Africa (De Villiers *et al.*, 1999). This area has a mean annual precipitation of 282 mm, of which rainfall constitutes 160 mm (De Villiers *et al.*, 1999). Advective sea fogs and heavy dewfalls supplement the low rainfall significantly. The mean daily temperature measured at the study site is 15.8°C.

According to Low & Rebelo (1998), the vegetation of the study area consists of Strandveld Succulent Karoo and Lowland Succulent Karoo, both of which are 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. 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). Small patches of Lowland Succulent Karoo vegetation, characterized 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).

A vegetation survey of the study area (De Villiers, *et al.*, 1999) resulted in the identification of six main plant communities (Figure 6.1). Seed bank sample plots were randomly located within each of five of these communities, and totalled 60 plots for the study site (Figure 6.1). These five communities are situated within the western mining area, which is being mined first. The sixth community almost solely constitutes the eastern mining area, and was not sampled.

At each of the 60 sampling locations (Figure 6.1), 15 soil samples were taken linearly at intervals of two meters. 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 soil sampling bags at ambient temperatures for approximately one week, before the seed content was estimated by means of the emergence method (De Villiers *et al.*, 1994). Sampling took place four times a year, for a total period of two years.

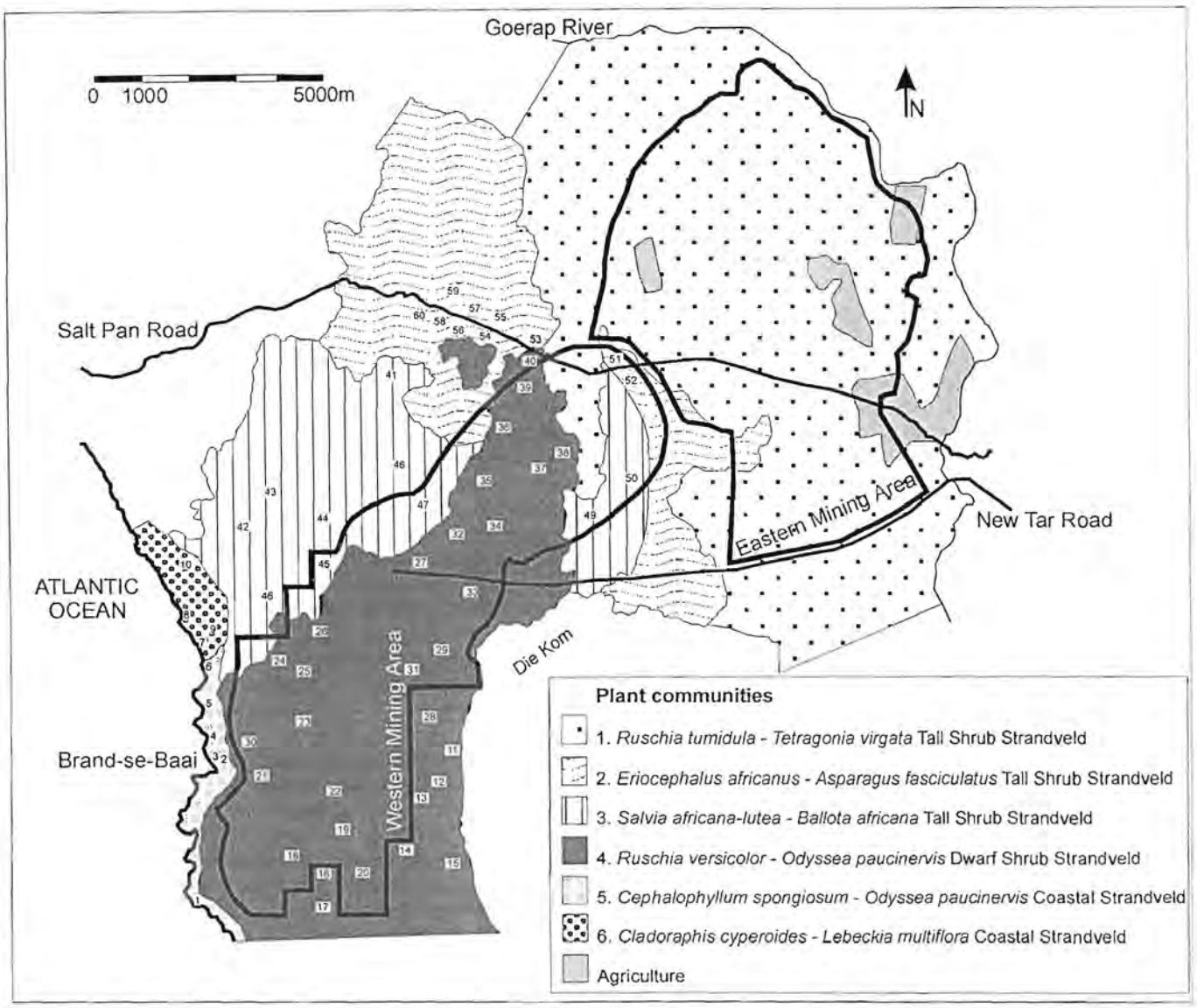

Figure 6.1. Vegetation map of the study area (De Villiers *et al.*, 1999), indicating 60 seed bank sampling locations.

Seedling identification was almost impossible, but at a more mature stage, the seedlings or young plants were identified, counted and removed. Examination of the samples continued for a period of six months. Species names conform to those of Arnold & De Wet (1999).

Seed bank abundance data obtained during the eight sampling seasons were lumped. These lumped seed bank 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. The first classification of the seed bank, based on the total floristic set, was obtained by the application of the TWINSPAN classification algorithm (Hill, 1979). Using the Zürich-Montpellier (Braun-Blanquet) approach (Werger, 1974), the species and relevés in the matrix were assembled to produce a phytosociological table (Table 6.1) for the seed bank. The seed bank units obtained in the phytosociological table (Table 6.1) closely resembled the main vegetation units obtained in the standing vegetation of the study area (De Villiers *et al.*, 1999; Chapter 3). For this reason, seed bank units were numbered in accordance with the allocated community numbers in the standing vegetation.

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.

To compare the species composition of the seed bank with that of the standing vegetation (De Villiers *et al.*, 1999), the data in the two sets had to correspond; *i.e.* some species had been lumped into larger units (genus, family or plant type). Similarity in species composition between the seed bank and the standing vegetation was determined by means of Sorensens' Presence Coefficient (IS_S) (Mueller-Dombois & Ellenberg, 1974):

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

where, in this case c is the number of species common to both standing vegetation and seed bank, A is the total number of species recorded in the standing vegetation, and B is the total number of species recorded in the soil seed bank.

Species composition data were analysed statistically at a 95% confidence level, using the least significant difference (LSD) one-way analysis of variance (ANOVA) and multiple range test of the Statgraphics 5.0[1] computer program.

[1] Statgraphics 5.0, 1989. STSC, Inc., U.S.A.

Table 6.1. A phytosociological table of the soil seed bank for the Brand-se-Baai area prior to mining. Values are according to the Turboveg scale. Numbering of seed bank units corresponds to community numbers in the standing vegetation (De Villiers *et al.*, 1999)

Seed bank unit	6	5	4			3	2	
			4.3	4.1	4.2		2.2	2.1
Relevé number	1 0 9 8	2 1 4 3 7 5 6	1 1 1 1 1 2 1 1 1 1 9 5 7 4 2 0 3 6 8 1	2 2 2 2 2 2 3 2 2 2 3 2 7 9 5 4 0 1 6 8	3 3 3 3 3 3 3 3 3 4 7 9 4 1 5 8 6 2 3 0	4 5 4 4 4 4 4 4 4 4 7 0 4 3 8 6 9 2 5 1	5 5 5 6 5 5 4 5 9 0 1 2	5 5 5 5 3 7 6 8
Species Group A								
Odyssea paucinervis (P)	1 1 1		1			1		
Lebeckia multiflora (P)	1					1		
Species Group B								
Arctotis spp. (P)		1 1 1						
Phyllobolus spp. (P)		1 1				1		
Cephalophyllum spongiosum (P)		1 1						
Lampranthus godmaniae (P)	1	1						1
Frankenia pulverulenta (A)*		1 1						
Species Group C								
Ruschia caroli (P)			1	1 1 1	1 1 1		1	
Ruschia versicolor (P)			1 1 1	1 1	1 1			
Wahlenbergia schlechteri (A)*			1 1 1	1	1		1	
Gazania leiopoda (P)			3 1	1	1 1			
Didelta carnosa (A)			1 1 1	1	1			
Species Group D								
Manulea pusilla (A)			1 5 3 1 1 1 1 1 1		5 1			
Hebenstretia repens (A)			1 1		1	1		
Species Group E								
Ruschia cymosa (P)				1 1				
Ruschia subpaniculata (P)				1 1				
Ocimum canum (A)*				1 1			1	
Species Group F								
Tripteris clandestina (A)			1 1 1	1			1	1
Brassica tournefortii (A)			1 1	1 1				
Ruschia tecta (P)			1	1				

Table 6.1. (Continued)

Community number	6			5							4																														3										2									
											4.3										4.1										4.2																				2.2						2.1			
Relevé number	10	9	8	2	1	4	3	7	5	6	19	15	17	14	12	20	13	16	18	11	23	22	27	29	25	24	30	21	26	28	37	39	34	31	35	38	36	32	33	40	47	50	44	43	48	46	49	42	45	41	54	55	59	60	51	52	53	57	56	58
Species Group G																																																												
Vanzijlia annulata (P)				1			1						1											1																																		1		
Lyperia tristis (A)								1												1			1																																					
Species Group H																																																											
Foveolina tenella (A)																															1	1	1	1	1																									
Crassula muscosa (P)									1								1														1	1																												
Galenia africana (P)																															1	1																						1						
Crotalaria humilis (A)																															1		1																											
Drosanthemum calycinum (P)					1			1																										3	1																	1								
Chrysocoma longifolia (P)																																				1	1																							
Species Group I																																																											
Pelargonium senecioides (A)																										1							1	1	1		1		1																					
Tripteris oppositifolia (P)																							1												1																			1						
Species Group J																																																											
Zaluzianskya villosa (A)			3		1	5	1	5	5	5		1		1	1		5			1	1	1		1	1						1	1	1	1	1	1	1	1	3	1																				
Pharnaceum aurantium (P)					1	1			1	1		1	1				1			1													1	1					1																					
Cardamine hirsuta (A)*			1			1		1	1	1			1		1						1				1	1										1																								
Stipagrostis zeyheri (P)								1									1											1							1																									
Species Group K																																																											
Chenopodium opulifolium (A)													1											1														1			1	1	1	1		1		6	1	1	1		1							
Tetragonia microptera (A)																															1												1		3	1		1												
Ballota africana (P)																																									1	1																		
Ruschia tumidula (P)																							1																				3																	
Species Group L																																																											
Conicosia pugioniformis (P)		1																					1						1							1	1				1	1																		

Table 6.1. (Continued)

Community number	6			5							4																														3										2									
											4.3										4.1										4.2																				2.2						2.1			
Relevé number	10	9	8	2	1	4	3	7	5	6	19	15	17	14	12	20	13	16	18	11	23	22	27	29	25	24	30	21	26	28	37	39	34	31	35	38	36	32	33	40	47	50	44	43	48	46	49	42	45	41	54	55	59	60	51	52	53	57	56	58
Species Group M																																																												
Hebenstretia dentata (A)											1								3					1			1	1		3		1	1	1			1	1	1					1		1	1													
Amellus microglossus (A)												1						1															1								1		1	3				8	1	3										
Amellus tenuifolius (P)																1								1												1		1					5																	
Species Group N																																																												
Chaetobromus dregeanus (P)						1				1										1											1			1						1	1																			
Arctotheca calendula (A)					1							1								1															1						1						1													
Species Group O																																																												
Lebeckia lotonoides (P)					1																																														1	1	1	1						
Pharnaceum lanatum (P)																																																			1				1					
Species Group P																																																												
Bromus pectinatus (A)									1										1																						1		1	5		1	1	6		1		1				1				
Nemesia bicornis (P)	1																1																								1				1							1	1		1					
Arctotis adpressa (A)																																															1							1			1			
Zygophyllum pygmaeum (P)																																																1	1				1							
Species Group Q																																																												
Mesembryanthemum crystallinum (A)		1	1	1		6	1	1	5	5				3	3		3							1				1	1	5					1	1		1	3	3		1		1		1	1	1			1									
Pharnaceum exiguum (A)						3					1	1		1		3			3			1	5		1		1	1	3		1	1	1		1	1	5	1	1	5							1					3	1	1						
Galenia sarcophylla (P)						1	1		1	1								1	3						1							1																1				1								
Grielum grandiflorum (P)	1					1	1	1																																				1	1					1	1		1							
Species Group R																																																												
Leysera gnaphalodes (P)																		1												1																											1	1	1	
Species Group S																																																												
Othonna floribunda (P)					1																															1		1	1			1								1	1		1				1			
Eriocephalus africanus (P)																																				1		5	1							1	1								1	1				1
Heliophila coronopifolia (A)																	1																	1					1				1			1														1

Table 6.1. (Continued)

Community number	6			5							4									
											4.3									
Relevé number	10	9	8	2	1	4	3	7	5	6	19	15	17	14	12	20	13	16	18	11
Species Group T																				
Nestlera biennis (P)						1														
Ursinia speciosa (A)																				
Ruschia bolusiae (P)						1														
Species Group U																				
Adenogramma littoralis (A)											5		5	1	1	5		3	1	
Polycarena pumila (A)												5	1	1				5		
Wahlenbergia paniculata (A)											1			1						1
Silene clandestina (A)												1		1	1		5			
Dimorphotheca pluvialis (A)															1			1	1	
Felicia merxmuelleri (A)													1							
Species Group V																				
Helichrysum marmarolepis (A)	1	1	1	5	5	3	3	5	3	3	3	5	3	1	1	3	3	1	1	1
Karroochloa schismoides (A)	1		1	1		1	1	6	1	5	6	1	6	5	7	5	6	1	7	6
Ehrharta calycina (P)	1	3		5		5	5	3	5	5	6	5	3	1	5	3	1	3	5	6
Crassula expansa (A)	1	1	1	3	1		1	1	1	1	1	3	1	5	6	3	7	3	1	5
Oncosiphon suffruticosum (A)	5	3	1	3	3	5	3	5	5	7	5	5	6	3	5	3	5	3	5	5
Senecio arenarius (A)	5	5	3	5	5	3	5	5	5	5	3	3	5	3	5	5	5	5	5	5
Pentaschistis patula (A)			1	1	1				1	3	7	1			5	7	3		5	5
Geophyte spp. (P)	1	1	1			1		1	1		1	1		1	1	1		1	1	1
Tetragonia virgata (P)		1	1		1		1		1				1	1	1			1	1	1
Ficinia argyropa (A)	1	1		1	1		1	1	1		1		1	1	1	1	1			1
Crassula umbellata (A)*			1								3	6	5	5	1	1	1	5	1	1
Mesembryanthemaceae (P)				3	5	1	1	1	1	1		1	1		1	1			1	1
Manochlamys albicans (P)		1						1							1		1			1
Manulea altissima (A)				1				1				1								
Ruschia brevicyma (P)	1			1		1			1		1	1						1	1	
Hypertelis salsoloides (P)					5		1		1		1		3	1		3	1		1	
Isolepis marginata (A)			1										1		1					
Cotula thunbergii (A)	1														1					1
Hermannia spp. (P)								3							1	1				1
Zygophyllum morgsana (P)									1						1		1	1		1

Community number	4																			
	4.1										4.2									
Relevé number	23	22	27	29	25	24	30	21	26	28	37	39	34	31	35	38	36	32	33	40
Species Group T																				
Nestlera biennis (P)	1	1		1	1		1						1	5			1			
Ursinia speciosa (A)	1					1							3	1						
Ruschia bolusiae (P)						1						1			1		1			1
Species Group U																				
Adenogramma littoralis (A)	1	1	1	1	5	5	3	5	5	1	5	6	3	7	6	3	5	3	5	5
Polycarena pumila (A)		1	1		1		1	1	1			1	1	1	1	1		1	1	3
Wahlenbergia paniculata (A)	1				3		1		1			1	1	1	3		1			
Silene clandestina (A)	1	1			1	1	1						1	1				1		
Dimorphotheca pluvialis (A)					1		1						1							
Felicia merxmuelleri (A)					1														1	
Species Group V																				
Helichrysum marmarolepis (A)	5	5	5	3	3	5	5	1	1	1	1	3	3	1	1	1	1	3	1	3
Karroochloa schismoides (A)	3	5	7	7	6	5	5	1	8	9	6	6	5	5	7	7	6	6	6	7
Ehrharta calycina (P)	1	5	3	1	5	1	1	5	3	1	1	1	3	3	1	1	5	5	5	5
Crassula expansa (A)	1	1	5	6	3	3	1	1	3	1	1	1	1	1	1	1	1	3	5	1
Oncosiphon suffruticosum (A)		1	5	5	1		1	1	5	6		1	3	1	3	3	1	5	5	5
Senecio arenarius (A)	5	5	1	3	5	5	1	1	1	5	1	1	3	5	1		1	1	3	
Pentaschistis patula (A)		3	1	1	1	1	5	1	1	1	5	3	5	5	6	5	5	5	5	5
Geophyte spp. (P)	1	3	1	1	1	3		1	1	1	1			1	1	1	3	1	1	1
Tetragonia virgata (P)	1		1	1		1	1		1	1	1	1		1	1		1	1	1	1
Ficinia argyropa (A)	1		1		1		1	1	1	3	1			1	1	1	1		1	
Crassula umbellata (A)*			3			1		1					1	1			1	1	1	
Mesembryanthemaceae (P)		1	1									1	1	1	1	1	1		1	
Manochlamys albicans (P)		1	1	1	1				1	1	1							1	1	1
Manulea altissima (A)								1				1	1			1			1	
Ruschia brevicyma (P)		1	1					1	1		1			1						1
Hypertelis salsoloides (P)											1		1		1		1	1		
Isolepis marginata (A)	1	1	1										1	3		1	1		1	
Cotula thunbergii (A)	1	1				1		1			1	1	1						1	
Hermannia spp. (P)		3					1					1	1							1
Zygophyllum morgsana (P)										1										

Community number	3										2									
											2.2						2.1			
Relevé number	47	50	44	43	48	46	49	42	45	41	54	55	59	60	51	52	53	57	56	58
Species Group T																				
Nestlera biennis (P)		1			1	1	1				1	1		1	3	1	1	1	1	1
Ursinia speciosa (A)												1			1	1	1	1		
Ruschia bolusiae (P)			1							1								1		
Species Group U																				
Adenogramma littoralis (A)	6	5		1	5	1	3		3	1			1	1		1		3		1
Polycarena pumila (A)	1	1	1		1	1				1				1	1	1	1	1		1
Wahlenbergia paniculata (A)							1		1			1	1		1			1		1
Silene clandestina (A)						1			1							1				1
Dimorphotheca pluvialis (A)	5			1	5	1				1					1			1	1	
Felicia merxmuelleri (A)									1		1				1	1	1	1	1	1
Species Group V																				
Helichrysum marmarolepis (A)		1	5	1	1	1	1	6	1	1	1	1	1	1	1	1	3	1	1	1
Karroochloa schismoides (A)	5	5	5	6	5	6	5	9	7	6	6	7	5	6	5	5	6	5	5	3
Ehrharta calycina (P)	5	1	3	3	3	5	1	1	1	1	1	1	1	1	1	1	1	1		1
Crassula expansa (A)	1	1	1		1	3	1	1	1		1	3	1	3	1	5	1	3	3	3
Oncosiphon suffruticosum (A)	1	5	3	6	1	5	5	5	5	5	3	1	1	1	5	3	1		1	1
Senecio arenarius (A)			1	5		5	1	1	3				1	1	1	1	1		1	
Pentaschistis patula (A)	1	1	1	1	1	1	1	1			1	1		1	1	1			1	1
Geophyte spp. (P)	3			1	1	3		1		1	3	3	1	1		1	1	1	1	1
Tetragonia virgata (P)	1	1	3	1		1	1	1	1		1	1	1	1		1	1			
Ficinia argyropa (A)	1	1		1	1	1			1	1		1	1				1	1	1	1
Crassula umbellata (A)*	1	3					5			1		5	1	1	5	7	1	6	6	5
Mesembryanthemaceae (P)		1	1		1	1	1		1	1	1									1
Manochlamys albicans (P)	1	1			1			1	1	1							1			
Manulea altissima (A)						1				1	1	3	3	1	1	3	1	1	3	1
Ruschia brevicyma (P)											1			1			1		1	1
Hypertelis salsoloides (P)						1							1	1					1	
Isolepis marginata (A)					1	1					1			1			1	1	1	
Cotula thunbergii (A)					1								1			1	1	1	3	3
Hermannia spp. (P)	1															1		1		
Zygophyllum morgsana (P)														1				1	1	

Table 6.1. (Continued)

Community number	6	5	4																														3										2					
			4.3										4.1										4.2																						2.2				2.1			
Relevé number	1		1	1	1	1	1	2	1	1	1	1	2	2	2	2	2	2	3	2	2	2	3	3	3	3	3	3	3	3	4	4	5	4	4	4	4	4	4	4	5	5	5	6	5	5	5	5	5	5
	0	9	8	2	1	4	3	7	5	6	9	5	7	4	2	0	3	6	8	1	3	2	7	9	5	4	0	1	6	8	7	9	4	1	5	8	6	2	3	0	7	0	4	3	8	6	9	2	5	1	4	5	9	0	1	2	3	7	6	8
Species Group W																																																			
Leipoldtia jacobeniana (P)	1																																																	
Hirpicium alienatum (P)		1																																																
Helichrysum incarnatum (A)				1																																														
Ruschia extensa (P)					1																																													
Ehrharta brevifolia (A)*						1																																												
Gymnodiscus capillaris (A)											1																																							
Atriplex semibaccata (P)																	1																																		
Ruschia namaquana (P)																					1																														
Portulaca quadrifida (A)*																						1																													
Exomis microphylla (P)																							1																												
Rhus longispina (P)																								1																											
Microloma sagittatum (P)																									1																										
Lampranthus lanatus (P)																										1																									
Lessertia benguellensis (A)																											1																								
Pteronia onobromoides (P)																																				1															
Sonderina tenuis (A)																																				1															
Cysticapnos cracca (A)																																					1														
Euphorbia spp. (P)																																																		
Psilocaulon spp. (P)																																																		
Diascia spp. (A)																																																		
Nemesia ligulata (A)																																																		

* - species not recorded in the standing vegetation

A - annual

P - perennial

RESULTS AND DISCUSSION

Five seed bank units were recognized, some of which were divided into sub-units (Table 6.1). These seed bank units closely resembled the plant communities described for the standing vegetation (De Villiers *et al.*, 1999), of which the hierarchical classification of the main vegetation units can be summarized as follows:

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

Since only the western mining area was sampled for seed bank size and composition estimations, Community 1 was not included in this seed bank study. In total, 230 species were recorded in the standing vegetation (De Villiers *et al.*, 1999), but when species were lumped for correspondence with seed bank data, a total of 216 species were recognized compared to the 108 species recorded in the seed bank. Species recorded only in the standing vegetation totalled 115 (20 annuals & 95 perennials) (De Villiers *et al.*, 1999), while seven annual species were unique to the soil seed bank (Table 6.1). These values represent 52% and 3% of the total species richness (standing vegetation & soil seed bank) of the area, respectively. Total, annual and perennial species' richness of all communities were higher in the standing vegetation than in the seed bank, with exception of annual species in Community 6 (Figure 6.2).

According to Sorensens' index (Table 6.2), similarity in total species composition between the standing vegetation and the soil seed bank was 54.3%. Higher similarity in annual (74.8%) than perennial (43.1%) species composition was obtained between the standing vegetation and the soil seed bank. This may be the result of the predominance of annual species in the seed bank, while many perennial species dominating the standing vegetation, were not recorded in the seed bank.

As a whole, the seed bank of the study area was characterized by species of Species Group V (Table 6.1). The most prominent species which occurred in almost all the seed bank units, were the perennials *Tetragonia virgata*, *Geophyte* spp., *Manochlamys albicans*, *Hypertelis salsoloides*, *Hermannia* spp., *Zygophyllum morgsana* and *Ruschia brevicyma*, the grasses *Ehrharta calycina*, *Pentaschistis patula* and *Karroochloa schismoides*, and the annuals *Senecio arenarius*, *Oncosiphon suffruticosum*, *Crassula expansa*, *Ficinia argyropa*, *Crassula umbellata*, *Manulea altissima*, *Isolepis marginata*, *Cotula thunbergii* and *Helichrysum marmarolepis*. These species will therefore not be repeatedly mentioned in the description of the seed bank units. Many of these species (Species Group V, Table 6.1) were also prominent in all

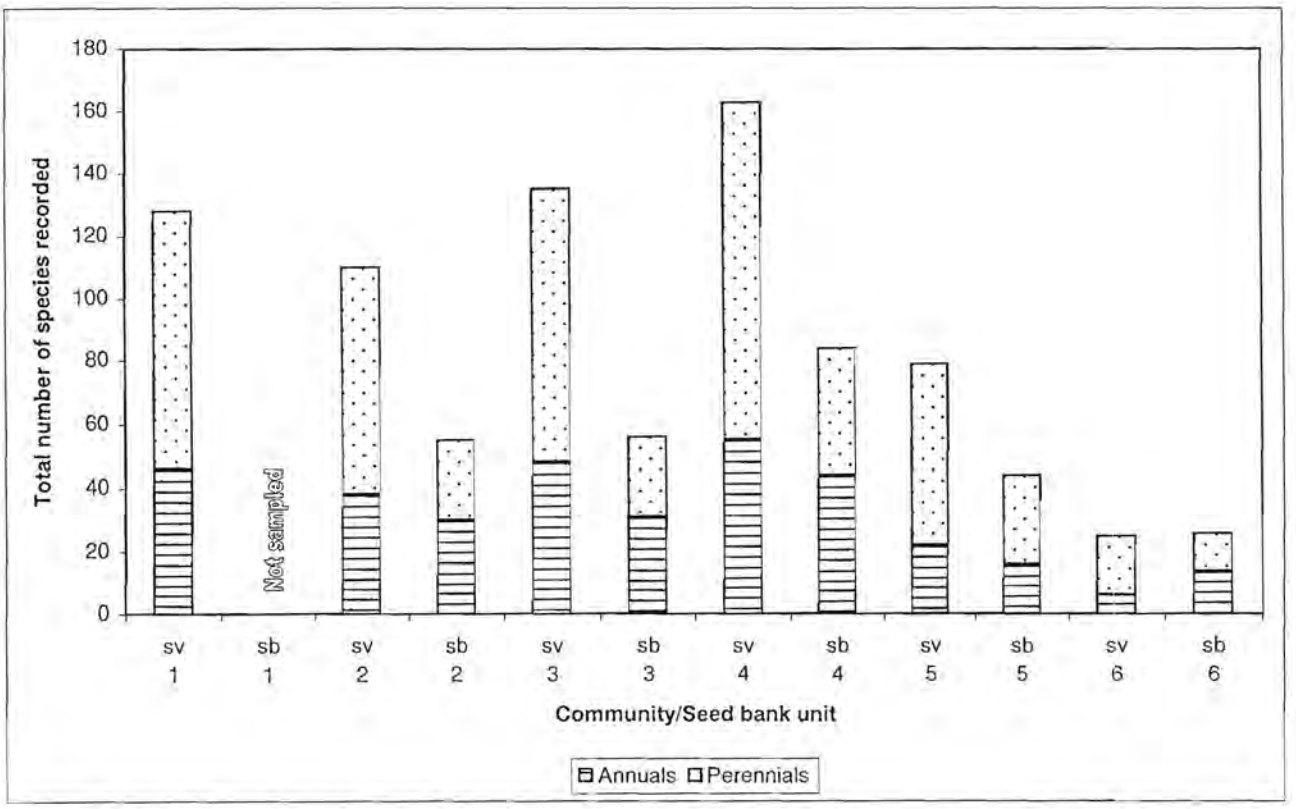

Figure 6.2. Total number of species recorded in the standing vegetation (sv) and the seed bank (sb) of six plant communities of the study area.

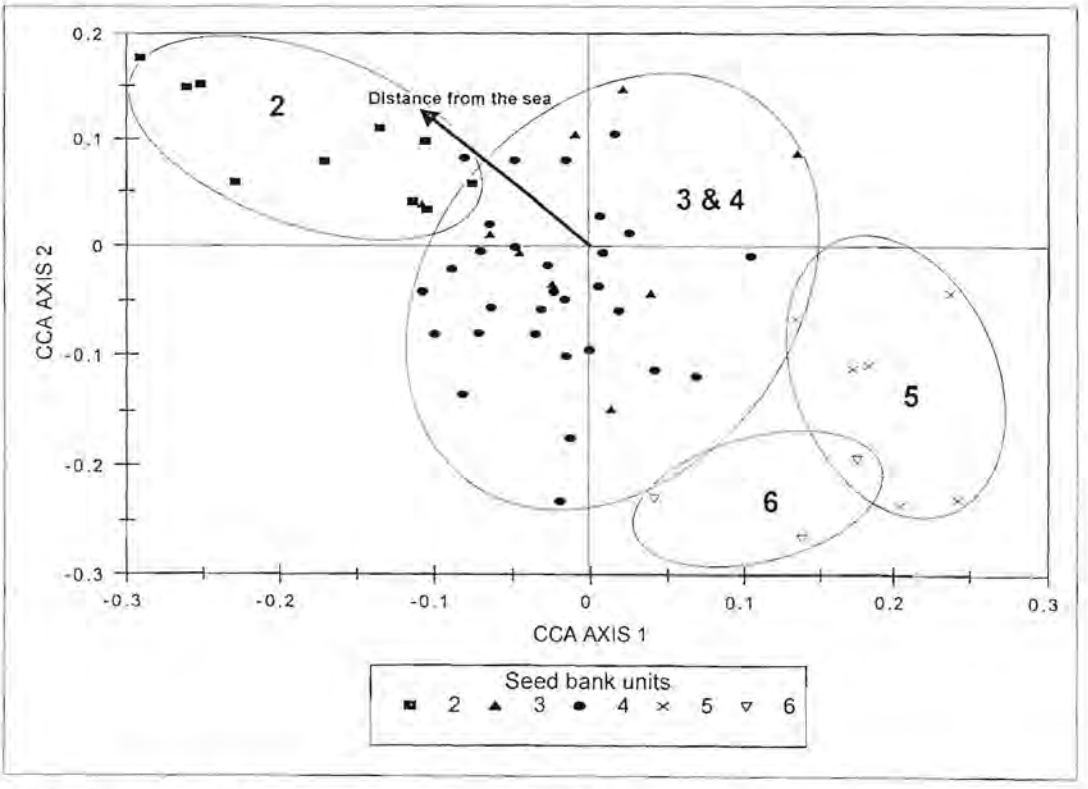

Figure 6.3. Canonical Correspondence Analysis (CCA) of floristic data of the soil seed bank along the first and second ordination axes (Eigen 1 = 0.195; eigen 2 = 0.101; scaling = 2).

Table 6.2. Sorensens' index of similarity (%) (Mueller-Dombois & Ellenberg, 1974) in species composition of plant communities, between the standing vegetation and the soil seed bank of the Strandveld Succulent Karoo. Plant communities correspond to that reported by De Villiers *et al.* (1999)

Plant communities	Plant type		
	Annuals	Perennials	All species
1. *Ruschia tumidula - Tetragonia virgata* Tall Shrub Strandveld	-	-	-
2. *Eriocephalus africanus - Asparagus fasciculatus* Tall Shrub Strandveld	64.7	33.0	46.1
3. *Salvia africana-lutea - Ballota africana* Tall Shrub Strandveld	68.4	33.9	48.2
4. *Ruschia versicolor - Odyssea paucinervis* Dwarf Shrub Strandveld	76.8	45.9	58.3
5. *Cephalophyllum spongiosum - Odyssea paucinervis* Coastal Strandveld	47.4	49.4	48.8
6. *Cladoraphis cyperoides - Lebeckia multiflora* Coastal Strandveld	30.0	45.2	39.2
All communities	74.8	43.1	54.3

- Communities for which the soil seed bank was not estimated

communities or characteristic of specific communities in the standing vegetation (De Villiers *et al.*, 1999). During revegetation efforts at the study site, topsoil replacement will be sufficient for the revegetation of species of Species Group V (Table 6.1). The fact that many of these species were also abundant in the standing vegetation, stresses the importance of the soil seed bank for revegetation efforts. Shrub species that were abundant in almost all communities in the standing vegetation (De Villiers *et al.*, 1999), but which were absent or less abundant in the soil seed bank, should probably be reintroduced to mined areas by means of transplanting and sowing, *e.g. Lycium ferocissimum, Asparagus retrofractus, Rhus longispina, Othonna floribunda* and *Lebeckia multiflora*. Annuals and perennial herb species falling in this category are *Limeum africanum, Lyperia tristis, Grielum grandiflorum, Microloma sagittatum, Hebenstretia dentata* and *Heliophila coronopifolia*.

While the communities recognized in the standing vegetation were grouped into two major units on account of the presence or absence of the perennial creeping grass *Odyssea paucinervis*, this species was not as abundant in the soil seed bank (Table 6.1), where this grouping (with exception of community/seed bank unit 6) was on account of species from Species Group J (Table 6.1). Although *Odyssea paucinervis* was not recorded in the vegetation of Community 6 (De Villiers *et al.*, 1999), this species was diagnostic for seed bank unit 6 (Species group A, Table 6.1). These results from the seed bank study indicate that plant Community 6 (De Villiers *et al.*, 1999) should probably be grouped with Communities 4 and 5 on account of the presence of *Odyssea paucinervis*, rather than with Communities 1, 2 and 3, where this species was found to be absent, both in the standing vegetation and the seed bank.

Seed bank unit 2

Seed bank unit 2 corresponds to the *Eriocephalus africanus - Asparagus fasciculatus* Tall Shrub Strandveld (Community 2, De Villiers *et al.*, 1999), but no diagnostic species for this unit were recorded in the seed bank. Conspicuous species for this unit included: *Nestlera biennis* (Species Group T), *Adenogramma littoralis* and *Felicia merxmuelleri* (Species Group U). These species were also abundant in the standing vegetation of Community 2. Two sub-units were recognized, which corresponds to variants 2.1 and 2.2 in the standing vegetation. These variants will probably not be restored individually, as they represent dune valley and dune crest vegetation of the same main community, respectively. Species richness for annual, perennial and the total number of species was higher in the standing vegetation than in the seed bank (Figure 6.2). Similarity in species composition between the standing vegetation and the seed bank was higher for annual species than for perennial species, with a similarity of 46.1% for all species (Table 6.2). Considering the 60% goal of revegetation, the topsoil replaced seed bank alone will not be sufficient for the restoration of Community 2.

Seed bank unit 3

This unit corresponds to the *Salvia africana-lutea - Ballota africana* Tall Shrub Strandveld (Community 3, De Villiers *et al.*, 1999), and species of Species Group K was diagnostic for this seed bank unit (Table 6.1). Species abundant in the seed bank of this unit were *Amellus microglossus* (Species Group M), *Bromus*

pectinatus (Species Group P), *Adenogramma littoralis, Polycarena pumila* and *Dimorphotheca pluvialis* (Species Group U). Most of these species were also abundant in the standing vegetation of Community 3. Species richness was higher in the standing vegetation than in the seed bank, for annuals, perennials and the total number of species (Figure 6.2). Similarity in species composition between standing vegetation and seed bank was higher for annuals than for perennial species. The total number of species yielded a similarity in species composition of 48.2% (Table 6.2). Therefore, if the revegetation goal is lowered from 60% to 30% (De Villiers *et al.*, 1999), topsoil replacement will be adequate for the restoration of Community 3 vegetation.

Seed bank unit 4

Corresponding to the *Ruschia versicolor - Odyssea paucinervis* Dwarf Shrub Strandveld (Community 4, De Villiers *et al.*, 1999), this unit was characterized by species of Species Group C (Table 6.1). *Ruschia caroli, Ruschia versicolor* and *Didelta carnosa* were diagnostic for the seed bank and were abundant in the standing vegetation, while *Gazania leiopoda* was diagnostic in the seed bank but not abundant in the standing vegetation. The annual *Wahlenbergia schlechteri* was unique and diagnostic to the seed bank. Species conspicuous in both the seed bank and the standing vegetation of this community included: *Zaluzianskya villosa* (Species Group J), *Hebenstretia dentata* (Species Group M), *Mesembryanthemum crystallinum, Pharnaceum exiguum* (Species Group Q), *Adenogramma littoralis, Polycarena pumila* and *Silene clandestina* (Species Group U) (Table 6.1). Three sub-units were recognized within this seed bank unit, which correspond to the three variants described by De Villiers *et al.* (1999). Total, annual and perennial species' richness was higher in the standing vegetation than in the seed bank. Similarity in annual species' composition, between the standing vegetation and the seed bank, was higher than that of perennial species (Table 6.2). Similarity in total species composition between the seed bank and the standing vegetation was 58.3%, which was the highest similarity value obtained for all communities, but was still less than the requirement of 60%. Topsoil replacement alone will not suffice for the revegetation of Community 4 with 60% of its original species.

Seed bank unit 5

This seed bank unit corresponds to the *Cephalophyllum spongiosum - Odyssea paucinervis* Coastal Strandveld (Community 5, De Villiers *et al.*, 1999). Species of Species Group B were diagnostic (Table 6.1) and included one annual species unique to the seed bank, *i.e. Frankenia pulverulenta*. Conspicuous species in this seed bank unit and its corresponding standing vegetation were *Zaluzianskya villosa, Pharnaceum aurantium* (Species Group J), *Mesembryanthemum crystallinum* and *Galenia sarcophylla* (Species Group Q). Species richness of annual, perennial and the total number of species was higher in the standing vegetation than in the seed bank (Figure 6.2), but perennial species predominated in both the standing vegetation and the seed bank. Consequently, perennial species' composition in the standing vegetation and the seed bank yielded the highest similarity for all communities (Table 6.2), and similarity in annual species' composition was lower than that for perennial species. Total species composition yielded a similarity of 48.8% between

the standing vegetation and the seed bank. With a revegetation goal of 60%, topsoil replacement alone will not be enough for the restoration of the vegetation of Community 5.

Seed bank unit 6

Seed bank unit 6 corresponds to the *Cladoraphis cyperoides* - *Lebeckia multiflora* Coastal Strandveld (Community 6, De Villiers *et al.*, 1999), and the two species of Species Group A (Table 6.1) are diagnostic for this unit, *i.e. Odyssea paucinervis* and *Lebeckia multiflora*. Species considered abundant in this seed bank unit but not in the standing vegetation included: *Zaluzianskya villosa* (Species Group J) and *Mesembryanthemum crystallinum* (Species Group Q). Species such as *Lampranthus godmaniae* and *Cladoraphis cyperoides* (De Villiers *et al.*, 1999) were diagnostic and/or conspicuous in the standing vegetation of Community 6, but were absent or less abundant in the seed bank (Table 6.1). Species abundant in both the seed bank and standing vegetation of this community were restricted to Species Group V. Annual and total species' richness was higher in the seed bank than in the standing vegetation, while that of perennial species was higher in the standing vegetation. Similarity in total species composition between the standing vegetation and the seed bank was 39.2% (Table 6.2), while that for annual species was lower than that of perennial species. This low similarity was probably due to the low species richness (Figure 6.2) recorded in both the standing vegetation and the seed bank. On its own, topsoil replacement will not be sufficient for the revegetation of Community 6.

Ordination

The positions of the different seed bank units on the CCA ordination diagram, along the first and second axes of the scatter diagram, are shown in Figure 6.3. Gradients associated with the first and second ordination axes could mainly be related to distance from the sea, which was also a main gradient associated with the standing vegetation. Factors associated with units situated closer to the coast, include: higher grass cover, salt spray and fog intensity (De Villiers *et al.*, 1999). Seed bank units 3 and 4 did not separate clearly on axis 1, 2, 3 or 4. The positions and composition of seed bank units on the ordination diagram correlated well with that obtained in the standing vegetation (De Villiers *et al.*, 1999).

CONCLUSIONS

The goal of revegetation of this area is to obtain a cover, which contains plant species from all the pre-mining communities of the mined area. The description of seed bank units and the comparison thereof with the standing vegetation can serve as a basis for determining the suitability of topsoil replacement as a sole means of post-mining revegetation of each of the plant communities identified prior to mining. Such descriptions will also aid in the selection of species that should be sown and/or transplanted.

An understanding of pre-mining seed bank units and their associated plant communities and habitats, is of vital importance for devising sound rehabilitation, management and conservation strategies.

The aim of the rehabilitation program in this area is to revegetate the area with indigenous plant species as soon as possible after mining has been completed (Environmental Evaluation Unit, 1990). It is recommended that this program concentrate on the perennial species, as these species dominate the standing vegetation and will help to stabilize the mined sand during the windy, dry and hot summer months (De Villiers *et al.*, 1999). However, annual species predominate in the soil seed bank of the study area, questioning the suitability of topsoil replacement as a sole means for revegetation.

Topsoil replacement should be sufficient for the revegetation of the entire area with species of Species Groups Q, T, U and V (Table 6.1), which contain 15% of the 216 lumped species recorded in the standing vegetation of the study area. Perennial species belonging to these Species Groups will contribute 6% to the restored species richness of the study area. Species groups J, M and N (4%) also contain species, which are abundant.

In general, total, annual and perennial species' richness of all communities to be mined was higher in the standing vegetation than in the seed bank. According to Sorensens' index, similarity in total species composition between the standing vegetation and the soil seed bank was 54.3%. Higher similarity in annual (74.8%) than perennial (43.1%) species composition was obtained between the standing vegetation and the soil seed bank.

Considering the dominance of perennial species in the standing vegetation, topsoil replacement alone will not be sufficient for the restoration of the mining area at the study site. However, 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 plant community boundaries may show little deviation from pre-mining plant community boundaries. The effectiveness of topsoil replacement for the restoration of a specific plant community will therefore depend mainly on the size and composition of the seed bank of that community.

The percentage of species occurring in Species Groups J, M, N, Q, T, U and V amounts to 19% (41 species) of the total standing vegetation species richness of the study area. Considering only perennials, species belonging to these groups will contribute 8% (17 species) to the total number of species recorded in the standing vegetation of this area. A revegetation goal of 30%, which approximately is the percentage of species common to almost all plant communities in the standing vegetation (De Villiers *et al.*, 1999), seems appropriate as a measure of the success of revegetation efforts in restoring the former structure and dominant species' composition by means of topsoil replacement. This percentage was confirmed also by Sorensens' indices for the study area as a whole and for individual communities. Even with a revegetation goal of 30%, sowing and transplanting of selected dominant species will be indispensable.

Perennial taxa, which could be recruited in sufficient numbers from the soil seed bank include: *Nestlera biennis, Ruschia bolusiae, Ehrharta calycina,* Geophyte spp., *Tetragonia virgata, Manochlamys albicans,*

Ruschia brevicyma, Hypertelis salsoloides, Hermannia spp. and *Zygophyllum morgsana*. Annual species abundant in the standing vegetation and the seed bank were *Senecio arenarius, Oncosiphon suffruticosum, Crassula expansa, Ficinia argyropa, Crassula umbellata, Manulea altissima, Isolepis marginata, Cotula thunbergii, Karroochloa schismoides, Pentaschistis patula* and *Helichrysum marmarolepis*. Most of these species were also abundant in the standing vegetation, proving the indispensable nature of topsoil replacement during revegetation efforts.

Shrub species such as *Lycium ferocissimum, Asparagus retrofractus, Rhus longispina, Othonna floribunda* and *Lebeckia multiflora* were abundant in almost all communities in the standing vegetation (De Villiers *et al.*, 1999), but were absent or less abundant in the soil seed bank, and should probably be reintroduced to mined areas by means of transplanting and sowing. Annuals and perennial herb species belonging to this category include *Limeum africanum, Lyperia tristis, Grielum grandiflorum, Microloma sagittatum, Hebenstretia dentata* and *Heliophila coronopifolia*.

Results from the seed bank study have indicated phytosociological affinities between communities in the standing vegetation. For example, Community 6 (De Villiers *et al.*, 1999) should be grouped with Communities 4 and 5 on account of the presence of *Odyssea paucinervis* in its seed bank, rather than with Communities 1, 2 and 3, where this species was found to be mostly absent, both in the standing vegetation and the seed bank. This phytosociological seed bank study therefore confirmed the affinity of Community 6 with Community 5 in the hierarchical classification of the standing vegetation.

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REFERENCES

ARNOLD, T.H. & DE WET, B.C. 1999. Plants of southern Africa: names and distribution. Electronic data-base, National Botanical Institute, Pretoria.

BOUCHER, C. & LE ROUX, A. 1990. Heavy mineral sand mining project assessment vegetation report. In: Environmental Evaluation Unit. *Anglo American Corporation: West Coast heavy mineral sands project - Supplementary Report*. Unpublished report. University of Cape Town, Cape Town. Section A5.

COFFIN, D.P. & LAUENROTH, W.K. 1989. Spatial and temporal variation in the seed bank of a semiarid grassland. *American Journal of Botany*, **76**: 53-58.

DE VILLIERS, A.J., VAN ROOYEN, M.W. & THERON, G.K. 1994. Comparison of two methods for estimating the size of the viable seed bank of two plant communities in the Strandveld of the West Coast, South Africa. *South African Journal of Botany*, **60**: 81-84.

DE VILLIERS, A.J., VAN ROOYEN, M.W., THERON, G.K. & VAN ROOYEN, N. 1999. Vegetation diversity of the Brand-se-Baai coastal dune area, West Coast, South Africa: A pre-mining benchmark survey for rehabilitation. *Land Degradation & Development*, **10**: 207-224.

ENVIRONMENTAL EVALUATION UNIT. 1990. *Anglo American Corporation: West Coast heavy mineral sands project.* Unpublished report. University of Cape Town, Cape Town.

FENNER, M. 1985. *Seed ecology.* Chapman & Hall, London.

GROSS, K.L. 1990. A comparison of methods for estimating seed numbers in the soil. *Journal of Ecology*, **78**: 1079-1093.

HENDERSON, C.B., PETERSEN, K.E. & REDAK, R.A. 1988. Spatial and temporal patterns in the seed bank and vegetation of a desert grassland community. *Journal of Ecology*, **76**: 717-728.

HENNEKEN, S. 1996a. *TURBOVEG – software package for input, processing, and presentation of phytosociological data.* IBN-DLO, University of Lancaster, Lancaster.

HENNEKEN, S. 1996b. *MEGATAB - a visual editor for phytosociological tables.* Giesen & Geurts, Ulft.

HILL, M.O. 1979. *TWINSPAN - A Fortran program for arranging multivariate data in an ordered two-way table by classification of the individuals and attributes.* Cornell University, New York.

HOOGERVORST, A. 1990. Legislation identification & authorities' consultation study. In: Environmental Evaluation Unit. *Anglo American Corporation: West Coast heavy mineral sands project - Supplementary Report.* Unpublished report. University of Cape Town, Cape Town. Section C7.

LOW, A.B. & REBELO, A. 1998. *Vegetation of South Africa, Lesotho and Swaziland.* Department of Environmental Affairs & Tourism, Pretoria.

MAJOR, J. & PYOTT, W.T. 1966. Buried, viable seeds in two California bunchgrass sites and their bearing on the definition of a flora. *Vegetatio*, **13**: 253-282.

MUELLER-DOMBOIS, D. & ELLENBERG, H. 1974. *Aims and methods of vegetation ecology.* Wiley, New York.

ROBERTS, H.A. 1981. Seed banks in soils. *Advances in Applied Biology*, **6**: 1-55.

TER BRAAK, C.J.F. 1997. *CANOCO – a Fortran program for canonical community ordination by [partial] [detrended] [canonical] correspondence analysis, principal component analysis and redundancy analysis (version 3.15).* Report LWA-88-02, Agricultural Mathematics Group, Wageningen.

THOMPSON, K. 1992. The functional ecology of seed banks. In: Fenner, M. (ed). *Seeds: The ecology of regeneration in plant communities.* CAB International, Wallingford. pp. 231-258.

WERGER, M.J.A. 1974. On concepts and techniques applied in the Zürich-Montpellier method of vegetation survey. *Bothalia*, **11**: 309-323.

CHAPTER 7

SIMILARITY BETWEEN THE SOIL SEED BANK AND THE STANDING VEGETATION IN THE STRANDVELD SUCCULENT KAROO, SOUTH AFRICA

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ABSTRACT

The similarity in species composition and abundance between the soil seed bank and its associated vegetation was studied in six vegetation units of the Strandveld Succulent Karoo, South Africa. A total of 103 taxa were recorded in the vegetation, of which 34 taxa were also present in the seed bank. Five taxa were unique to the soil seed bank. In general, the taxa most abundant in the vegetation were also recorded in the seed bank and *vice versa*. Mean seed bank density varied between different plant types. Perennial taxa were most abundant in the vegetation, while annual taxa were most abundant in the seed bank. Annual taxa (excluding grasses) yielded the highest similarity between vegetation and seed bank (67.9%), while that of perennial (excluding grasses) and grass taxa were 34.2% and 40.0% respectively. An overall similarity of 47.0% between the seed bank and its associated vegetation was obtained for this part of the Strandveld Succulent Karoo. The seed bank of the study site will be a good source of future annual vegetation, but not of perennial vegetation. Topsoil replacement, sowing and transplanting of selected species will be essential for the success of post-mining revegetation efforts following complete destruction of the existing vegetation. Annual species may be recruited from the soil stored seed bank, while many perennial species will have to be reintroduced by means of sowing and/or transplanting.

Key words: Mining; Namaqualand; revegetation; seed bank density; species composition; vegetation density

INTRODUCTION

A soil seed bank is defined as the number, store, or density of viable seeds in the soil at a given time, representing a living record of the recent vegetation of an area. Not all species growing at a site are represented in its seed bank, but seeds of species not currently growing at the site may be present (Leck *et al.*, 1989; Van der Valk *et al.*, 1992; Warr *et al.*, 1993). Spatial patterns of vegetation and seed banks may have a direct effect on the dynamics, conservation and sustainable management of arid ecosystems (Bertiller, 1998).

The majority of seed bank studies have been carried out in grasslands and arable fields. There are less data available from woodlands, heathlands, dunes, deserts, marshes, arctic/alpine and aquatic communities (Bakker *et al.*, 1996). Only a small number of studies have been conducted on the seed banks of the arid areas of South Africa (Van Rooyen & Grobbelaar, 1982; Dean *et al.*, 1991; Esler *et al.*, 1992; Esler, 1993; De

Villiers *et al.*, 1994). The role of the seed bank in restoration and revegetation studies, other than arable land, has been the subject of a number of studies in recent years (Levassor *et al.*, 1990; Aerts *et al.*, 1995; Bakker *et al.*, 1996; Kotanen, 1996).

The degree of correlation between the species composition of the seed bank and that of the associated plant community is of considerable interest in restoration projects. A lack of correspondence between the species present in the seed bank and in the current vegetation has been observed in a range of vegetation types (Thompson & Grime, 1979; Smith & Kadlec, 1983; Pratt *et al.*, 1984; Bakker, 1989). In frequently disturbed habitats, the species composition of the seed bank and the vegetation is usually similar, for example in arable fields (Wilson *et al.*, 1985). In undisturbed habitats there is generally less correspondence between the species present in the seed bank and the vegetation (Warr *et al.*, 1993).

The mining of heavy minerals along the western coast of South Africa will lead to the total destruction of the vegetation in mined areas. Rehabilitation of the area, which is required by law, should restore the mined area to a state as close as possible to the state of the area before mining commenced, as soon as possible after mining of an area has been completed (Environmental Evaluation Unit, 1990). One of the viable options to revegetate the area is topsoil replacement. The seeds present in the soil are potentially useful in restoration projects where establishment of plant cover is desired (Skoglund, 1992; Kotanen, 1996). However, if the similarity between the seed bank and its associated vegetation is limited, the seed bank alone cannot be used for the restoration of that plant community (Warr *et al.*, 1993).

The aim of this study was to determine whether topsoil replacement would be sufficient for the restoration of the pre-mining standing vegetation of mined areas in the Strandveld Succulent Karoo. The degree of similarity between the seed bank and standing vegetation was used to predict species which will most probably be recruited from replaced topsoil, and those which will have to be reintroduced by means other than the seed bank contained in replaced topsoil.

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 (De Villiers *et al.*, 1999). 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 (De Villiers *et al.*, 1999). The average annual temperature is 15.8°C 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) (De Villiers *et al.*, 1999). Frequent easterly berg winds, which blow from the interior, bring hot, dry conditions to the coast (Environmental Evaluation Unit, 1990).

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

Only the five communities situated in the vicinity of the western mining area (Communities 2 – 6), which is being mined first, were investigated. Community 1 almost solely constitutes the eastern mining area, and was not investigated. The three variants of Community 4 were investigated individually, while the two variants of Community 2 were not. Since the coastal Communities 5 and 6 are not included in the area to be mined, these communities have been investigated as a single vegetation unit.

Within each of these vegetation units, two sites were randomly selected using 1:50 000 aerial photographs. At each site, both the density and species richness of the standing vegetation and the soil seed bank were determined. During autumn 1995, 15 soil samples were collected linearly at intervals of two meters, at each site. 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.

From each of the 15 samples per site, a subsample of 100 cm^3 was spread evenly on top of sterile sand in a 1.5 dm^3 pot and placed at ambient conditions at the University of Pretoria, some 1 200 km north-east of Brand-se-Baai. The samples were watered daily and emerged seedlings were marked and counted. Half strength Arnon and Hoagland's complete nutrient solution (Hewitt, 1952) was applied fortnightly. Emerged seedlings were identified and removed. Treatment of the samples continued for a period of three months, whereafter the top layer of soil in the pots was stirred. A second germination period lasted three months. After a total germination period of six months, only the pots containing species not yet identified, were retained.

During early spring of 1995, 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 all perennial and annual plant species (excluding grass species) were recorded. For grass species (Poaceae), percentage cover was estimated in each quadrant. In this paper, grass species are not included in the perennial and annual plant type categories, but are dealt with as a separate category. Species names conform to those of Arnold & De Wet (1999).

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 standing vegetation density/cover values for each species (individuals m^{-2}) from each plot were transformed to scores on a 1 – 9 abundance scale (Standing vegetation (excluding grasses): 1 = >0 – 0.05, 2 = >0.05 – 0.1, 3 = >0.1 – 0.5, 4 = >0.5 – 1, 5 = >1 – 2, 6 = >2 – 5, 7 = >5 – 10, 8 = >10 – 20, 9 = >20) (Grasses: 1 = >0 - 0.05, 2 = >0.05 – 0.1, 3 = >0.1 – 0.5, 4 = >0.5 – 1, 5 = >1 – 2, 6 = >2 – 3, 7 = >3 – 5, 8 = >5 – 10, 9 = >10). The seed bank data (emerged seedlings m^{-2}) were also transformed to scores on a 1 – 9 abundance scale (Seed bank: 1 = >0 - 100, 2 = >100 - 200, 3 = >200 - 300, 4 = >300 - 500, 5 = >500 - 750, 6 = >750 – 1 000, 7 = >1 000 – 1 500, 8 = >1 500 – 2 000, 9 = >2 000). These limits were chosen so that the density distribution of the nine classes would be similar for the vegetation and seed bank data.

For vegetation and soil seed bank, the density of individual m^{-2}, frequency (%) as well as the mean number of taxa per vegetation unit 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 (*ISs*)(Mueller-Dombois & Ellenberg, 1974):

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

where in this case c is the number of species common to both vegetation and seed bank, A is the total number of species recorded in the standing vegetation, and B is the total number of species recorded in the soil seed bank.

Spatial distribution of the soil seed bank was determined by calculating the variance/mean ratio (Odum, 1971). If this ratio is found to be greater than 1, the distribution is clumped; if it is less than 1, distribution is regular; if not different from 1, the distribution is random.

Results were analysed statistically using the least significant difference (LSD) one-way analysis of variance (ANOVA), multi-factor ANOVA and multiple range test of the Statgraphics 5.0[1] computer program, to test for significant differences at a 95% confidence level.

[1] Statgraphics 5.0, 1989. STSC, Inc., U.S.A.

RESULTS

Standing vegetation

A total of 103 taxa were recorded in the standing vegetation of the Strandveld Succulent Karoo (Table 7.1). The four most abundant taxa were Geophyte spp. (4.792 plants m^{-2}), *Odyssea paucinervis* (1.886 % cover m^{-2}), *Gazania leiopoda* (1.308 plants m^{-2}) and *Tetragonia microptera* (1.157 plants m^{-2}). With the exception of *Ehrharta calycina*, no species obtained a frequency of more than 50% in the vegetation.

Vegetation unit 2 and vegetation unit 1 yielded the highest and lowest number of taxa, respectively (Figure 7.1a). In general, perennials constituted the highest number of taxa, while grass species constituted the lowest number of taxa recorded in each vegetation unit (Figure 7.1a).

The mean perennial plant density (Table 7.2) varied from 1.8 plants m^{-2} in vegetation unit 4 to 20.8 plants m^{-2} in vegetation unit 6. For annual plants, the highest and lowest densities were recorded in vegetation units 5 (11.0 plants m^{-2}) and 6 (2.3 plants m^{-2}) respectively. Percentage grass cover m^{-2} was highest in vegetation unit 3 (7.4 %) and lowest in vegetation unit 5 (0.3 %).

Seed bank

The soil seed bank within these samples of the Strandveld Succulent Karoo yielded a total number of 39 taxa (Table 7.1). Due to the high mortality of emerged seedlings, a total of 1714 seedlings m^{-2} were not identified (Table 7.1). The four most abundant taxa in the seed bank were annuals, *i.e. Karroochloa schismoides* (457 seedlings m^{-2}), *Crassula expansa* (316 seedlings m^{-2}), *Oncosiphon suffruticosum* (254 seedlings m^{-2}) and *Adenogramma littoralis* (231 seedlings m^{-2}). The annual grass *Karroochloa schismoides* also obtained the highest frequency in the seed bank (19.5%).

At the vegetation unit level, the highest number of taxa present in the seed bank was recorded in vegetation unit 2, while the lowest number of taxa was recorded in vegetation unit 1 (Figure 7.1b). Annual taxa constituted the highest number of taxa recorded in each vegetation unit, and grass taxa the lowest (Figure 7.1b).

Mean seedling densities of perennial taxa ranged from 101.5 seedlings m^{-2} in vegetation unit 1 to 575.2 seedlings m^{-2} in vegetation unit 2 (Table 7.2). Vegetation unit 2 yielded the highest seedling density for annual taxa. The highest mean seedling density of grass taxa were recorded in vegetation unit 4, while that of unidentified taxa were recorded in vegetation unit 6. With the exception of vegetation unit 4 of which the seed bank was predominated by unidentified taxa, the seed bank of all other vegetation units were predominated by annual taxa (Table 7.2).

Table 7.1. Mean density (plants/seeds per m^2), mean percentage cover (grass taxa in the standing vegetation) and frequency (%) of taxa in the Strandveld Succulent Karoo. Data from two replicates in each of six vegetation units have been lumped. Vegetation data based on 1 200 square-metre subplots and seed bank data based on 180 soil samples

Species	Mean number of plants/seeds or % cover per m^2		Frequency (%)	
	Vegetation	Seed bank	Vegetation	Seed bank
Taxa recorded only in the vegetation				
Amellus tenuifolius (P)	0.006		0.5	
Arctotheca calendula (A)	0.102		5.9	
Arctotis adpressa (A)	0.041		2.6	
Aspalathus divaricata (P)	0.006		0.6	
Asparagus aethiopicus (P)	0.003		0.3	
Asparagus asparagoides (P)	0.066		4.1	
Asparagus capensis (P)	0.073		5.8	
Asparagus fasciculatus (P)	0.048		3.1	
Asparagus retrofractus (P)	0.006		0.6	
Ballota africana (P)	0.001		0.1	
Brassica tournefortii (A)	0.262		7.5	
Cephalophyllum spongiosum (P)	0.022		1.8	
Chaetobromus dregeanus (P)	0.058		3.7	
Cissampelos capensis (P)	0.002		0.2	
Cladoraphis cyperoides (P)	0.004		0.3	
Coelanthum semiquinquefidum (A)	0.015		1.2	
Crassula muscosa (P)	0.001		0.1	
Crassula tomentosa (P)	0.051		0.9	
Cucurbitaceae (P)	0.181		7.5	
Didelta carnosa (A)	0.144		6.8	
Drosanthemum calycinum (P)	0.004		0.2	
Euphorbia caput-medusae (P)	0.006		0.6	
Euphorbia mauritanica (P)	0.003		0.3	
Euphorbia sp.(P)	0.006		0.5	
Exomis microphylla (P)	0.005		0.4	
Felicia dregei (P)	0.001		0.1	
Ficinia argyropa (A)	0.004		0.3	
Galenia africana (P)	0.001		0.1	
Galenia sarcophylla (P)	0.029		1.9	
Galium tomentosum (P)	0.003		0.3	
Grielum grandiflorum (P)	0.404		17.3	
Grielum humifusum (A)	0.087		5.9	
Hebenstretia repens (A)	0.068		4.2	
Helichrysum hebelepis (P)	0.018		1.5	
Heliophila coronopifolia (A)	0.058		4.3	
Lebeckia lotonoides (P)	0.083		4.1	
Lebeckia multiflora (P)	0.059		4.1	
Leipoldtia jacobeniana (P)	0.019		1.3	
Limeum africanum (A)	0.318		14.9	
Lycium ferocissimum (P)	0.015		1.5	
Lycium sp. (P)	0.006		0.6	
Manulea cinerea (P)	0.010		0.7	
Melolobium exudans (P)	0.013		1.3	
Microloma sagittatum (P)	0.017		1.7	
Nemesia ligulata (A)	0.025		1.8	
Odyssea paucinervis (P)	1.886		38.2	
Othonna floribunda (P)	0.103		7.3	
Pelargonium gibbosum (P)	0.003		0.3	
Pelargonium senecioides (A)	0.320		5.8	
Pelargonium sp. (P)	0.001		0.1	
Phyllobolus spp. (P)	0.001		0.1	
Pteronia onobromoides (P)	0.002		0.2	
Ruschia bolusiae (P)	0.086		5.3	
Ruschia brevicyma (P)	0.043		4.1	
Ruschia cymosa (P)	0.045		3.3	
Ruschia tecta (P)	0.023		1.8	
Ruschia tumidula (P)	0.002		0.2	
Ruschia versicolor (P)	0.013		1.0	
Salvia africana-lutea (P)	0.005		0.5	
Senecio bulbinifolius (P)	0.001		0.1	
Sonderina tenuis (A)	0.090		2.8	
Stipagrostis zeyheri (P)	0.010		1.0	
Sutera triste (A)	0.110		5.9	
Thesium spinescens (P)	0.014		1.4	
Tribolium hispidum (A)	0.001		0.1	
Trichogyne ambigua (P)	0.008		0.4	
Tripteris clandestina (A)	0.085		4.7	
Tripteris oppositifolia (P)	0.013		1.3	
Zygophyllum morgsana (P)	0.114		10.6	

Table 7.1. (Continued)

Species	Mean number of plants/seeds or % cover per m^2		Frequency (%)	
	Vegetation	Seed bank	Vegetation	Seed bank
Taxa recorded only in the seed bank				
Bromus pectinatus (A)		11.283		1.1
Crassula umbellata (A)		78.950		5.6
Pentaschistis patula (A)		33.833		2.2
Wahlenbergia schlechteri (A)		16.917		1.7
Zaluzianskya villosa (A)		28.183		2.8
Unidentified species		1714.283		65.0
Taxa recorded in the vegetation and seed bank				
Adenogramma littoralis (A)	0.448	231.200	10.2	7.3
Arctotis spp.(P)	0.033	5.633	2.6	0.6
Chrysocoma longifolia (P)	0.002	11.283	0.2	1.1
Conicosia pugioniformis (A)	0.108	5.633	5.9	0.6
Crassula expansa (A)	0.018	315.783	1.3	11.2
Dimorphotheca pluvialis (A)	0.406	107.133	8.8	5.6
Ehrharta calycina (P)	0.968	140.967	50.3	11.7
Eriocephalus africanus (P)	0.073	16.917	6.2	1.7
Felicia merxmuelleri (A)	0.013	5.633	1.0	0.6
Gazania leiopoda (P)	1.308	39.467	5.8	2.8
Geophyte spp. (P)	4.792	78.950	42.6	7.8
Hebenstretia dentata (P)	0.038	11.283	3.0	1.1
Helichrysum marmarolepis (A)	0.454	33.833	12.3	2.8
Hermannia spp. (P)	0.550	5.633	18.4	0.6
Isolepis marginata (A)	0.184	22.567	5.5	2.2
Karroochloa schismoides (A)	0.144	456.767	13.9	19.5
Manochlamys albicans (P)	0.008	22.567	0.8	1.7
Manulea altissima (A)	0.062	28.183	4.0	2.8
Manulea pusilla (A)	0.001	22.567	0.1	2.2
Mesembryanthemaceae (P)	0.002	11.283	0.2	1.1
Mesembryanthemum crystalinum (A)	0.455	22.567	14.3	2.3
Nemesia bicornis (A)	0.193	16.917	9.8	1.7
Nestlera biennis (P)	0.258	16.917	7.7	1.7
Oncosiphon suffruticosum (A)	0.128	253.750	8.8	16.7
Pharnaceum aurantium (P)	0.095	11.283	5.9	1.1
Pharnaceum exiguum (A)	0.143	33.833	6.9	3.3
Polycarena pumila (A)	0.178	56.383	8.8	4.5
Senecio arenarius (A)	0.255	191.717	15.2	11.1
Silene clandestinum (A)	0.212	22.567	7.3	2.3
Tetragonia microptera (A)	1.157	39.467	8.5	3.9
Tetragonia virgata (P)	0.299	28.183	22.3	2.8
Ursinia speciosa (A)	0.011	11.283	1.0	1.1
Vanzijlia annulata (P)	0.243	16.917	10.7	1.7
Wahlenbergia paniculata (A)	0.174	28.183	7.6	2.8

P - perennial
A - annual

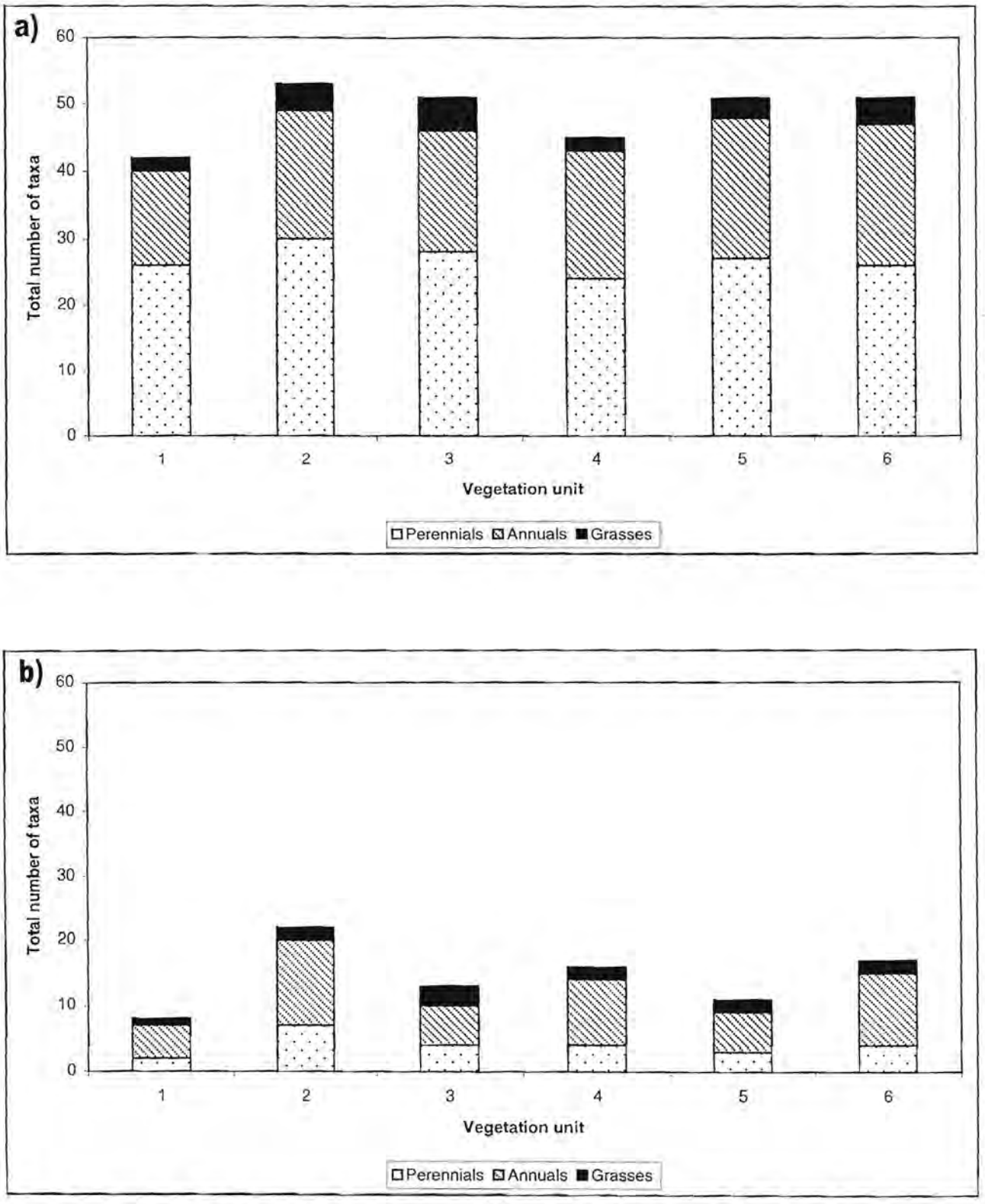

Figure 7.1. Total number of perennial, annual and grass taxa recorded in the a) standing vegetation and the b) seed bank, for six vegetation units of the Strandveld Succulent Karoo.

Table 7.2. Mean plant/seed density and mean % cover (grass taxa in the vegetation)(± standard deviation), for both the standing vegetation and the soil seed bank determined in six vegetation units

Vegetation unit number	Plant type	Number of plants m^{-2} or % cover in the vegetation	Number of seedlings m^{-2} in the seed bank
1	Perennials	6.1 ± 1.7	101.5 ± 33.8
	Annuals	5.2 ± 1.8	981.2 ± 236.8
	Grasses	6.2 ± 4.5	101.5 ± 33.8
	Unidentified	0.0 ± 0.0	1184.2 ± 710.5
2	Perennials	15.5 ± 13.3	575.2 ± 236.8
	Annuals	4.6 ± 1.0	3417.3 ± 372.2
	Grasses	7.3 ± 5.8	372.2 ± 33.8
	Unidentified	0.0 ± 0.0	1150.4 ± 406.0
3	Perennials	5.1 ± 2.0	236.8 ± 33.8
	Annuals	8.4 ± 2.1	609.0 ± 338.3
	Grasses	7.4 ± 1.5	473.7 ± 67.7
	Unidentified	0.0 ± 0.0	1184.2 ± 169.2
4	Perennials	1.8 ± 0.4	236.8 ± 101.5
	Annuals	4.0 ± 1.0	1827.0 ± 1285.7
	Grasses	1.2 ± 0.1	2199.2 ± 778.2
	Unidentified	0.0 ± 0.0	2334.6 ± 642.9
5	Perennials	5.8 ± 4.3	169.2 ± 33.8
	Annuals	11.0 ± 10.2	1082.7 ± 812.0
	Grasses	0.3 ± 0.1	406.0 ± 67.7
	Unidentified	0.0 ± 0.0	1691.7 ± 135.3
6	Perennials	20.8 ± 8.9	338.3 ± 0.0
	Annuals	2.3 ± 0.4	1454.9 ± 372.2
	Grasses	0.6 ± 0.5	304.5 ± 169.2
	Unidentified	0.0 ± 0.0	2639.1 ± 203.0

Standing vegetation *versus* seed bank

Of the 103 taxa recorded in the standing vegetation of the Strandveld Succulent Karoo, only 34 taxa (31%) were present in the seed bank (Table 7.1). However, it has to be borne in mind that the total area sampled for determining species composition and density of the soil seed bank represented only 0.06% of the total area sampled in the standing vegetation. Most of the taxa present only in the vegetation (64%) had low densities (< 0.5 plants m^{-2} for perennial and annuals), percentage cover (< 2% for grasses) and frequencies (< 40%). Five taxa (5%) were recorded only in the seed bank, all of which had frequencies lower than 6% and densities lower than 80 seeds m^{-2}. Generally, the taxa most abundant in the vegetation were also recorded in the seed bank and *vice versa*.

In general, perennial species predominated in the standing vegetation, while annual species predominated the soil seed bank (Figures 7.1a & 7.1b). In all six vegetation units, seed density in the seed bank was higher than plant density in the standing vegetation (Table 7.2). The soil seed bank of this part of the Strandveld Succulent Karoo had a clumped spatial distribution (Table 7.3a). This was also the distribution pattern within each of the vegetation units individually. Perennial species approached a random distribution in the seed bank (Table 7.3b), while annual, grass and unidentified species had a clumped spatial distribution pattern.

The PCA ordination separated seed bank and vegetation data along the first ordination axis (Figure 7.2), which could be attributed to differences in species composition between the soil seed bank and the standing vegetation. Poor separation between soil seed bank vegetation units along the second ordination axis could be ascribed to the similarity in annual species, as these predominate in the seed bank (Figure 7.1b). With the exception of vegetation unit 5, clear separation between vegetation units in the standing vegetation (Figure 7.2) could be attributed to the dissimilarity in perennial species, as these predominate in the standing vegetation (Figure 7.1a). The affinity between the standing vegetation and seed bank of vegetation unit 2 (Figure 7.2) was possibly due to the high similarity in annual species, compared to other plant types (Figure 7.3). High similarity in grass species (Figure 7.3) may be responsible for the grouping of the standing vegetation of one site of vegetation unit 5 with its corresponding seed bank (Figure 7.2). Although the similarity in grass species was 100% for vegetation unit 4 (Figure 7.3), clear separation between the standing vegetation and the seed bank of this vegetation unit (Figure 7.2) was probably due to the low similarity in perennial species and/or the low grass species richness (Figure 7.1).

Calculation of Sorensen's index indicated a 47.9% similarity between the vegetation and the seed bank of the study area (Figure 7.3). Highest similarity occurred between annual taxa (67.9%) recorded in the vegetation and the seed bank, while perennial and grass taxa had low similarities, *i.e.* 34.2% and 40.0% respectively. Sorensen's index indicated that similarity between the vegetation and the seed bank ranged from 29.0% in vegetation unit 5 to 45.3% in vegetation unit 2 (Figure 7.3). With the exception of vegetation units 2 and 6, grass taxa yielded the highest similarities between the vegetation and the seed bank (> 33% - 100%). Perennial taxa yielded the lowest similarity (< 33%) between vegetation and seed bank, in all vegetation units. Similarity in annual taxa between seed bank and standing vegetation ranged from 35 – 65%.

Table 7.3a. Mean, variance, and spatial distribution of the soil seed bank (sample $^{-1}$) determined in six vegetation units of the Strandveld Succulent Karoo

Vegetation unit	Mean (*m*)	Variance (*V*)	*V*/*m*	Distribution
1	2.33	6.71	2.88	Clumped
2	5.40	18.59	3.44	Clumped
3	2.47	5.57	2.26	Clumped
4	6.60	35.01	5.30	Clumped
5	3.27	9.37	2.87	Clumped
6	4.67	12.16	2.61	Clumped
All	4.12	16.63	4.03	Clumped

Table 7.3b. Mean, variance, and spatial distribution of the soil seed bank (sample $^{-1}$) determined for different plant types in the Strandveld Succulent Karoo

Plant type	Mean (*m*)	Variance (*V*)	*V*/*m*	Distribution
Perennials	0.27	0.24	0.90	Random
Annuals	1.54	6.22	4.04	Clumped
Grasses	0.64	2.35	3.65	Clumped
Unidentified	1.68	3.81	2.27	Clumped

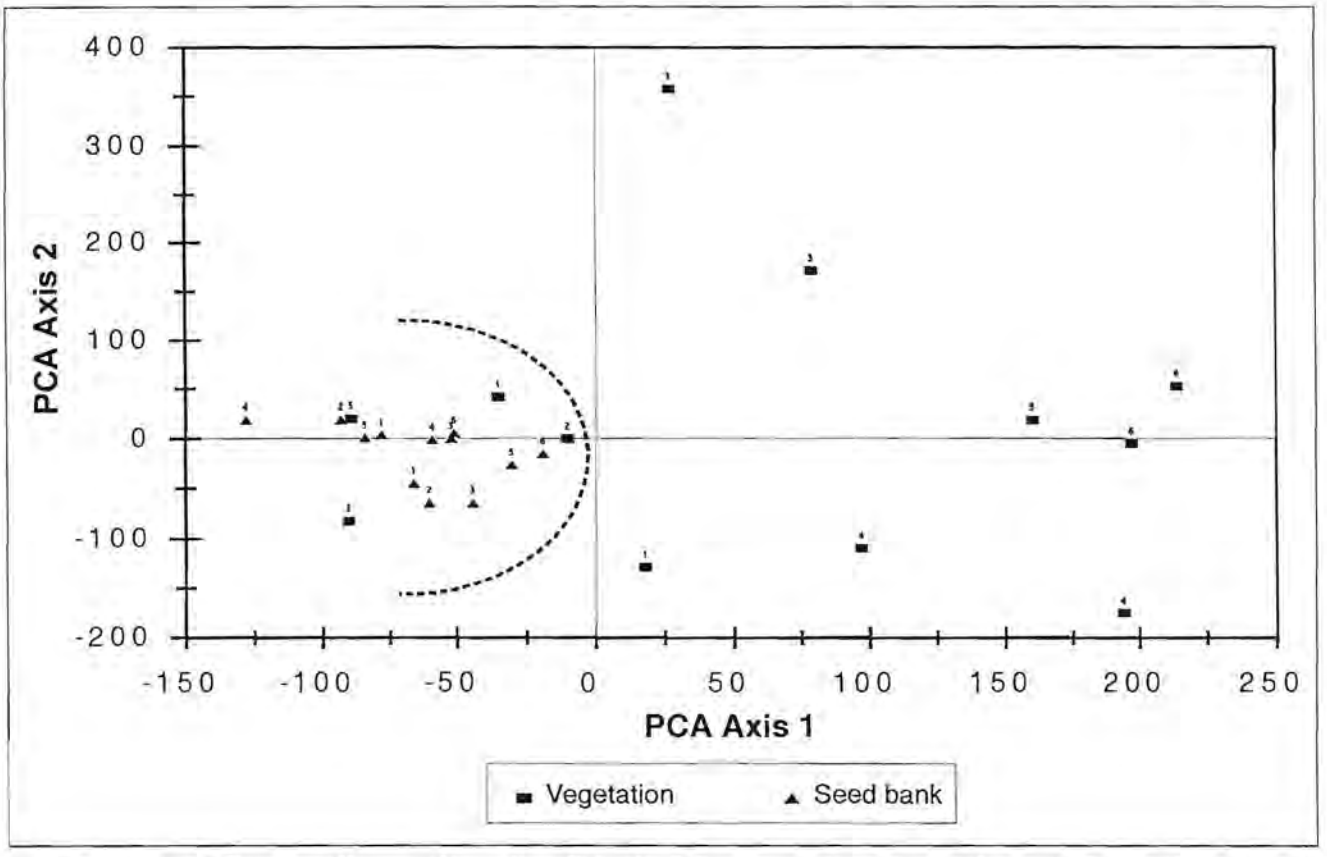

Figure 7.2. Ordination diagram based on Principal Component analysis of vegetation and seed bank density data, for six Strandveld Succulent Karoo vegetation units (Eigen1 = 0.153; eigen2 = 0.119; scaling = 2).

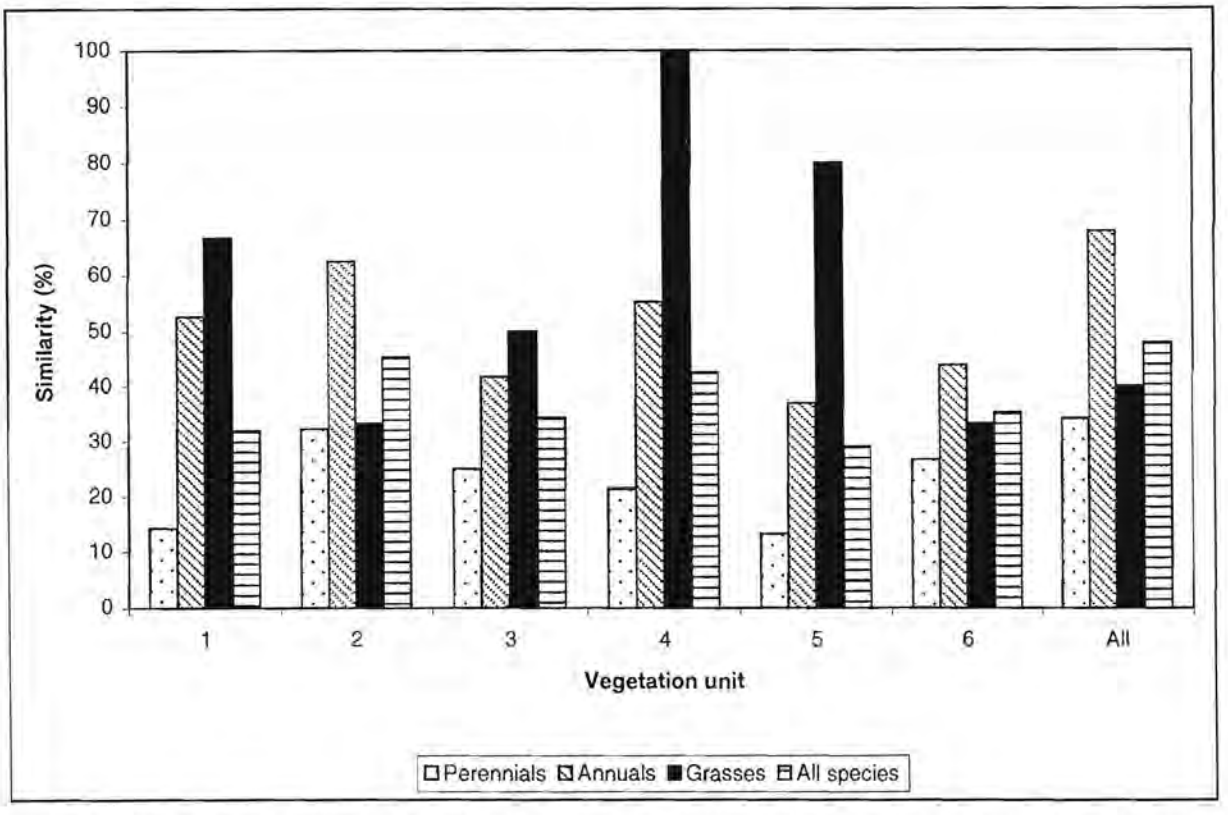

Figure 7.3. Similarity in number of taxa (%) according to Sorensen's Index of Similarity, between the standing vegetation and the seed bank, for different plant types in the Strandveld Succulent Karoo.

DISCUSSION

The general dissimilarity between the seed bank and its associated vegetation was manifested by dissimilarities in species composition, plant/seedling densities and frequencies. Similar lack of correspondence between vegetation and seed banks have been reported for agricultural habitats (Roberts & Stokes, 1966; Caixinhas *et al.*, 1998), grassland communities (Milberg & Persson, 1994), forests (Granstrom, 1982), coastal plain forests (Matlack & Good, 1990), sand dunes (Planisek & Pippen, 1984) and desert environments (Khan, 1993; Aziz & Khan, 1996), and reflects such factors as absolute seed production, rate and depth of burial, and loss of viability (Archibold, 1981). However, in some desert ecosystems the species composition of the seed bank proved to be similar to the standing vegetation (Henderson *et al.*, 1988; Ohga, 1992). In general, Fenner (1985) suggested that similarity of vegetation and seed bank is greatest in frequently disturbed communities, and difference increases as succession progresses. Species represented in the seed bank may have been derived from vegetation present at the site in previous years (Warr *et al.*, 1993).

In most habitats, densities of seeds in the soil do not correlate well with densities of plants in time or space (Harper, 1977; Kemp, 1989; Silvertown & Lovett-Doust, 1995). The existing vegetation at the study site was not well represented in the seed bank samples, but the seed bank taxa were well represented in the standing vegetation. The soil seed bank was predominated mainly by annual taxa, while perennials were scarce and infrequent. Also, annual taxa in the vegetation had higher similarities with their seed banks, than did perennial taxa. Several perennial species of the Karoo have large seeds (> 5 mm) and accumulate transient seed banks, while small, persistent seeds are characteristic of many annual species (Esler, 1999). Large seeds of long-lived perennials are more likely to be predated than small seeds of annual species (Bertiller, 1998). This, and their low seed production, the retention of seeds in the canopy, possible seed dormancy and short longevity, might be some of the causes of their small numbers observed in the seed bank (Van Rooyen & Grobbelaar, 1982; Esler *et al.*, 1992; Chambers, 1993; Bertiller, 1998). The contrasting pattern of the soil seed bank of annual compared with perennial species (small and numerous vs. large and scarce seeds) has previously been reported and associated with seed size and availability of safe sites for germination and plant establishment (Graham & Hutchings, 1988; Hegde *et al.*, 1991; Ohga, 1991). Most of the annual species from the Succulent Karoo accumulate a persistent seed bank (Van Rooyen & Grobbelaar, 1982; De Villiers *et al.*, 1994).

The reduced seed bank of perennial taxa does not seem to be critical in maintaining their cover in the short term, since the density of standing individuals of this group does not depend on successful annual seed set, germination and establishment of young plants. Additionally, recruitment by perennial taxa is probably more limited by the availability of safe sites (Andersen, 1989; Esler, 1993). The reverse applies for annual taxa, which depend on the periodic re-establishment of new individuals to maintain their populations in an area. In this case, spatial and temporal patterns of the soil seed bank may play an important role in their conservation (Bertiller, 1998).

Those taxa recorded only in the seed bank were mainly annuals with relatively low densities and frequencies. The magnitude of the discrepancy in abundance between the seed bank and vegetation is

recognized as an indicator of its seed bank persistency (Thompson & Grime, 1979; Bakker, 1989; Kirkham & Kent, 1997). The five taxa recorded only in the seed bank were observed in nearby plant communities, stressing the fact that seed bank taxa were well represented in the standing vegetation.

Some habitats like deserts are risky for the survival of plant species, especially for annuals, because conditions may become so severe in some years that all individuals die before they have a chance to reproduce. One way for a species to survive in risky environments is to have a persistent seed bank. Thus, if a species fails to produce seeds in one year, the presence of a seed bank ensures that the species can persist at the site without immigration (Baskin & Baskin, 1998).

As in most arid ecosystems, the frequency distribution of seeds in soil samples is highly kurtotic (Kemp, 1989; Ohga, 1992; Bertiller, 1998), since most samples had a few or no seeds and only a minor proportion had a large number of seeds. This general spatial pattern may in part be the result of the relatively short seed dispersal distances that characterize the majority of desert plants (Ellner & Shmida, 1981), or the consequence of directed dispersal by ants or rodents (Van Rheede van Oudtshoorn & Van Rooyen, 1999). Spatial and temporal heterogeneity is important to the entire community through the relationships between seeds, germination and seedling competition, plant populations, and seed predation by granivores (Reichman, 1984).

In this study, as in most restoration and creation projects, a precise estimate of seed density for a particular species in the seed bank was not needed. An estimate of the relative abundance of species is usually sufficient. Even a list of species present in the seed bank is enough to establish which desirable and undesirable species are present or absent (Van der Valk *et al.*, 1992).

Revegetation

Seed banks may be important in the long-term survival of individual species, as well as plant communities. However, not all species in a community are represented in the seed bank, and some species are present in the seed bank, but do not occur in the extant vegetation (Baskin & Baskin, 1998). Since mining activities will destroy the standing vegetation at the study site and topsoil will be used in the revegetation process, the size and composition of the seed bank will predict the future vegetation. This is true for at least the early stages of succession in the mined area. According to Kotanen (1996), theory predicts that at least the early stages of revegetation should be influenced by the way in which disturbance interacts with the seed bank.

Post-mining vegetation should conform as close as possible to the vegetation present prior to mining activities. Factors such as species richness, plant abundance and cover will be important measures for estimating the success of revegetation efforts. The pre-mining standing vegetation was predominated by perennial species and the goal of restoration efforts should concentrate on the revegetation of these species. However, perennial species were poorly represented in the soil seed bank, and most of the large seeded perennials that were present accumulate a transient rather than a persistent seed bank. For the long-term revegetation goals at the study site, recruitment from the seed bank alone will therefore not be sufficient.

The large seeded perennials will probably not be recruited in sufficient numbers from the topsoil replaced seed bank. However, the seeds of some of these species are wind dispersed and reintroduction of these species to the post-mining area may occur naturally from surrounding vegetation. Artificially established patches of perennial vegetation may also act as sources of seeds that may eventually reach other patches of bare soil (Bouza & Del Valle, 1993; Bertiller, 1998). Many small seeded perennial species (mainly belonging to the Mesembryanthemaceae) accumulate persistent aerial seed banks (Chapter 11), but their seeds are not well adapted to long range dispersal. Because the standing vegetation, including aerial seed banks, will be destroyed during the mining process, adult plants of these species should be transplanted on mined areas during revegetation efforts. In some species, transplanting may also result in a beneficial shortening of the period between revegetation and seed production. Revegetation of mined areas at the study site with perennials should therefore involve topsoil replacement, sowing and transplanting of selected species.

The topsoil stored seed bank will be a vital source of annual species recruitment. Seeds are the only mechanism of reproduction in annuals, and many of these species accumulate large persistent seed banks (Esler, 1999). The seeds present in the seed bank are potentially useful in restoration projects where establishment of plant cover is desired, for example to reduce soil erosion (Skoglund, 1992).

Buried seeds can also have important implications for conservation management where preferred species have been lost from the vegetation but survive in the seed bank. Species recorded only in the seed bank were previously observed in neighbouring vegetation, but detailed seed bank studies in these areas will determine the status of rare or endangered seed bank species.

Topsoil replacement, sowing and transplanting should all be considered for the revegetation of mined areas in the Strandveld Succulent Karoo. Annual species will be recruited from the topsoil stored seed bank. However, all will depend on the period of stockpiling before being used in restoration, as this can negatively influence recruitment (Van der Valk *et al.*, 1992). 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. Selected perennial species should be considered for transplanting and sowing.

Seed banks are important in revegetating lands that have been severely disturbed by mining activities (Baskin & Baskin, 1998). The seed bank can be activated, but if the right conditions for establishment are not fulfilled it may result in exhaustion of a long-term persistent seed bank. Environmental conditions (soil moisture, temperature and salinity in particular) can greatly influence recruitment from the seed bank (Van der Valk *et al.*, 1992), and the success or failure of a project can depend as much on environmental conditions as on the composition of the seed bank.

The large seeded perennials will probably not be recruited in sufficient numbers from the topsoil replaced seed bank. However, the seeds of some of these species are wind dispersed and reintroduction of these species to the post-mining area may occur naturally from surrounding vegetation. Artificially established patches of perennial vegetation may also act as sources of seeds that may eventually reach other patches of bare soil (Bouza & Del Valle, 1993; Bertiller, 1998). Many small seeded perennial species (mainly belonging to the Mesembryanthemaceae) accumulate persistent aerial seed banks (Chapter 11), but their seeds are not well adapted to long range dispersal. Because the standing vegetation, including aerial seed banks, will be destroyed during the mining process, adult plants of these species should be transplanted on mined areas during revegetation efforts. In some species, transplanting may also result in a beneficial shortening of the period between revegetation and seed production. Revegetation of mined areas at the study site with perennials should therefore involve topsoil replacement, sowing and transplanting of selected species.

The topsoil stored seed bank will be a vital source of annual species recruitment. Seeds are the only mechanism of reproduction in annuals, and many of these species accumulate large persistent seed banks (Esler, 1999). The seeds present in the seed bank are potentially useful in restoration projects where establishment of plant cover is desired, for example to reduce soil erosion (Skoglund, 1992).

Buried seeds can also have important implications for conservation management where preferred species have been lost from the vegetation but survive in the seed bank. Species recorded only in the seed bank were previously observed in neighbouring vegetation, but detailed seed bank studies in these areas will determine the status of rare or endangered seed bank species.

Topsoil replacement, sowing and transplanting should all be considered for the revegetation of mined areas in the Strandveld Succulent Karoo. Annual species will be recruited from the topsoil stored seed bank. However, all will depend on the period of stockpiling before being used in restoration, as this can negatively influence recruitment (Van der Valk *et al.*, 1992). 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. Selected perennial species should be considered for transplanting and sowing.

Seed banks are important in revegetating lands that have been severely disturbed by mining activities (Baskin & Baskin, 1998). The seed bank can be activated, but if the right conditions for establishment are not fulfilled it may result in exhaustion of a long-term persistent seed bank. Environmental conditions (soil moisture, temperature and salinity in particular) can greatly influence recruitment from the seed bank (Van der Valk *et al.*, 1992), and the success or failure of a project can depend as much on environmental conditions as on the composition of the seed bank.

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REFERENCES

AERTS, R., HUISZOON, A., VAN OOSTRUM, J.H.A., VAN DE VIJVER, C.A.D.M. & WILLEMS, J.H. 1995. The potential for heathland restoration on formerly arable land at a site in Drenthe, The Netherlands. *Journal of Applied Ecology*, **32**: 827-835.

ANDERSEN, A.N. 1989. How important is seed predation to recruitment in stable populations of long-lived perennials? *Oecologia*, **81**: 310-315.

ARCHIBOLD, O.W. 1981. Buried viable propagules in native prairie and adjacent agricultural sites in central Saskatchewan. *Canadian Journal of Botany*, **59**: 701-706.

ARNOLD, T.H. & DE WET, B.C. 1999. Plants of southern Africa: names and distribution. Electronic data-base, National Botanical Institute, Pretoria.

AZIZ, S. & KHAN, M.A. 1996. Seed bank dynamics of a semi-arid coastal shrub community in Pakistan. *Journal of Arid Environments*, **34**: 81-87.

BAKKER, J. P. 1989. *Nature management by grazing and cutting.* Kluwer Academic, Dordrecht.

BAKKER, J.P., POSCHLOD, P., STRYKSTRA, R.J., BEKKER, R.M. & THOMPSON, K. 1996. Seed banks and seed dispersal: important topics in restoration ecology. *Acta Botanica Neerlandica*, **45**: 461-490.

BASKIN, C.C. & BASKIIN J.M. 1998. *Seeds: Ecology, biogeography, and evolution of dormancy and germination.* Academic Press, New York.

BERTILLER, M.B. 1998. Spatial patterns of the germinable soil seed bank in northern Patagonia. *Seed Science Research*, **8**: 39-45.

BOUZA, P. & DEL VALLE, H.F. 1993. Micromorphological, physical, and chemical characteristics of soil crust types of the central Patagonia region, Argentina. *Arid Soil Research and Rehabilitation*, **7**: 355-368.

CAIXINHAS, M.L., JERONIMO, A., ROCHA, F. & LEITAO, A. 1998. Relationship between the seedbank and actual weed flora in one agricultural soil in the Tapada da Ajuda (Lisboa). *Aspects of Applied Biology*, **51**: 51-57.

CHAMBERS, J.C. 1993. Seed and vegetation dynamics in an alpine herb field: effects of disturbance type. *Canadian Journal of Botany*, **71**: 471-485.

DEAN, M.R.J., MILTON, S.J., WATKEYS, M.K. & HOCKEY, P.A.R. 1991. Distribution, habitat preference and conservation status of the Red Lark *Certhilauda burra* in Cape Province, South Africa. *Biological Conservation*, **58**: 257-274.

DE VILLIERS, A.J., VAN ROOYEN, M.W. & THERON, G.K. 1994. Comparison of two methods for estimating the size of the viable seed bank of two plant communities in the Strandveld of the West Coast, South Africa. *South African Journal of Botany*, **60**: 81-84.

DE VILLIERS, A.J., VAN ROOYEN, M.W., THERON, G.K. & VAN ROOYEN, N. 1999. Vegetation diversity of the Brand-se-Baai coastal dune area, West Coast, South Africa: A pre-mining benchmark survey for rehabilitation. *Land Degradation & Development*, **10**: 207-224.

ELLNER, S. & SHMIDA, A. 1981. Why are adaptations for long-range seed dispersal rare in desert plants? *Oecologia*, **51**: 133-144.

ENVIRONMENTAL EVALUATION UNIT. 1990. *Anglo American Corporation: West Coast heavy mineral sands project.* Unpublished report. University of Cape Town, Cape Town.

ESLER, K.J. 1993. Vegetation patterns and plant reproductive processes in the Succulent Karoo. Ph.D. thesis, University of Cape Town, Cape Town.

ESLER, K.J. 1999. Plant reproductive ecology. In: Dean, W.R.J. & Milton, S.J. (eds). *The Karoo – Ecological patterns and processes.* Cambridge University Press, Cambridge. pp. 123-144.

ESLER, K.J., COWLING, R.N. & IVEY, P. 1992. Seed biology of three species of Mesembryanthema in the southern Succulent Karoo. *South African Journal of Botany*, **58**: 343-348.

FENNER, M. 1985. *Seed ecology.* Chapman & Hall, London.

GRAHAM, D.J. & HUTCHINGS, M.J. 1988. Estimation of the seed bank of a chalk grassland ley established on former arable land. *Journal of Applied Ecology*, **25**: 241-252.

GRANSTRöM, A. 1982. Seed banks in five boreal forest stands originating between 1810 and 1963. *Canadian Journal of Botany*, **60**: 1815-1821.

HARPER, J.L. 1977. *Population biology of plants.* Academic Press, London.

HEDGE, S.G., LOKESHA, R. & GANESHAIAH, K.N. 1991. Seed size distribution in plants: an explanation based on fractal geometry. *Oikos*, **62**: 100-101.

HENDERSON, C.B., PETERSEN, K.E. & REDAK, R.A. 1988. Spatial and temporal patterns in the seed bank and vegetation of a desert grassland community. *Journal of Ecology*, **76**: 717-728.

HEWITT, E.J. 1952. *Sand and water culture methods used in the study of plant nutrition.* Farnham Royal, Bucks, Commonwealth Agricultural Bureau.

KEMP, P.R. 1989. Seed banks and vegetation processes in deserts. In: Leck, M.A., Parker, V.T. & Simpson, R.L. (eds). *Ecology of soil seed banks.* Academic Press, London. pp. 257-281.

KHAN, M.A. 1993. Relationship of seed bank to plant distribution in saline arid communities. *Pakistan Journal of Botany*, **25**: 73-82.

KIRKHAM, F.W. & KENT, M. 1997. Soil seed bank composition in relation to the standing vegetation in fertilized and unfertilized hay meadows on a Somerset peat moor. *Journal of Applied Ecology*, **34**: 889-902.

KOTANEN, P.M. 1996. Revegetation following soil disturbance in a California meadow: the role of propagule supply. *Oecologia*, **108**: 652-662.

LECK, M.A., PARKER, V.T. & SIMPSON, R.L. 1989. *Ecology of soil seed banks.* Academic Press, London.

LEVASSOR, C., ORTEGA, M. & PECO, B. 1990. Seed bank dynamics of Mediterranean pastures subjected to mechanical disturbance. *Journal of Vegetation Science*, **1**: 339-344.

MATLACK, G.R. & GOOD, R.E. 1990. Spatial heterogeneity in the soil seed bank of a mature coastal plain forest. *Bulletin of the Torrey Botanical Club*, **117**: 143-152.

MILBERG, P. & PERSSON, T.S. 1994. Soil seed bank and species recruitment in road verge grassland vegetation. *Annales Botanici Fennici*, **31**: 155-162.

MUELLER-DOMBOIS, D. & ELLENBERG, H. 1974. *Aims and methods of vegetation ecology*. Wiley, New York.

ODUM, E.P. 1971. *Fundamentals of ecology*. W.B. Saunders Company, London.

OHGA, N. 1991. Distribution patterns of buried seeds in the herbaceous lomas community over the entire plateau on Loma Ancon in the coastal desert of central Peru. *Journal of Arid Land Studies*, **1**: 41-51.

OHGA, N. 1992. Buried seed population in the herbaceous lomas on Loma Ancon in the coastal desert of central Peru. *Ecological Research*, **7**: 341-353.

PLANISEK, S.L. & PIPPEN, R.W. 1984. Do sand dunes have seed banks? *Michigan Botany*, **23**: 169-177.

PRATT, D.W., BLACK, R.A. & ZAMORA, B.A. 1984. Buried viable seed in a ponderosa pine community. *Canadian Journal of Botany*, **62**: 44-52.

REICHMAN, O.J. 1984. Spatial and temporal variation of seed distributions in Sonoran Desert soils. *Journal of Biogeography*, **11**: 1-11.

ROBERTS, H.A. & STOKES, F.G. 1966. Studies on the weeds of vegetable crops. VI. Seed populations of soil under commercial cropping. *Journal of Applied Ecology*, **3**: 181-190.

SILVERTOWN, J.W. & LOVETT-DOUST, J.L. 1995. *Introduction to plant population biology*. Blackwell Science Ltd., Oxford.

SKOGLUND, J. 1992. The role of seed banks in vegetation dynamics and restoration of dry tropical ecosystems. *Journal of Vegetation Science*, **3**: 357-360.

SMITH, L.M. & KADLEC, J.A. 1983. Seed banks and their role during drawdown of a North American marsh. *Journal of Applied Ecology*, **20**: 673-684.

TER BRAAK, C.J.F. 1997. *CANOCO – a Fortran program for canonical community ordination by [partial] [detrended] [canonical] correspondence analysis, principal component analysis and redundancy analysis (version 3.15)*. Report LWA-88-02, Agricultural Mathematics Group, Wageningen.

THOMPSON, K. & GRIME, J.P. 1979. Seasonal variation in the seed banks of herbaceous species in ten contrasting habitats. *Journal of Ecology*, **67**: 893-921.

VAN DER VALK, A.G., PEDERSON, R.L. & DAVIS, C.B. 1992. Restoration and creation of freshwater wetlands using seed banks. *Wetlands Ecology and Management*, **1**: 191-197.

VAN RHEEDE VAN OUDTSHOORN, K. & VAN ROOYEN, M.W. 1999. *Dispersal biology of desert plants*. Springer-Verlag, Berlin.

VAN ROOYEN, M.W. & GROBBELAAR, N. 1982. Saadbevolkings in die grond van die Hester Malan-natuurreservaat in die Namakwalandse Gebrokeveld. *South African Journal of Botany*, **1**: 41-50.

WARR, S.J., THOMPSON, K. & KENT, M. 1993. Seed banks as a neglected area of biogeographic research: a review of literature and sampling techniques. *Progress in Physical Geography*, **17**: 329-347.

WILSON, R.G., KERR, E.D. & NELSON, L.A. 1985. Potential for using weed seed content in the soil to predict future weed problems. *Weed Science*, **33**: 171-175.

CHAPTER 8

GERMINATION STRATEGIES OF STRANDVELD SUCCULENT KAROO PLANT SPECIES FOR REVEGETATION PURPOSES: I. TEMPERATURE AND LIGHT REQUIREMENTS

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ABSTRACT

The timing of germination and seedling establishment is critical for the existence and survival of plants in arid environments. Both innate seed characteristics and environmental factors such as temperature and light influence the timing of germination. Optimum germination requirements of 28 Strandveld Succulent Karoo species (including 31 seed types) were examined. Of these species, *c.* 50% achieved highest germination percentages in the absence of light and over a wide range of temperatures. Most of these were perennial species. Twenty-five percent of the species (nine seed types) obtained highest germination percentages at intermediate temperatures in the light. Most of these were annual species. Another 25% of the species achieved highest germination percentages at low and intermediate temperatures, irrespective of light conditions. In 57% of the species, mean time to germination was not influenced by light, whereas 86% of the species yielded shortest mean times to germination at intermediate temperatures. Most species were characterised by intermediate mean optimum temperatures for germination. An understanding of the germination requirements of these species will allow the local mining industry to maximize their revegetation efforts on post-mining areas.

Key words: Germination; light; mining; Namaqualand; revegetation; temperature

INTRODUCTION

The germination of seeds is one of the most important processes in the life-cycle of plants. When a seed germinates under natural conditions the individual has in a sense "bet its life" on the favourability of environmental conditions for seedling establishment. Consequently, selection favours environmental cueing mechanisms that decrease the probability of encountering unacceptable growth conditions following germination (Badger & Ungar, 1989; Probert, 1992).

Determining what controls the timing of seed germination in the field requires information on the seed, environmental conditions in the habitat, and how the two interact from time of seed maturation to germination (Baskin & Baskin, 1998). Germination can depend on certain environmental factors to release the seed from dormancy. Once dormancy has been broken, these factors are no longer required for germination itself (Bewley & Black, 1982; Probert, 1992). The extent and rate at which the germination process occurs in a

non-dormant seed is affected by various factors. Temperature is most important; equally significant in many cases are light, oxygen, carbon dioxide and other substances, and factors affecting the availability of water (Mayer & Poljakoff-Mayber, 1975; Bewley & Black, 1982, 1994; Copeland & McDonald, 1995). Germination requirements are species specific (Datta, 1965) and are determined both by the conditions which prevail during seed formation (Gutterman, 1992; 1993) and even more by hereditary factors (Freeman *et al.*, 1977; Gutterman, 1993; Visser, 1993). Frequently there is some correlation between the environmental requirement for germination and the ecological conditions in the habitat of the species (Mayer & Poljakoff-Mayber, 1975; Gutterman, 1993).

Under arid and semi-arid conditions seeds are exposed to a variety of environmental stresses. Arid habitats are characterised by temperature fluctuations extending beyond the limiting temperatures for germination, by recurrence of moisture deficiency and sometimes by deficiencies of nutrients in the soil (El-Sharkawi *et al.*, 1989).

The present study on germination strategies of Strandveld Succulent Karoo plant species was prompted by the need to ensure optimal germination of seeds during the revegetation of mined areas. Revegetation of these areas will depend mainly on the use of the soil stored seed bank, as well as seeding and transplanting of selected species (Environmental Evaluation Unit, 1990). These methods ensure the re-establishment of local plant species, which are already adapted to the local environmental conditions.

The aim of this study was to identify Strandveld Succulent Karoo species with the highest probabilities to be revegetated successfully by means of topsoil replacement and/or sowing. Knowledge of which extrinsic factors, as well as the degree to which these factors control the timing of germination in individual species, will also aid in predicting the periods/seasons and methods best suited for revegetation efforts.

This study forms part of a project aimed at describing the seed bank dynamics of the Strandveld Succulent Karoo to guide mining authorities on appropriate revegetation strategies. This paper is the first in a series of three, aimed at identifying some of the germination strategies of Strandveld Succulent Karoo species, and deals with the temperature and light requirements for optimum germination. Subjects addressed in the other two papers concern after-ripening, dormancy-breaking, endogenous germination patterns and the effect of relative humidity on viability.

MATERIAL AND METHODS

Mature diaspores (henceforth referred to as seeds) of 28 plant species (31 seed types) were collected from natural populations in the vicinity of Brand-se-Baai (31°18'S, 17°54'E) on the Cape West Coast, South Africa (De Villiers *et al.*, 1999). This area falls within the Namaqualand coastal belt and has an average precipitation of 282 mm per annum, measured over a period of four years at the study site (Figure 8.1). Rainfall occurs mainly during winter, with an average of 160 mm per annum at the study site. The average annual temperature at the study site is 15.8°C with a relatively small fluctuation due to the marine influence (De Villiers *et al.*, 1999). Average monthly minimum and maximum temperatures recorded at the study site were

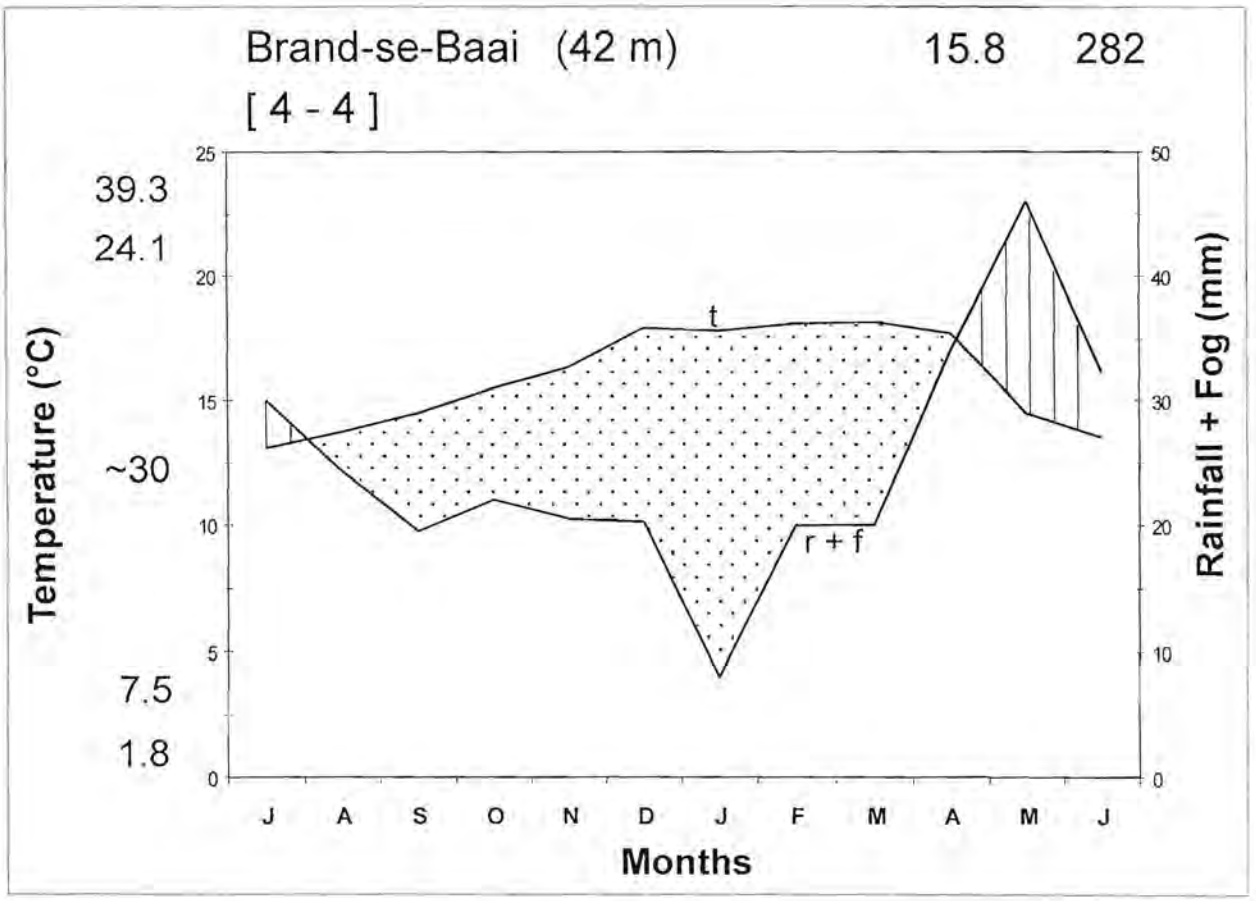

Figure 8.1. Climate diagram (following Walter & Lieth, 1960) of the Brand-se-Baai station for the period March 1993 – February 1997.

7.5°C and 24.1°C respectively (Figure 8.1). 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 at the University of Pretoria, for 28 weeks.

Species used in this experiment included the following perennials: *Albuca exuviata* Bak., *Amellus tenuifolius* Burm., *Arctotis stoechadifolia* Berg., *Ballota* africana (L.) Benth., *Cephalophyllum spongiosum* (L.Bol.) L.Bol., *Chrysocoma longifolia* DC., *Conicosia elongata* (Haw.) N.E.Br., *Conicosia pugioniformis* (L.) N.E.Br., *Dimorphotheca tragus* (Ait.) T.Norl., *Ehrharta calycina* J.E.Sm., *Eriocephalus africanus* L., *Gazania leiopoda* (DC.) Rössl., *Grielum grandiflorum* (L.) Druce, *Pharnaceum aurantium* (DC.) Druce, *Pteronia divaricata* (Berg.) Less., *Ruschia bolusiae* Schwant., *Stoeberia* sp. and *Vanzijlia annulata* (Berger) L.Bol..

Annual species investigated were: *Brassica tournefortii* Gouan, *Dimorphotheca pluvialis* (L.) Moench. (ray floret achenes), *Hebenstretia repens* Jarosz, *Heliophila coronopifolia* L., *Pharnaceum exiguum* Adamson, *Polycarena pumila* (Benth.) Levyns, *Senecio arenarius* Thunb., *Silene clandestina* Jacq., *Ursinia anthemoides* (L.) Poir. (black, grey & white achenes) and *Ursinia speciosa* DC. (black & white achenes).

Seeds were germinated in Petri dishes with a diameter of either 90 mm or 50 mm (depending on the seed size), containing two layers of filter paper (Schleicher & Schüll, no. 595, Dassel, Germany) to which approximately 6 cm^3 or 4 cm^3 distilled water was added respectively. Germination tests were conducted in germination cabinets and each treatment consisted of five replicates of 50 seeds for each species. To determine the optimum light and temperature requirements for 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}) 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. Germination of dark replicates was determined under a green safety light (Baskin & Baskin, 1998).

Petri dishes were examined every second day, and germinated seeds counted and removed over a period of 30 days. Radicle protrusion was the germination criterion.

The optimal temperature for germination (To) of a specific species was calculated as:

$$To = \frac{\sum tp}{\sum p}$$

where p is the percentage germination at temperature t (Olff *et al.*, 1994).

For each treatment and species the mean time to germination (*mtg*) was calculated using the equation:

$$mtg = \frac{\sum Dn}{\sum n}$$

where n is the number of seeds which germinate on day D and D is the number of days counted from the beginning of the test (Ellis & Roberts, 1981).

The least significant difference (LSD) one-way analysis of variance (ANOVA) and multiple range test (Statgraphics 5.0, 1989, STSC, Inc., U.S.A.) were used to determine significant differences ($P \leq 0.05$), in germination percentages and mean times to germination, between treatments within a species. The LSD multi-factor ANOVA of the Statgraphics 5.0 computer program was used to determine significant differences between light and dark treatments at a $P \leq 0.05$ level.

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

RESULTS

The temperature and light requirements for germination of the 28 Strandveld Succulent Karoo species (31 seed types) investigated, are presented in Tables 8.1, 8.2 and 8.3. Species and seed types were grouped according to their germination responses to light conditions (Table 8.4) as well as to the range of temperatures where highest germination percentages (Table 8.1) or mean times to germination (Table 8.2) were obtained.

Fifteen species (*c.* 50%) obtained significantly higher germination percentages in the dark treatments (Table 8.1, Table 8.4). Most of these belong to perennial species, requiring low (7 & 12°C) and/or intermediate (17 & 22°C) temperatures to obtain highest germination percentages. Annual species that yielded higher germination percentages in the dark than in the light (Table 8.4), required intermediate and/or high temperatures. Seeds of the geophyte *Conicosia elongata* required high temperatures (27 & 32°C) for optimum germination.

Species that required light for optimum germination included two perennial and five annual species (nine seed types)(Table 8.1, Table 8.4), and constituted 25% of all species investigated. These species/seed types obtained highest germination percentages at low and/or intermediate temperatures.

The germination of seeds of four perennial and three annual species (seven seed types) (25%) was not significantly affected by light (Table 8.1, Table 8.4). Low and/or intermediate temperatures were required by these species/seed types for optimal germination.

Table 8.1. Mean germination percentages of 28 Strandveld Succulent Karoo plant species (31 seed types), at different temperature treatments under light and dark conditions. Within each species/seed type, values followed by the same letter are not significantly different at $P \leq 0.05$

Species/seed type	Temperature (°C)														Significance level ($P \leq 0.05$)
	Light							Dark							
	7°C	12°C	17°C	22°C	27°C	32°C	12/22°C	7°C	12°C	17°C	22°C	27°C	32°C	12/22°C	
Species/seed types where mean germination percentages were significantly higher in the dark than in the light															
Highest germination percentages at low and intermediate temperatures (7, 12, 17 & 22°C)															
Albuca exuviata (P)	96.5 i	97.0 i	94.5 i	62.5 d	10.0 bc	6.0 ab	-	98.0 i	97.0 i	97.5 i	85.5 e	14.0 c	1.5 a	-	0.0000
Arctotis stoechadifolia (P)	0.0 a	0.0 a	0.5 ab	0.0 a	0.0 a	0.0 a	0.0 a	1.0 b	1.0 b	1.0 b	0.0 a	0.0 a	0.0 a	0.0 a	0.0402
Ballota africana (P)	0.0 a	11.7 bcd	24.2 ef	4.2 abc	0.0 a	0.0 a	0.0 a	21.7 def	20.8 def	25.8 f	17.5 def	0.8 ab	0.0 a	14.2 cde	0.0000
Dimorphotheca tragus (P)	77.5 g	70.0 f	52.0 d	38.5 c	20.5 b	3.5 a	-	79.5 g	81.0 g	62.0 e	37.5 c	21.5 b	8.5 a	-	0.0000
Ehrharta calycina (P)	4.0 a-d	5.5 cde	7.0 c-f	7.5 c-f	5.0 b-e	1.0 ab	3.5 abc	9.0 ef	14.0 g	14.0 g	11.0 fg	8.0 def	0.5 a	10.0 fg	0.0000
Gazania leiopoda (P)	76.5 fgh	68.0 def	58.5 cd	64.5 de	41.0 b	7.0 a	43.5 b	81.0 gh	87.0 h	71.0 efg	48.0 bc	40.0 b	4.0 a	60.5 de	0.0000
Grielum grandiflorum (P)	7.0 ab	9.0 abc	15.0 bcd	18.0 cde	3.0 a	-	-	12.0 a-d	21.0 de	25.0 e	19.0 de	9.0 abc	-	-	0.0003
Pharnaceum aurantium (P)	6.0 ab	43.0 d	47.5 d	15.5 c	5.5 a	0.0 a	15.0 bc	83.0 i	90.0 i	84.5 i	15.0 bc	0.0 a	0.0 a	61.5 e	0.0000
Ruschia bolusiae (P)	5.5 abc	10.0 cd	14.5 de	5.5 abc	1.5 ab	0.5 a	9.5 cd	7.0 bc	14.5 de	25.0 f	9.5 cd	9.5 cd	0.0 a	16.5 e	0.0000
Vanzijlia annulata (P)	85.5 d	87.5 de	90.0 def	59.5 c	46.5 b	0.0 a	61.5 c	89.0 def	97.5 f	96.0 ef	83.5 d	56.0 bc	0.0 a	97.0 ef	0.0000
Highest germination percentages at intermediate and high temperatures (17, 22 & 27°C)															
Brassica tournefortii (A)	0.5 a	0.0 a	0.0 a	4.0 a	4.5 a	1.5 a	0.0 a	0.0 a	2.5 a	17.5 b	46.5 c	19.0 b	3.0 a	20.0 b	0.0000
Conicosia pugioniformis (P)	0.0 a	2.5 ab	1.5 ab	13.0 bc	24.0 cd	-	-	4.0 ab	40.0 ef	32.5 de	47.5 f	42.0 ef	-	-	0.0000
Hebenstretia repens (A)	0.0	0.0	0.0	0.0	0.5	0.0	-	0.0	1.0	1.0	1.0	1.0	0.0	-	0.2962
Polycarena pumila (A)	0.0 a	1.5 a	12.5 c	2.5 a	1.0 a	0.0 a	-	0.0 a	3.5 ab	19.0 d	13.0 c	8.0 bc	0.0 a	-	0.0000
Highest germination percentages at high temperatures (27 & 32°C)															
Conicosia elongata (P)	0.0 a	0.0 a	0.0 a	0.0 a	0.0 a	0.0 a	0.0 a	0.0 a	0.0 a	2.5 ab	5.0 bc	8.8 c	7.5 c	2.5 ab	0.0028
Species/seed types where mean germination percentages were significantly higher in the light than in the dark															
Highest germination percentages at low and intermediate temperatures (7, 12, 17 & 22°C)															
Stoeberia sp. (P)	46.0 fg	65.0 h	57.0 gh	43.0 ef	14.5 bc	2.0 a	66.0 h	22.0 cd	33.0 de	21.0 c	13.5 bc	5.5 ab	2.0 a	35.5 ef	0.0000
Senecio arenarius (A)	63.5 d	48.0 d	50.5 d	27.0 bc	46.0 cd	-	-	23.5 ab	22.0 ab	10.5 ab	15.0 ab	6.5 a	-	-	0.0000
Ursinia anthemoides - gray (A)	15.5 c	40.0 f	33.5 e	25.5 d	13.0 c	0.0 a	-	1.0 ab	6.0 b	5.0 ab	1.0 ab	0.5 a	0.0 a	-	0.0000
Ursinia speciosa - white (A)	16.0 cd	33.5 e	36.5 e	11.5 bcd	7.5 abc	0.0 a	11.5 bcd	15.0 cd	17.0 cd	18.0 d	2.0 ab	2.5 ab	0.0 a	8.0 a-d	0.0000
Highest germination percentages at intermediate temperatures (17 & 22°C)															
Cephalophyllum spongiosum (P)	12.0 ab	29.5 cd	45.5 e	39.5 de	19.5 bc	-	-	0.0 a	2.0 a	35.5 de	20.5 bc	17.5 bc	-	-	0.0000
Dimorphotheca pluvialis - ray (A)	9.5 b	37.5 d	64.5 f	11.0 bc	0.5 a	0.0 a	8.5 ab	4.5 ab	23.0 d	41.5 e	19.0 cd	6.0 ab	0.0 a	13.0 bc	0.0000
Silene clandestina (A)	0.5 ab	7.0 bc	20.0 e	39.5 f	7.0 bc	0.0 a	-	7.5 c	12.0 cd	14.5 de	12.5 cd	6.0 abc	0.0 a	-	0.0000
Ursinia anthemoides - black (A)	1.0 a	10.5 c	5.0 b	17.0 d	2.5 ab	0.0 a	-	1.0 a	5.5 b	2.5 ab	1.0 a	0.0 a	0.5 a	-	0.0000
Ursinia anthemoides - white (A)	1.5	2.0	3.5	2.0	0.0	0.0	-	1.0	0.5	0.0	0.0	0.0	0.0	-	0.0747
Species/seed types where mean germination percentages were not significantly different between light and dark treatments															
Highest germination percentages at low and intermediate temperatures (7, 12, 17 & 22°C)															
Amellus tenuifolius (P)	22.5 bc	58.0 f	38.0 de	39.5 de	28.5 cd	0.0 a	23.0 bc	49.0 ef	39.5 de	51.0 ef	38.0 de	11.0 ab	0.0 a	28.5 cd	0.0000
Chrysocoma longifolia (P)	71.5 c	84.5 d	75.0 cd	64.5 c	39.5 b	8.5 a	67.0 c	67.0 c	72.0 c	76.0 cd	67.0 c	42.5 b	3.5 a	64.5 c	0.0000
Eriocephalus africanus (P)	1.5	1.0	0.0	1.0	0.5	-	-	0.0	1.5	1.0	2.0	0.5	-	-	0.4032
Heliophila coronopifolia (A)	8.0 bcd	9.0 cd	11.5 d	9.0 cd	4.0 abc	0.5 a	-	7.0 bcd	9.0 cd	9.0 cd	17.0 e	3.5 ab	0.5 a	-	0.0000
Pteronia divaricata (P)	44.5 de	48.5 e	48.0 e	19.0 b	40.0 cd	2.0 a	15.0 b	44.5 de	41.5 cde	44.5 de	14.5 b	35.5 c	2.0 a	20.0 b	0.0000
Ursinia speciosa - black (A)	23.0 de	39.0 f	10.0 bc	13.0 c	3.5 ab	0.0 a	9.5 bc	29.0 g	27.0 e	12.5 c	16.0 cd	2.5 ab	0.5 a	10.0 bc	0.0000
Highest germination percentages at intermediate temperatures (17 & 22°C)															
Pharnaceum exiguum (A)	0.0	0.0	0.5	0.5	0.0	0.5	-	0.5	1.5	0.5	0.5	0.0	0.0	-	0.2718

A - Annual
P - Perennial
- Treatment not used for this species/seed type.

Table 8.2. Mean time to germination (days), of 28 Strandveld Succulent Karoo plant species (31 seed types), at different temperature treatments under light and dark conditions. Within each species/seed type, values followed by the same letter are not significantly different at $P \leq 0.05$

Species/seed type	Temperature (°C)														Significance level ($P \leq 0.05$)
	Light							Dark							
	7°C	12°C	17°C	22°C	27°C	32°C	12/22°C	7°C	12°C	17°C	22°C	27°C	32°C	12/22°C	
Species/seed types where mean time to germination were significantly shorter in the dark than in the light															
Shortest mean time to germination at low and intermediate temperatures (7, 12 & 17°C)															
Albuca exuviata (P)	7.2 abc	4.4 a	4.3 a	9.6 bc	15.5 d	20.0 d	-	5.5 a	4.1 a	3.6 a	6.4 ab	10.6 c	20.0 d	-	0.0000
Shortest mean time to germination at intermediate temperatures (17 & 22°C)															
Amellus tenuifolius (P)	14.7 d	13.2 cd	12.7 cd	14.3 d	15.1 d	--	15.1 d	10.2 bc	7.7 ab	5.1 a	5.7 a	18.6 e	--	8.4 ab	0.0000
Chrysocoma longifolia (P)	17.3 ef	10.4 abc	9.9 abc	11.3 bcd	10.5 abc	21.9 f	10.2 abc	15.6 de	8.8 abc	7.8 ab	6.6 a	7.8 ab	15.1 cde	7.7 ab	0.0000
Gazania leiopoda (P)	13.4 de	12.3 cde	13.2 de	15.4 e	19.9 f	19.7 f	12.7 de	12.5 de	7.7 a	9.0 ab	10.9 bcd	14.6 de	12.5 bcd	9.3 abc	0.0000
Heliophila coronopifolia (A)	11.1 bcf	5.2 a-e	6.3 a-e	6.9 a-f	12.8 bcf	4.0 ab	-	11.0 bcf	4.4 a-e	4.0 abc	2.9 a	3.1 a	4.0 a-d	-	0.0024
Pharnaceum aurantium (P)	23.7 e	17.7 cd	15.5 cd	15.9 cd	18.2 de	--	14.2 bc	13.1 bc	7.9 a	7.4 a	8.8 ab	--	--	10.3 ab	0.0000
Stoeberia sp. (P)	15.0 cd	8.8 ab	9.0 ab	15.2 cd	21.8 e	26.0 f	8.4 ab	18.2 de	9.7 ab	6.9 a	12.0 bc	13.6 bc	8.5 ab	7.3 a	0.0000
Senecio arenarius (A)	14.7 d	11.5 bc	8.8 a	8.7 a	12.6 cd	-	-	13.8 d	11.5 c	8.5 a	7.4 a	8.8 ab	-	-	0.0000
Vanzijlia annulata (P)	17.9 g	10.4 cde	10.0 b-e	12.2 ef	11.6 def	--	13.7 f	17.4 g	10.9 cde	7.2 a	8.8 abc	9.7 bcd	--	7.7 ab	0.0000
Shortest mean time to germination at high temperatures (27 & 32°C)															
Conicosia elongata (P)	--	--	--	--	--	--	--	--	--	11.0	7.5	5.7	8.0	5.0	0.0801
Species/seed types where mean time to germination were significantly shorter in the light than in the dark															
Shortest mean time to germination at intermediate temperatures (17 & 22°C)															
Ursinia anthemoides - gray (A)	13.2 cd	8.1 abc	6.5 a	6.4 a	7.9 ab	--	-	23.0 f	12.0 bcd	16.4 de	18.0 def	22.0 ef	--	--	0.0001
Ursinia anthemoides - white (A)	16.7	13.5	16.0	8.5	--	--	-	24.0	26.0	--	--	--	--	-	0.0988
Ursinia speciosa - white (A)	12.1 a	7.0 cd	5.1 ab	5.0 ab	5.6 ab	--	6.3 abc	13.1 a	7.8 d	6.3 a-d	5.5 abc	4.0 a	--	7.3 bcd	0.0000
Species/seed types where mean time to germination were not significantly different between light and dark treatments															
Shortest mean time to germination at intermediate temperatures (17 & 22°C)															
Arctotis stoechadifolia (P)	--	--	14.0	--	--	--	--	22.0	21.0	10.0	--	--	--	--	0.4513
Ballota africana (P)	--	22.7 c	14.1 ab	16.8 bc	--	--	--	24.0 c	14.4 ab	9.0 a	16.3 ab	22.0 bc	--	16.6 b	0.0016
Cephalophyllum spongiosum (P)	18.6 d	13.2 c	17.0 d	13.2 c	13.3 c	-	-	--	17.5 d	11.6 bc	10.4 b	7.1 a	-	-	0.0000
Conicosia pugioniformis (P)	--	18.0 cd	14.0 abc	16.9 cd	14.4 abc	-	-	20.8 d	16.3 bc	11.4 a	13.8 ab	14.0 ab	-	-	0.0011
Dimorphotheca pluvialis - ray (A)	9.6 b	6.6 a	5.5 a	5.9 a	18.0 c	--	8.0 a	15.1 c	7.0 ab	6.3 a	5.5 a	5.7 a	--	5.8 a	0.0000
Dimorphotheca tragus (P)	6.3 cd	5.3 abc	4.7 a	5.8 a-d	6.1 a-d	10.3 a	-	6.1 bcd	5.1 abc	4.9 ab	7.0 d	7.1 d	9.8 a	-	0.0000
Eriocephalus africanus (P)	18.0	15.0	--	16.0	22.0	-	-	--	14.7	14.0	15.5	16.0	-	-	0.3742
Grielum grandiflorum (P)	19.0 d	12.5 bc	7.0 a	7.4 a	9.3 abc	-	-	16.9 d	12.7 c	8.4 ab	7.4 a	7.8 a	-	-	0.0000
Hebenstretia repens (A)	--	--	--	--	6.0	--	-	--	17.0	10.0	8.0	7.0	--	-	0.7214
Pharnaceum exiguum (A)	--	--	4.0	6.0	--	6.0	-	16.0	7.3	4.0	4.0	--	--	-	0.0692
Polycarena pumila (A)	--	24.7	17.4	20.0	13.0	--	-	--	19.7	18.4	12.5	13.1	--	-	0.1469
Pteronia divaricata (P)	17.4 e	13.3 cd	10.2 ab	9.1 ab	13.6 d	24.0 f	10.7 ab	17.5 e	11.5 bcd	10.6 abc	8.8 a	16.1 e	23.0 f	10.3 ab	0.0000
Ruschia bolusiae (P)	19.5 e	10.1 a	13.0 abc	12.6 abc	14.7 a-d	12.0 ab	12.5 a	19.4 bcd	13.5 abc	10.2 a	10.5 a	9.0 a	--	10.4 a	0.0003
Silene clandestina (A)	8.0 f	4.4 a	3.8 cde	3.7 abc	3.7 bcd	--	-	7.1 f	4.5 de	4.1 cde	3.0 a	3.2 ab	--	-	0.0000
Ursinia anthemoides - black (A)	12.0 a	9.6 a	8.2 a	6.4 a	10.8 a	--	-	21.0 b	11.6 a	10.4 a	12.0 a	--	26.0 b	-	0.0028
Ursinia speciosa - black (A)	10.5 b	5.6 a	6.9 a	4.7 a	7.1 a	--	7.0 a	9.7 b	6.4 a	5.7 a	4.4 a	5.2 a	4.0 a	5.9 a	0.0009
Shortest mean time to germination at intermediate and high temperatures (17, 22, 27 & 32°C)															
Brassica tournefortii (A)	26.0 c	--	--	7.3 ab	8.7 ab	11.3 b	--	--	6.4 ab	4.3 ab	3.2 a	4.1 a	9.0 ab	5.5 ab	0.0004
Ehrharta calycina (P)	22.5 d	11.1 bc	11.9 c	13.1 c	11.8 bc	4.0 a	10.9 bc	24.7 d	12.8 c	10.2 bc	9.7 abc	6.9 ab	10.0 abc	11.7 c	0.0000

- Treatment not used for this species/seed type.
-- No mean germination time as mean germination percentage was 0.

P - Perennial
A - Annual

Table 8.3. Optimum germination temperatures (°C) calculated for 28 Strandveld Succulent Karoo species (31 seed types)

Species/seed type	Temperature (°C)	
	Light	Dark
Low temperatures in light & dark		
Ursinia speciosa - black (A)	13.33	13.43
Low temperatures in light & intermediate temperatures in dark		
Albuca exuviata (P)	14.41	14.78
Dimorphotheca tragus (P)	14.42	14.69
Intermediate temperatures in light & low temperatures in dark		
Arctotis stoechadifolia (P)	17.00	12.00
Ballota africana (P)	16.06	14.40
Pharnaceum aurantium (P)	15.79	12.58
Pharnaceum exiguum (A)	23.67	13.67
Senecio arenarius (A)	15.81	14.35
Ursinia speciosa - white (A)	15.14	13.33
Ursinia anthemoides - white (A)	15.33	8.67
Intermediate temperatures in light & dark		
Amellus tenuifolius (P)	16.83	14.94
Cephalophyllum spongiosum (P)	17.86	20.54
Chrysocoma longifolia (P)	16.15	16.34
Conicosia pugioniformis (P)	24.13	19.52
Dimorphotheca pluvialis - ray (A)	15.19	16.95
Ehrharta calycina (P)	18.17	16.69
Eriocephalus africanus (P)	14.50	18.50
Gazania leiopoda (P)	16.15	15.35
Grielum grandiflorum (P)	17.10	16.53
Heliophila coronopifolia (A)	16.23	17.27
Stoeberia sp. (P)	15.26	14.60
Polycarena pumila (A)	17.86	19.93
Pteronia divaricata (P)	16.20	15.93
Ruschia bolusiae (P)	15.53	17.00
Silene clandestina (A)	20.07	16.76
Ursinia anthemoides - black (A)	18.32	14.62
Ursinia anthemoides - gray (A)	16.24	14.78
Vanzijlia annulata (P)	15.56	16.05
High temperatures in light & intermediate temperatures in dark		
Brassica tournefortii (A)	24.86	22.14
Hebenstretia repens (A)	27.00	19.50
High temperatures in dark		
Conicosia elongata (P)	--	26.47

-- No optimum temperature as all germination percentages were 0

P - Perennial

A - Annual

Table 8.4. Multi-factor ANOVA significance levels for 28 Strandveld Succulent Karoo plant species (31 seed types), treated at different temperatures and light conditions. Significance levels for both germination percentages and mean time to germination are presented

Species/seed type	Source of variation					
	Germination percentage			Mean time to germination		
	Main effects		Interaction of Light/Dark & Temperature	Main effects		Interaction of Light/Dark & Temperature
	Light/Dark	Temperature		Light/Dark	Temperature	
Species/seed types where mean germination percentages were significantly higher in the dark than in the light						
Albuca exuviata (P)	0.0027	0.0000	0.0000	0.0126	0.0000	0.1717
Arctotis stoechadifolia (P)	0.0307	0.0492	0.2933	1.0000	1.0000	1.0000
Ballota africana (P)	0.0001	0.0000	0.0584	0.5988	0.0005	0.5243
Brassica tournefortii (A)	0.0000	0.0000	0.0000	0.0093	0.0358	0.0000
Conicosia elongata (P)	0.0002	0.0358	0.0358	1.0000	1.0000	1.0000
Conicosia pugioniformis (P)	0.0000	0.0000	0.0024	0.0084	0.0161	0.0247
Dimorphotheca tragus (P)	0.0033	0.0000	0.1291	0.4378	0.0000	0.2856
Ehrharta calycina (P)	0.0000	0.0000	0.0551	0.6581	0.0000	0.2123
Gazania leiopoda (P)	0.0344	0.0000	0.0006	0.0000	0.0000	0.1382
Grielum grandiflorum (P)	0.0028	0.0003	0.5508	0.9869	0.0000	0.6227
Hebenstretia repens (A)	0.0253	0.4317	0.6674	0.0311	0.6968	0.5878
Pharnaceum aurantium (P)	0.0000	0.0000	0.0000	0.0000	0.0042	0.3147
Polycarena pumila (A)	0.0003	0.0000	0.0361	0.3827	0.0496	0.6129
Ruschia bolusiae (P)	0.0002	0.0000	0.2324	0.1558	0.0001	0.2459
Vanzijlia annulata (P)	0.0000	0.0000	0.0000	0.0000	0.0000	0.0046
Species/seed types where mean germination percentages were significantly higher in the light than in the dark						
Cephalophyllum spongiosum (P)	0.0000	0.0000	0.0566	0.0000	0.0244	0.0000
Dimorphotheca pluvialis - ray (A)	0.0368	0.0000	0.0000	0.8704	0.0000	0.0002
Stoeberia sp. (P)	0.0000	0.0000	0.0003	0.0001	0.0000	0.0000
Senecio arenarius (A)	0.0000	0.0281	0.1862	0.0272	0.0000	0.1907
Silene clandestina (A)	0.0112	0.0000	0.0000	0.1269	0.0000	0.2165
Ursinia anthemoides - black (A)	0.0000	0.0000	0.0000	0.3422	0.5111	0.8057
Ursinia anthemoides - gray (A)	0.0000	0.0000	0.0000	0.0000	0.0049	0.1667
Ursinia anthemoides - white (A)	0.0139	0.2208	0.2711	0.0383	0.1975	0.4377
Ursinia speciosa - white (A)	0.0003	0.0000	0.0766	0.1617	0.0000	0.5410
Species/seed types where mean germination percentages were not significantly different between light and dark treatments						
Amellus tenuifolius (P)	0.6980	0.0000	0.0006	0.0000	0.0000	0.0000
Chrysocoma longifolia (P)	0.1126	0.0000	0.6192	0.0002	0.0000	0.4081
Eriocephalus africanus (P)	0.6260	0.4073	0.2768	0.9374	0.5994	0.1083
Heliophila coronopifolia (A)	0.5552	0.0000	0.1201	0.0103	0.0019	0.2232
Pharnaceum exiguum (A)	0.2643	0.4653	0.1774	0.1599	0.7403	0.1693
Pteronia divaricata (P)	0.1633	0.0000	0.3895	0.8342	0.0000	0.2950
Ursinia speciosa - black (A)	0.9609	0.0000	0.0531	0.7003	0.0000	0.3969

P - Perennial
A - Annual

Ten species (mostly perennial) obtained significantly shorter mean times to germination (*mtg*) (days) (Table 8.2) in the dark than in the light (Table 8.4), of which 50% also obtained highest germination percentages in the absence of light (Table 8.1). Three seed types belonging to two annual *Ursinia* species, obtained shortest *mtg* under light and intermediate temperature conditions (Table 8.2), all of which obtained highest germination percentages under similar conditions. The seeds of 16 species obtained shortest mean times to germination at intermediate temperatures, irrespective of the presence or absence of light (Table 8.2). Only 25% of these species obtained highest germination percentages under similar conditions (Table 8.1).

The mean germination percentages (Table 8.1) and/or mean times to germination (Table 8.2) obtained did not differ significantly between constant and alternating incubation temperatures, in any of the species/seed types investigated.

Approximately 93% of the species/seed types had optimal germination temperatures (Table 8.3) at intermediate temperatures (>14.5°C - <24.5°C), in either light or dark treatments. The optimal germination temperature of *Conicosia elongata* was high, and that of *Ursinia speciosa* (black achenes) low, in both light and/or darkness.

The Canonical Correspondence Analysis (CCA) separated the germination data along light, darkness and temperature gradients (Figure 8.2). In general, annual species were associated with a light requirement for optimum germination and correlated well with temperature requirements for germination. Perennial species were associated with the absence of light for optimum germination and correlation of these species with temperature requirements was less pronounced than that of annual species.

DISCUSSION

While moisture, oxygen, and a favourable temperature are essential for germination of all seeds, certain species also require light (Bewley & Black, 1994; Copeland & McDonald, 1995). The influence of light and temperature on germination of seeds has long been recognised (Mayer & Poljakoff-Mayber, 1975; Bewley & Black, 1982, 1994; Pons, 1991, 1992; Copeland & McDonald, 1995; Baskin & Baskin, 1998). Numerous studies on the flora of Namaqualand and the Succulent Karoo have included some aspects of light and/or temperature requirements for seed germination (Blomerus, 1992; Esler *et al.*, 1992; Beneke *et al.*, 1993; Visser, 1993; De Villiers *et al.*, 1994).

Light requirements

In many of the annual species investigated in this study, light promoted germination (Table 8.1). For most desert winter annuals, germination is promoted by light but the seeds of only a few species have an absolute light requirement for germination (Baskin & Baskin, 1985). The germination of two perennial species belonging to the Mesembryanthemaceae was promoted by light.

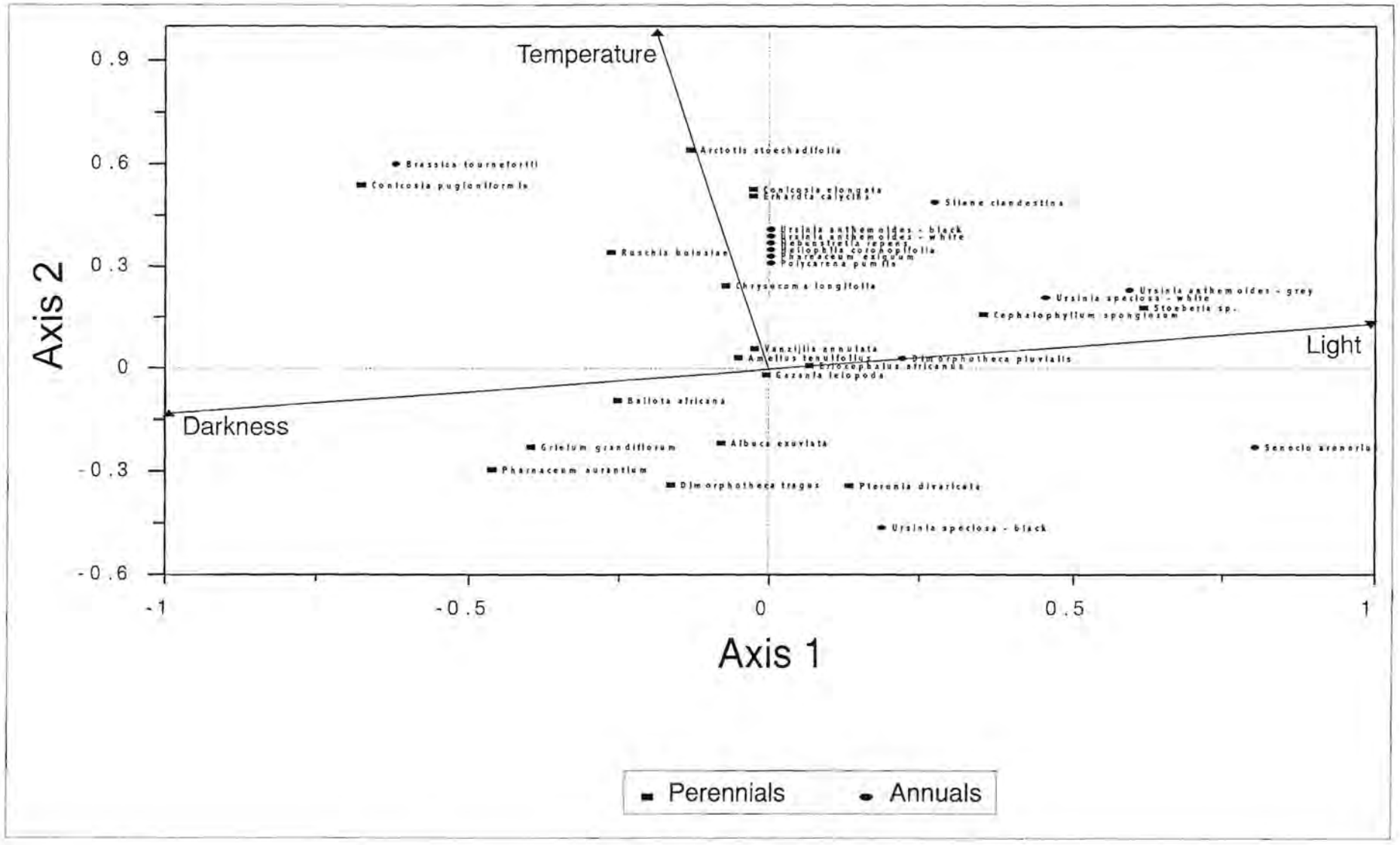

Figure 8.2. Ordination diagram based on Canonical Correspondence Analysis of the species germination percentage data with respect to three environmental variables (temperature, light & darkness). The species/environment correlation of the first two axes is 0.936 and 0.839 respectively. (Eigen1 = 0.094; eigen2 = 0.063; scaling = 2).

Light is one of the principal factors controlling dormancy and germination of seeds (Grime *et al.*, 1981; Bewley & Black, 1994; Baskin & Baskin, 1998). The plant pigment phytochrome is the physiological sensor of light in seeds, and light-controlled seed germination has been associated with this pigment since the pioneer studies on lettuce seeds (Borthwick *et al.*, 1952). Both light intensity and light quality influence germination (Copeland & McDonald, 1995). Seeds requiring light for germination are called positive photoblastic, and this has two ecological roles: the preservation of dormancy of buried seeds, and preventing germination of heliophyte seeds dispersed to shaded sites (Vazquez-Yanes & Orozco-Segovia, 1993).

The significance of a light requirement in seeds seems primarily to be avoidance of germination too deep in soil for the seedlings to reach the surface with the available seed reserves. Only when a seed is somehow brought to the surface is it exposed to light and its dormancy broken (Pons, 1992). Small seeds in particular, rely on dark-dormancy to avoid germination at great depths in the soil and hence, for the formation of a persistent seed bank (Grime *et al.*, 1981; Bewley & Black, 1982, 1994; Milberg, 1994). This mechanism delays the germination of seeds until they are brought onto or close to the soil surface again as may occur during soil disturbance. Competition by established plants is less likely after disturbance, thus improving the seedlings' chances for survival and high reproductive output (Pons, 1991).

Several of the perennial species and few of the annual species investigated obtained significantly higher germination percentages and shorter mean times to germination in the absence of light (Tables 8.1 & 8.2). Inhibition of germination due to prolonged exposure to light has been described for several species, *i.e.* negative photoblastic seeds (Pons, 1992; Bewley & Black, 1994), e.g. *Conicosia elongata*. In desert annuals, darkness is not required for seed germination, but the seeds of several species may germinate to higher percentages in darkness (Baskin & Baskin, 1998). Photoinhibition probably avoids germination on the soil surface in exposed sites where conditions are not suitable for establishment, since the seedling may suffer desiccation (Keren & Evenari, 1974; Bewley & Black, 1982; Pons, 1992). In the field, exposure to light could prevent the germination of negatively photoblastic seeds until factors such as high or low temperatures induced secondary dormancy. The actual germination response of a seed to light depends on the interaction with other environmental factors such as temperature, water potential and chemicals (Pons, 1992; Bewley & Black, 1994).

Temperature requirements

Most annual species in this study obtained highest germination percentages and shortest mean times to germination at intermediate temperatures (Tables 8.1 & 8.2). The perennial species in this study obtained highest germination percentages at low and intermediate (Table 8.1), and shortest mean times to germination at intermediate temperatures (Table 8.2). The mean optimal germination temperature of 93% of the species investigated occurred in the intermediate temperature range in either light or darkness (Table 8.3). Several studies on the germination requirements of Succulent Karoo ephemerals indicated that these species achieve optimum germination at intermediate temperatures (Beneke *et al.*, 1993; Visser, 1993; De Villiers *et al.*, 1994).

Several environmental factors simultaneously affect germination, but temperature is often regarded as the most important factor in determining the timing of germination (Badger & Ungar, 1989). Seed germination is a complex process involving many individual reactions and phases, each of which is affected by temperature (Bewley & Black, 1982, 1994; Copeland & McDonald, 1995).

Seeds of winter annuals lose their dormancy during summer (Baskin & Baskin, 1998). As dormancy loss progresses, the rate of germination increases and seeds of some species lose their light requirement for germination (Corbineau *et al.*, 1992; Baskin & Baskin, 1998). Germination in winter annuals is prevented during summer because the maximum temperature at which seeds can germinate are below those occurring in the habitat. Seeds germinate in autumn because the maximum temperature for germination has increased and habitat temperatures have declined until there is an overlap between the two. If environmental conditions (e.g. burial in the soil) prevent the seeds of obligate winter annuals from germinating in autumn, low winter temperatures induce them into dormancy (Baskin & Baskin, 1998).

As is the case with winter annual species, the seeds of many Succulent Karoo perennial species after-ripen during summer and germinate in autumn, the start of the rainy season. As most of these species germinated over a wide range of temperatures and did not require light for germination (Table 8.1), they probably do not accumulate a persistent seed bank. In the southern Karoo, artificially sown seeds of large-seeded, non-succulent shrubs placed in the field in summer germinated only in the first year (Milton, 1994; Esler, 1999), indicating that these seeds do not remain viable in the field for long periods. Little is known about what happens to seeds of perennials if they come out of dormancy in summer but fail to germinate in autumn (Baskin & Baskin, 1998).

Seeds of many species with low germination capacity at constant temperatures are stimulated by alternating temperatures (Harty & McDonald, 1972; Bewley & Black, 1982; Brown, 1987; Myers & Couper, 1989; Probert, 1992; Baskin & Baskin, 1998). The need for fluctuating temperatures during germination seems to be associated with dormancy, but alternating temperatures may accelerate germination of non-dormant seeds as well (Copeland & McDonald, 1995). In other species, including those in this study, alternating temperatures had no positive effect on germination (Mott & Groves, 1981; Fenner, 1985; Bell *et al.*, 1993; Beneke *et al.*, 1993; Copeland & McDonald, 1995).

Another way in which species can increase their probability of survival is the production of seeds having different germination requirements or dispersal characteristics (heterocarpy) (Mott & Groves, 1981; Van Rheede van Oudtshoorn & Van Rooyen, 1999). The grey seeds of *Ursinia anthemoides* obtained highest germination percentages at low and intermediate temperatures in the light (Table 8.1), while the black and white seeds of this species had highest germination percentages at intermediate temperatures in the light. The white seeds of *Ursinia speciosa* obtained highest germination percentages at low and intermediate temperatures in the light (Table 8.1), while the black seeds of this species obtained highest germination percentages at low temperatures, irrespective of light conditions.

Heterocarpy has been described in many species found in unpredictable environments, such as frequently disturbed habitats (Harper, 1977) and arid environments (Beneke *et al.*, 1993; Van Rheede van Oudtshoorn

& Van Rooyen, 1999). The possession of heterocarpic seeds enables species to adopt two strategies when unsuitable conditions arise: an escape in space (seed dispersal strategies) and an escape in time (fractional or delayed seed germination)(Venable & Lawlor, 1980; Fenner, 1985; Venable, 1985). While some individuals are able to exploit rainfall immediately, a seed reserve is maintained in the soil to enable repopulation should the initial germination fail (Gutterman, 1993).

In general, perennial species obtained highest germination percentages at a wide range of temperatures in the absence of light (Table 8.1). Many annual species on the other hand required light and/or intermediate temperatures for optimum germination. The interaction of light and temperature on germination is not well understood. However, it is clear that the response to each can sometimes be increased, decreased, or changed qualitatively by the other, while in other cases it cannot (Gutterman *et al.*, 1992; Copeland & McDonald, 1995). The role of temperature in regulating emergence in the field is not restricted to its action on germination but also involves its effects on dormancy. These two effects combine to control the time of germination (Bewley & Black, 1982, 1994).

Effect on revegetation

The impact of environmental conditions on recruitment from seed banks is a phenomenon whose significance has been inadequately appreciated (Lyle, 1987), and whose management potential has not been fully realised (Van der Valk & Pederson, 1989). The restoration of mined areas in the Strandveld Succulent Karoo will involve the revegetation of the area to a state which conforms to that of the pre-mining vegetation, *i.e.* both in species composition and abundance, as soon as possible after the mining of an area has been completed. Possible means to achieve these goals include topsoil replacement, sowing and transplanting of selected local species (Environmental Evaluation Unit, 1990). Sowing and transplanting, however, are expensive, and sometimes impossible because sufficient sources of seeds or plants are not available. Alternatively, there is the option to recruit from the seed bank if seeds of required or preferred species are present. The presence of species in a seed bank disposes of many of the problems associated with collecting, storing, and sowing seeds or transplanting individuals, but it does not eliminate uncertainties associated with seed germination and seedling survival (Van der Valk & Pederson, 1989).

Since the soil seed bank of the Strandveld Succulent Karoo is predominated by annual species that accumulate persistent seed banks (Chapters 4 & 5), these species have the potential to be recruited when topsoil replacement is used in the revegetation process. The depth to which topsoil is replaced will be critical in determining the success of recruitment from its seed bank. If the replaced topsoil layer extends too deep, recruitment from the seed bank will be low. On the other hand, if the replaced topsoil layer is too shallow, prevailing winds may deplete the seed bank during the dry summer months due to a lack of buffering vegetation in the mined areas. The transplanting of perennial shrubs from neighbouring vegetation into topsoil replaced areas may help in reducing the wind-speed at ground level (Environmental Evaluation Unit, 1990). Artificial wind-speed reducing mechanisms (e.g. mulch or shade-cloth) may achieve the same results.

When considering irrigation in revegetation efforts, it must be borne in mind that the Strandveld Succulent Karoo has a mean annual rainfall which rarely exceeds 150 mm (Environmental Evaluation Unit, 1990). Also, many species present in the seed bank require intermediate temperatures for germination. Seedling recruitment from the replaced topsoil should be restricted to the period of natural field emergence, *i.e.* autumn and winter. During this period, both moisture and temperature are usually non-limiting for the germination of local species. Seedling recruitment from the seed bank after summer irrigation would be minimal, but perennial plants will benefit from irrigation during the hot and dry season.

Perennial species usually predominate the aboveground vegetation in the Strandveld Succulent Karoo and most of these species have seeds forming transient seed banks, and are therefore not well represented in the soil seed bank (Chapters 6 & 7; Esler, 1999). These species will have to be returned to the revegetation areas by means of sowing, transplanting or dispersal from surrounding vegetation. However, natural dispersal is often slow and unreliable (Bauer, 1973; Van der Valk & Pederson, 1989) and transplanting is labour intensive (Lyle, 1987). Because many of these perennial species obtained higher germination percentages in darkness than in light, revegetation efforts must ensure that after sowing, seeds of these species are not merely left on top of the soil.

A solution to some of these problems may be the replacement of topsoil after sowing, ensuring that the light requirements for germination of both perennial and annual species are met. Also, irrigation of areas where topsoil replacement and sowing have been completed should only commence at the start of the rainy season, in an attempt to provide favourable moisture and temperature conditions for germination.

Understanding the germination ecology of Strandveld Succulent Karoo species will allow the mining industry to maximise the species' return to these highly diverse communities once mining has been completed. The importance of an understanding of seed germination ecology has also been expressed by Willis and Groves (1991) in relation to the rehabilitation of conservation reserves in Australia. Further knowledge of germination syndromes will continue to improve the restoration of destroyed Strandveld Succulent Karoo ecosystems.

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REFERENCES

BADGER, K.S. & UNGAR, I.A. 1989. The effects of salinity and temperature on the germination of the inland halophyte *Hordeum jubatum*. *Canadian Journal of Botany*, **67**: 1420-1425.

BASKIN, C.C & BASKIN, J.M. 1998. *Seeds: Ecology, biogeography, and evolution of dormancy and germination*. Academic Press, New York.

BASKIN, J.M & BASKIN, C.C. 1985. The annual dormancy cycle in buried weed seeds: A continuum. *BioScience*, **35**: 492-498.

BAUER, H.J. 1973. Ten years' studies of biocoenological succession in the excavated mines of the Cologne lignite district. In: Hutnik, R.J. & Davis, G. (eds). *Ecology and reclamation of devastated land.* Gordon & Breach, New York. pp. 271-283.

BELL, D.T., PLUMMER, J.A. & TAYLOR, S.K. 1993. Seed germination ecology in Southwestern Western Australia. *The Botanical Review*, **59**: 24-73.

BENEKE, K., VAN ROOYEN, M.W., THERON, G.K. & VAN DE VENTER, H.A. 1993. Fruit polymorphism in ephemeral species of Namaqualand: III. Germination differences between the polymorphic diaspores. *Journal of Arid Environments*, **24**: 333-344.

BEWLEY, J.D. & BLACK, M. 1982. *Physiology and biochemistry of seeds*. Springer-Verlag, Heidelberg.

BEWLEY, J.D. & BLACK, M. 1994. *Seeds: Physiology of development and germination*. Plenum Press, London.

BLOMERUS, J.J. 1992. 'n Voorlopige outekologiese ondersoek na die seleksie van plante vir hervestiging in verbrakte omgewings in Suid-Afrika. M.Sc. dissertation. University of Stellenbosch, Stellenbosch.

BORTHWICK, H.A., HENDRICKS, S.B., TOOLE, E.H. & TOOLE, V.K. 1952. A reversible photoreaction controlling seed germination. *Proceedings of the National Academy of Science*, **38**: 662-666.

BROWN, R.F. 1987. Germination of *Aristida armata* under constant and alternating temperatures and its analysis with the accumulative Weibull distribution as a model. *Australian Journal of Botany*, **35**: 581-591.

COPELAND, L.O. & McDONALD, M.B. 1995. *Principles of seed science and technology*. Chapman & Hall, New York.

CORBINEAU, F., BELAID, D. & COME, D. 1992. Dormancy of *Bromus rubens* L. seeds in relation to temperature, light and oxygen effects. *Weed Research*, **32**: 303-310.

DATTA, S.C. 1965. Germination of seeds of two arid zone species. *Bulletin of the Botanical Society of Bengal*, **19**: 51-53.

DE VILLIERS, A.J., VAN ROOYEN, M.W., THERON, G.K. & VAN DE VENTER, H.A. 1994. Germination of three Namaqualand pioneer species, as influenced by salinity, temperature and light. *Seed Science & Technology*, **22**: 427-433.

DE VILLIERS, A.J., VAN ROOYEN, M.W., THERON, G.K. & VAN ROOYEN, N. 1999. Vegetation diversity of the Brand-se-Baai coastal dune area, West Coast, South Africa: A pre-mining benchmark survey for rehabilitation. *Land Degradation & Development*, **10**: 207-224.

ELLIS, R.H. & ROBERTS, E.H. 1981. The quantification of ageing and survival in orthodox seeds. *Seed Science & Technology*, **9**: 373-409.

EL-SHARKAWI, H.M., FARGALI, K.A. & SAYED, S.A. 1989. Interactive effects of water stress, temperature and nutrients in the seed germination of three desert plants. *Journal of Arid Environments*, **17**: 307-317.

ENVIRONMENTAL EVALUATION UNIT. 1990. *Anglo American Corporation: West Coast heavy mineral sands project.* Unpublished report. University of Cape Town, Cape Town.

ESLER, K.J. 1999. Plant reproductive ecology. In: Dean, W.R.J. & Milton, S.J. (eds). *The Karoo – Ecological patterns and processes*. Cambridge University Press, Cambridge. pp. 123-144.

ESLER, K.J., COWLING, R.N. & IVEY, P. 1992. Seed biology of three species of Mesembryanthema in the Southern Succulent Karoo. *South African Journal of Botany*, **58**: 343-348.

FENNER, M. 1985. *Seed Ecology*. Chapman & Hall, London.

FREEMAN, C.E., TIFFANY, R.S. & REID, W.H. 1977. Germination responses of *Agave lecheguilla*, *Agave parryi*, and *Fouquieria splendens*. *The Southwestern Naturalist*, **22**: 195-204.

GRIME, J.P., MASON, G., CURTIS, A.V., RODMAN, J., BAND, S.R., MOWFORTH, M.A.G., NEAL, A.M. & SHAW, S. 1981. A comparative study of germination characteristics in a local flora. *Journal of Ecology*, **69**: 1017-1059.

GUTTERMAN, Y. 1992. Maternal effects on seed during development. In: Fenner, M. (ed). *Seeds: The ecology of regeneration in plant communities*. CAB International, Wallingford. pp. 145-162.

GUTTERMAN, Y. 1993. *Seed germination in desert plants*. Springer-Verlag, Berlin.

GUTTERMAN, Y., CORBINEAU, F. & COME, D. 1992. Interrelated effects of temperature, light and oxygen on *Amaranthus caudatus* L. seed germination. *Weed Research*, **32**: 111-117.

HARPER, J.L. 1977. *Population biology of plants*. Academic Press, London.

HARTY, R.L. & McDONALD, T.J. 1972. Germination behaviour in beach spinifex (*Spinifex hirsutus* Labill.). *Australian Journal of Botany*, **20**: 241-251.

KEREN, A. & EVENARI, M. 1974. Some ecological aspects of distribution and germination of *Pancratium maritimum* L.. *Israel Journal of Botany*, **23**: 202-215.

LYLE, E.S. Jr.. 1987. *Surface mine reclamation manual*. Elsevier, New York.

MAYER, A.M. & POLJAKOFF-MAYBER, A. 1975. *The germination of seeds*. Pergamon Press, Oxford.

MILBERG, P. 1994. Annual dark dormancy cycle in buried seeds of *Lychnis flos-cuculi*. *Annales Botanici Fennici*, **31**: 163-167.

MILTON, S.J. 1994. Small-scale reseeding trials in arid rangelands: effects of rainfall, clearing and grazing on seedling survival. *African Journal of Range and Forage Science*, **11**: 54-58.

MOTT, J.J. & GROVES, R.H. 1981. Germination strategies. In: Pate, J.S. & McComb, A.J. (eds). *The Biology of Australian Plants*. University of Western Australia Press, Nedlands. pp. 307-341.

MYERS, B.A. & COUPER, D.I. 1989. Effects of temperature and salinity on the germination of *Puccinellia ciliata* (Bor) cv. Menemen. *Australian Journal of Agricultural Research*, **40**: 561-571.

OLFF, H., PEGTEL, D.M., VAN GROENENDAEL, J.M. & BAKKER, J.P. 1994. Germination strategies during grassland succession. *Journal of Ecology*, **82**: 69-77.

PONS, T.L. 1991. Induction of dark dormancy in seeds: its importance for the seed bank in the soil. *Functional Ecology*, **5**: 669-675.

PONS, T.L. 1992. Seed responses to light. In: Fenner, M. (ed). *Seeds: The ecology of regeneration in plant communities*. CAB International, Wallingford. pp. 259-284.

PROBERT, T.L. 1992. The role of temperature in germination ecophysiology. In: Fenner, M. (ed). *Seeds: The ecology of regeneration in plant communities*. CAB International, Wallingford. pp. 285-325.

TER BRAAK, C.J.F. 1997. *CANOCO – a Fortran program for canonical community ordination by [partial] [detrended] [canonical] correspondence analysis, principal component analysis and redundancy analysis (version 3.15)*. Report LWA-88-02. Agricultural Mathematics Group, Wageningen.

VAN DER VALK, A.G. & PEDERSON, R.L. 1989. Seeds banks and the management and restoration of natural vegetation. In: Leck, M.A., Parker, V.T. & Simpson, R.L. (eds). *Ecology of soil seed banks*. Academic Press, New York. pp. 329-346.

VAN RHEEDE VAN OUDTSHOORN, K. & VAN ROOYEN, M.W. 1999. *Dispersal biology of desert plants*. Springer-Verlag, Berlin.

VAZQUEZ-YANES, C. & OROZCO-SEGOVIA, A. 1993. Patterns of seed longevity and germination in the tropical rainforest. *Annual Review of Ecology and Systematics*, **24**: 69-87.

VENABLE, D.L. 1985. The evolutionary ecology of seed heteromorphism. *American Naturalist*, **126**: 577-595.

VENABLE, D.L. & LAWLOR, L. 1980. Delayed germination and escape in desert annuals: escape in space and time. *Oecologia*, **46**: 272-282.

VISSER, L. 1993. Saadontkiemingstudies van geselekteerde Namakwalandse efemeerspesies. M.Sc. dissertation, University of Pretoria, Pretoria.

WALTER, H. & LIETH, H. 1960. *Klimadiagramm - Weltatlas*. Fischer, Jena.

WILLIS, A.J & GROVES, R.H. 1991. Temperature and light effects on the germination of seven native forbs. *Australian Journal of Botany*, **39**: 219-228.

CHAPTER 9

GERMINATION STRATEGIES OF STRANDVELD SUCCULENT KAROO PLANT SPECIES FOR REVEGETATION PURPOSES: II. DORMANCY-BREAKING TREATMENTS

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ABSTRACT

In arid environments, the timing of germination and seedling establishment is critical for the survival of plants. Environmental factors as well as innate seed characteristics such as dormancy, influence the timing of germination. The requirement of an after-ripening period was investigated in 27 plant species from the Strandveld Succulent Karoo, South Africa. The seeds of seven species were examined for the presence of endogenous germination patterns. The influence of alternative dormancy-breaking treatments on germination percentage and rate was examined in ten species. The germination of 14 species (including annuals and perennials) was promoted by a summer after-ripening period, indicating that the seeds of these species are characterised by nondeep physiological dormancy. The germination percentage of 13 species was not promoted by an after-ripening period. Of these, the fresh seeds of six perennial species obtained germination percentages equal to or higher than 10%, while fresh seeds of the remaining seven species (mainly annuals) obtained germination percentages less than 10%. Chemical scarification of the seeds of several annual and perennial species, prior to seeding, will enhance the probability of germination in these species. In areas where topsoil replacement and sowing have been completed, irrigation should not be applied prior to the start of the rainy season, as the seeds of most species present in the seed bank will be in a state of dormancy or conditional dormancy.

Key words: After-ripening; dormancy; endogenous germination pattern; germination; leaching; mining; revegetation; scarification

INTRODUCTION

The timing of germination can significantly determine the success of plants growing in arid habitats, if germination is cued by predictors of favourable environmental conditions (Badger & Ungar, 1989). Many seeds do not germinate when placed under conditions, which are normally regarded as favourable for germination, namely an adequate water supply, a favourable temperature and the normal composition of the atmosphere. If these seeds can be shown to be viable, they are said to be dormant, and can be induced to germinate by various special treatments (Mayer & Poljakoff-Mayber, 1975; Lyle, 1987). However, seed dormancy is not equivalent to the absence of germination. Seed dormancy should rather be defined as: a seed characteristic, the degree of which defines what conditions should be met to make the seed germinate (Vleeshouwers *et al.*, 1995).

If freshly matured seeds fail to germinate when incubated over a range of test conditions, they are primary dormant. This is the most common type of dormancy and has two forms: endogenous and exogenous dormancy (Copeland & McDonald, 1995; Baskin & Baskin, 1998). In endogenous dormancy, some characteristic of the embryo prevents germination, whereas in exogenous dormancy, some characteristic of the structures covering the embryo prevents germination (Nikolaeva, 1977; Baskin & Baskin, 1998). Endogenous dormancy broadly comprises physiological, morphological and morphophysiological dormancy, while exogenous dormancy broadly comprises physical, chemical and mechanical dormancy (Baskin & Baskin, 1998).

After-ripening may be defined as any changes which occur in seeds during storage as a result of which germination is improved (Mayer & Poljaloff-Mayber, 1975). During after-ripening (dormancy loss), the range of external conditions under which germination can occur broadens considerably. The transitional state between dormancy and non-dormancy is called conditional dormancy. Non-dormant seeds of some species may re-enter dormancy, *i.e.* secondary dormancy, if environmental conditions are unfavourable for germination (Baskin & Baskin, 1998).

Seed dormancy is a common phenomenon in species from arid, unpredictable environments and probably represents an adaptation which prevents the seeds from responding to occasional, unpredictable showers which occur in the dry season, but which do not provide sufficient moisture for establishment and growth (Freas & Kemp, 1983; Fenner, 1985; Gutterman, 1993). Seed dormancy has been the subject of numerous studies (Mayer & Poljakoff-Mayber, 1975; Copeland & McDonald, 1995; Baskin & Baskin, 1998), but the role of dormancy in revegetation processes has not been adequately investigated (Lyle, 1987). After-ripening can be seen as a mechanism controlling the timing of germination (Leck *et al.*, 1994), which is critical in revegetation efforts.

Plants are able to regulate certain growth and developmental processes due to their apparent ability to measure time independently of the outside environment (Cummings & Wagner, 1968; Copeland & McDonald, 1995). This orderly sequence of growth and development is referred to as 'endogenous' rhythms, which also seem to influence the pattern of seed germination. Both endogenous rhythms and environmental factors such as temperature, are responsible for loss or induction of dormancy in seeds (Copeland & McDonald, 1995; Baskin & Baskin, 1998).

The present study on germination strategies of Strandveld Succulent Karoo plant species was necessitated by the need to ensure optimal germination of seeds to revegetate mined areas along the arid West Coast of South Africa (Environmental Evaluation Unit, 1990). Revegetation of these areas will depend mainly on the use of the soil stored seed bank, as well as seeding and/or transplanting of selected species (Environmental Evaluation Unit, 1990). These methods ensure the re-establishment of local plant species, which are already adapted to the local environmental conditions.

The objectives of this study were to determine the contribution of seed dormancy to the seed bank dynamics of the Strandveld Succulent Karoo, and to determine whether seed dormancy mechanisms and the breaking of dormancy in local species would affect species recruitment during post-mining revegetation efforts. An

understanding of such dormancy mechanisms will aid in the identification of seed bank strategies, *i.e.* transient or persistent, characteristic of specific species or plant types.

This study forms part of a project aimed at describing the seed bank dynamics of the Strandveld Succulent Karoo to guide mining authorities on appropriate revegetation strategies. This paper is the second in a series of three, aimed at identifying some of the seed germination strategies. The first paper in the series deals with temperature and light requirements for germination, while the third concerns the effect of relative humidity on seed viability.

MATERIAL AND METHODS

Mature diaspores (henceforth referred to as seeds) of 27 plant species were collected during spring 1994 and/or 1995, from natural populations in the vicinity of Brand-se-Baai (31°18'S, 17°54'E) on the Cape West Coast, South Africa (De Villiers *et al.*, 1999). This area falls within the Namaqualand coastal belt, an arid region in the north western part of the Republic of South Africa. Rainfall occurs mainly during winter and an average of 160 mm per annum was measured over a period of four years at the study site (De Villiers *et al.*, 1999). The average annual temperature at the study site is 15.8°C with a relatively small fluctuation due to the marine influence (De Villiers *et al.*, 1999).

Collected seeds 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 with a diameter of either 90 mm or 50 mm (depending on the seed size), containing two layers of filter paper (Schleicher & Schüll, no. 595, Dassel, Germany) to which approximately 6 cm^3 or 4 cm^3 distilled water was added respectively. Germination tests were conducted in germination cabinets and radicle protrusion was the germination criterion.

The least significant difference (LSD) one-way analysis of variance (ANOVA) and multiple range test (Statgraphics 5.0, 1989, STSC, Inc., U.S.A.) were used to ascertain significant differences ($P \leq 0.05$), in germination percentages and mean times to germination, between treatments.

After-ripening

Seeds used in the after-ripening experiment were collected during spring 1994 and included the following species: *Albuca exuviata* Bak., *Amellus tenuifolius* Burm., *Arctotis stoechadifolia* Berg., *Ballota africana* (L.) Benth., *Brassica tournefortii* Gouan, *Cephalophyllum spongiosum* (L.Bol.) L.Bol., *Chrysocoma longifolia* DC., *Conicosia pugioniformis* (L.) N.E.Br., *Dimorphotheca pluvialis* (L.) Moench. (disc & ray achenes), *Dimorphotheca tragus* (Ait.) T.Norl., *Ehrharta* calycina J.E.Sm., *Gazania leiopoda* (DC.) Rössl., *Grielum grandiflorum* (L.) Druce, *Hebenstretia repens* Jarosz, *Heliophila coronopifolia* L., *Pharnaceum aurantium* (DC.) Druce, *Pharnaceum exiguum* Adamson, *Polycarena pumila* (Benth.) Levyns, *Ruschia bolusiae* Schwant., *Senecio arenarius* Thunb., *Silene clandestina* Jacq., *Stoeberia* sp., *Tetragonia microptera* Fenzl,

Tripteris oppositifolia (Ait.) T.Norl., *Ursinia anthemoides* (L.) Poir. (black, grey & white achenes) and *Ursinia speciosa* DC. (black & white achenes).

To determine the requirement for an after-ripening period, freshly collected seeds of each 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 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. This temperature was found to be optimal for the germination of seeds of several Namaqualand plant species (Van Rensburg, 1978; Beneke *et al.*, 1993; De Villiers *et al.*, 1994; Visser, 1993). Each treatment consisted of five replicates of 50 seeds per replicate, for each species. The Petri dishes were examined every second day for a period of 30 days, and germinated seeds counted and removed.

Endogenous germination patterns

Seeds collected in spring 1994 were used in this experiment and included the following seven species: *Amellus tenuifolius* Burm., *Conicosia pugioniformis* (L.) N.E.Br., *Dimorphotheca pluvialis* (L.) Moench. (disc & ray achenes), *Gazania leiopoda* (DC.) Rössl., *Pteronia divaricata* (Berg.) Less., *Senecio arenarius* Thunb. and *Ursinia speciosa* DC. (white achenes).

Collected seeds 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. For analysis and presentation of endogenous germination patterns, 6^{th} order polynomial functions (Microsoft Excel 97, 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 used in these experiments were collected during spring 1995 and included the following species: *Albuca exuviata* Bak., *Amellus tenuifolius* Burm., *Brassica tournefortii* Gouan, *Conicosia pugioniformis* (L.) N.E.Br., *Dimorphotheca pluvialis* (L.) Moench. (disc & ray achenes), *Ehrharta* calycina J.E.Sm., *Senecio arenarius* Thunb., *Tetragonia microptera* Fenzl, *Tripteris oppositifolia* (Ait.) T.Norl., and *Ursinia speciosa* DC. (white achenes).

Seeds were stored dry in paper bags at ambient temperatures at the University of Pretoria for periods of 15 – 26 weeks, before conducting alternative dormancy-breaking treatments. Because sowing of selected species during revegetation efforts at Brand-se-Baai would probably not commence prior to the summer after seed dispersal (Chapter 8), a storage period prior to the conducting of alternative dormancy-breaking treatments were used. Untreated seeds were used as a control. Five main dormancy-breaking treatments were applied:

1) Seeds were scarified mechanically by pricking the seed coat, whereafter they were germinated directly or leached in distilled water for four hours prior to conducting germination tests. Seeds of *Conicosia pugioniformis* were not pricked, but scarified with sandpaper. Both sandpaper or pricking of the seed coat were used for mechanical scarification of the seeds of *Brassica tournefortii.*
2) Chemical scarification entailed the submergence of the seeds in 98% sulphuric acid for periods of 0.5, 1, 2, 4, 8 or 16 minutes. Untreated seeds of *Tetragonia microptera* and *Brassica tournefortii* were also submerged for periods of 32 minutes and 32 or 64 minutes, respectively. After the period of submergence, seeds were rinsed with running 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 treated in the reverse order.
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). Seeds of *Amellus tenuifolius, Dimorphotheca pluvialis* (disc & ray achenes), *Senecio arenarius, Tetragonia microptera, Tripteris oppositifolia* and *Ursinia speciosa* (white achenes) were germinated 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. Seeds of *Albuca exuviata* and *Ehrharta calycina* were germinated in darkness at a constant temperature of 17°C. Seeds of *Brassica tournefortii* and *Conicosia pugioniformis* were germinated in darkness at a constant temperature of 22°C. The Petri dishes of the dark treatments were placed in cardboard boxes and sealed with aluminium foil to eliminate light. Each treatment consisted of five replicates of 50 seeds per replicate, for each species. The Petri dishes were examined every second day for a period of 30 days, and germinated seeds counted and removed. Germination of dark replicates was determined under a green safety light.

The mean time to germination (*mtg*) was calculated for each species and treatment using the equation:

$$mtg = \frac{\sum Dn}{\sum n}$$

where n is the number of seeds which germinate on day D and D is the number of days counted from the beginning of the test (Ellis & Roberts, 1981).

RESULTS

After-ripening

Of the 27 species examined, the germination percentages of the perennials *Cephalophyllum spongiosum* and *Albuca exuviata* improved significantly after an after-ripening period of only six weeks (Group 2, Table 9.1). An after-ripening period of 28 weeks significantly improved the germination of 12 species, *i.e.* six perennials and six annuals (Group 1, Table 9.1). In only two perennial species, *Stoeberia* sp. and *Albuca exuviata*, belonging to these groups, did fresh seeds yield germination percentages of more than 10% (Table 9.1).

Thirteen species yielded germination percentages that did not differ between fresh and 28 weeks after-ripened seeds (Groups 3a & 3b Table 9.1). Of these, the fresh seeds of six perennial species yielded germination percentages equal to or more than 10%. Five annual as well as two perennial species had low germination capacities (< 10%) irrespective of the after-ripening treatment. Ten percent was chosen as a cut-off, as this percentage yielded the best separation between annual and perennial species.

Endogenous germination patterns

The polynomial function for *Amellus tenuifolius* (Figure 9.1a) indicated that after 12 weeks of storage (early summer), the germination percentage increased and peaked (87%) during winter, whereafter germination decreased for the remaining period of the experiment. Germination of *Conicosia pugioniformis*' seeds (Figure 9.1b) increased during summer and peaked (4%) during late autumn. The polynomial functions of both seed types of *Dimorphotheca pluvialis* (Figures 9.1c & d) indicated that after an initial after-ripening period, germination peaked (>90% - disc floret seeds; >60% - ray floret seeds) during early winter. For *Gazania leiopoda* (Figure 9.1e), the polynomial function indicated a single germination peak (>80%) in winter. After dispersal, germination percentages of *Pteronia divaricata* (Figure 9.1f) increased gradually and peaked (>70%) during the second summer, wherafter germination declined rapidly during autumn. The polynomial function indicated that seeds of *Senecio arenarius* (Figure 9.1g) after-ripened during the summer, autumn and winter period following dispersal, and germination peaked (>50%) during spring. After a small decline during the following summer, germination increased during autumn. Germination of *Ursinia speciosa* (white achenes) (Figure 9.1h) increased during summer and early autumn after seed dispersal, peaking

Table 9.1. Mean germination percentages at 17°C in the light, of 27 Strandveld Succulent Karoo plant species, stored for different periods. Within each species, values followed by the same letter are not significantly different at $P \leq 0.05$

Species	Fresh seeds (air-dried for 2 weeks at 20°C)	Seeds stored dry at 20°C for 6 weeks	Seeds stored dry at 20°C for 28 weeks	Significance level ($P \leq 0.05$)
Group 1 - Germination percentage increased significantly after 28 weeks of storage				
Dimorphotheca pluvialis - disc (A)	0.0 a	0.4 a	86.4 b	0.0000
Dimorphotheca pluvialis - ray (A)	0.0 a	0.0 a	64.5 b	0.0000
Ehrharta calycina (P)	0.0 a	0.0 a	7.0 b	0.0000
Gazania leiopoda (P)	2.0 a	8.4 a	58.5 b	0.0000
Grielum grandiflorum (P)	0.0 a	0.0 a	15.0 b	0.0000
Pharnaceum aurantium (P)	0.0 a	2.0 a	47.5 b	0.0000
Ruschia bolusiae (P)	0.0 a	2.0 a	14.5 b	0.0001
Senecio arenarius (A)	0.0 a	0.0 a	50.5 b	0.0000
Silene clandestina (A)	0.0 a	0.0 a	20.0 b	0.0000
Stoeberia sp. (P)	24.0 a	10.0 a	57.0 b	0.0001
Tetragonia microptera (A)	0.0 a	0.0 a	1.6 b	0.0334
Ursinia anthemoides - black (A)	0.0 a	0.0 a	5.0 b	0.0001
Ursinia anthemoides - grey (A)	0.0 a	0.0 a	33.5 b	0.0000
Ursinia anthemoides - white (A)	0.0 a	0.0 a	3.5 b	0.0001
Ursinia speciosa - black (A)	0.0 a	0.0 a	10.0 b	0.0000
Ursinia speciosa - white (A)	0.4 a	0.4 a	36.5 b	0.0000
Group 2 - Germination percentage increased significantly after 6 weeks of storage				
Albuca exuviata (P)	38.0 a	96.0 b	94.5 b	0.0000
Cephalophyllum spongiosum (P)	2.0 a	32.0 b	45.5 b	0.0003
Group 3 - Germination percentage did not increase significantly after 6 or 28 weeks of storage				
Group 3a - Germination of fresh seeds ≥ 10%				
Amellus tenuifolius (P)	50.0	36.0	38.0	0.2614
Ballota africana (P)	10.0	10.0	24.2	0.2831
Chrysocoma longifolia (P)	72.0	70.0	75.0	0.6696
Dimorphotheca tragus (P)	44.0	54.0	52.0	0.1600
Pteronia divaricata (P)	12.0	16.0	12.0	0.4769
Tripteris oppositifolia (P)	37.0	52.0	32.4	0.1312
Group 3b - Germination of fresh seeds < 10%				
Arctotis stoechadifolia (P)	0.0	0.0	0.5	0.2298
Brassica tournefortii (A)	0.0	0.8	0.0	0.1101
Conicosia pugioniformis (P)	0.0	0.0	1.5	0.2298
Hebenstretia repens (A)	0.0	0.0	0.0	-
Heliophila coronopifolia (A)	6.0 ab	2.0 a	11.5 b	0.0433
Pharnaceum exiguum (A)	0.0	0.0	0.5	0.2298
Polycarena pumila (A)	4.0	4.0	12.5	0.0971

A - annual
P - perennial

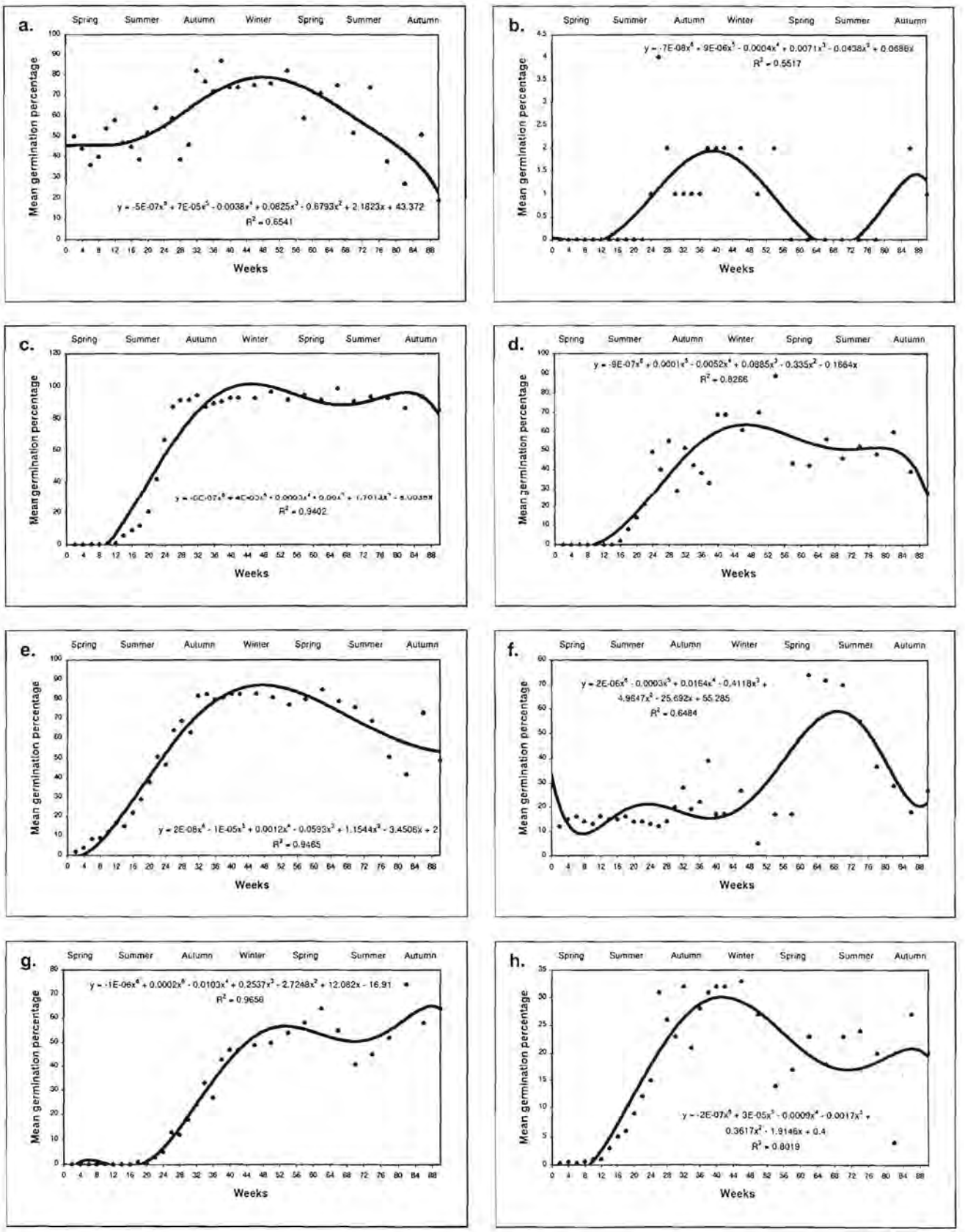

Figure 9.1. Sixth order polynomial functions fitted to mean germination percentages of a) *Amellus tenuifolius* (perennial), b) *Conicosia pugioniformis* (annual), c) *Dimorphotheca pluvialis* disc floret seeds (annual), d) *Dimorphotheca pluvialis* ray floret seeds (annual), e) *Gazania leiopoda* (perennial), f) *Pteronia divaricata* (perennial), g) *Senecio arenarius* (annual) and h) white seeds of *Ursinia speciosa* (annual), determined over a period of 88 weeks. Germination tests at 17°C in the light were conducted fortnightly over the first period of 40 weeks, whereafter germination tests were conducted every four weeks for a period of 48 weeks.

(33%) during late autumn and early winter. A second lesser germination peak occurred during the second autumn after dispersal.

Alternative dormancy-breaking treatments

Results of the alternative dormancy-breaking treatments are shown in Tables 9.2 and 9.3. Mechanical scarification improved the mean germination percentages of both *Senecio arenarius* and *Brassica tournefortii* (Table 9.2), as well as the mean time to germination of *Conicosia pugioniformis* (Table 9.3). Scarification by means of sulphuric acid improved the mean germination percentages of six species and mean time to germination of seven species, for some scarification periods.

Hydration/dehydration treatments improved the germination percentages (Table 9.2) of two species, while the mean time to germination (Table 9.3) of five species was improved by this treatment.

Heat pre-treatment did not improve the germination of any of the species investigated, while cold pre-treatment and heat+cold pre-treatment improved the germination percentages (Table 9.2) of *Ursinia speciosa* and *Tetragonia microptera*, and the mean time to germination (Table 9.3) of *Conicosia pugioniformis* and *Ehrharta calycina*. A cold-pre-treatment also decreased the mean time to germination of *Albuca exuviata*. Cold+heat pre-treatment improved the mean germination percentage of *Dimorphotheca pluvialis* disc floret seeds.

Leaching for one hour and for four hours improved the germination percentage (Table 9.2) of *Albuca exuviata* and the mean time to germination (Table 9.3) of *Tetragonia microptera*, respectively.

DISCUSSION

After-ripening

In at least 52% of the species investigated (Groups 1 & 2, Table 9.1), the regulation of germination timing involves safe-guards against precocious summer germination (*i.e.* seed dormancy and/or slow germination) and subsequent loss of these regulatory mechanisms in time for autumn germination. One of these processes, by which a species loses these protective mechanisms, is after-ripening (Evenari, 1965; Bewley & Black, 1994; Baskin & Baskin, 1998).

The seeds of *Albuca exuviata* and *Cephalophyllum spongiosum* (Group 2, Table 9.1) require a short after-ripening period (*c.* 2 – 6 weeks), whereafter they may germinate at the first fall of sufficient rain, providing temperature and light requirements are met. Species of Group 1 (Table 9.1) require after-ripening periods longer than six weeks.

Table 9.2. Mean germination percentages of ten Strandveld Succulent Karoo plant species, after various dormancy-breaking treatments. Plant type, temperature and light condition at which germination was conducted, and the number of weeks that seeds were stored, are indicated between brackets

Treatment	Time	Species										
		Senecio arenarius (A; 17L; 24)	*Brassica tournefortii* (A; 22D; 20)	*Conicosia pugioniformis* (P; 22D; 23)	*Amellus tenuifolius* (P; 17L; 17)	*Tripteris oppositifolia* (P; 17L; 15)	*Ursinia speciosa* white (A; 17L; 19)	*Tetragonia microptera* (A; 17L; 22)	*Dimorphotheca pluvialis* disc (A; 17L; 25)	*Albuca exuviata* (P; 17D; 26)	*Dimorphotheca pluvialis* ray (A; 17L; 21)	*Ehrharta calycina* (P; 17D; 18)
Control		66.4	64.8	53.0	58.8	32.4	9.2	1.6	86.4	93.2	19.2	24.4
Scarify (prick)		81.6 *	84.4 *	-	62.0	14.4 $	0.0 $	0.8	85.2	88.4 $	22.4	9.2 $
Scarify + Leaching		80.4 *	81.6 *	-	76.0	14.0 $	0.0 $	0.0	87.2	88.4 $	10.8 $	20.0
Scarify 2 (sandpaper)		-	46.0 $	34.0 $	-	-	-	-	-	-	-	-
Scarify2 + Leaching		-	46.0 $	31.0 $	-	-	-	-	-	-	-	-
Sulphuric Acid	0.5 min.	79.6 *	65.6	91.0 *	86.0 *	41.2	16.0 *	0.4	91.6	0.4 $	14.0	21.2
	1 min.	68.8	64.4	92.0 *	54.8	37.6	7.6	1.6	91.2	1.2 $	14.8	27.6
	2 min.	52.8 $	51.2 $	93.0 *	43.6	20.4 $	5.6	0.4	91.2	5.2 $	9.2 $	28.0
	4 min.	17.2 $	80.4 *	93.0 *	22.0 $	39.2	2.4 $	0.4	92.4	9.6 $	10.4 $	26.8
	8 min.	6.8 $	99.2 *	82.0 *	13.2 $	44.4 *	4.4	1.6	88.4	5.2 $	8.4 $	16.8
	16 min.	0.8 $	98.0 *	69.0 *	0.0 $	22.4	12.4	0.4	86.0	3.6 $	7.6 $	10.8 $
	32 min.	-	98.4 *	-	-	-	-	0.8	-	-	-	-
	64 min.	-	3.6	-	-	-	-	-	-	-	-	-
Hydration/ dehydration	1 Hour	66.4	62.4	55.0	62.8	31.2	23.2 *	5.2 *	89.2	95.2	16.8	22.4
	2 Hours	68.4	59.6	46.0	68.0	30.8	25.2 *	6.4 *	90.0	95.2	23.2	21.6
	4 Hours	44.8 $	50.0 $	48.0	63.2	29.2	19.6 *	4.8 *	90.4	96.8	17.6	31.6
	8 Hours	27.2 $	49.2 $	48.0	64.4	39.2	12.8	4.8 *	91.2	94.0	14.0	27.2
	16 Hours	14.8 $	35.6 $	49.0	58.8	41.6	7.2	3.2	88.8	96.4	10.4 $	23.6
Heat pre-treatment (1 week at 45°C)		59.6	47.2 $	44.0	59.2	19.6 $	12.4	3.2	81.2	82.0 $	4.0 $	15.6 $
Cold pre-treatment (1 week at 5°C)		54.0	43.2 $	42.0	54.4	28.0	18.0 *	4.0 *	91.6	92.4	9.2 $	18.8
Heat + Cold pre-treatment		70.0	62.0	54.0	46.8	14.4 $	15.6 *	5.2 *	91.2	90.0	6.4 $	29.2
Cold + Heat pre-treatment		54.0	60.4	46.0	49.2	15.6 $	12.0	3.2	95.2 *	82.8 $	6.4 $	24.4
Leaching	1 Hour	56.8	58.0	58.0	55.6	20.4 $	3.6 $	1.6	85.2	98.4 *	8.4 $	24.4
	2 Hours	66.0	57.2	46.0	66.4	16.0 $	1.6 $	0.4	76.4 $	95.2	10.0 $	26.0
	4 Hours	50.8 $	48.8 $	54.0	65.2	22.0	1.6 $	1.2	88.0	94.8	10.4 $	14.8 $
	8 Hours	34.4 $	49.2 $	56.0	64.0	19.6 $	2.0 $	0.0	90.0	96.8	10.8 $	29.2
	16 Hours	21.6 $	30.0 $	52.0	59.2	34.8	0.8 $	0.0	89.2	93.2	10.4 $	17.6

- Treatment not used for this species

P - Perennial

A - Annual

* Mean germination percentage significantly higher than that of the control treatment ($P \leq 0.05$)

$ Mean germination percentage significantly lower than that of the control treatment ($P \leq 0.05$)

Table 9.3. Mean time to germination (days) of ten Strandveld Succulent Karoo plant species, after various dormancy-breaking treatments. Plant type, temperature and light condition at which germination was conducted, and the number of weeks that seeds were stored, are indicated between brackets

Treatment	Time	Species										
		Senecio arenarius (A; 17L; 24)	*Brassica tournefortii* (A; 22D; 20)	*Conicosia pugioniformis* (P; 22D; 23)	*Amellus tenuifolius* (P; 17L; 17)	*Tripteris oppositifolia* (P; 17L; 15)	*Ursinia speciosa* white (A; 17L; 19)	*Tetragonia microptera* (A; 17L; 22)	*Dimorphotheca pluvialis* disc (A; 17L; 25)	*Albuca exuviata* (P; 17D; 26)	*Dimorphotheca pluvialis* ray (A; 17L; 21)	*Ehrharta calycina* (P; 17D; 18)
Control		5.7	2.5	10.7	12.4	9.1	9.8	18.0	4.0	3.6	6.3	10.4
Scarify (prick)		6.8	2.6	-	9.7	8.6	--	22.0	3.6	3.5	6.3	7.0 *
Scarify + Leaching		7.1 $	3.7 $	-	11.0	8.5	--	--	4.2	3.6	7.9	9.0
Scarify 2 (sandpaper)		-	2.9 $	5.4 *	-	-	-	-	-	-	-	-
Scarify2 + Leaching		-	2.9 $	6.5 *	-	-	-	-	-	-	-	-
Sulphuric Acid	0.5 min.	4.7	2.3	5.2 *	11.9	10.4	11.7	26.0	4.2	6.0 $	7.7	8.0 *
	1 min.	5.3	2.3	5.2 *	14.6	10.3	12.4	18.0	3.6	2.7 *	8.5	7.8 *
	2 min.	5.1	2.3	5.7 *	9.7	11.1 $	12.3	18.0	3.2	2.6 *	9.4	7.3 *
	4 min.	4.5 *	2.1	5.1 *	8.2 *	10.5	11.7	22.0	2.9 *	2.8 *	10.1	7.0 *
	8 min.	4.8	2.1 *	5.4 *	9.0	10.0	10.2	21.5	3.2 *	2.9 *	12.1 $	7.2 *
	16 min.	4.0 *	2.1 *	8.4 *	--	10.4 $	9.7	26.0	3.0 *	3.1	9.7	7.1 *
	32 min.	-	2.2	-	-	-	-	16.0	-	-	-	-
	64 min.	-	4.0 $	-	-	-	-	-	-	-	-	-
Hydration/ dehydration	1 Hour	5.8	2.4	9.9	12.8	8.8	11.3	15.5	3.2	2.9	6.6	10.0
	2 Hours	5.4	2.5	11.1	11.9	7.8	11.3	14.3	2.8 *	3.2	5.1	10.3
	4 Hours	6.2	2.8	11.1	12.4	8.4	10.6	11.8	3.1 *	2.9	7.0	9.5
	8 Hours	7.6 $	2.7	10.5	15.2	7.5 *	9.8	14.2	3.6	2.9	5.3	7.6 *
	16 Hours	8.1 $	3.6 $	10.5	13.4	7.5	10.6	8.5 *	3.2 *	2.8 *	8.4	7.4 *
Heat pre-treatment (1 week at 45°C)		5.3	2.8	10.7	14.1	9.2	7.7	24.0	4.4	14.2 $	9.6 $	9.0
Cold pre-treatment (1 week at 5°C)		6.4	2.5	9.1 *	12.6	8.9	7.0	19.8	3.6	2.7 *	6.4	8.4 *
Heat + Cold pre-treatment		8.7 $	2.1	9.3 *	13.2	10.1	8.3	22.8	4.4	10.1 $	7.0	8.1 *
Cold + Heat pre-treatment		7.7 $	2.2	10.0	13.8	9.6	6.7	22.5	3.7	12.8 $	7.8 $	8.9
Leaching	1 Hour	6.4	2.7	10.5	12.4	8.2	10.7	17.5	3.9	3.9	9.6	10.4
	2 Hours	7.2 $	2.6	11.9 $	13.5	8.0	7.0	14.0	4.1	3.8	8.0	10.0
	4 Hours	7.8 $	3.2 $	9.8	11.5	8.9	6.5	10.0 *	4.1	3.8	7.5	9.8
	8 Hours	8.0 $	3.4 $	10.4	11.7	8.4	9.2	--	3.7	3.4	6.4	9.3
	16 Hours	8.3 $	3.7 $	9.7	12.4	9.1	16.0	--	3.6	3.3	10.2	10.7

- Treatment not used for this species

* Mean time to germination significantly higher than that of the control treatment ($P \leq 0.05$)

$ Mean time to germination significantly lower than that of the control treatment ($P \leq 0.05$)

P - Perennial

A - Annual

Many perennial and annual species of Namaqualand require a summer after-ripening period to enable them to germination in autumn (Beneke *et al.*, 1993; Visser, 1993). In species where germination is promoted by after-ripening, fresh seeds have low germination percentages (high dormancy) and germinate very slowly, while after-ripened seeds are non-dormant or conditionally dormant and germinate quickly (Beckstead *et al.*, 1996). Both the high temperature and the low moisture conditions during summer probably promote loss of dormancy in many species from winter rainfall habitats (Baskin & Baskin, 1976a, 1998). Non-dormant and conditionally dormant seeds that did not germinate during the rainy season may enter secondary dormancy due to low winter temperatures (Baskin & Baskin, 1976a; Visser, 1993; Bewley & Black, 1994).

As after-ripening (dormancy loss) occurs in seeds of winter annuals, they first gain the ability to germinate at low temperatures, and then with additional dormancy loss also at high temperatures (Copeland & McDonald, 1995; Baskin & Baskin, 1998). As dormancy loss progresses, the rate of germination increases and seeds of some species lose their light requirement for germination. Germination is prevented during summer because the maximum temperatures at which seeds can germinate are below those occurring in the habitat. Seeds germinate in autumn because the maximum temperature for germination has increased and habitat temperatures have declined until there is an overlap between the two (Baskin & Baskin, 1976b, 1998). Clearly, after-ripening is a function of environment as well as time (Murdoch & Ellis, 1992).

The requirement of an after-ripening period by seeds indicate a delay in germination until the probability of seedling survival and plant growth is high (Tevis, 1958; Baskin & Baskin, 1976a, 1976b, 1998; Bewley & Black, 1994). In the Strandveld Succulent Karoo, this germination strategy ensures that newly shed seeds do not germinate during occasional summer precipitation, as few seedlings will survive during the hot season.

Many seeds of the six perennial species of Group 3a (Table 9.1) may germinate at the first fall of sufficient rain after dispersal, providing favourable temperature and light conditions. With the exception of *Tripteris oppositifolia*, these species obtained higher germination percentages and/or rates in darkness than in light treatments (Chapter 8). Temperature and moisture in the habitat probably determine the timing of germination in these species.

Species of Group 3b probably require germination conditions other than 17°C in the light, a longer period of after-ripening, and/or specific conditions for the breaking of dormancy (see alternative dormancy-breaking treatments), to obtain optimum germination. Germination of *Brassica tournefortii, Conicosia pugioniformis, Hebenstretia repens* and *Polycarena pumila* was improved in the absence of light (Chapter 8). With the exception of *Polycarena pumila*, these species also obtained higher germination percentages at temperatures higher than 17°C.

Endogenous germination patterns

No clear germination patterns could be ascertained for the species investigated (Figures 9.1a, b, c, d, e, f, g & h). This experiment continued for a period of 88 weeks, whereas a period of 104 weeks will be necessary

to confirm the presence or absence of germination rhythms in most species. Such periodicity in seed germination has been observed in the seeds of numerous species (Crocker & Barton, 1957; Bünning, 1965; Maguire, 1969; Gutterman, 1980, 1993; Copeland & McDonald, 1995), including several species from Namaqualand (Beneke *et al.*, 1993).

After dispersal in spring, the dormant seeds of winter annual species become conditionally dormant or non-dormant (after-ripen) during summer and autumn (Baskin & Baskin, 1998). Because germination of seeds occurs at times of low or no dormancy, the non-dormant (after-ripened) seeds simply await the availability of moisture and suitable temperatures for germination (Bouwmeester, 1990; Murdoch & Ellis, 1992). During late autumn and early winter, the germination of *Conicosia pugioniformis* and *Ursinia speciosa* peaked (Figures 9.1b & h). In the field, this is also the period when environmental conditions (temperature & moisture) are most favourable for the germination, emergence and survival of these species (Chapter 8). Exposure to light, nitrate, fluctuations of temperature or combinations of these treatments may be needed to relieve residual innate and induced dormancy at times of low dormancy (Murdoch & Ellis, 1992).

A decrease in germination during winter and spring (Figures 9.1b & h) may be due to a decrease in seed viability and/or the seeds of such species have been induced into secondary dormancy. Seeds of winter annual species entering secondary dormancy are usually correlated with low winter temperatures and/or darkness (Bewley & Black, 1994; Copeland & McDonald, 1995; Baskin & Baskin, 1998). The seasonal temperature cycle is usually responsible for annual dormancy cycles observed in seeds of winter annuals, i.e. germination increases after exposure to high summer temperatures and decreases after exposure to low winter temperatures (Derkx & Karssen, 1994; Baskin & Baskin, 1998). In this study, seeds were not exposed to low winter temperatures and although seeds were stored in darkness, germination was conducted in the light. Therefore, seeds of these species have innate mechanisms controlling the weak endogenous germination patterns observed. These endogenous germination responses help explain the periodicity of seedling emergence which characterises many species (Roberts, 1964; Beneke *et al.*, 1993; Murdoch & Ellis, 1992; Visser, 1993). From an ecological point of view, such endogenous germination patterns may ensure that germination is restricted to autumn and early winter, the normal rainy season where these species naturally occur (Gutterman, 1980; Beneke *et al.*, 1993; Murdoch & Ellis, 1992; Visser, 1993).

The low germination capacity ($\leq$ 4%) recorded for *Conicosia pugioniformis* may be due to the fact that conditions for germination were not optimal. A study on the temperature and light requirements of this species indicated optimum germination conditions to be 19.5°C in darkness (Chapter 8). For this species, unfavourable germination conditions may also be the reason for the large difference in germination capacity observed between this experiment ($\leq$ 4%) and the control treatment of the alternative dormancy-breaking treatments (53%, Table 9.2). Differences in seed dormancy between seeds collected during different seasons (1994 & 1995) may also be responsible for the observed discrepancy, as reported for several species from arid environments (Gutterman, 1993).

Some of the seeds of the perennial species, i.e. *Amellus tenuifolius* and *Pteronia divaricata* were non-dormant or conditionally dormant at the start of the experiment, while other seeds (including the seeds of

Gazania leiopoda) became conditionally dormant or non-dormant during the summer and autumn months following dispersal. The seeds of *Amellus tenuifolius* and *Gazania leiopoda* obtained maximum germination during winter, while the seeds of *Pteronia divaricata* continued to after-ripen during winter and spring, and obtained maximum germination during early summer. Germination of *Pteronia divaricata* seeds may therefore occur after occasional rainfall during summer, but the resulting seedlings will probably not survive.

The decrease in germination percentage of these perennial species, following the peak in germination, probably indicates a loss in seed viability and these species will not be able to accumulate large persistent seed banks (Chapter 11). However, seed viability for these species was not determined in this experiment. Because no clear germination patterns were evident, environmental factors such as temperature and moisture probably determine the timing of germination (Mayer & Poljakoff-Mayber, 1975) in these perennial species.

In non-dormant or conditionally dormant orthodox seeds of dry regions, such as *Amellus tenuifolius* and *Pteronia divaricata*, persistence is usually associated with enforced quiescence (lack of suitable environmental conditions for germination) (Murdoch & Ellis, 1992). However, most of these species germinate rapidly after shedding as soon as sufficient moisture is available, and are therefore transient in the soil seed bank (Chapter 11; Murdoch & Ellis, 1992).

Alternative dormancy-breaking treatments

Non-deep physiological dormancy appears to be characteristic of at least eight of the ten species investigated (Tables 9.1 & 9.2). Methods for breaking such dormancy include warm and/or cold stratification (Baskin & Baskin, 1998), leaching and scarification of the pericarp (Copeland & McDonald, 1995).

In nine of the species investigated (4 annuals and 5 perennials, including the 2 species that do not require an after-ripening period), pericarp scarification resulted in increased germination percentages and/or shorter mean times to germination (Tables 9.2 & 9.3) for some scarification periods. Dormancy in these species is probably due to the mechanical restriction and/or the low permeability of the pericarp to oxygen, while the light requirement may also be controlled by the pericarp. Since germination percentages and mean times to germination did not improve when mechanical scarification was followed by a leaching period, water soluble growth inhibitors are probably not present in the embryos of these species.

The requirement for pericarp scarification prior to germination has been reported by several authors (Went, 1961; Haas *et al.*, 1973; Burrows, 1994; Copeland & McDonald, 1995) and was usually associated with breaking of the mechanical constraint imposed by the pericarp (Conner & Conner, 1988; Burrows, 1989; Fountain & Outred, 1991). In many cases, seeds with pericarp imposed dormancy contribute to the formation of a persistent seed bank (Fountain & Outred, 1991).

In this study, chemical scarification proved to be less labour intensive, and resulted in increased germination percentages and/or shorter mean times to germination in more species than did mechanical scarification.

Due to its positive effect on the germination of perennial species, chemical scarification is recommended should alternative dormancy-breaking treatments be required during the revegetation of mined areas in the Strandveld Succulent Karoo. However, the specific scarification period should be determined individually for each species to be sown.

The germination percentages of two annual species increased when hydration of the seeds was followed by a dehydration period, or when seeds were given a cold or a heat+cold pre-treatment (Table 9.2). Hydration followed by dehydration may result in specific changes in the pericarp without the loss of probable germination promoting substances. Similar changes in the structure of the pericarp may result from cold pre-treatment or heat+cold pre-treatment. Improved germination by means of hydration/dehydration has been reported for several species (Barbour, 1968; Morgan & Myers, 1989), including species from Namaqualand (Visser, 1993), and may involve the leaching of germination inhibitors. Because the seeds of most winter annual species occur mainly on or just below the soil surface after dispersal, it is expected that alternating wet and dry conditions will influence germination (Mott, 1974). Embryo development may be initiated by alternating wet and dry conditions, resulting in a faster rate of germination when temperature and moisture conditions are favourable (Hegarthy, 1978).

Increased germination percentages (2 annuals) and mean times to germination (3 perennials) due to cold and/or heat+cold treatments (Tables 9.2 & 9.3) may indicate a safe-guard against precocious summer rains. In these species, a cold requirement ensures that germination occurs in winter, when moisture is usually non-limiting at the study area. Prolonged exposure of seeds to low temperatures during winter may induce secondary dormancy, to prevent germination in spring (Baskin & Baskin, 1998). Requirement of cold pre-treatment (stratification) is usually associated with species germinating in spring (Bewley & Black, 1994; Baskin & Baskin, 1998). The mean germination percentages of these species were low (<30%), which make presumptions about specific treatments difficult.

Since many winter annuals require high summer temperatures to after-ripen (Gutterman, 1993; Visser, 1993; Baskin & Baskin, 1998), it was expected that a heat pre-treatment would be beneficial for seed germination in the annual species examined. However, this treatment did not result in increased germination percentages or mean times to germination in any of the species investigated. A cold+heat treatment did result in higher germination percentages in the disc floret seeds of *Dimorphotheca pluvialis* (Table 9.2). The requirement of long periods of high temperature before seeds are "ready to germinate" is an important survival mechanism because it prevents germination in the wrong season (Capon & Van Asdall, 1967; Gutterman, 1993).

Only one geophyte species, *i.e. Albuca exuviata*, yielded higher germination percentages after a leaching treatment than in the control (Table 9.2), and only at a treatment period of one hour. The presence of water soluble germination inhibitors seem to be the main cause of the observed increase in germination percentages in this species. Increased germination due to the leaching of water soluble germination inhibitors has been reported for numerous species (Copeland & McDonald, 1995), including several species from arid environments (Koller, 1955; Capon & Van Asdall, 1967; Bell *et al.*, 1993; Visser, 1993).

A leaching requirement in seeds may be ascribed to the role of water soluble compounds preventing germination in climates with seasonal rainfall (Bell *et al.*, 1993). In deserts, the leaching of germination inhibitors from seeds is one explanation for the germination of seeds following a rain storm, in addition to there being enough water present for the seeds to become fully imbibed. Thus, the amount of rain required to remove the inhibitors is thought to equal the amount of moisture required for seedling establishment and eventual maturation of the plant (Went, 1955; Gutterman, 1993; Visser, 1993; Baskin & Baskin, 1998).

By the time that additional dormancy-breaking treatments started for *Albuca exuviata* (after 26 weeks storage) and the disc floret seeds of *Dimorphotheca pluvialis* (after 25 weeks storage), most of the seeds have already after-ripened, yielding mean germination percentage of 93% and 86% respectively, in the control treatment (Table 9.2). Nonetheless, leaching for one hour increased the germination percentage of *Albuca exuviata* to 98%, while a cold+heat treatment increased that of *Dimorphotheca pluvialis* (disc) to 95%. Under field conditions, after-ripening will be sufficient for breaking dormancy as well as recruitment of these species.

Revegetation

The ecological function of primary dormancy appears to be twofold (Murdoch & Ellis, 1992). Firstly, along with the inhibition of germination of developing seeds by the mother plant, dormancy helps to prevent precocious germination on the mother plant (Bewley & Black, 1982). Secondly, in many species, dormancy persists after maturation and shedding to ensure the temporal dispersal of seeds by preventing the immediate and approximately synchronous germination of seeds. Therefore, dormancy is an adaptive trait that optimises the distribution of germination over time within a population of seeds (Simpson, 1990; Bewley & Black, 1994).

Dormancy is claimed to be a device for preventing germination during short periods of favourable conditions (Vleeshouwers *et al.*, 1995), rather than a device for surviving prolonged periods of unfavourable conditions (Went, 1961; Baskin & Baskin, 1976a; Bradbeer, 1988; Visser, 1993). During unfavourable conditions (dry summer months) the lack of germination-stimulating factors (temperature & moisture) will prevent germination, and the seeds will survive ungerminated in the soil, independent of their dormancy state (Vleeshouwers *et al.*, 1995).

The soil seed bank of the Strandveld Succulent Karoo is dominated mainly by species with annual life strategies (Chapters 4 & 5). These species depend on the production and survival of seeds for regeneration (Crawford, 1989). Since the physiological state of seeds is an important aspect in the control of timing of germination (Baskin & Baskin, 1998), the dormancy status of the annual species from the study area will aid in the determination of the appropriate timing for revegetation. Most of the annual species investigated exhibited nondeep physiological dormancy, and germination was promoted by a summer after-ripening period. The germination of these seeds may also follow specific endogenous germination patterns. In the Strandveld Succulent Karoo, these endogenous germination strategies have the ability to ensure that most

seeds do not germinate during occasional summer precipitation, as few seedlings will survive during the hot season.

The recruitment of annual species from the topsoil stored seed bank can be maximised by ensuring that irrigation commences only at the start of the rainy season. During the summer period, after-ripening of seeds of many annual species proceeds. Several of the annuals investigated require dormancy-breaking mechanisms supplementary to after-ripening for maximum germination in autumn (Table 9.2). Natural scarification or hydration/dehydration cycles in the habitat (Gutterman, 1993), however, may be sufficient for the recruitment of these species from the topsoil stored seed bank. Seeds that persist in the soil after initial recruitment may contribute to future recruitment events.

In species with dimorphic seeds, e.g. *Dimorphotheca pluvialis*, reproduction is at a maximum if the seeds with the best dispersal mechanism are nondormant (disc diaspores) and those that are not so easily dispersed are dormant (ray diaspores)(Baskin & Baskin, 1998). The possession of dimorphic seed types by a species reduces the chances of extinction of a complete generation (Berger, 1985). The thick pericarp of the ray diaspores possibly ensures their longevity and allows their maintenance in the seed bank, thereby enabling the species to escape in time (Beneke *et al.*, 1993). Species with dimorphic seed types, such as *Dimorphotheca pluvialis*, may play an important role in revegetation efforts in the Strandveld Succulent Karoo. Apart from an initial germination flush, these species may be recruited from the topsoil stored seed bank over a long period (by dormant ray floret seeds) and, if present in surrounding vegetation, will probably be dispersed from such vegetation (disc floret seeds).

Perennial grass species such as *Ehrharta calycina* were abundant in the soil seed bank of the study area (Chapter 5). Germination of these species is promoted by a summer after-ripening period and recruitment from the topsoil stored seed bank should be sufficient during revegetation efforts.

After mining of an area has been completed, many perennial species will have to be reintroduced by means of seeding or transplanting (Chapter 7), because of the low abundance of these species in the soil seed bank (Chapter 4). As the perennial shrub species investigated were either nondormant or conditionally dormant soon after being dispersed, irrigation should not commence prior to the start of the rainy season. In these species, it may be adventageous not to break the dormancy of those seeds that remained dormant, as to ensure the presence of these species in the seed bank for future recruitment. The germination of those perennial and annual species with hard pericarps and low germination percentages (< 10%) could probably be improved by means of chemical scarification prior to seeding. However, financial and practical implications will determine the viability of this approach to enhance germination in seeds with pericarp imposed dormancy.

Similar to other plant species from Namaqualand (Beneke *et al.*, 1993; Visser, 1993), Strandveld Succulent Karoo plant species possess innate seed characteristics and have developed many different dormancy strategies, to ensure survival. Some species have hard seed coats which require scarification, some need a specific minimum amount of rain for germination, while in others, germination is promoted by a summer after-ripening period. These dormancy strategies, together with the amount of rainfall, temperature and light

(Chapter 8), will be the main mechanisms determining the timing of germination in these species. In turn, the timing of germination will influence the timing and management of revegetation efforts. Utilisation of seed germination characteristics, such as dormancy and germination requirements, of local plant species should therefore yield the highest probability of success in the revegetation of the area after completion of mining.

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REFERENCES

BADGER, K.S. & UNGAR, I.A. 1989. The effects of salinity and temperature on the germination of the inland halophyte *Hordeum jubatum*. *Canadian Journal of Botany*, **67**: 1420-1425.

BARBOUR, M.G. 1968. Germination requirements of the desert shrub *Larrea divaricata*. *Ecology*, **49**: 915-923.

BASKIN, C.C & BASKIN, J.M. 1998. *Seeds: Ecology, biogeography, and evolution of dormancy and germination.* Academic Press, New York.

BASKIN, J.M. & BASKIN, C.C. 1976a. High temperature requirement for afterripening in seeds of winter annuals. *New Phytologist*, **77**: 619-624.

BASKIN, J.M. & BASKIN, C.C. 1976b. Effect of photoperiod on germination of *Cyperus inflexus* seeds. *Botanical Gazette*, **137**: 269-273.

BECKSTEAD, J., MEYER, S.E. & ALLEN, P.S. 1996. *Bromus tectorum* seed germination: between-population and between-year variation. *Canadian Journal of Botany*, **74**: 875-882.

BELL, D.T., PLUMMER, J.A. & TAYLOR, S.K. 1993. Seed germination ecology in Southwestern western Australia. *The Botanical Review*, **59**: 24-73.

BENEKE, K., VAN ROOYEN, M.W., THERON, G.K. & VAN DE VENTER, H.A. 1993. Fruit polymorphism in ephemeral species of Namaqualand: III. Germination differences between the polymorphic diaspores. *Journal of Arid Environments*, **24**: 333-344.

BERGER, A. 1985. Seed dimorphism and germination behaviour in *Salicornia patula*. *Vegetatio*, **61**: 137-143.

BEWLEY, J.D. & BLACK, M. 1982. *Physiology and biochemistry of seeds.* Springer-Verlag, Heidelberg.

BEWLEY, J.D. & BLACK, M. 1994. *Seeds: Physiology of development and germination.* Plenum Press, London.

BOUWMEESTER, H.J. 1990. The effect of environmental conditions on the seasonal dormancy pattern and germination of weed seeds. Ph.D. thesis, Agricultural University in Wageningen, Wageningen.

BRADBEER, J.W. 1988. *Seed dormancy and germination.* Chapman & Hall, London.

BÜNNING, E. 1965. Endogenous rhythmic activities. *Encyclopedia of Plant Physiology*, **15**: 879-907.

BURROWS, C.J. 1989. Patterns of delayed germination in seeds. *New Zealand Natural Sciences*, **16**: 13-19.

BURROWS, C.J. 1994. The seeds always know best. *New Zealand Journal of Botany*, **32**: 349-363.

CAPON, B. & VAN ASDALL, W. 1967. Heat pre-treatment as a means of increasing germination of desert annual seeds. *Ecology*, **48**: 305-306.

CONNER, L.N. & CONNER, A.J. 1988. Seed biology of *Chordospartium stevensonii*. *New Zealand Journal of Botany*, **26**: 473-475.

COPELAND, L.O. & McDONALD, M.B. 1995. *Principles of seed science and technology*. Chapman & Hall, New York.

CRAWFORD, R.M.M. 1989. *Studies in plant survival. Ecological case histories of plant adaptation to adversity*. Blackwell Scientific Publications, Oxford.

CROCKER, W. & BARTON, L.V. 1957. *Physiology of seeds: An introduction to the experimental study of seed and germination problems*. Chronica Botany Company, Waltham, Massachusetts.

CUMMINGS, B.C. & WAGNER, E. 1968. Rhythmic processes in plants. *Annual Review of Plant Physiology*, **19**: 381-416.

DERKX, M.P.M. & KARSSEN, C.M. 1994. Are seasonal dormancy patterns in *Arabidopsis thaliana* regulated by changes in seed sensitivity to light, nitrate and gibberellin ? *Annals of Botany*, **73**: 129-136.

DE VILLIERS, A.J., VAN ROOYEN, M.W., THERON, G.K. & VAN DE VENTER, H.A. 1994. Germination of three Namaqualand pioneer species, as influenced by salinity, temperature and light. *Seed Science & Technology*, **22**: 427-433.

DE VILLIERS, A.J., VAN ROOYEN, M.W., THERON, G.K. & VAN ROOYEN, N. 1999. Vegetation diversity of the Brand-se-Baai coastal dune area, West Coast, South Africa: A pre-mining benchmark survey for rehabilitation. *Land Degradation & Development*, **10**: 207-224.

ELLIS, R.H. & ROBERTS, E.H. 1981. The quantification of ageing and survival in orthodox seeds. *Seed Science & Technology*, **9**: 373-409.

ENVIRONMENTAL EVALUATION UNIT. 1990. *Anglo American Corporation: West Coast heavy mineral sands project*. Unpublished report. University of Cape Town, Cape Town.

EVENARI, M. 1965. Physiology of seed dormancy, after-ripening and germination. *Proceedings of the International Seed Testing Association*, **30**: 49-71.

FENNER, M. 1985. *Seed Ecology*. Chapman & Hall, London.

FOUNTAIN, D.W. & OUTRED, H.A. 1991. Germination requirements of New Zealand native plants: a review. *New Zealand Journal of Botany*, **29**: 311-316.

FREAS, K.E. & KEMP, P.R. 1983. Some relationships between environmental reliability and seed dormancy in desert annual plants. *Journal of Ecology*, **71**: 211-217.

GUTTERMAN, Y. 1980. Annual rhythm and position effect in the germinability of *Mesembryanthemum nodiflorum*. *Israel Journal of Botany*, **29**: 93-97.

GUTTERMAN, Y. 1993. *Seed germination in desert plants*. Springer-Verlag, Berlin.

HAAS, R.H., MEYER, R.E., SCIFRIES, C.J. & BROCK, J.H. 1973. *Growth and development of mesquite*. Texas A&M Agr. Exp. Sta., Texas.

HEGARTHY, T.W. 1978. The physiology of seed hydration and relation between water stress and control of germination: a review. *Plant, Cell and Environment*, **1**: 101-119.

KOLLER, D. 1955. The regulation of germination in seeds. *Israel Research Council Bulletin*, **5**: 85-108.

LECK, M.A., BASKIN, C.C. & BASKIN, J.M. 1994. Germination ecology of *Bidens laevis* (Asteraceae) from a tidal freshwater wetland. *Bulletin of the Torrey Botanical Club*, **121**: 230-239.

LYLE, E.S. Jr.. 1987. *Surface mine reclamation manual.* Elsevier, New York.

MAGUIRE, J.D. 1969. Endogenous germination rhythms in seeds. *Proceedings of the Association of Official Seed Analysts*, **59**: 95-100.

MAYER, A.M. & POLJAKOFF-MAYBER, A. 1975. *The germination of seeds.* Pergamon Press, Oxford.

MORGAN, W.C. & MYERS, B.A. 1989. Germination of the salt-tolerant grass *Diplachne fusca*. I. Dormancy and temperature responses. *Australian Journal of Botany*, **37**: 225-237.

MOTT, J.J. 1974. Factors affecting seed germination in three annual species from an arid region of western Australia. *Journal of Ecology*, **62**: 699-709.

MURDOCH, A.J. & ELLIS, R.H. 1992. Longevity, viability and dormancy. In: Fenner, M. (ed). *Seeds: The ecology of regeneration in plant communities.* CAB International, Wallingford. pp. 193-229.

NIKOLAEVA, M.G. 1977. Factors controlling the seed dormancy pattern. In: Khan, A.A. (ed). *The physiology and biochemistry of seed dormancy and germination.* North-Holland, New York. pp. 51-74.

ROBERTS H.A. 1964. Emergence and longevity in cultivated soil of seeds of some annual weeds. *Weed Research*, **4**: 296-307.

SIMPSON, G.M. 1990. *Seed dormancy in grasses.* Cambridge University Press, Cambridge.

TEVIS, L. Jr.. 1958. Germination and growth of ephemerals induced by sprinkling a sandy desert. *Ecology*, **39**: 681-688.

VAN RENSBURG, D.J. 1978. Fenologiese aspekte van enkele Namakwalandse spesies. B.Sc.(Hons.) project, University of Pretoria, Pretoria.

VISSER, L. 1993. Saadontkiemingstudies van geselekteerde Namakwalandse efemeerspesies. M.Sc. dissertation, University of Pretoria, Pretoria.

VLEESHOUWERS, L.M., BOUWMEESTER, H.J. & KARSSEN, C.M. 1995. Redefining seed dormancy: an attempt to integrate physiology and ecology. *Journal of Ecology*, **83**: 1031-1037.

WENT, F.W. 1955. The ecology of desert plants. *Science America*, **192**: 68-75.

WENT, F.W. 1961. Problems in seed viability and germination. *Proceedings of the International Seed Testing Association*, **26**: 674-685.

CHAPTER 10

GERMINATION STRATEGIES OF STRANDVELD SUCCULENT KAROO PLANT SPECIES FOR REVEGETATION PURPOSES: III. EFFECT OF RELATIVE HUMIDITY ON VIABILITY

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ABSTRACT

The effect of relative humidity and locality on seed viability was investigated in six plant species from the Strandveld Succulent Karoo, South Africa. An increase in relative humidity generally resulted in a decrease in seed viability. High summer temperatures in the field probably hastened the loss of seed viability at a relative humidity of 43%, while high summer temperatures exerted only a minimal deteriorative effect on seeds stored at a low relative humidity (7%). Low winter temperatures in the field probably induced the seeds of the annual species into secondary dormancy at a relative humidity of 43%. Changes in seed viability due to fluctuations in environmental conditions (temperature and relative humidity) are crucial factors to consider during post-mining revegetation efforts in the Strandveld Succulent Karoo.

Key words: Germination; locality; longevity; mining; relative humidity; revegetation; seed moisture content; temperature; viability

INTRODUCTION

Seeds are uniquely equipped to survive as viable regenerative organisms until the time and place are right for the beginning of a new generation; however, they cannot retain their viability indefinitely and eventually deteriorate and die (Copeland & McDonald, 1995). The period for which seeds remain viable is determined genetically, by internal factors of the seed as well as by environmental factors. The latter will have a decisive effect on the life span of any given seed (Mayer & Poljakoff-Mayber, 1975; Copeland & McDonald, 1995).

Ecological longevity of seeds can be defined as the mean duration of dormancy under natural conditions: the mean interval elapsing between seed maturation and seed germination or death in the soil, whereas potential longevity is the maximum duration of germination capacity (viability) of dormant seeds under optimal storage conditions (Vazquez-Yanes & Orozco-Segovia, 1993). Plant species with long-lived seeds may accumulate large persistent seed banks (Murdoch & Ellis, 1992) which are, *inter alia*, important in revegetating lands that have been severely disturbed by mining activities (Vivian-Smith & Handel, 1996; Baskin & Baskin, 1998).

The revegetation of mined areas along the arid West Coast of South Africa will depend mainly on the use of the soil stored seed bank by means of topsoil replacement, as well as on sowing and/or transplanting of selected species (Environmental Evaluation Unit, 1990). Consequently, successful revegetation of the mined areas will depend largely on the timing of germination, which in turn is determined by factors such as temperature, dormancy strategies and viability of seeds.

The present study forms part of a project aimed at describing the seed bank dynamics of the Strandveld Succulent Karoo to guide mining authorities on appropriate revegetation strategies. This study on germination strategies of Strandveld Succulent Karoo plant species was prompted by the need to ensure optimal germination of seeds in the revegetation process. This paper is the third in a series of three, aimed at identifying some of the seed germination strategies of Strandveld Succulent Karoo species, and deals with changes in seed viability due to different relative humidities and storage locations. The first and second papers in the series were concerned with temperature and light conditions for germination, and dormancy-breaking treatments respectively.

MATERIAL AND METHODS

During spring 1994, mature diaspores (henceforth referred to as seeds) of six plant species were collected from natural populations near Brand-se-Baai (31°18'S, 17°54'E) on the arid Cape West Coast, South Africa. This area falls within the Namaqualand coastal belt and has an average precipitation of 282 mm per annum, measured over a period of four years at the study site. Rainfall occurs mainly during winter, with an average of 160 mm per annum. The average annual temperature at the study site is 15.8°C with a relatively small fluctuation due to the marine influence (De Villiers *et al.*, 1999).

Species used in this experiment included: *Conicosia pugioniformis* (L.) N.E.Br., *Dimorphotheca pluvialis* (L.) Moench. (disc & ray achenes), *Gazania leiopoda* (DC.) Rössl., *Tripteris oppositifolia* (Ait.) T.Norl., *Senecio arenarius* Thunb., and *Ursinia speciosa* DC. (white achenes).

Collected seeds 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 relative humidity in the dessicator results in a corresponding moisture content within the seeds present in the specific dessicator. The following solutions were used to obtain the required relative humidities at *c.* 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 of *Conicosia pugioniformis* and *Senecio arenarius* were not included in the field burial treatments. Seeds stored dry

(ambient RH) in paper bags at 20°C for 6 or 30 months were used as an initial control and final control treatment, respectively.

After 27 months of storage or burial (autumn), five replicates of each treatment and species were germinated in Petri dishes with a diameter of 50 mm, containing two layers of filter paper (Schleicher & Schüll, no. 595, Dassel, Germany) to which approximately 4 cm^3 distilled water was added. 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). The Petri dishes of the dark treatments were placed in cardboard boxes and sealed with aluminium foil to eliminate light. Petri dishes were inspected every second day for a period of 30 days, and germinated seeds counted and removed. Germination of dark replicates was determined under a green safety light. Radicle protrusion was the germination criterion.

The mean time to germination (mtg) was calculated for each species and treatment using the equation:

$$mtg = \frac{\sum Dn}{\sum n}$$

where n is the number of seeds which germinate on day D and D is the number of days counted from the beginning of the test (Ellis & Roberts, 1981).

Data were analysed statistically by the least significant difference (LSD) one-way and multi-factor analysis of variance (ANOVA), and multiple range test (Statgraphics 5.0, 1989, STSC, Inc., U.S.A.) at $P \leq 0.05$.

RESULTS

For all species, germination of seeds stored at relative humidities of 75% or 93% was lower than that of seeds stored at relative humidities of 7% and 43% (Table 10.1). In general, the mean germination percentages of seeds decreased with an increase in relative humidity when stored under field and laboratory conditions (Table 10.1). The ray floret seeds of *Dimorphotheca pluvialis* obtained significantly higher germination percentages at a relative humidity of 43%, when stored under laboratory conditions. These seeds obtained a mean germination percentage of 64.5% in the initial control treatment, which was significantly higher than that of all other treatments. In both *Conicosia pugioniformis* and *Tripteris oppositifolia*, the mean germination percentages obtained in the initial control and final control treatments were significantly lower than that of the other treatments, except for the storage of *Conicosia pugioniformis* seeds at a relative humidity of 75/93% (Table 10.1).

Table 10.1. Mean germination percentage for seeds of six Strandveld Succulent Karoo plant species, after storage in the laboratory or the field for 27 months, at different relative humidities. Plant type as well as the temperature (°C) and light condition for the germination of each species are indicated between brackets. For each species, values followed by the same letter are not significantly different at $P \leq 0.05$

Species	Initial Control (stored dry in the laboratory at 20°C for 6 months)	Final Control (stored dry in the laboratory at 20°C for 30 months)	Relative Humidity (%)						Significance level ($P \leq 0.05$)
			Stored in the laboratory at 20°C for 27 months			Buried in the field for 27 months			
			7	43	75/93	7	43	75/93	
Conicosia pugioniformis (P; 17D)	32.5 $_{b}$	74.0 $_{c}$	97.0 $_{e}$	89.0 $_{d}$	2.0 $_{a}$	-	-	-	0.0000
Dimorphotheca pluvialis - disc (A; 17L)	86.4 $_{bc}$	77.0 $_{b}$	83.0 $_{bc}$	90.0 $_{c}$	-	86.0 $_{bc}$	53.0 $_{a}$	-	0.0000
Dimorphotheca pluvialis - ray (A; 17L)	64.5 $_{e}$	25.0 $_{bc}$	18.0 $_{b}$	41.0 $_{d}$	0.0 $_{a}$	44.0 $_{d}$	35.0 $_{cd}$	0.0 $_{a}$	0.0000
Gazania leiopoda (P; 17D)	71.0 $_{c}$	30.0 $_{b}$	88.0 $_{c}$	84.0 $_{c}$	9.0 $_{ab}$	30.0 $_{b}$	16.0 $_{ab}$	0.0 $_{a}$	0.0000
Tripteris oppositifolia (P; 17L)	32.4 $_{a}$	45.0 $_{a}$	62.0 $_{b}$	75.0 $_{b}$	-	68.0 $_{b}$	67.0 $_{b}$	-	0.0000
Senecio arenarius (A; 17L)	50.5 $_{abc}$	75.0 $_{c}$	53.0 $_{bc}$	41.0 $_{ab}$	23.0 $_{a}$	-	-	-	0.0196
Ursinia speciosa - white (A; 17L)	36.5 $_{c}$	9.0 $_{ab}$	27.0 $_{c}$	31.0 $_{c}$	14.0 $_{b}$	30.0 $_{c}$	2.0 $_{ab}$	0.0 $_{a}$	0.0000

A - annual
P - perennial
L - light
D - dark
- Treatment not used for this species

Table 10.2. Mean time to germination for seeds of six Strandveld Succulent Karoo plant species, after storage in the laboratory or the field for 27 months, at different relative humidities. Plant type as well as the temperature (°C) and light condition for the germination of each species are indicated between brackets. For each species, values followed by the same letter are not significantly different at $P \leq 0.05$

Species	Initial Control (stored dry in the laboratory at 20°C for 6 months)	Final Control (stored dry in the laboratory at 20°C for 30 months)	Relative Humidity (%)						Significance level ($P \leq 0.05$)
			Stored in the laboratory at 20°C for 27 months			Buried in the field for 27 months			
			7	43	75/93	7	43	75/93	
Conicosia pugioniformis (P; 17D)	11.3 $_{b}$	4.8 $_{a}$	4.0 $_{a}$	4.1 $_{a}$	5.0 $_{a}$	-	-	-	0.0000
Dimorphotheca pluvialis - disc (A; 17L)	4.0 $_{ab}$	5.9 $_{c}$	3.8 $_{ab}$	4.8 $_{bc}$	-	3.1 $_{a}$	7.6 $_{d}$	-	0.0000
Dimorphotheca pluvialis - ray (A; 17L)	5.5	5.9	5.8	4.6	--	4.6	5.1	--	0.6111
Gazania leiopoda (P; 17D)	9.0 $_{b}$	19.4 $_{e}$	6.1 $_{a}$	6.0 $_{a}$	14.0 $_{d}$	10.6 $_{bc}$	12.5 $_{cd}$	--	0.0000
Tripteris oppositifolia (P; 17L)	9.0 $_{b}$	9.1 $_{b}$	14.3 $_{c}$	5.8 $_{a}$	-	8.0 $_{b}$	7.3 $_{ab}$	-	0.0000
Senecio arenarius (A; 17L)	8.7	9.5	8.4	8.7	11.0	-	-	-	0.6419
Ursinia speciosa - white (A; 17L)	5.2 $_{a}$	8.0 $_{ab}$	4.5 $_{a}$	4.3 $_{a}$	10.3 $_{b}$	4.6 $_{a}$	8.0 $_{ab}$	--	0.0329

A - annual
P - perennial
L - light
D - dark
- Treatment not used for this species
-- No mean time to germination as germination percentage was 0%

The perennial species, *Gazania leiopoda* and *Tripteris oppositifolia* as well as the annual *Ursinia speciosa* (white) obtained the shortest mean times to germination after storage at a relative humidity of 43% in the laboratory (Table 10.2). The perennial *Conicosia pugioniformis* obtained a shortest mean time to germination after storage in the laboratory at a relative humidity of 7% (Table 10.2). Mean time to germination of other species investigated did not differ significantly between treatments.

According to the multi-factor ANOVA (Table 10.3), storage location as well as relative humidity affected both the germination percentage and rate of *Dimorphotheca pluvialis* (disc) and *Gazania leiopoda* seeds significantly. The germination percentage of *Dimorphotheca pluvialis* ray floret seeds was affected significantly only by relative humidity. Both storage location and relative humidity influenced the germination percentage of *Ursinia speciosa* (white) seeds, but the germination rate was affected only by the relative humidity during storage. Although the germination percentage of *Tripteris oppositifolia* seeds was not influenced by storage location or relative humidity, the mean time to germination of this species was influenced significantly by both treatments. The interaction between storage location and relative humidity (LO x RH, Table 10.3) significantly influenced the germination percentage of *Dimorphotheca pluvialis* (disc & ray), *Gazania leiopoda* and *Ursinia speciosa* (white) seeds, while this interaction affected the mean time to germination of *Dimorphotheca pluvialis* (disc) and *Tripteris oppositifolia* seeds.

DISCUSSION

In general, the germination percentages of the species investigated decreased with an increase in relative humidity from 7% or 43% to 75% or 93% (Table 10.1). Seeds of dry climate plants generally remain viable for longer periods of time when stored dry (Went, 1961; Mayer & Poljakoff-Mayber, 1975) and Ellis *et al.* (1982) reported a negative logarithmic relationship between seed moisture and longevity. The moisture content of seeds is determined, at least in part, by the relative humidity of the air surrounding them (Mayer & Poljakoff-Mayber, 1975). Seeds stored at moisture contents above 14% begin to exhibit increased respiration, heating, and fungal invasion that destroy seed viability more rapidly than in seeds stored at lower moisture contents (Harrington, 1972; Bewley & Black, 1982, 1994; Copeland & McDonald, 1995). However, the activity of fungi, and other contaminants of stored seeds, are more strictly related to the relative humidity of the intra-seed atmosphere than to the moisture content of the seeds themselves (Bewley & Black, 1982, 1994). Below 5% seed moisture, a breakdown of membrane structure hastens seed deterioration. This is probably a consequence of reorientation of hydrophyllic cell membranes due to the loss of the water molecules necessary to retain their configuration. Thus, storage of most seeds between 5 and 6% seed moisture appears to be ideal for maximum longevity (Copeland & McDonald, 1995).

Hygroscopic moisture equilibrium curves (Copeland & McDonald, 1995) indicates three different stages of water absorption or desorption (Bewley & Black, 1994):

1) very tightly held water that may actually be a part of the chemical structure of the seed, and cannot be removed without destruction of the seed tissue,
2) more loosely held water that can be easy or difficult to remove by drying, and may contribute to seed deterioration during storage, and

Table 10.3. Multi-factor ANOVA ($P \leq 0.05$) for seeds of four Strandveld Succulent Karoo plant species stored in the laboratory or in the field for 27 months, at different relative humidities

Parameter	Species	Main effects				2-Factor interaction	
		Storage location (LO)		Relative humidity (RH)		LO x RH	
		F-ratio	Significance level	F-ratio	Significance level	F-ratio	Significance level
Mean germination percentage	*Dimorphotheca pluvialis* - disc (A)	31.671	0.0000	18.521	0.0005	43.836	0.0000
	Dimorphotheca pluvialis - ray (A)	2.067	0.1634	25.364	0.0000	4.486	0.0221
	Gazania leiopoda (P)	34.747	0.0000	19.529	0.0000	5.703	0.0094
	Tripteris oppositifolia (P)	0.049	0.8303	1.756	0.2037	2.390	0.1416
	Ursinia speciosa - white (A)	12.308	0.0018	10.715	0.0005	5.915	0.0082
Mean time to germination	*Dimorphotheca pluvialis* - disc (A)	4.854	0.0426	32.626	0.0000	12.311	0.0029
	Dimorphotheca pluvialis - ray (A)	0.206	0.6611	0.258	0.6234	1.496	0.2390
	Gazania leiopoda (P)	77.338	0.0000	48.424	0.0000	2.729	0.1268
	Tripteris oppositifolia (P)	16.016	0.0010	61.126	0.0000	43.593	0.0000
	Ursinia speciosa - white (A)	0.449	0.5199	7.101	0.0068	0.916	0.3636

A - annual

P - perennial

3) loosely held water by very weak bonding and free water in the intercellular and intertissue spaces, easily removed by drying, but if not eliminated, contributes to rapid seed deterioration.

Water classified as stage one must be retained by the seed for maintaining metabolic functions, in order to prevent loss of viability due to low moisture content. Increases in relative humidity may also be important for the longevity of seeds, as it enables damage that occurs during storage to be repaired (Karssen *et al.*, 1989; Gutterman, 1993).

With the exception of seeds stored at a relative humidity of 7%, the germination percentages were lower when stored under field than under laboratory conditions (Table 10.1). Because the seeds were stored under similar relative humidities and light conditions, one of the main factors responsible for the observed differences in germination percentages may have been temperature. Seeds in the laboratory were stored at a constant temperature of 20°C, while those in the field probably experienced high temperatures during summer and low temperatures during the winter period (De Villiers *et al.*, 1999). Temperature was found to regulate the germination of seeds of winter annuals not only during germination, but also during the period of storage prior to germination (Gutterman, 1986).

It has long been known that the major factors which influence the longevity of seeds in storage are temperature, oxygen pressure and moisture content (Roberts, 1972), of which the latter is considered to be the most critical (Copeland & McDonald, 1995). Seed ageing is a function not only of time, but also of temperature and moisture (Ellis & Roberts, 1981). The interdependence of temperature and relative humidity and its subsequent influence on seed longevity have been the subject of numerous studies (Roberts, 1972; Mayer & Poljakoff-Mayber, 1975; Bewley & Black, 1982; 1994; Murdoch & Eilis, 1992; Copeland & McDonald, 1995). Generally, seed longevity increases with a decrease in temperature and relative humidity (Roberts, 1972; Murdoch & Ellis, 1992; Copeland & McDonald, 1995), and both influence seed metabolism. High relative humidities increase seed moisture content, which results in biochemical events such as increased hydrolytic enzyme activity, enhanced respiration, and increases in free fatty acids. High temperatures serve to enhance the rate at which many enzymatic and metabolic reactions occur, causing a more rapid rate of deterioration.

The majority of species conform to certain rules of thumb that predict the pattern of loss of viability in relation to storage environment (Harrington, 1973):

1. For each 1% decrease in seed moisture content the storage life of the seed is doubled.
2. For each 5.6°C decrease in seed storage temperature the storage life of the seed is doubled.
3. The arithmetic sum of the storage temperature (in °F) and the per cent relative humidity should not exceed 100, with no more than half the sum contributed by the temperature.

These rules of thumb reflect the interactions between seed moisture, storage temperature, and seed longevity (Copeland & McDonald, 1995).

At a relative humidity of 7%, the germination percentages and rates were not affected by storage location (Tables 10.1 & 10.2). In general, seeds stored at a relative humidity of 43% obtained highest germination percentages and shortest mean times to germination when stored at a constant temperature of 20°C, rather than in the field. At a relative humidity of 43%, the viability of seeds stored in the field was probably negatively affected by high temperatures during summer. Low temperatures during winter may also have induced these seeds to enter secondary dormancy.

Revegetation

Irrigation during the summer months may solve seedling recruitment problems related to low moisture, but the dormancy status of most annual species will prevent the germination of these species (Chapter 9). An increase in relative humidity due to irrigation may also result in increased seed moisture contents, which may repair damage that occurs during storage (Gutterman, 1993) in the seed bank. However, prevailing high summer temperatures and high relative humidities will enhance seed deterioration and consequently, seed viability and longevity will be reduced.

Collected seeds of perennial shrub species should not be stored for too long, as they are probably not as long-lived as seeds of the annual species investigated (Chapters 9 & 11). The loss of viability is only the final stage in seed deterioration (Murdoch & Ellis, 1992; Bewley & Black, 1994). Prior to death, ageing results in a decline in many aspects of a seed's potential performance such as the rate of germination (Ellis & Roberts, 1981). Recruitment of these species should occur during autumn and winter following topsoil replacement and/or sowing, as germination during this season should provide sufficient time for seedling establishment and growth.

Irrigation during summer would result in the germination of many perennial shrub species, required for successful revegetation of the study area (Chapters 6 & 7), but seed viability of most annuals and perennial herbs (Chapter 11) will be reduced under prevailing environmental conditions. All seedling recruitment efforts should rather be concentrated during the autumn and winter rainfall period, when conditions may also be favourable for germination, seedling survival and growth. Irrigation during the second summer after topsoil replacement and/or sowing will be beneficial for the survival of perennial species. Although the viability of annual and perennial herb species' seeds may be reduced by irrigation during this period, survival of perennial species will be more critical during this phase of revegetation efforts.

Extreme temperature conditions, occasional high humidities due to out of season rainfall, decay and germination will all decrease the number of viable seeds in the soil. For this reason, studies on seed longevity under field conditions, for as many local plant species as possible, are essential for developing sound revegetation strategies concerning topsoil replacement and sowing in the Strandveld Succulent Karoo. A major drawback is the large number of local plant species with very small seeds, making natural burial experiments almost impossible.

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REFERENCES

BASKIN, C.C & BASKIN, J.M. 1998. *Seeds: Ecology, biogeography, and evolution of dormancy and germination.* Academic Press, New York.

BEWLEY, J.D. & BLACK, M. 1982. *Physiology and biochemistry of seeds.* Springer-Verlag, Heidelberg.

BEWLEY, J.D. & BLACK, M. 1994. *Seeds: Physiology of development and germination.* Plenum Press, London.

COPELAND, L.O. & McDONALD, M.B. 1995. *Principles of seed science and technology.* Chapman & Hall, New York.

DE VILLIERS, A.J., VAN ROOYEN, M.W., THERON, G.K. & VAN ROOYEN, N. 1999. Vegetation diversity of the Brand-se-Baai coastal dune area, West Coast, South Africa: A pre-mining benchmark survey for rehabilitation. *Land Degradation & Development*, **10**: 207-224.

ELLIS, R.H., OSEI-BONSU, K. & ROBERTS, E.H. 1982. The influence of genotype, temperature and moisture on seed longevity in Chickpea, Cowpea and Soya bean. *Annals of Botany*, **50**: 69-82.

ELLIS, R.H. & ROBERTS, E.H. 1981. The quantification of ageing and survival in orthodox seeds. *Seed Science & Technology*, **9**: 373-409.

ENVIRONMENTAL EVALUATION UNIT. 1990. *Anglo American Corporation: West Coast heavy mineral sands project.* Unpublished report. University of Cape Town, Cape Town.

GUTTERMAN, Y. 1986. Are plants which germinate and develop during winter in the Negev Desert highlands of Israel, winter annuals ? *Environmental Quality and Ecosystem Stability*, **3**: 135-144.

GUTTERMAN, Y. 1993. *Seed germination in desert plants.* Springer-Verlag, Berlin.

HARRINGTON, J.F. 1972. Seed storage and longevity. In: Kozlowski, T.T. (ed). *Seed biology.* Academic Press, New York. pp. 145-240.

HARRINGTON, J.F. 1973. Biochemical basis of seed longevity. *Seed Science and Technology*, **1**: 453-461.

KARSSEN, C.M., HAIGH, A., VAN DER TOORN, P. & WEGES, R. 1989. Physiological mechanisms involved in seed priming. In: Taylorson, R.B. (ed). *Recent advances in the development and germination of seeds.* Plenum, New York. pp. 269-280.

MAYER, A.M. & POLJAKOFF-MAYBER, A. 1975. *The germination of seeds.* Pergamon Press, Oxford.

MURDOCH, A.J. & ELLIS, R.H. 1992. Longevity, viability and dormancy. In: Fenner, M. (ed). *Seeds: The ecology of regeneration in plant communities.* CAB International, Wallingford. pp. 193-229.

ROBERTS, E.H. 1972. *Viability of seeds.* Syracuse University Press, Great Britain.

VAZQUEZ-YANES, C. & OROZCO-SEGOVIA, A. 1993. Patterns of seed longevity and germination in the tropical rainforest. *Annual Review of Ecology and Systematics*, **24**: 69-87.

VIVIAN-SMITH, G. & HANDEL, S.N. 1996. Freshwater wetland restoration of an abandoned sand mine: Seeds bank recruitment dynamics and plant colonization. *Wetlands*, **16**: 185-196.

WENT, F.W. 1961. Problems in seed viability and germination. *Proceedings of the International Seed Testing Association*, **26**: 674-685.

WINSTON, P.W. & BATES, D.H. 1960. Saturated solutions for the control of humidity in biological research. *Ecology*, **41**: 232-237.

CHAPTER 11

SEED BANK CLASSIFICATION OF THE STRANDVELD SUCCULENT KAROO, SOUTH AFRICA

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ABSTRACT

The laboratory characteristics of seeds of 37 species (41 seed types) from the Strandveld Succulent Karoo were used to predict seed bank types according to the modified key of Grime & Hillier (1981). Five seed bank strategies were recognised for this vegetation type, *i.e.* two with transient and three with persistent seed bank strategies. Of the 37 species investigated, 32% (all perennial species) had transient seed bank strategies, while 68% had persistent seed bank strategies. Seed dispersal mechanisms of these species were mainly anemochorous and antitelechoric dispersal mechanisms such as myxospermy, hygrochasy, heterodiaspory and synaptospermy occurred in these species. Topsoil stored seed banks will be used in post-mining revegetation efforts in the Strandveld Succulent Karoo. The seed bank alone will not be sufficient for revegetation in this area, as many of the species dominant in the vegetation do not produce a persistent seed bank. Many of these species may, however, be dispersed by wind into revegetation areas from surrounding vegetation. Topsoil replacement, seeding and transplanting of selected species will be essential for the successful revegetation of mined areas in this part of Namaqualand.

Key words: Mining; Namaqualand; persistent seed bank; revegetation; seed bank types; seed characteristics; seed dispersal; transient seed bank

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). 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 seed bank of a plant community represents the "memory" of previous conditions and it is an important component of the potential of the community to respond to conditions in the present and future (Coffin & Lauenroth, 1989). 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, however, 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 recovery of a plant community after disturbance is related to the germination of seeds and establishment of seedlings after emergence, although in some communities

vegetative reproduction by perennial plants is another important process (Coffin & Lauenroth, 1989; Warr *et al.*, 1993).

Restoration ecology deals with the scientific and ecological background of nature management practices aiming at the re-establishment of plant species, which have disappeared (Bakker *et al.*, 1996). The re-appearance of plant species may depend on their persistence in the soil seed bank. If the species has been lost from the persistent soil seed bank, it has to be transported to the site of re-appearance by some vector, e.g. wind, water, animals, man, and incorporated into the fresh seed bank. The re-appearance of a species either from the old seed bank or from the fresh seed bank depends on the availability of safe sites (Harper, 1977). Without the presence or arrival of seeds no re-appearance will be possible.

During the mining of heavy minerals along the arid western coast of South Africa, the topography, vegetation, soil chemical and physical characteristics and animal life, are destroyed (Environmental Evaluation Unit, 1990). The aim of the rehabilitation programme in this area 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 (Environmental Evaluation Unit, 1990). If the topsoil of the area to be mined is removed and used in the revegetation process, knowledge on persistence of individual species present in the seed bank will be essential. Data on the seed bank strategies of individual species will also guide revegetation efforts towards local species that were dominant in the vegetation prior to mining activities and that may not re-establish by means of topsoil replacement or dispersal from surrounding vegetation. These species will have to be reintroduced by processes such as seeding and transplanting.

Thompson & Grime (1979) recognised two seed bank strategies for temperate zones; transient (Types I & II), in which no seeds remain viable for more than one year, and persistent (Types III & IV), in which some seeds remain viable for longer than one year. The type III seed bank was further subdivided into type IIIa and IIIb categories (Grime, 1981). Since many seeds remain viable in the soil for long periods of time, Bakker (1989) suggested the further division of the persistent seed bank strategy into persistent, for species with seeds which survive in the soil for more than one year, and permanent, for species with seeds which persist for longer than five years. These two strategies have been renamed short-term persistent and long-term persistent respectively (Thompson, 1993; Warr *et al.*, 1993). These two strategies together with the transient strategy form a useful seed bank classification (Thompson, 1993).

A further elaboration of the seed bank classification, which relies on the dynamics of the seed bank and seed rain was published by Poschlod & Jackel (1993). In an attempt to formalise all the above-mentioned criteria into a more usable form, Thompson *et al.* (1996) devised a key to seed bank types. The drawback of this key is the information required on the period since a species was last present in the vegetation at the site. The data needed to apply it to most species, especially in the Strandveld Succulent Karoo, are simply not available.

The key of Grime & Hillier (1981) is based on laboratory characteristics of seeds which can be used to predict seed bank types (Thompson & Grime, 1979). This key was compiled for the North West European region and modifications may be necessary for successful use in other regions, as more than four seed bank

strategies have already been reported for soil seed banks of other regions (Garwood, 1989; Baskin & Baskin, 1998).

The classification of species according to seed bank strategies has long been recognised as an important tool for understanding species and environmental relationships (Thompson & Grime, 1979; Bakker, 1989; Leck *et al.*, 1989; Thompson, 1992; Leck & Simpson, 1993; Badger & Ungar, 1994; Kirkham & Kent, 1997). Only recently has it been recognised as important in biogeography, conservation, restoration ecology and revegetation processes (Warr *et al.*, 1993; Bakker *et al.*, 1996).

The aim of this study was to determine the suitability of Grime & Hillliers' key (1981) for the classification and prediction of seed bank strategies in the Strandveld Succulent Karoo, South Africa. Knowledge of the seed bank dynamics of local species was used as a basis for the recommendation of suitable revegetation strategies. Species that accumulate a persistent seed bank have the potential for regeneration from replaced topsoil, while species with a transient seed bank will probably have to be introduced by dispersal of seeds (Bakker *et al.*, 1996), sowing or transplanting.

MATERIAL AND METHODS

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

Mature seeds of 37 local plant species (41 seed types) were collected during spring, from natural populations in the vicinity of the area to be mined at Brand-se-Baai (31°18'S, 17°54'E), South Africa (De Villiers *et al.*, 1999). This area falls within the Namaqualand coastal belt and has an average winter rainfall of 160 mm per annum. The average annual temperature at the study site is 15.8°C, with a relatively small annual fluctuation due to the marine influence (De Villiers *et al.*, 1999). The vegetation of the area is classified as Strandveld Succulent Karoo (Low & Rebelo, 1998) and contains many drought resistant and succulent species associated with areas of calcareous sand. The vegetation varies in height depending on 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).

The following perennial species were included in this study: *Albuca exuviata* Bak., *Amellus tenuifolius* Burm., *Arctotis acaulis* L., *Arctotis stoechadifolia* Berg., *Ballota africana* (L.) Benth., *Cephalophyllum spongiosum* (L.Bol.) L.Bol., *Chrysocoma longifolia* DC., *Conicosia pugioniformis* (L.) N.E.Br., *Dimorphotheca tragus* (Ait.) T.Norl., *Ehrharta calycina* J.E.Sm., *Gazania leiopoda* (DC.) Rössl., *Grielum grandiflorum* (L.) Druce, *Hypertelis salsoloides* (Burch.) Adamson, *Pharnaceum aurantium* (DC.) Druce, *Pharnaceum lanatum* Bartl., *Pteronia divaricata* (Berg.) Less., *Ruschia bolusiae* Schwant., *Stoeberia* sp., *Tetragonia virgata* Schltr., *Tripteris oppositifolia* (Ait.) T.Norl. and *Zygophyllum morgsana* L..

Annual species investigated were *Arctotheca calendula* (L.) Levyns, *Cotula thunbergii* Harv., *Cysticapnos cracca* (Cham. & Schlechtd.) Liden, *Didelta carnosa* (L.f.) Ait., *Dimorphotheca pluvialis* (L.) Moench. (disc &

ray achenes), *Nemesia bicornis* (L.) Pers., *Hebenstretia dentata* L., *Hebenstretia repens* Jarosz, *Heliophila coronopifolia* L., *Pharnaceum exiguum* Adamson, *Polycarena pumila* (Benth.) Levyns, *Senecio arenarius* Thunb., *Silene clandestina* Jacq., *Ursinia anthemoides* (L.) Poir. (black, grey & white achenes), *Ursinia speciosa* DC. (black & white achenes) and *Wahlenbergia paniculata* (Thunb.) A.DC..

Both fresh seeds (air-dried for two weeks) and seeds stored dry at 20°C for one month after the initial air-drying period of two weeks, were used in the germination experiments. Seeds were germinated in Petri dishes, on two layers of moist filter paper (Schleicher & Schüll, no. 595, Dassel, Germany). Germination tests were carried out in germination cabinets at a constant temperature of 17°C, in light and darkness. This temperature was found to be favourable for the germination of many Namaqualand species (Beneke *et al*, 1993; Visser, 1993; De Villiers *et al.*, 1994). Seeds of the light treatments were exposed to constant fluorescent light with a photosynthetic photon flux density of 9.3 μmol m^{-2} s^{-1}. Petri dishes of the dark treatments were sealed in cardboard boxes and covered with aluminium foil, to eliminate light. Five replicates of 50 seeds were used for each species.

Germination tests were continued for a period of 30 days, during which seeds were examined every second day and germinated seeds counted and removed. Germination counts for the dark treatments were carried out under a green safety light (Baskin & Baskin, 1998). Distilled water was added when necessary to prevent the filter paper from drying out. Emergence of the radicle was used as germination criterion.

Mean diaspore length was determined by measuring the length of 100 diaspores for each species. Small diaspores 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_U) was determined from data on stored seeds of these species, germinated at various temperatures (Chapter 8). Species names follow that of Arnold & De Wet (1999).

The following seed dispersal types were distinguished:

a) Telechoric – mechanisms which promote long range dispersal.
   i) Anemoballistic – mechanism whereby wind does nor exert its influence on the diaspore directly, but on the capsule or follicle enclosing the diaspores (Van Rheede van Oudtshoorn & Van Rooyen, 1999).
   ii) Anemochory – wind-dispersal of diaspores with characters (*e.g.* pappus, bristles) slowing their terminal velocity of descent (Van der Pijl, 1982; Van Rooyen *et al.*, 1990; Van Rheede van Oudtshoorn & Van Rooyen, 1999).
   iii) Epizoochory – mechanism where seeds are transported externally on animals (Van Rheede van Oudtshoorn & Van Rooyen, 1999).
   iv) Rain ballistic – mechanism whereby raindrops falling onto open capsules are responsible for the dispersal of some (but not all) of the seeds, and ensuring that seeds will only germinate when sufficient moisture is available (Van Rooyen *et al.*, 1990; Gutterman, 1993, 1994; Baskin & Baskin, 1998; Van Rheede van Oudtshoorn & Van Rooyen, 1999).

b) Atelechory – no mechanisms for long distance dispersal.

c) Antitelechory – mechanisms which hamper dispersal.

i) Bradyspory – mechanisms whereby dispersal of diaspores from the mother plant is delayed and spread over time (Van Rheede van Oudtshoorn & Van Rooyen, 1999).

ii) Heterodiaspory – the production of two or more morphologically distinct types of seeds by an individual plant (Harper, 1977; Ellner & Shmida, 1981; Beneke *et al.*, 1993).

iii) Hygrochasy – mechanism in which the fruit opens when moistened to allow the seeds to escape, and close again during dry weather (Van Rooyen *et al.*, 1990). Consequently, some seeds remain undispersed and viable for a number of years (Gutterman, 1972, 1993).

iv) Myxospermy – mechanism in which the seeds form a superficial layer of mucilage upon moistening as a mechanism of anchorage and enhanced water uptake due to increased seed-soil contact (Van Rooyen *et al.*, 1990).

v) Synaptospermy – mechanism in which the diaspore contains more than one seed (Van Rooyen *et al.*, 1990).

RESULTS AND DISCUSSION

The modified key used to predict seed bank types of species from the Strandveld Succulent Karoo is shown in Figure 11.1. The original key of Grime and Hillier (1981) distinguished four main seed bank types: (I) Annual and perennial grasses of dry or disturbed habitats capable of immediate germination; (II) Annual and perennial herbs, colonising vegetation gaps in early spring; (III) Annual and perennial herbs, mainly germinating in the autumn but maintaining a small seed bank; and (IV) Annual and perennial herbs and shrubs with large, persistent seed banks. Type III seed bank strategy was subdivided into types IIIa) perennial herb species germinating mainly in autumn, and IIIb) annual species which germinate during autumn (Grime, 1981). The seeds of species with type IIIa or IIIb seed bank strategies usually have a light requirement for germination. Consequently, seeds that become buried prior to the first germination promoting rainfall contribute to the formation of a persistent seed bank.

Since the Strandveld Succulent Karoo falls within a winter rainfall region and rain during the summer months is extremely uncommon (Environmental Evaluation Unit, 1990), germination of most local species is limited to the autumn months, *i.e.* there are probably no winter transient species. For this reason, the seed bank type characterised by spring germinating species (Grime & Hillier, 1981, Type II) has been omitted. As germination occurs mainly in autumn, a dry heat pre-treatment (Baskin & Baskin, 1998) is more representative of the hot summer months preceding germination than cold stratification for after-ripening of the seeds.

The key of Grime and Hillier (1981) does not make provision for small non-photoblastic seeds with high initial germination percentages. Both germination percentages of fresh and stored (20°C for one month) seeds were taken into consideration for categorising small seeds. Also, the time taken by seeds stored dry at 20°C for one month to reach 50% germination (t^{50}, Grime & Hillier, 1981), was not included as a means of

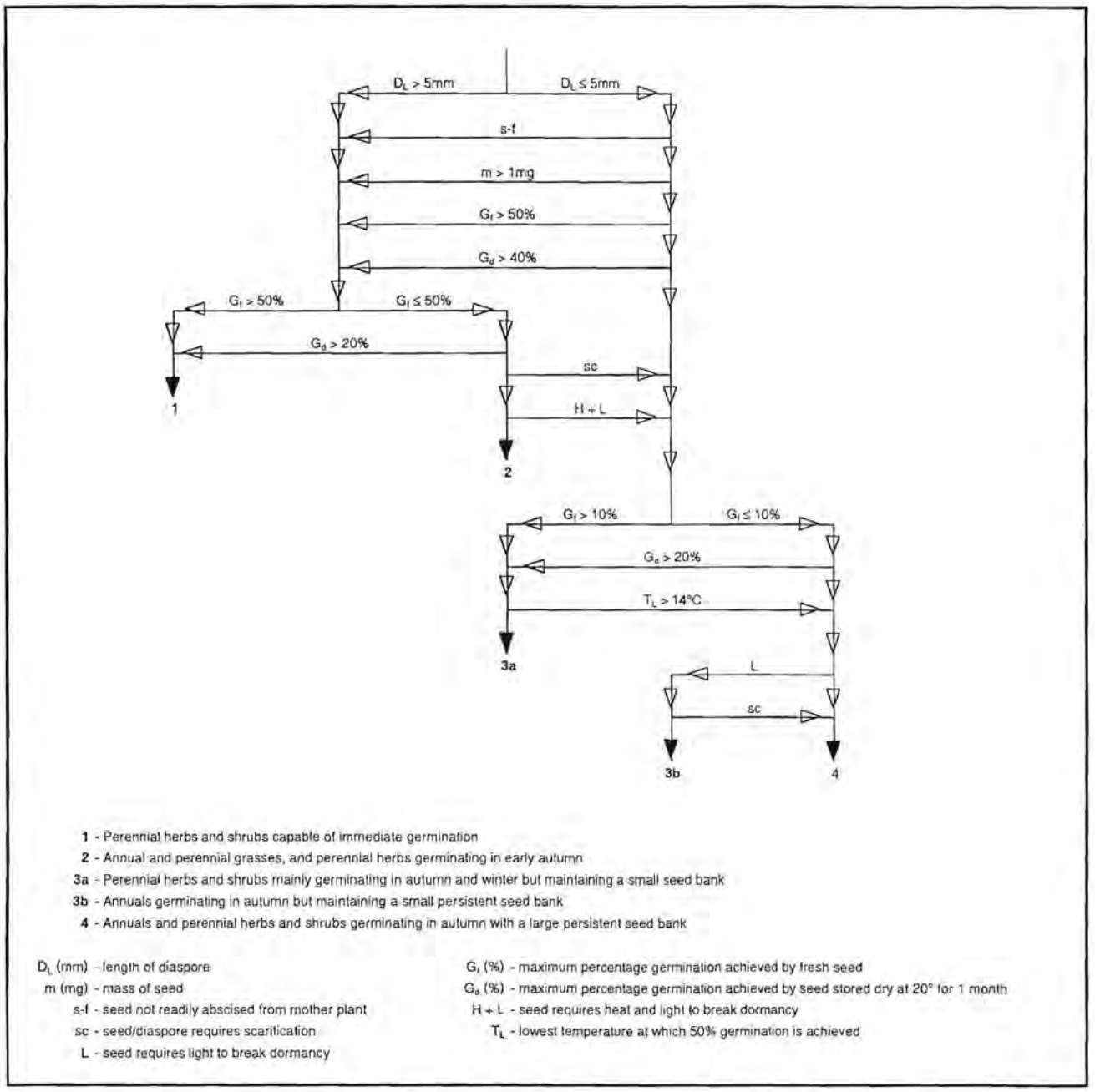

Figure 11.1. A key with laboratory characteristics of seeds developed to predict five seed bank types in the Strandveld Succulent Karoo (after Grime & Hillier, 1981).

distinguishing between seed bank types 3a and 3b or 4, as none of the species in these categories reached 50% germination in this study (Figure 11.1; Table 11.1).

Type 3 seed bank strategy was subdivided into types 3a and 3b (Figure 11.1) according to the type IIIa and IIIb strategies described by Grime (1981). Type 3a was obtained similar to the original type III (Grime & Hillier, 1981), but type 3b was derived from seed bank type IV (Grime & Hillier, 1981) *i.e.* species requiring light but not scarification for optimum germination.

Seed characteristics such as mass, size and shape may be linked to both seed longevity and dispersal distance. Whether one considers species, genera or families, small, light, and round seeds, with smooth coats, are more likely to build persistent seed banks than large, heavy, flattened and/or elongated seeds, that have hooks, awns, spines or other kinds of projections on the seed coat (Thompson *et al.*, 1993, 1998; Bakker *et al.*, 1996; Baskin & Baskin, 1998). The underlying cause of this relationship is assumed to be relative ease of burial. Large seeds do not readily become buried by rain, animals or gravity, and suffer high levels of predation while on the soil surface (Thompson *et al.*, 1993).

The seed characteristics of 37 species (41 seed types) from the Strandveld Succulent Karoo, determined in the laboratory, are shown in Tables 11.1 and 11.2. Species/seed types have been grouped according to the five predicted seed bank types: 1, 2, 3a, 3b and 4 (Figure 11.1).

Seed bank type 1

Of the 37 species investigated, eight species exhibited the type 1 seed bank strategy (Table 11.1; Figure 11.2), all of which were perennial or geophyte species with wind dispersed seeds (Table 11.2). The plant species of Namaqualand were found to be predominantly anemochorous (66.3% of all species)(Van Rooyen *et al.*, 1990). In contrast to the type I strategy of Grime and Hillier (1981) (annual and perennial grasses of dry or disturbed habitats capable of immediate germination), this group (type 1) can be described as perennial herbs and shrubs capable of immediate germination. This strategy includes both large and small seeded species, while grass species did not fall in this category (Table 11.1).

The anemochorous seeds of six of the eight species with the type 1 seed bank strategy have wing-like appendages (Table 11.2), *i.e. Albuca exuviata*, *Amellus tenuifolius, Chrysocoma longifolia, Dimorphotheca tragus, Tripteris oppositifolia* and *Zygophyllum morgsana*. The seeds of *Pteronia divaricata* have a pappus, while the atelechoric seeds of *Hypertelis salsoloides* are dispersed by anemoballistic mechanisms (Table 11.2). Although the diaspores of *Zygophyllum morgsana* are wind dispersed, the true seeds are atelechoric. In this seed bank category, antitelechoric mechanisms employed by *Tripteris oppositifolia* and *Zygophyllum morgsana* were myxospermy and synaptospermy respectively (Table 11.2).

Seed bank type 1 species can germinate over a wide range of temperatures and at different light conditions (Chapter 8) and rainfall will play a crucial role in the timing of germination in these species for successful seedling establishment and survival. Occasional out of season rainfall may result in the germination of

Table 11.1. Seed characteristics of 37 Strandveld Succulent Karoo plant species (41 seed types) used in predicting seed bank types

Seed bank type	Species/seed type	Seed characteristic								
		D_L (mm)	S-F	m (mg)	G_f (%)	G_d (%)	sc	H	L	T_L > 14°C
1	*Albuca exuviata* (PH)	4.2	Y	0.8	38.0	96.0				
	Amellus tenuifolius (PS)	3.1	Y	0.4	51.0	36.0				
	Chrysocoma longifolia (PS)	1.2	Y	0.2	72.0	53.0				
	Dimorphotheca tragus (PH)	10.1	Y	4.3	44.0	54.0				
	Hypertelis salsoloides (PH)	0.8	Y	0.1	94.0	90.0				
	Pteronia divaricata (PS)	3.7	Y	2.2	23.0	47.0				
	Tripteris oppositifolia (PS)	11.6	Y	13.6	37.0	52.0				
	Zygophyllum morgsana (PS)	33.3	N	8.8	88.0	72.0				
2	*Arctotis acaulis* (PH)	3.0	Y	4.5	0.0	0.0	N	Y	N	
	Arctotis stoechadifolia (PH)	2.9	Y	4.0	0.0	0.0	N	Y	N	
	Ehrharta calycina (PG)	5.3	N	1.0	0.0	0.0	N	Y	N	
	Gazania leiopoda (PH)	3.5	Y	2.4	2.0	8.4	N	Y	N	
3a	*Cephalophyllum spongiosum* (PH)	0.6	Y	0.1	2.0	32.0	N	Y	Y	N
	Stoeberia sp. (PS)	0.7	Y	0.0	24.0	10.0	N	Y	Y	N
3b	*Arctotheca calendula* (A)	2.9	Y	0.7	0.0	0.0	N	Y	Y	Y
	Cotula thunbergii (A)	1.5	Y	0.3	1.2	5.6	N	Y	Y	Y
	Dimorphotheca pluvialis (disc)(A)	8.8	Y	3.3	0.0	0.4	N	Y	Y	Y
	Nemesia bicornis (A)	2.1	Y	0.3	0.0	0.0	N	Y	Y	Y
	Senecio arenarius (A)	2.9	Y	0.3	0.0	0.0	N	Y	Y	N
	Ursinia anthemoides (grey)(A)	5.5	Y	2.1	0.0	0.0	N	Y	Y	Y
	Ursinia speciosa (white)(A)	2.9	Y	1.2	0.4	0.4	N	Y	Y	Y
	Wahlenbergia paniculata (A)	0.4	Y	0.0	0.0	0.0	N	Y	Y	Y
4	*Ballota africana* (PS)	2.0	Y	0.8	10.0	10.0	Y	Y	N	
	Conicosia pugioniformis (PH)	1.1	Y	0.7	0.0	0.0	Y	Y	N	
	Cysticapnos cracca (A)	1.3	Y	0.5	0.0	0.0	Y	Y	N	
	Didelta carnosa (A)	8.8	N	73.5	6.0	8.0	Y	Y	N	
	Dimorphotheca pluvialis (ray)(A)	7.1	Y	5.2	0.0	0.0	Y	Y	Y	
	Grielum grandiflorum (PH)	19.1	N	791.0	0.0	0.0	Y	N	N	
	Hebenstretia dentata (A)	3.8	Y	1.0	0.0	0.0	Y	Y	N	
	Hebenstretia repens (A)	1.9	Y	0.5	0.0	0.0	Y	Y	N	
	Heliophila coronopifolia (A)	0.8	Y	0.1	6.0	2.0	N	Y	N	
	Pharnaceum aurantium (PH)	0.5	Y	0.1	0.0	2.0	N	Y	N	
	Pharnaceum exiguum (A)	0.5	Y	0.1	0.0	0.0	N	Y	N	
	Pharnaceum lanatum (PH)	0.8	Y	0.1	0.0	6.0	N	Y	N	
	Polycarena pumila (A)	0.3	Y	0.0	4.0	4.0	N	Y	N	
	Ruschia bolusiae (PS)	1.0	Y	0.3	0.0	2.0	N	Y	N	
	Silene clandestina (A)	1.2	Y	0.3	0.0	0.0	Y	Y	Y	
	Tetragonia virgata (PS)	6.9	N	40.4	0.0	0.0	Y	Y	N	
	Ursinia anthemoides (black)(A)	5.7	Y	2.1	0.0	0.0	Y	Y	Y	
	Ursinia anthemoides (white)(A)	5.5	Y	2.2	0.0	0.0	Y	Y	Y	
	Ursinia speciosa (black)(A)	2.9	Y	1.3	0.0	0.0	Y	Y	N	

D_L (mm) - length of diaspore
m (mg) - mass of seed
G_f (%) - maximum percentage germination achieved by fresh seed
G_d (%) - maximum percentage germination achieved by seed stored dry at 20° for 1 month

S-F - seed not readily abscised from mother plant
H - seed requires heat to break dormancy (after-ripen)
T_L - lowest temperature at which 50% germination is achieved
L - seed requires light to break dormancy
sc - seed/diaspore requires scarification
A - annual
PS - perennial shrub
PH - perennial herb
PG - perennial grass

1 - Perennial herbs and shrubs capable of immediate germination
2 - Annual and perennial grasses, and perennial herbs germinating in early autumn
3a - Perennial herbs and shrubs mainly germinating in autumn and winter but maintaining a small seed bank
3b - Annuals germinating in autumn but maintaining a small persistent seed bank
4 - Annuals and perennial herbs and shrubs germinating in autumn with a large persistent seed bank

Table 11.2. Seed dispersal types of 37 Strandveld Succulent Karoo plant species (41 seed types), grouped according to predicted seed bank types

Seed bank type	Species/seed type	Dispersal type	
		Telechoric	Atelechoric / Antitelechoric
1	*Albuca exuviata* (PH)	Anemochory	
	Amellus tenuifolius (PS)	Anemochory	
	Chrysocoma longifolia (PS)	Anemochory	
	Dimorphotheca tragus (PH)	Anemochory	
	Hypertelis salsoloides (PH)	Anemoballistic	Atelechory
	Pteronia divaricata (PS)	Anemochory	
	Tripteris oppositifolia (PS)	Anemochory	Myxospermy
	Zygophyllum morgsana (PS)	Anemochory	Atelechory/Synaptospermy
2	*Arctotis acaulis* (PH)	Anemochory	
	Arctotis stoechadifolia (PH)	Anemochory	
	Ehrharta calycina (PG)	Anemochory	
	Gazania leiopoda (PH)	Anemochory	Myxospermy
3a	*Cephalophyllum spongiosum* (PH)	Rain ballistic	Hygrochasy
	Stoeberia sp. (PS)	Rain ballistic	Hygrochasy
3b	*Arctotheca calendula* (A)	Anemochory	
	Cotula thunbergii (A)	Anemochory	Myxospermy
	Dimorphotheca pluvialis (disc)(A)	Anemochory	Heterodiaspory
	Nemesia bicornis (A)	Anemochory	
	Senecio arenarius (A)	Anemochory	Myxospermy
	Ursinia anthemoides (grey)(A)	Anemochory	Myxospermy/Heterodiaspory
	Ursinia speciosa (white)(A)	Anemochory	Myxospermy/Heterodiaspory
	Wahlenbergia paniculata (A)	Anemoballistic	
4	*Ballota africana* (PS)	Anemoballistic	Myxospermy
	Conicosia pugioniformis (PH)	Anemochory	Atelechory/Synaptospermy
	Cysticapnos cracca (A)	Anemochory	Atelechory/Synaptospermy
	Didelta carnosa (A)	Anemochory/Epizoochory	Synaptospermy
	Dimorphotheca pluvialis (ray)(A)		Heterodiaspory
	Grielum grandiflorum (PH)	Epizoochory	Synaptospermy
	Hebenstretia dentata (A)	Anemoballistic	Heterodiaspory
	Hebenstretia repens (A)		Atelechory
	Heliophila coronopifolia (A)	Anemochory	Myxospermy
	Pharnaceum aurantium (PH)	Anemochory	
	Pharnaceum exiguum (A)	Anemochory	
	Pharnaceum lanatum (PH)	Anemochory	
	Polycarena pumila (A)	Anemoballistic	Atelechory
	Ruschia bolusiae (PS)	Rain ballistic	Hygrochasy
	Silene clandestina (A)	Anemoballistic	
	Tetragonia virgata (PS)	Anemochory	Synaptospermy
	Ursinia anthemoides (black)(A)	Anemochory	Myxospermy/Heterodiaspory
	Ursinia anthemoides (white)(A)	Anemochory	Myxospermy/Heterodiaspory
	Ursinia speciosa (black)(A)	Anemochory	Myxospermy/Heterodiaspory

A - annual
PH - perennial herb
PG - perennial grass
PS - perennial shrub

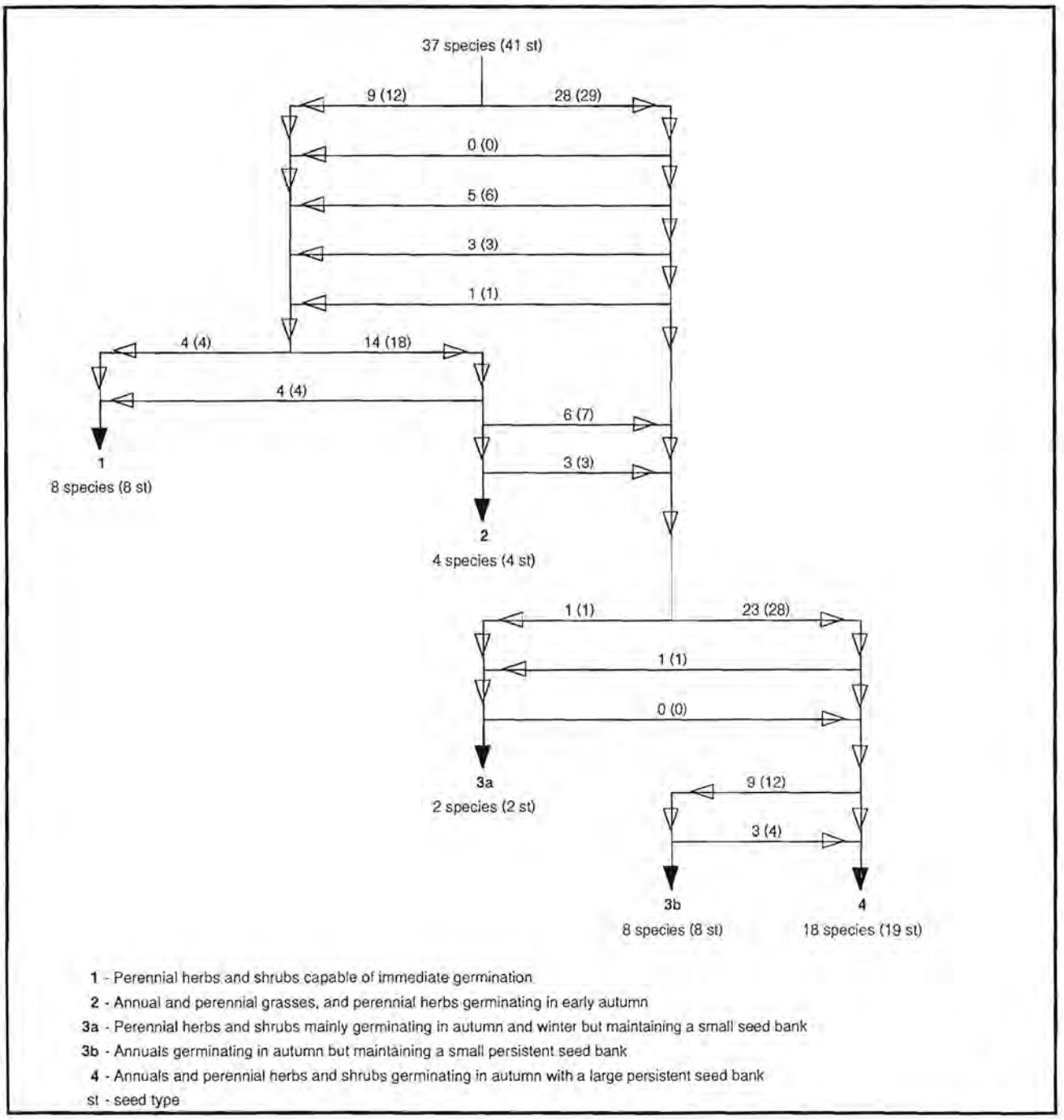

Figure 11.2. Distribution of 37 Strandveld Succulent Karoo species (41 seed types) between seed bank strategies predicted by using a modified key with laboratory characteristics of seeds.

seeds of these species, but many seedlings will not survive the dry summer months. However, the loss of offspring will be buffered by the perennial nature of these species. *Amellus tenuifolius* is a short-term bradysporic species and the mature seeds are retained on the mother plant for a relatively short period.

Diaspores of these anemochorous species (seed bank type 1, Table 11.2) have the potential to be dispersed by wind over long distances (Sheldon & Burrows, 1973; Bakker *et al.*, 1996). Many species are specialised either towards good dispersal capacity or building a persistent seed bank (Klinkhamer *et al.*, 1987; Poschlod & Jackel, 1993; Bakker *et al.*, 1996).

Although Strandveld Succulent Karoo species with a type 1 seed bank strategy do not produce a persistent seed bank, which will be beneficial for the rehabilitation process in mined areas by means of topsoil replacement, they may disperse to the revegetation areas from surrounding vegetation. However, natural dispersal is often slow and unreliable (Bauer, 1973; Van der Valk & Pederson, 1989). Although transplanting of adult plants is labour intensive, this method is recommended for the initial revegetation of mined areas with seed bank type 1 shrub species. These shrubs may reduce wind speed at ground level and thereby combat wind erosion on the reclamation sites. After transplanting, the reintroduction of these shrub species by means of sowing could be limited. Seed bank type 1 herb species should be reintroduced to the mined areas by means of sowing.

Seed bank type 2

Species characteristic of seed bank type 2, typically have large seeds (diaspores longer than 5 mm and/or seed with a mass of more than 1 mg) and/or seeds not readily abscised from the mother plant (Figure 11.1). Also, the seeds of these species have low germination percentages when fresh or stored dry at 20°C for one month, they do not require scarification or light to germinate, but they do require heat to after-ripen (Table 11.1).

This seed bank strategy was observed in four of the species examined, all of which were perennials with anemochorous seeds (Figure 11.2, Table 11.2). A few other local perennial and annual grass species are expected to have this type of seed bank strategy, as their temporal germination strategies were similar to that of *Ehrharta calycina* in seed bank studies of the Strandveld Succulent Karoo (Chapter 5).

The seeds of species with this type of seed bank strategy require an after-ripening period (Table 11.1), whereafter most of them are able to germinate at the first fall of sufficient rains, usually in autumn. Seeds of these species can germinate over a wide range of temperatures in both light and darkness (Chapter 8). These species have a summer transient seed bank, but some seeds may persist in the soil for a short-term. The seed bank type 2 strategy was exhibited by seeds of grass and perennial herb species (Table 11.1). The seeds of species with a seed bank type 2 strategy are dispersed by wind, but antitelechoric mechanisms are also evident, such as myxospermy in *Gazania leiopoda* (Table 11.2).

Species in this seed bank category build no long-term persistent seed banks (Table 11.1). They may occur in environments which produce predictable circumstances for establishment in space as well as in time, probably relying on clonal colonisation (Bakker *et al.*, 1996). These species are likely to re-establish easily during natural regeneration, but may need deliberate reintroduction, to initial safe-sites for establishment, by man.

Seed bank type 3a

The seed bank type 3a strategy is characterised by species with small photoblastic seeds (< 5 mm) which require a short after-ripening period. These seeds can obtain germination percentages of more than 50% at temperatures lower than 14°C (Table 11.1, Figures 11.1 & 11.2), indicating that germination may also occur during the winter months. Once after-ripened, seeds of seed bank type 3a species may experience considerable depletion of the seed bank after sufficient rainfall, but due to a light requirement for germination (Table 11.1), have a portion of seeds that persists. Two perennial species, both belonging to the Mesembryanthemaceae, had seed bank strategies typical of seed bank type 3a (Table 11.1). Therefore, seed bank type 3a include perennial herbs and shrubs mainly germinating during autumn and winter but maintaining a small seed bank.

In both *Cephalophyllum spongiosum* and *Stoeberia* sp., rain ballistic seed dispersal is restricted in time by means of hygrochasy (Table 11.2). Both species in this seed bank category occur in plant communities close to the ocean (De Villiers *et al.*, 1999), where high levels of atmospheric moisture (rain or fog) lead to the opening of seed bearing capsules (Pers. obs.). Once after-ripened, the seeds of these species may germinate (Table 11.1, Figure 11.2), provided that sufficient moisture and favourable temperatures and light conditions prevail.

Similar to species with the seed bank type 1 and 2 strategies, mass germination and the loss of seedlings during following unfavourable conditions will be buffered by the perennial nature of the seed bank type 3a species (Table 11.1). Since the probability of seedling establishment, under severe competition from other plants, is lower in species with small seeds than in species with large seeds (Hodgson & Thompson, 1993), establishment of these small seeded species (type 3a) may depend on the availability of sites where there is less biotic competition. Because light is required for germination, burial causes an inhibition of germination, which results in the formation of a small seed bank. Topsoil replacement should be sufficient for the revegetation of mined areas with seed bank type 3a species, provided that the topsoil is not stored for long periods prior to replacement. Due to the limited distribution of these species (De Villiers *et al.*, 1999), post-mining reintroduction by means of sowing should be considered in areas where these species were previously abundant, *i.e.* communities close to the ocean.

Seed bank type 3b

Seeds of seed bank type 3b species usually are small, require a high temperature after-ripening period and light but not scarification to germinate, and have a narrow temperature range for germination (Figure 11.1, Table 11.1). Eight annual species (8 seed types) were classified in this category (Figure 11.2). During the start of the rainy season (autumn), a large portion of the seeds of these species germinates, but many seeds may persist in the soil for more than one year. In species with this seed bank type, some seeds become buried during the summer after-ripening period, and a light requirement for germination prevents the germination of buried seeds after sufficient rains in autumn (Baskin & Baskin, 1998). Consequently, seed bank type 3b has been classified as annual species with seeds germinating in autumn with a short-term persistent seed bank.

Seed dispersal of seed bank type 3b species is mainly by wind (Table 11.2). Antitelechoric mechanisms such as myxospermy and heterodiaspory are abundant in these winter annual species. Myxospermy was recorded for four of the eight species, *i.e. Cotula thunbergii, Senecio arenarius*, *Ursinia anthemoides* (grey seeds) and *Ursinia speciosa* (white seeds)(Table 11.2). Heterodiaspory occurred in three species (one seed type each in this category), *i.e. Dimorphotheca pluvialis, Ursinia anthemoides* and *Ursinia speciosa,* and greatly enhances the ability of the species to live in highly variable environments and can be important in the recruitment of new individuals into the population (Baskin & Baskin, 1998).

Seed bank type 3b species are expected to make a major contribution towards revegetation by means of topsoil replacement, as these species accumulate short-term persistent seed banks (Table 11.1). However, all will depend on the period of topsoil storage. Stockpiling soils before they are used for revegetation can negatively influence recruitment in 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). For these species, seed input by man (sowing) should not be necessary once the topsoil has been replaced. Furthermore, most of these species are anemochorous and may be reintroduced by dispersal from surrounding vegetation.

Seed bank type 4

Type 4 seed bank strategy species are those for which the seed bank is large relative to annual input. These species commonly have small seeds or seeds with hard, water permeable or impermeable seed coats and usually require a summer after-ripening period (Figure 11.1, Table 11.1). Eighteen of the species (19 seed types) investigated had this type of seed bank strategy, including seven perennial and 11 annual species (Figure 11.2, Table 11.1). Seed bank type 4 species can therefore be described as annuals and perennial herbs and shrubs of which the seeds germinate in autumn and can produce a long-term persistent seed bank (Figure 11.1). If the environment is moderately predictable on a time scale and confined spatially, building a persistent seed bank was found to be a common strategy (Bakker *et al.*, 1996).

Seeds of species with this seed bank type are mainly anemochorous, but several species were found to be epizoochorous and rain ballistic (Table 11.2). Antitelechorous mechanisms employed by species with a seed bank type 4 strategy include synaptospermy, heterodiaspory, hygrochasy and myxospermy. The unwinged ray floret seeds of the polymorphic species *Dimorphotheca pluvialis* has this persistent seed bank strategy, *i.e.* dispersal in time, while the winged disc floret seeds of this species (type 3b) will disperse horizontally in space. Heteromorphism in morphologically different seeds is important since it provides a two-way strategy. On the one hand the disc floret seeds, which show a high germination percentage under favourable conditions, are responsible for the relative abundance and the range extension of the species. On the other hand the ray floret seeds, with delayed germination (Chapter 8) protect the species against unpredictable, disastrous events. Seed dimorphism which involves dormancy of one type may lead to distribution of germination in time, thus reducing the chances of extinction of a complete generation (Berger, 1985).

Both the black and white seeds of *Ursinia anthemoides* and the black seeds of *Ursinia speciosa* were categorised with type 4 seed bank strategies. In these heteromorphic species, differences in seed colour and timing of germination is correlated with differences in the surface structure of the pericarp (Van Rheede van Oudtshoorn & Van Rooyen, 1999), and has no real effect on dispersal.

Due to the persistent nature of seed bank type 4 species' seeds in the soil seed bank, their germination is dispersed temporally. The importance of seed bank type 4 species in revegetation efforts is stressed by this long-term persistence. During long periods of topsoil stockpiling, seeds with this seed bank strategy may have lower mortality rates than seeds of seed bank type 3b species. Also, high temperatures experienced during summer stockpiling may not be as detrimental for the hard seeds of seed bank type 4 species, than for the seeds of type 3b species. Topsoil replacement should be sufficient for the reintroduction of seed bank type 4 species during post-mining revegetation processes. Due to the hard pericarp of these species' seeds, sowing should most probably involve the scarification and/or heat pre-treatment of these seeds prior to sowing.

Seed bank type and revegetation

The seeds present in the soil are potentially useful in restoration projects where establishment of plant cover is desired, for example to reduce soil erosion (Skoglund, 1992). Buried seeds can have important implications for conservation management where preferred species have been lost from the vegetation but survive in the seed bank. However, seed banks cannot be used for the restoration of all plant communities (Warr *et al.*, 1993). Also, the species composition of the seed bank will determine which species could possibly be recruited. This, in turn, will be determined by the seed bank strategy employed by the different species.

Restoration management has only recently taken into account that dispersal is an important key for the establishment of 'target' communities or species (Bakker *et al.*, 1996). Dispersal was found to be the most important factor in a second phase of restoration, after activating the present seed bank (Salonen, 1987;

Poschlod, 1995). However, it was also shown that even species occurring close to restoration sites, were absent from the seed rain (Poschlod, 1995).

Species of all five seed bank types will be important in the revegetation of mined areas of the Strandveld Succulent Karoo, as each contain species dominant in specific vegetation types (De Villiers *et al.*, 1999). The revegetation strategies will, however, differ for species with different seed bank types. The seed bank alone will not be sufficient for the revegetation of this area, as many of the species which are dominant in the aboveground vegetation do not produce persistent seed banks (types 1 & 2). The use of topsoil replacement will, however, be essential because of difficulties involved in the collection, treatment and sowing of small persistent seeds of many species present in the seed bank (types 3a, 3b & 4).

During recolonization, species with type 3a, 3b and 4 seed bank strategies will probably originate from the seed bank contained in the replaced topsoil. Due to the limited distribution of seed bank type 3a species, their seeds should also be reintroduced to selected mined areas by means of sowing. The predominantly anemochorous seeds of species with seed bank types 1, 2, 3b and 4 strategies may be dispersed by wind into restoration areas from surrounding vegetation, but revegetation efforts should not rely on dispersal alone for the reintroduction of these species. Sowing of seed bank types 1 and 2 herb species' seeds will be necessary, while adult plants of shrub species with the type 1 seed bank strategy should be transplanted on mined areas to serve as wind-breaks.

CONCLUSIONS

The modified key with laboratory characteristics of seeds developed to predict the seed bank types (after Grime & Hillier, 1981) seems to be well suited for the classification of seed banks of the Strandveld Succulent Karoo. A few adaptations had to be made to Grime & Hillier's (1981) key. Firstly, the requirement of a dry heat pre-treatment rather than cold stratification during the summer after-ripening of the seeds was evident. Secondly, the mean germination percentages of fresh and stored seeds (20°C for one month) were considered for both large and small seeds. Consequently, the size (length or mass) and abscised status (from the mother plant) of a seed were not the only criteria for classification into transient or persistent seed bank types. Thirdly, because many species apparently had persistent seed banks (type IV, Grime & Hillier, 1981), this category was subdivided into type 3b and type 4 according to the categories (types IIIb & IV) described by Grime (1981). Lastly, the time taken by seeds stored dry at 20°C for one month to reach 50% germination was not incorporated as a means of distinguishing between seed bank types 3a and 3b or 4, as these species did not obtain 50% germination when stored for such a short period. In contrast to the four main seed bank types predicted by the original key, results from this study predicted five seed bank types, two of which have transient seed bank strategies (types 1 and 2) and three of which accumulate persistent seed banks (types 3a, 3b and 4).

Of the 37 species investigated, 32% have seeds with a transient seed bank strategy, while 68% exhibited persistent seed bank strategies. Five percent of the species produce small persistent seed banks, while 22% and 49% of the species have seed types which accumulate small short-term persistent seed banks and

large persistent seed banks respectively. Therefore, species with persistent seed bank strategies were by far the most numerous in the Strandveld Succulent Karoo. Predicted seed bank strategies should, however, be examined and checked in the field for each species.

Species abundance in the aboveground vegetation should be incorporated during the planning phase of revegetation projects in this area, as both species richness and abundance or cover will be important in fulfilling the revegetation requirements. The seed bank alone will not be sufficient for the revegetation of this area, as many of the species dominant in the vegetation do not produce persistent seed banks. Topsoil replacement will, however, be essential because of difficulties involved in the collection, treatment and sowing of many species. Also, prior or during the period of mining, many species may be present only in the seed bank. The inclusion of these species in the revegetation process will therefore rely solely on the use of topsoil replacement.

For the successful revegetation of mined areas in the Strandveld Succulent Karoo, topsoil replacement, seeding and transplanting of selected species will be essential. Species of all five seed bank types will be important during the revegetation of these mined areas. The anemochorous seeds of seed bank types 1, 2, 3b and 4 species may disperse into the post-mining revegetation areas from surrounding vegetation, but this would not be sufficient for revegetation purposes. During revegetation, species with types 3a, 3b and 4 seed bank strategies should originate from replaced topsoil. Seeds of species with the seed bank type 3a strategy should also be sown in selected areas, as these species have a restricted spatial distribution. Seeds of herb species with types 1 and 2 seed bank strategies should be reintroduced to post-mining areas by means of sowing, while adult plants of seed bank type 1 shrub species should be transplanted to serve as wind-breaks.

Finally, it is very important to realise that seed dispersal distance and seed bank formation form only part of the total reproductive strategy of a species. Other parts of this strategy, such as seed production, predation, seed release time and duration, timing of germination, seedling survival and, after establishment, clonal and sexual reproduction speed may be equally important in restoration. The arrival of a certain species before others may determine succession through shifts in competition between species (Bakker *et al.*, 1996). The timing of restoration measures will therefore be important in obtaining the proposed revegetation goals.

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REFERENCES

ARNOLD, T.H. & DE WET, B.C. 1999. Plants of Southern Africa: names and distribution. Electronic database, National Botanical Institute, Pretoria.

BADGER, K.S. & UNGAR, I.A. 1994. Seed bank dynamics in an inland salt marsh, with special emphasis on the halophyte *Hordeum jubatum* L.. *International Journal of Plant Science*, **155**: 66-72.

BAKKER, J.P. 1989. *Nature management by grazing and cutting*. Kluwer Academic, Dordrecht.

BAKKER, J.P., POSCHLOD, P., STRYKSTRA, R.J., BEKKER, R.M. & THOMPSON, K. 1996. Seed banks and seed dispersal: important topics in restoration ecology. *Acta Botanica Neerlandica*, **45**: 461-490.

BASKIN, C.C. & BASKIN, J.M. 1998. *Seeds: Ecology, biogeography, and evolution of dormancy and germination*. Academic Press, London.

BAUER, H.J. 1973. Ten years' studies of biocoenological succession in the excavated mines of the Cologne lignite district. In: Hutnik, R.J. & Davis, G. (eds). *Ecology and reclamation of devastated land*. Gordon & Breach, New York. pp. 271-283.

BENEKE, K., VAN ROOYEN, M.W., THERON, G.K. & VAN DE VENTER, H.A. 1993. Fruit polymorphism in ephemeral species of Namaqualand: III. Germination differences between the polymorphic diaspores. *Journal of Arid Environments*, **24**: 333-344.

BERGER, A. 1985. Seed dimorphism and germination behaviour in *Salicornia patula*. *Vegetatio*, **61**: 137-143.

BOUCHER, C. & LE ROUX, A. 1990. Heavy mineral sand mining project assessment vegetation report. In: Environmental Evaluation Unit. *Anglo American Corporation: West Coast heavy mineral sands project - Supplementary Report*. Unpublished report. University of Cape Town, Cape Town. Section A5.

COFFIN, D.P. & LAUENROTH, W.K. 1989. Spatial and temporal variation in the seed bank of a semi-arid grassland. *American Journal of Botany*, **76**: 53-58.

DE VILLIERS, A.J., VAN ROOYEN, M.W., THERON, G.K. & VAN DE VENTER, H.A. 1994. Germination of three Namaqualand pioneer species, as influenced by salinity, temperature and light. *Seed Science & Technology*, **22**: 427-433.

DE VILLIERS, A.J., VAN ROOYEN, M.W., THERON, G.K. & VAN ROOYEN, N. 1999. Vegetation diversity of the Brand-se-Baai coastal dune area, West Coast, South Africa: A pre-mining benchmark survey for rehabilitation. *Land Degradation & Development*, **10**: 207-224.

ELLNER, S. & SHMIDA, A. 1981. Why are adaptations for long-range seed dispersal rare in desert plants? *Oecologia*, **51**: 133-144.

ENVIRONMENTAL EVALUATION UNIT. 1990. *Anglo American Corporation: West Coast heavy mineral sands project*. Unpublished report. University of Cape Town, Cape Town.

GARWOOD, N.C. 1989. Tropical soil seed banks: a review. In: Leck, M.A., Parker, V.T. & Simpson, R.L. (eds). *Ecology of soil seed banks*. Academic Press, London. pp. 149-209.

GRIME, J.P. 1981. The role of seed dormancy in vegetation dynamics. *Annals of Applied Biology*, **98**: 555-558.

GRIME, J.P. & HILLIER, S.H. 1981. *Predictions based upon the laboratory characteristics of seeds*. Annual Report 1981, Unit of Comparative Plant Ecology (NERC), University of Sheffield, Sheffield.

GROSS, K.L. 1990. A comparison of methods for estimating seed numbers in the soil. *Journal of Ecology*, **78**: 1079-1093.

GUTTERMAN, Y. 1972. Delayed seed dispersal and rapid germination as survival mechanisms of the desert plant *blepharis persica* (Burm.) Kuntze. *Oecologia*, **10**: 145-149.

GUTTERMAN, Y. 1993. *Seed germination in desert plants.* Springer-Verlag, Berlin.

GUTTERMAN, Y. 1994. Strategies of seed dispersal and germination in plants inhabiting deserts. *The Botanical Review*, **60**: 373-425.

HARPER, J.L. 1977. *Population biology of plants.* Academic Press, London.

HODGSON, J.G. & THOMPSON, K. 1993. Seeds: Size. In: Hendry, G.A.F. & Grime, J.P. (eds). *Methods in comparative plant ecology.* Chapman & Hall, London. pp. 202-205.

KIRKHAM, F.W. & KENT, M. 1997. Soil seed bank composition in relation to the aboveground vegetation in fertilized and unfertilized hay meadows on a Somerset peat moor. *Journal of Applied Ecology*, **34**: 889-902.

KLINKHAMER, P.G.L., DE JONG, T.J., METZ, J.A.J. & VAL, J. 1987. Life history tactics of annual organisms: the joint effects of dispersal and delayed germination. *Theoretical Population Biology*, **32**: 127-156.

LECK, M.A., PARKER, V.T. & SIMPSON, R.L. 1989. *Ecology of soil seed banks.* Academic Press, London.

LECK, M.A. & SIMPSON, R.L. 1993. Seeds and seedlings of the Hamilton marshes, a Delaware river tidal freshwater wetland. *Proceedings of The Academy of Natural Sciences of Philadelphia*, **144**: 267-281.

LOW, A.B. & REBELO, A. 1998. *Vegetation of South Africa, Lesotho and Swaziland.* Department of Environmental Affairs & Tourism, Pretoria.

POSCHLOD, P. 1995. Diaspore rain and diaspore bank in raised bogs and its implication for the restoration of peat mined sites. In: Wheeler, B.D., Shaw, S.C., Fojt, W.J. & Robertson, R.A. (eds). *Restoration of Temperate Wetlands.* Wiley, Chichester. pp. 471-494.

POSCHLOD, P. & JACKEL, A.K. 1993. Untersuchungen zur Dynamik von generativen Diasporenbanken von Samenpflanzen in Kalkmagerrasen. I. Jahreszeitliche Dynamik des Diasporenregens und der Diasporenbank auf zwei Kalkmagerrasenstandorten der Schwäbischen Alp. *Flora*, **188**: 49-71.

ROBERTS, H.A. 1981. Seed banks in soils. *Advances in Applied Biology*, **6**: 1-55.

SALONEN, V. 1987. Relationship between the seed rain and the establishment of vegetation in two areas abandoned after peat harvesting. *Holarctic Ecology*, **10**: 171-174.

SHELDON, J.C. & BURROWS, F.M. 1973. The effectiveness of the achene-pappus units of selected Compositae in steady winds with convection. *New Phytologist*, **72**: 665-675.

SKOGLUND, J. 1992. The role of seed banks in vegetation dynamics and restoration of dry tropical ecosystems. *Journal of Vegetation Science*, **3**: 357-360.

THOMPSON, K. 1992. The functional ecology of seed banks. In: Fenner, M. (ed). *Seeds: the ecology of regeneration in plant communities.* CAB International, Wallingford. pp. 231-258.

THOMPSON, K. 1993. Persistence in soil. In: Henry, G.A.F. & Grime, J.P. (eds). *Methods in comparative plant ecology.* Chapman & Hall, London. pp. 199-202.

THOMPSON, K., BAKKER, J.P. & BEKKER, R.M. 1996. *Soil seed banks of North-west Europe: Methodology, density and longevity.* Cambridge University Press, Cambridge.

THOMPSON, K., BAND, S.R. & HODGSON, J.G. 1993. Seed size and shape predict persistence in soil. *Functional Ecology*, **7**: 236-241.

THOMPSON, K., BEKKER, R.M. & BAKKER, J.P. 1998. Weed seed banks; evidence from the north-west European seed bank database. *Aspects of Applied Biology*, **51**: 105-112.

THOMPSON, K. & GRIME, J.P. 1979. Seasonal variation in the seed banks of herbaceous species in ten contrasting habitats. *Journal of Ecology*, **67**: 893-921.

VAN DER PIJL, L. 1982. *Principles of dispersal in higher plants.* Springer Verlag, Berlin.

VAN DER VALK, A.G. & PEDERSON, R.L. 1989. Seeds banks and the management and restoration of natural vegetation. In: Leck, M.A., Parker, V.T. & Simpson, R.L. (eds). *Ecology of soil seed banks.* Academic Press, New York. pp. 329-346.

VAN DER VALK, A.G., PEDERSON, R.L. & DAVIS, C.B. 1992. Restoration and creation of freshwater wetlands using seed banks. *Wetlands Ecology and Management*, **1**: 191-197.

VAN RHEEDE VAN OUDTSHOORN, K. & VAN ROOYEN, M.W. 1999. *Dispersal biology of desert plants.* Springer-Verlag, Berlin.

VAN ROOYEN, M.W., THERON, G.K. & GROBBELAAR, N. 1990. Life form and dispersal spectra of the flora of Namaqualand, South Africa. *Journal of Arid Environments*, **19**: 133-145.

VISSER, L. 1993. Saadontkiemingstudies van geselekteerde Namakwalandse efemeer-spesies. M.Sc. dissertation, University of Pretoria, Pretoria.

WARR, S.J., THOMPSON, K. & KENT, M. 1993. Seed banks as a neglected area of biogeographic research: a review of literature and sampling techniques. *Progress in Physical Geography*, **17**: 329-347.

CHAPTER 12

EFFECTS OF SEED PRODUCTION, PREDATION, SEED-BORNE FUNGI AND RECRUITMENT ON SEED BANK DYNAMICS OF SELECTED STRANDVELD SUCCULENT KAROO (SOUTH AFRICA) PLANT SPECIES

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ABSTRACT

Seed production, pre- and post-dispersal seed predation, abundance of seed-borne fungi and seedling recruitment were studied in selected species from the Strandveld Succulent Karoo, South Africa. Information on the factors which control seedling abundance and survival provided a predictive basis for assessing the feasibility of post-mining revegetation by means of topsoil replacement and seeding. Pre-dispersal predation was interspecific density dependent and decreased the number of seeds entering the seed pool. Post-dispersal predation did not affect seedling recruitment during the first peak germination period following dispersal, but the number of seeds that persisted in the soil decreased significantly. Seed-borne fungi occurred at percentages lower than two percent and will not be a major source of seed mortality during the revegetation process. Although seedling mortality was high, the presence of a large persistent seed bank will ensure the survival of annual species during harsh environmental conditions. Supplementary irrigation during the seasons following initial germination in autumn, may ensure the survival of seedlings of several perennial species.

Key words: mining; predation; revegetation; seed-borne fungi; seedling recruitment; seed production; Strandveld Succulent Karoo

INTRODUCTION

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).

Seed production is a critical stage in the life history of plants. Seeds contribute to adult replacement and to increases in local population size, and are also the means of dispersal to areas distant from the local population (De Steven, 1983; Van Rheede van Oudtshoorn & Van Rooyen, 1999). Most plant species can produce large numbers of seeds. Only very few of these seeds eventually become seedlings (Cavers, 1983), and even fewer established plants (Sheldon, 1973; Klinkhamer *et al.*, 1988).

The enormous seed production of most plants, coupled with the general paucity of seedlings, is vivid testimony to the intensity of seed mortality (Crawley, 1992). Once a seed is released from the plant it can suffer one of the following fates: germination followed by emergence; germination followed by death before emergence; persistence; predation or decay (O'Connor, 1997). Many kinds of seeds harbour a great variety of microflora, especially fungi, which might reduce their germinability, be involved in and responsible for deterioration of dormant seeds, or result in disease in the growing plant (Christensen, 1972).

Seed predation by animals has important consequences for plant abundance, distribution, and evolution (De Steven, 1983). Seed predation can be the critical factor limiting population recruitment (Klinkhamer *et al.*, 1988). The seeds of desert plants are known to support large populations of granivorous ants and seed-eating vertebrates (Inouye *et al.*, 1980; Heithaus, 1981; Kerley, 1991; Gutterman, 1993; Van Rheede van Oudtshoorn & Van Rooyen, 1999).

Germination and recruitment are thought to be critical stages in the life cycles of many plants from arid and semi-arid environments. For annual species, seedling establishment is vital for population maintenance. The survival of seedlings of any species does not depend entirely on the characteristics of the seedlings themselves. Various features of the parent plant can increase the chances of seedling survival, e.g. effective dispersal, dormancy mechanisms, and synchronous fruiting and germination (Fenner, 1987). These methods can, however, do no more than ensure that the seedlings are favourably placed for establishment. Once germination has occurred, the seedling depends on its own morphological and physiological characteristics to cope with the various factors threatening its survival. Although a minimum amount of rain may be required for a germination event (Gutterman, 1993), seedling survival depends on adequate post-germination rainfall (Wiegand *et al.*, 1995), which is not always predictable (Esler & Phillips, 1994).

Knowledge on the factors which control seedling abundance and survival, *e.g.* seed production, pre- and post-dispersal seed predation, germination and seed-borne fungi, would provide a predictive basis for assessing topsoil replacement and seeding as feasible methods for post-mining revegetation in the Strandveld Succulent Karoo, South Africa. Few results about the processes contributing to the seed bank dynamics of this area have been published (Van Rooyen & Grobbelaar, 1982; Esler *et al.*, 1992; De Villiers *et al.*, 1994). Even less reported on the consequences of these processes on recruitment (Esler & Phillips, 1994), especially concerning restoration projects (Milton, 1995).

The aim of this study was to determine whether recruitment of several Strandveld Succulent Karoo species is seed limited, and the factors possibly responsible. The null hypotheses that in this area (1) seedling recruitment was independent of seed production, seed-borne fungi and pre- and post-dispersal seed predation, and that (2) plant survival was independent of seedling predation, were tested by direct counting, agar tests and by carrying out small-scale exclosure experiments.

MATERIAL AND METHODS

This study was conducted in the vicinity of Brand-se-Baai (31°18'S, 17°54'E) on the Cape West Coast, South Africa (Environmental Evaluation Unit). The study area falls within the Namaqualand coastal belt, which has an average precipitation of 282 mm per annum, measured over a period of four years at Brand-se-Baai. Rainfall occurs mainly during winter with an average of 160 mm per annum at the study area. The average annual temperature at the study site is 15.8°C, with a relatively small annual fluctuation due to the marine influence (De Villiers *et al.*, 1999a).

The 17 species used in this study, as well as the specific experiments in which each were examined, are shown in Table 12.1.

Seed production and pre-dispersal seed predation

During spring 1994, the diaspore (henceforth referred to as seed) production of *Eriocephalus africanus*, *Lebeckia multiflora*, *Salvia africana-lutea*, *Stoeberia* sp., *Tripteris oppositifolia* and *Zygophyllum morgsana* 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. With the exception of *Tripteris oppositifolia* of which seeds are dispersed soon after maturation, pre-dispersal seed predation in 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. This method proved to be more reliable than the conventional method of assessing seed losses due to predation by inspecting mature seeds and fruit for signs of attack (Andersen, 1988). 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 the prostrate species, *Tetragonia microptera* do not disperse directly after maturation and seed production was determined by counting the total number of fruits produced by each of 10 randomly selected plants. Seed production of *Dimorphotheca pluvialis*, *Gazania leiopoda* and *Senecio arenarius* under laboratory conditions have been reported elsewhere (De Villiers *et al.*, 1999b).

For the determination of pre-dispersal seed predation in *Dimorphotheca pluvialis, Gazania leiopoda, Senecio arenarius, Tetragonia microptera* and *Tripteris oppositifolia*, 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 correlations between seed production and pre-dispersal seed predation or the number of seeds entering the seed pool.

Table 12.1. Plant species used in different experiments for determining the pre-mining seed bank dynamics of the Strandveld Succulent Karoo

Experiment		Seed production		Predation			Seed-borne fungi	Recruitment
				Pre-dispersal		Post-dispersal		
Method		Field	Laboratory	Bagging	Inspection	Burial	Agar test	Burial
Year of seed collection		1994	1993	1994	1994	1994	1995	1994
Species	*Albuca exuviata* (P)						X	
	Amellus tenuifolius (P)						X	
	Arctotis stoechadifolia (P)					X		
	Brassica tournefortii (A)						X	
	Dimorphotheca pluvialis (disc)(A)		X		X	X		
	Dimorphotheca pluvialis (ray)(A)		X		X			X
	Eriocephalus africanus (P)	X		X				
	Gazania leiopoda (P)		X		X	X		
	Lebeckia multiflora (P)	X		X				
	Pteronia divaricata (P)							X
	Salvia africana-lutea (P)	X		X				
	Senecio arenarius (A)		X		X	X	X	
	Silene clandestina (A)						X	
	Stoeberia sp. (P)	X		X				
	Tetragonia microptera (A)				X			
	Tripteris oppositifolia (P)	X			X	X		X
	Ursinia speciosa (white)(A)							X
	Zygophyllum morgsana (P)	X		X				

P - perennial
A - annual

Table 12.2. Mean seed production and pre-dispersal seed predation (± standard deviation) of ten Strandveld Succulent Karoo plant species

Species	Average number of seeds produced plant^{-1}	Pre-dispersal predation (%)	Average number of seeds plant^{-1} entering the seed pool
Dimorphotheca pluvialis (disc + ray)(A)	77.2 ± 12.5	3.1 ± 2.1	74.8 ± 12.1
Eriocephalus africanus (P)	1590.7 ± 222.2	67.8 ± 12.5	508.2 ± 212.2
Gazania leiopoda (P)	9.1 ± 5.5	1.1 ± 1.1	9.0 ± 5.5
Lebeckia multiflora (P)	2574.9 ± 468.9	81.6 ± 8.4	499.7 ± 232.8
Salvia africana-lutea (P)	421.8 ± 114.5	1.8 ± 2.9	415.0 ± 120.0
Senecio arenarius (A)	807.8 ± 169.8	36.8 ± 8.9	510.5 ± 107.3
Stoeberia sp. (P)	27444.1 ± 2770.0	82.8 ± 8.6	4851.8 ± 2816.2
Tetragonia microptera (A)	91.4 ± 39.1	7.7 ± 5.1	84.4 ± 36.1
Tripteris oppositifolia (P)	4457.4 ± 793.2	10.7 ± 5.5	3980.4 ± 708.4
Zygophyllum morgsana (P)	261.7 ± 64.2	11.5 ± 7.2	228.5 ± 49.1

P - perennial
A - annual

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 investigated species (Table 12.1), present in the soil, were removed prior to replacement 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). Draining holes at the bottom of the containers were not covered to exclude soil fauna. 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 species examined (Table 12.1) 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 and plant survival

Prior to the start of the rainy season (early autumn 1995), treatments similar to those used to determine post-dispersal seed predation were set out for each of four species (Table 12.1). After three months of burial in the field (winter 1995), the mesh covering each container was removed and the number of emerged seedlings recorded. After an additional three months (spring 1995), the number of remaining plants were recorded.

For all experiments, the least significant difference (LSD) one-way analysis of variance (ANOVA) and multiple range test (Statgraphics 5.0, 1989, STSC, Inc., U.S.A.) were used to determine significant differences at $P \leq 0.05$.

RESULTS AND DISCUSSION

Seed production and pre-dispersal seed predation

In the perennial species investigated, seed yield ranged from 9.1 seeds plant^{-1} for *Gazania leiopoda* to 27 444.1 seeds plant^{-1} for *Stoeberia* sp. (Table 12.2). In *Gazania leiopoda* the lowest level of pre-dispersal seed predation (1.1%) as well as the lowest number of seeds entering the seed pool (9.0) were observed. Both the highest level of seed predation (82.8%) and the highest number of seeds entering the seed pool (4851.8 seeds plant^{-1}) occurred in *Stoeberia* sp.. Of the annual species investigated, *Senecio arenarius* had the highest seed production (807.8 seeds plant^{-1}), level of pre-dispersal seed predation (36.8%) as well as number of seeds entering the seed pool (510.5 seeds plant^{-1}) (Table 12.1). For the annual species, the lowest number of seeds produced (77.2 seeds plant^{-1}), level of seed predation (3.1%) and number of seeds entering the seed pool (74.8 seeds plant^{-1}) were observed for *Dimorphotheca pluvialis*.

In general, high levels of seed production were associated with high levels of pre-dispersal seed predation (Table 12.2; Figure 12.1). Seed production and the net number of seeds entering the seed pool yielded a logarithmic correlation ($R^2 = 0.59$): species yielding low numbers of seeds plant^{-1} had a high fraction of seeds entering the seed pool, while in species producing high numbers of seeds plant^{-1} a decrease in the fraction of seeds entering the seed pool was observed.

In the ten species investigated, large variation in seed production occurred between species (Table 12.2). Within species, seed production may depend on the weather, plant density, plant size, pollination rates, level of defoliation and recent history of seed production (Crawley, 1992; Gutterman, 1993). Only one species, *Gazania leiopoda*, yielded less than 50 seeds plant^{-1} (Table 12.2), but this may have been due to suboptimal laboratory conditions at which its seed production was investigated. Since the number of seeds produced by most of these species is so large, a small percentage change in seed mortality may make a massive difference in the number of seedlings that can be recruited (Blum, 1988; Misra *et al.*, 1997).

A great number of studies have documented the impact of pre-dispersal seed predation on plant fecundity (Green & Palmbald, 1975; Sork & Boucher, 1977; Zimmerman, 1980; Louda, 1982, 1983; De Steven, 1983; Andersen, 1988; Crawley, 1992; Gedge & Maun, 1994; Ehrlén, 1996; Vaughton, 1998), including several studies in desert habitats (Keeley *et al.*, 1984; Crawley, 1992). Most of the fauna species involved in pre-dispersal seed predation are considered to be small, sedentary, specialist feeders belonging to the insect orders (Crawley, 1992).

The apparent density dependent pre-dispersal seed predation (at the between species comparison level) (Table 12.2; Figure 12.1) suggests that pre-dispersal seed predators may have the potential to regulate

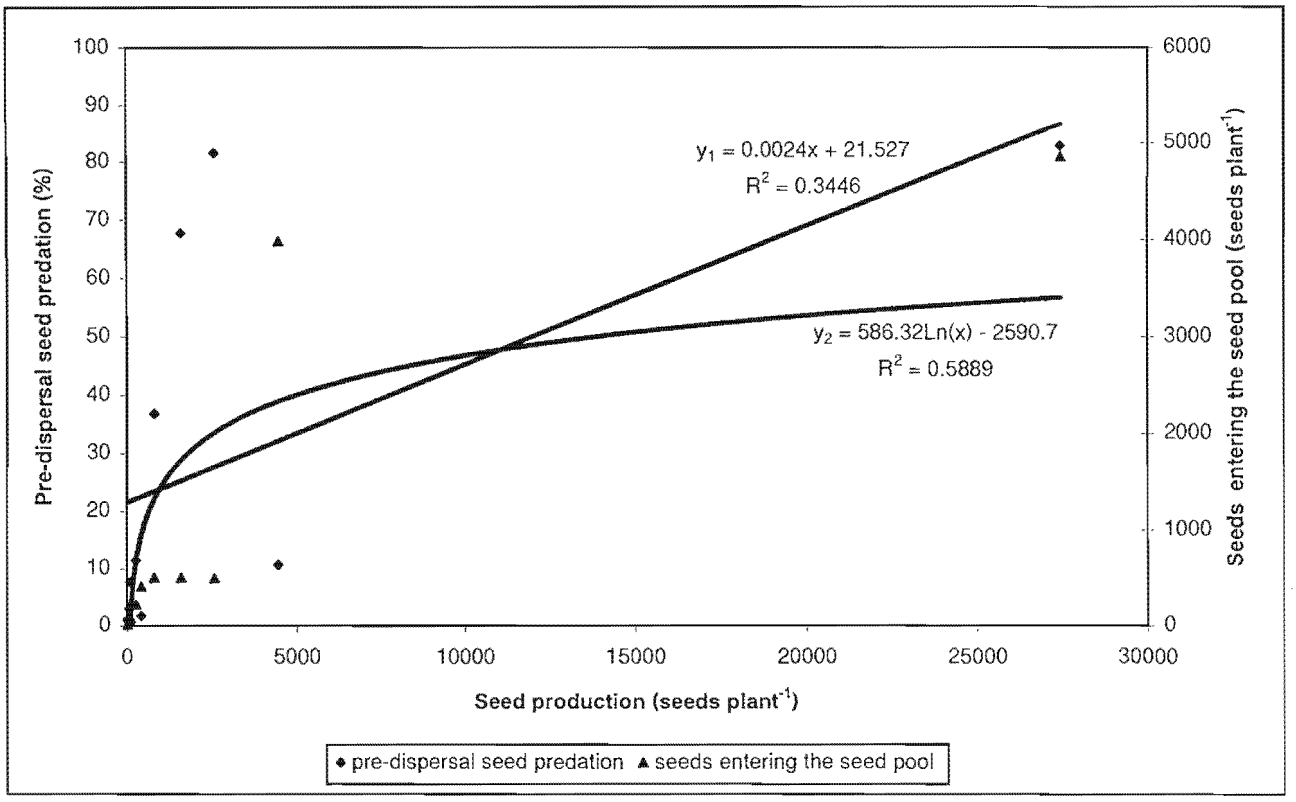

Figure 12.1. Interspecific regression analysis indicating the relationship between seed production and pre-dispersal seed predation (y_1 – axis), as well as between seed production and the number of seeds entering the seed pool (y_2 – axis).

species recruitment, especially in those species which do not accumulate a persistent seed bank such as *Tripteris oppositifolia* and *Zygophyllum morgsana* (Chapter 11). In species which accumulate persistent seed banks, *e.g. Dimorphotheca pluvialis, Stoeberia* sp., *Senecio arenarius* and *Tetragonia microptera* (Chapter 11), pre-dispersal seed predation may not have such a pronounced effect on seedling recruitment in a specific year. Seed dormancy provides an extremely powerful buffer against the ravages of seed predation, and the existence of a large bank of dormant seeds may mean that wide fluctuations in pre-dispersal seed predation have little or no impact on plant dynamics (Crawley, 1992).

Post-dispersal seed predation

In all five species investigated, exclosure treatments yielded significantly more surviving seeds compared with open (non-exclosure) treatments (Table 12.3), although the mean percentage of seedlings did not differ significantly between treatments. Due to the large contribution by the surviving seed fraction, the percentage of surviving individuals was significantly higher in the exclosure treatments (Table 12.3).

In the annual species *Senecio arenarius*, no individuals survived in the open treatment and survival in the exclosures was low (< 10%) (Table 12.3). Small insects such as ants may have been responsible for the consumption of the small seeds (Crawley, 1992) of this species *in situ*. The perennial *Tripteris oppositifolia* yielded the highest percentage of surviving individuals when post-dispersal predation was prevented (93.4%), but had the highest percentage post-dispersal seed predation. The highest percentage surviving individuals in the open treatments was obtained by *Gazania leiopoda* (45.4%) (Table 12.3).

Studies on post-dispersal seed predation are voluminous (Borchert & Jain, 1978; Inouye *et al.*, 1980; Heithaus, 1981; Goldberg, 1985; Fenner, 1987; Klinkhamer *et al.*, 1988; Valiente-Banuet & Ezcurra, 1991; Crawley, 1992; Curtis, 1996; Johnson & Fryer, 1996; Vaughton, 1998). In general, post-dispersal seed predators tend to be large, mobile, generalist herbivores like rodents and granivorous birds (Kerley, 1991; Crawley, 1992; Kerley & Whitford, 1994), which forage selectively for large, energetically rewarding seeds (Inouye *et al.*, 1980). Some insects like ants are important post-dispersal seed predators, especially in deserts and nutrient-poor communities (Rissing, 1986; Crawley, 1992), where they often specialize in the predation of certain abundant species (Inouye *et al.*, 1980). In this study, the specific seed predators were not identified.

Several authors have reported on very high post-dispersal seed predation rates (Soholt, 1973; Hay & Fuller, 1981; Valiente-Banuet & Ezcurra, 1991) and the extreme spatial and temporal variation thereof in arid environments (O'Dowd & Hay, 1980; Boyd & Brum, 1983; Casper, 1988; Klinkhamer *et al.*, 1988; Kerley, 1991, 1992; Crawley, 1992; Dean & Milton, 1999). Factors such as seed density, depth of burial, seed size (Crawley, 1992) and soil type (Goldberg, 1985; Price & Podolsky, 1989) have been shown to affect post-dispersal seed predation rates.

Post-dispersal seed predation did not influence seedling recruitment during the growing season following dispersal (Table 12.3). Predation may, however, influence seedling recruitment from the same seed lot in

Table 12.3. Mean percentages of surviving individuals (seeds and number of seedlings) for five Strandveld Succulent Karoo species, after nine months of burial. Between treatments, values followed by the same letter are not significantly different at $P \leq 0.05$

Species	Treatment	Surviving seeds (%)	Number of seedlings (%)	Total % of surviving individuals	Post-dispersal predation (%)
Arctotis stoechadifolia (P)	Exclosure	70.0 c	3.6 a	73.6 b	50.6
	Open	22.4 b	0.6 a	23.0 a	
Dimorphotheca pluvialis (disc)(A)	Exclosure	62.8 b	15.0 a	77.8 b	41.0
	Open	22.0 a	14.8 a	36.8 a	
Gazania leiopoda (P)	Exclosure	77.2 c	10.6 a	87.8 b	42.4
	Open	36.8 b	8.6 a	45.4 a	
Senecio arenarius (A)	Exclosure	7.2 b	2.4 ab	9.6 b	9.6
	Open	0.0 a	0.0 a	0.0 a	
Tripteris oppositifolia (P)	Exclosure	89.2 c	4.2 a	93.4 b	76.6
	Open	16.6 b	0.2 a	16.8 a	

A - annual
P - perennial

Table 12.4. Mean percentage (± standard deviation) of seeds of five Strandveld Succulent Karoo plant species infected with seed-borne fungi

Plant species	Fungus taxa			Total
	Pithomyces spp.	*Rhizopus* spp.	Other	
Albuca exuviata (P)	-	-	1.00 ± 1.70	1.00 ± 1.70
Amellus tenuifolius (P)	0.50 ± 0.90	-	0.75 ± 1.28	1.25 ± 1.88
Brassica tournefortii (A)	0.50 ± 0.90	0.25 ± 0.48	0.75 ± 1.28	1.50 ± 2.40
Senecio arenarius (A)	-	-	1.00 ± 1.60	1.00 ± 1.60
Silene clandestina (A)	0.50 ± 0.90	-	-	0.50 ± 0.90

A - annual
P - perennial

Table 12.5. Mean recruitment percentages of four Strandveld Succulent Karoo plant species, sown in the field. Within species, values followed by the same letter are not significantly different at $P \leq 0.05$

Species	Treatment	Number of plants (%)	
		Winter	Spring
Dimorphotheca pluvialis (ray)(A)	Exclosure	44.0 c	0.8 a
	Open	23.6 bc	3.2 ab
Pteronia divaricata (P)	Exclosure	0.0 a	1.2 b
	Open	0.0 a	0.0 a
Tripteris oppositifolia (P)	Exclosure	0.0 a	0.0 a
	Open	0.2 a	0.0 a
Ursinia speciosa (white)(A)	Exclosure	6.0 b	3.2 ab
	Open	0.0 a	0.0 a

A - annual
P - perennial

following years, because the number of surviving seeds was significantly higher in exclosures (Table 12.3). Seed predation rather than germination has previously been shown to cause the greater loss to the seed bank of Engelmann spruce in the southern Canadian Rockies (Johnson & Fryer, 1996).

Seed-borne fungi

In general, seed-borne fungi infected only a small percentage of seeds (< 2%) (Table 12.4). The introduced annual, *Brassica tournefortii* yielded the highest percentage (1.5%) of seed-borne fungi, which included species of the genera *Pithomyces* and *Rhizopus* (Table 12.4). The genus *Pithomyces* was also recorded for the seeds of *Amellus tenuifolius* and *Silene clandestina*. The latter species yielded the lowest percentage (0.5%) of seeds infected with seed-borne fungi.

Ecologically, seed-borne fungi can be divided into field fungi and storage fungi (Roberts, 1972; Bewley & Black, 1982, 1994; Copeland & McDonald, 1995). Field fungi invade seeds almost exclusively during development or after physiological maturity and have usually completed their damage prior to dispersal. In contrast to field fungi, storage fungi actively invade seeds and cause damage under conditions that are encountered during storage (Copeland & McDonald, 1995), and in the soil seed bank. Both pathogenic and saprophytic fungi are recognised (Copeland & McDonald, 1995; Maude, 1996) within the storage fungi. The two fungi genera identified in this study (*Pithomyces* & *Rhizopus;* Table 12.4) belong to the latter category (Copeland & McDonald, 1995). Suitable growing conditions for storage fungi include moisture conditions and temperatures higher than 75% RH and 25°C, respectively (Naumova, 1972; Roberts, 1972; Copeland & McDonald, 1995; Maude, 1996). The major effects of storage fungi upon seeds are: a decrease in germinability (Naumova, 1972), discolouration, production of mycotoxins, heating, development of mustiness and caking, and total decay (Roberts, 1972; Bewley & Black, 1994).

Seedling recruitment and plant survival

In general, the percentage of recruited plants did not differ significantly between the exclosure and open treatments (Table 12.5). In *Ursinia speciosa* during the winter count and *Pteronia divaricata* during the spring count, the mean percentage of seedlings recorded was significantly higher in the exclosures. Post-dispersal seed or seedling predation may therefore be of vital important during seedling recruitment of these species in revegetation efforts.

In the exclosure treatment, the mean percentage of *Dimorphotheca pluvialis* plants decreased significantly from 44.0% recorded during winter to 0.8% recorded during spring (Table 12.5). Factors such as increased competition and predation (Gutterman, 1993), promoted by high seedling density, may have been responsible for the observed increase in seedling mortality in this species.

In the Succulent Karoo, seed production of adult plants as well as germination and survival of seedlings depend on timing and amount of rainfall (Milton, 1995). To survive the critical post-germination period,

young seedlings require a total rainfall that exceeds a species-specific threshold and which is fairly evenly distributed. In extremely good years, all seedlings at safe sites establish, whereas in normal years only 10% of seedlings survive (Wiegand *et al.*, 1995). In other desert habitats, Gutterman (1993) reported that in most cases at least 50% of the seedlings that appear survive, flower and produce seeds. There is a tendency for short-lived plants to have low seedling mortality (Gutterman, 1993) and for long-lived plants to have high seedling mortality (Fenner, 1987).

In general, seedling recruitment was low (Table 12.5). In harsh habitats like deserts, seedling mortality tends to be due to abiotic factors such as drought (Sharitz & McCormick, 1973; Burdon *et al.*, 1983; Gutterman, 1993), soil salinity, high temperature (Misra *et al.*, 1997) and surface disturbances (Mack, 1976). In contrast, in more mesic habitats, biotic factors such as competition and grazing may account for relatively more seedling deaths (Fenner, 1987). In the Succulent Karoo, Wiegand *et al.* (1995) found that in the absence of grazing, survival of seedlings depends on their competitive ability during the seedling stage and their ability to compete with established neighbouring plants. A characteristic of Succulent Karoo plant communities is that considerable mortality occurs only during the seedling stage and when plants have reached their maximal age. Occasionally, large proportions of a population may die after catastrophic events such as extreme drought.

Revegetation

During post-mining revegetation efforts at Brand-se-Baai, predation will affect the number of seeds present in replaced topsoil, but seedling recruitment will probably not be affected to the same extent. In annual species, seed production within the same year following germination will compensate for high post-dispersal predation losses. In seasons when the rainfall is above the annual average, many of the desert annual species produce large quantities of seeds, which enlarge the seed bank for many years. In many perennial species, however, plants mature and reproduce only after a number of years, and replenishment of the soil seed bank occurs only after a number of years have passed since the initial topsoil replacement or seeding process. The transplanting of juvenile or mature individuals of selected perennial species may be beneficial in reducing the period between initial revegetation and reproduction. Suitable conditions for the germination of seeds and the survival of seedlings to fill empty gaps in populations of desert perennial species are very rare, and occurs only once in several years (Gutterman, 1993; Wiegand *et al.*, 1995).

When seed densities in the soil are low, as reported for many perennial species in the Strandveld Succulent Karoo (Chapter 4), then seed predation may reduce plant recruitment (Crawley, 1992). When seed densities in the soil are high, as reported for many annual species at the study site (Chapter 4), then there may be intense competition for access to suitable recruitment microsites and seed predation is unlikely to have any impact on mature plant density (Crawley, 1992). For many annual species, the impact of seed predation is buffered by recruitment from the bank of dormant seeds in the soil (Leck *et al.*, 1989), or by the immigration of wind-borne propagules from elsewhere (Keddy, 1981). Thus, quite large changes in the seed predation rate may have no measurable impact on recruitment of these species.

Due to the low (< 2%) occurrence of seed-borne fungi in Strandveld Succulent Karoo plant species, these pathogens will probably play only a minor role in the depletion of the seed bank of post-mining replaced topsoil. The transmission rates of fungi are reportedly reduced under the warm, less moist soil conditions of semi-arid and arid climates (Maude, 1996). During the moist winter periods, low environmental temperatures at the study site will prohibit optimal fungal growth. During summer, low moisture conditions will have the same effect. At seed moisture contents that are in equilibrium with RH below 68%, micro-organisms were found to be virtually ineffective (Bewley & Black, 1982). If, however, revegetation efforts include irrigation treatments during the period of low rainfall (summer), growth conditions for storage fungi may become favourable. For this reason, irrigation during the revegetation process should be considered as a supplement only during the seasons following the initial germination flush (first autumn/winter after topsoil replacement), to ensure the survival of seedlings during the dry period.

In perennial species, possible high seedling mortality (Fenner, 1987) during initial revegetation may be buffered by the sowing of seeds of selected species under the canopies of transplanted individuals. Several desert plant species (Franco & Nobel, 1989; Curtis, 1996), including some species that occur at the study site (Chapter 13) have been shown to require a perennial 'nurse plant' for successful seedling establishment. These perennial 'nurse plants' modify the environment beneath their canopies (Valiente-Banuet & Ezcurra, 1991) and aid in the formation of 'fertile islands' (Pugnaire *et al.*, 1996), which will enhance the revegetation process (Gutiérrez *et al.*, 1993). However, proximity to mature perennials has been reported to reduce both survival and growth of Karoo annuals and perennials (Milton, 1995).

CONCLUSIONS

During the revegetation of mined areas in the Strandveld Succulent Karoo, factors such as seed production, pre-dispersal seed predation, post-dispersal seed predation and mortality due to fungi, will affect seedling recruitment. At the between species level, the relationship between seed production and pre-dispersal seed predation appeared to be density-dependent (Table 12.2; Figure 12.1). Pre-dispersal seed predators may have the potential to regulate species recruitment, especially in species which do not accumulate a persistent seed bank such as the perennials *Tripteris oppositifolia* and *Zygophyllum morgsana* (Chapter 11).

Seedling recruitment during the peak germination season (autumn) following dispersal was largely unaffected by post-dispersal predators. For many perennial species at the study site, seed densities in the soil are low (Chapter 4), and plant recruitment may be reduced by seed predation. On the other hand, soil seed densities of several annual species occurring at the study site were found to be high. This may result in intense competition for access to suitable recruitment microsites and as a consequence, seed predation is unlikely to have any impact on mature plant density (Crawley, 1992).

Seed-borne fungi will not affect seed numbers in the soil to a great extent, under natural environmental conditions. In the Strandveld Succulent Karoo, low seed mortality due to fungal attack could be ascribed to the combination of low occurrence (< 2%) and unfavourable environmental conditions for growth (low moisture during summer, low temperature during moist winters). Although supplementary irrigation in the

hot, dry seasons may induce seed decay due to fungal attack, irrigation during the seasons following initial germination in autumn, will be beneficial for the survival of seedlings of many species. Apart from their role as wind-breaks, transplanting of adult perennial plants may also reduce the period between revegetation and reproduction in these species.

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REFERENCES

ANDERSEN, A.N. 1988. Insect seed predators may cause far greater losses than they appear to. *Oikos*, **52**: 337-340.

BEWLEY, J.D. & BLACK, M. 1982. *Physiology and biochemistry of seeds*. Springer-Verlag, Heidelberg.

BEWLEY, J.D. & BLACK, M. 1994. *Seeds: Physiology of development and germination*. Plenum Press, London.

BLUM, A. 1988. Plant breedings for stress environments. *CRC Critical Review in Plant Science*, **2**: 199-238.

BORCHERT, M.I. & JAIN, S.K. 1978. The effect of rodent seed predation on four species of California annual grasses. *Oecologia*, **33**: 101-113.

BOYD, R.S. & BRUM, G.D. 1983. Post-dispersal reproductive biology of Mojave desert population of *Larrea tridentata* (Zygophyllaceae). *American Midland Naturalist*, **110**: 25-36.

BURDON, J.J., MARSHALL, D.R. & BROWN, A.H.D. 1983. Demographic and genetic changes in populations of *Echium plantagineum*. *Journal of Ecology*, **71**: 667-679.

CASPER, B.B. 1988. Post-dispersal seed predation may select for wind dispersal but not seed number per dispersal unit in *Cryptantha flava*. *Oikos*, **52**: 27-30.

CAVERS, P. 1983. Seed demography. *Canadian Journal of Botany*, **61**: 3578-3590.

CHRISTENSEN, C.M. 1972. Microflora and seed deterioration. In: Roberts, E.H. (ed). *Viability of seeds*. Syracuse University Press, U.S.A. pp. 59-93.

COPELAND, L.O. & McDONALD, M.B. 1995. *Principles of seed science and technology*. Chapman & Hall, New York.

CRAWLEY, M.J. 1992. Seed predators and plant population dynamics. In: Fenner, M. (ed). *Seeds – The ecology of regeneration in plant communities*. CAB International, Wallingford. pp. 157-191.

CURTIS, N.P. 1996. Germination and seedling survival studies of *Xanthorrhoea australis* in the Warby Range State Park, North-eastern Victoria, Australia. *Australian Journal of Botany*, **44**: 635-647.

DEAN, W.R.J. & MILTON, S.J. 1999. Animal foraging and food. In: Dean, W.R.J. & Milton, S.J. (eds). *The Karoo – Ecological patterns and processes.* Cambridge University Press, Cambridge. pp. 164-177.

DE STEVEN, D. 1983. Reproductive consequences of insect seed predation in *Hamamelis virginiana*. *Ecology*, **64**: 89-98.

DE VILLIERS, A.J., VAN ROOYEN, M.W. & THERON, G.K. 1994. Comparison of two methods for estimating the size of the viable seed bank of two plant communities in the Strandveld of the West Coast, South Africa. *South African Journal of Botany*, **60**: 81-84.

DE VILLIERS, A.J., VAN ROOYEN, M.W., THERON, G.K. & VAN ROOYEN, N. 1999a. Vegetation diversity of the Brand-se-Baai coastal dune area, West Coast, South Africa: A pre-mining benchmark survey for rehabilitation. *Land Degradation & Development*, **10**: 207-224.

DE VILLIERS, A.J., VAN ROOYEN, M.W. & THERON, G.K. 1999b. Seed production of four Namaqualand pioneer plant species grown on saline soil. *South African Journal of Botany*, **65**: 110-112.

EHRLÉN, J. 1996. Spatiotemporal variation in predispersal seed predation intensity. *Oecologia*, **108**: 708-713.

ENVIRONMENTAL EVALUATION UNIT. 1990. *Anglo American Corporation: West Coast heavy mineral sands project.* Unpublished report. University of Cape Town, Cape Town.

ESLER,K.J., COWLING, R.N. & IVEY, P. 1992. Seed biology of three species of Mesembryanthema in the southern Succulent Karoo. *South African Journal of Botany*, **58**: 343-348.

ESLER, K.J. & PHILLIPS, N. 1994. Experimental effects of water stress on semi-arid Karoo seedlings: implications for field seedling survivorship. *Journal of Arid Environments*, **26**: 325-337.

FENNER, M. 1987. Seedlings. *New Phytologist*, **106**: 35-47.

FRANCO, A.C. & NOBEL, P.S. 1989. Effect of nurse plants on the microhabitat and growth of Cacti. *Journal of Ecology*, **77**: 870-886.

GEDGE, K.E. & MAUN, M.A. 1994. Compensatory response of two dune annuals to simulated browsing and fruit predation. *Journal of Vegetation Science*, **5**: 99-108.

GOLDBERG, D.E. 1985. Effects of soil pH, competition, and seed predation on the distributions of two tree species. *Ecology*, **66**: 503-511.

GREEN, T.W. & PALMBALD, I.G. 1975. Effects of insect seed predators on *Astragalus cibarius* and *Astragalus utahensis* (Leguminosae). *Ecology*, **56**: 1435-1440.

GUTIéRREZ, J.R., MESERVE, P.L., CONTRERAS, L.C., VáSQUEZ, H. & JAKSIC, F.M. 1993. Spatial distribution of soil nutrients and ephemeral plants underneath and outside the canopy of *Porlieria chilensis* shrubs (Zygophyllaceae) in arid coastal Chile. *Oecologia*, **95**: 347-352.

GUTTERMAN, Y. 1993. *Seed germination in desert plants.* Springer-Verlag, Berlin.

HAY, M.E. & FULLER, P.J. 1981. Seed escape from heteromyid rodents: the importance of microhabitat and seed preference. *Ecology*, **62**: 1395-1399.

HEITHAUS, E.R. 1981. Seed predation by rodents on three ant-dispersed plants. *Ecology*, **62**: 136-145.

HOWE, C.D. & CHANCELLOR, R.J. 1983. Factors affecting the viable seed content of soils beneath lowland pastures. *Journal of Applied Ecology*, **20**: 915-922.

INOUYE, R.S., BYERS, G.S. & BROWN, J.H. 1980. Effects of predation and competition on survivorship, fecundity, and community structure of desert annuals. *Ecology*, **61**: 1344-1351.

JOHNSON, E.A. & FRYER, G.I. 1996. Why Engelmann spruce does not have a persistent seed bank. *Canadian Journal of Forestry Research*, **26**: 872-878.

KEDDY, P.A. 1981. Experimental demography of the sand-dune annual, *Cakile edentula*, growing along an environmental gradient in Nova Scotia. *Journal of Ecology*, **69**: 615-630.

KEELEY, J.E., KEELEY, S.C., SWIFT, C.C. & LEE, J. 1984. Seed predation due to the Yucca-moth symbiosis. *American Midland Naturalist*, **112**: 187-191.

KERLEY, G.I.H. 1991. Seed removal by rodents, birds and ants in the semi-arid Karoo, South Africa. *Journal of Arid Environments*, **20**: 63-69.

KERLEY, G.I.H. 1992. Small mammal seed consumption in the Karoo, South Africa, further evidence for divergence in desert biotic process. *Oecologia*, **89**: 471-475.

KERLEY, G.I.H. & WHITFORD, W.G. 1994. Desert-dwelling small mammals as granivores: intercontinental variations. *Australian Journal of Zoology*, **42**: 543-555.

KLINKHAMER, P.G.L., DE JONG, T.J. & VAN DER MEIJDEN, E. 1988. Production, dispersal and predation of seeds in the biennial *Cirsium vulgare*. *Journal of Ecology*, **76**: 403-414.

LECK, M.A., PARKER, V.T. & SIMPSON, R.L. 1989. *Ecology of soil seed banks*. Academic Press, London.

LIMONARD, T. 1968. Ecological aspects of seed health testing. *Proceedings of the International Seed Testing Association*, **33**: 343-513.

LOUDA, S.M. 1982. Limitation of the recruitment of the shrub *Haplopappus squarrosus* (Asteraceae) by flower- and seed-feeding insects. *Journal of Ecology*, **70**: 43-53.

LOUDA, S.M. 1983. Seed predation and seedling mortality in the recruitment of a shrub, *Haplopappus venetus* (Asteraceae), along a climatic gradient. *Ecology*, **64**: 511-521.

MACK, R.N. 1976. Survivorship of *Cerastium atrovirens* at Aberffraw, Anglesey. *Journal of Ecology*, **64**: 309-312.

MAUDE, R.B. 1996. *Seedborne diseases and their control – Principles & Practice*. CAB International, Wallingford.

MILTON, S.J. 1995. Spatial and temporal patterns in the emergence and survival of seedlings in arid Karoo shrubland. *Journal of Applied Ecology*, **32**: 145-156.

MISRA, A.N., SAHU, S.M., MEERA, I., MOHAPATRA, P., DAS, N. & MISRA, M. 1997. Root growth of a salt susceptible and a salt resistant rice (*Oryza sativa* L.) during seedling establishment under NaCl salinity. *Journal of Agronomy & Crop Science*, **178**: 9-14.

NAUMOVA, N.A. 1972. *Testing of seeds for fungous and bacterial infections*. Israel Program for Scientific Translations, Jerusalem.

O'CONNOR, T.G. 1997. Micro-site influence on seed longevity and seedling emergence of a bunchgrass (*Themeda triandra*) in a semi-arid savanna. *African Journal of Range & Forage Science*, **14**: 7-11.

O'DOWD, D.J. & HAY, M.E. 1980. Mutualism between harvester ants and a desert ephemeral: seed escape from rodents. *Ecology*, **61**: 531-540.

PRICE, M.V. & PODOLSKY, R.H. 1989. Mechanisms of seed harvest by heteromyid rodents: soil texture effects on harvest rate and seed size selection. *Oecologia*, **81**: 267-273.

PUGNAIRE, F.I., HAASE, P. & PUIGDEFáBREGAS, J. 1996. Facilitation between higher plant species in a semiarid environment. *Ecology*, **77**: 1420-1426.

RISSING, S.W. 1986. Indirect effects of granivory by harvester ants: plant species composition and reproductive increase near ant nests. *Oecologia*, **68**: 231-234.

ROBERTS, E.H. 1972. *Viability of seeds*. Syracuse University Press, Great Britain.

SHARITZ, R.R. & McCORMICK, J.F. 1973. Population dynamics of two competing annual plant species. *Ecology*, **54**: 723-740.

SHELDON, J.C. 1973. The behaviour of seeds in soil. III. The influence of seed morphology and the behaviour of seedlings on the establishment of plants from surface-lying seeds. *Journal of Ecology*, **62**: 47-66.

SOHOLT, L.F. 1973. Consumption of primary production by a population of kangaroo rats (*Dipodomys merriami*) in the Mojave desert. *Ecological Monographs*, **43**: 357-376.

SORK, V.L. & BOUCHER, D.H. 1977. Dispersal of sweet pignut hickory in a year of low fruit production, and the influence of predation by a Curculionid beetle. *Oecologia*, **28**: 289-299.

VALIENTE-BANUET, A. & EZCURRA, E. 1991. Shade as a cause of the association between the cactus *Neobuxbaumia tetetzo* and the nurse plant *Mimosa luisana* in the Tehuacán Valley, Mexico. *Journal of Ecology*, **79**: 961-971.

VAN RHEEDE VAN OUDTSHOORN, K. & VAN ROOYEN, M.W. 1999. *Dispersal biology of desert plants*. Springer-Verlag, Berlin.

VAN ROOYEN, M.W. & GROBBELAAR, N. 1982. Saadbevolkings in die grond van die Hester Malan-natuurreservaat in die Namakwalandse Gebrokeveld. *South African Journal of Botany*, **1**: 41-50.

VAUGHTON, G. 1998. Soil seed bank dynamics in the rare obligate seeding shrub, *Grevillea barklyana* (Proteaceae). *Australian Journal of Ecology*, **23**: 375-384.

WIEGAND, T., MILTON, S.J. & WISSEL, C. 1995. A simulation model for a shrub ecosystem in the semiarid Karoo, South Africa. *Ecology*, **76**: 2205-2221.

ZIMMERMAN, M. 1980. Reproduction in *Polemonium*: pre-dispersal seed predation. *Ecology*, **61**: 502-506.

CHAPTER 13

THE ROLE OF FACILITATION IN SEEDLING RECRUITMENT AND SURVIVAL PATTERNS, IN THE STRANDVELD SUCCULENT KAROO, SOUTH AFRICA

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ABSTRACT

Adult plant distribution may be determined by processes operating during regeneration. Seedling emergence and survival beneath as well as in open spaces between selected perennial shrub species were investigated at five localities in the Strandveld Succulent Karoo, each dominated by a different shrub species. Seedling emergence and survival were also examined at three localities dominated by annual species. In general, species richness and seedling numbers were significantly higher in open areas than underneath shrubs, while seedling survival percentages did not differ significantly between microhabitats. None of the shrub species investigated seem to facilitate recruitment and survival of other species. The pattern of seedling distribution partly conformed to the model of Succulent Karoo vegetation dynamics. Knowledge on factors such as seedling recruitment and survival, underneath and in open areas between the canopies of selected shrub species, provided a predictive basis for assessing possible methods for revegetation of mined areas in the Strandveld Succulent Karoo.

Key words: Mining; Namaqualand; revegetation; seedling survival; shrub canopies; topsoil replacement; transplanting

INTRODUCTION

Events occurring during the seed and seedling stages are the primary determinants of the distribution of adult plants (Grubb, 1977; De Jong & Klinkhamer, 1988; Mustart & Cowling, 1993). A knowledge of the dynamics of germination and early seedling growth is important for an understanding of the structure and dynamics of communities (Valiente-Banuet & Ezcurra, 1991).

In most arid ecosystems, vegetation displays a heterogeneous spatial array consisting of vegetation patches alternating with areas of bare soil (Bertiller, 1998). Studies on arid ecosystems have demonstrated that seedling establishment and survival may depend on the shelter provided by shrub species (Carlsson & Callaghan, 1991; Hobbie, 1992; Yeaton & Esler, 1990). The communities of shrubs and their understoreys may maintain diversity in areas where otherwise only poor vegetation of stress-tolerant species would survive (Pugnaire *et al.*, 1996a).

An understanding of seedling responses to environmental differences provides some insight into restoration management problems. For example, information on differential survival characteristics of seedlings can be used to assist in the selection of species for reintroduction into disturbed vegetation. Furthermore, an understanding of the mechanisms and rates of recruitment is important for managers, since these processes influence population turnover and therefore maintenance of cover (Esler & Phillips, 1994).

The mining of heavy minerals along the arid West Coast of South Africa involves the total destruction of the existing vegetation (Environmental Evaluation Unit, 1990). Successful seedling establishment and survival will be crucial during the revegetation of these mined areas, irrespective of the method of revegetation *i.e.* sowing or topsoil replacement.

This study focused on seedling recruitment and survival underneath and in open areas between each of five shrub species dominant in the pre-mining standing vegetation of the Strandveld Succulent Karoo. An experimental analysis of seedling recruitment and survival at three localities predominated by annual species is also described. We predicted that these reproductive processes of the plant life-cycle would yield higher values underneath the canopies of Strandveld Succulent Karoo shrub species, since the amelioration of the physical environment produced by such shrub species is important in the patch-structured population dynamics of many communities of desert plants. Knowledge on these processes may also indicate local species and methods best suited for achieving post-mining revegetation goals.

MATERIAL AND METHODS

During the winter of 1995, eight localities were selected in the vicinity of Brand-se-Baai (31°18'S, 17°54'E), South Africa. The vegetation at each locality was predominated by a different perennial shrub (P) or annual (A) plant species *i.e. Eriocephalus africanus* L. (P), *Othonna floribunda* Schltr. (P), *Salvia africana-lutea* L. (P), *Senecio arenarius* Thunb. (A), *Tripteris oppositifolia* (Aiton) B.Nord. (P), *Ursinia speciosa* DC. (A), *Zygophyllum morgsana* L. (P) and a community with a number of dominant annual species.

At 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 microhabitat and species. At localities dominated by annual species, ten replicates were used in total and the metal frame was randomly placed within each locality.

The position of each frame was marked semi-permanently with 150 mm long plastic pegs. Within each frame, all seedlings were identified and counted. For some seedlings, identification to species level was not possible and these seedlings have been grouped according to taxa or plant types, *e.g.* Mesembryanthemaceae, *Babiana* spp. and geophytes.

After three months (spring 1995), the surveys were repeated. Seedlings that emerged after the initial winter count were not incorporated in the calculation of seedling survival percentages. Nomenclature follows that of Arnold & De Wet (1999).

The least significant difference (LSD) one-way and multi-factor analyses of variance (ANOVA) as well as the multiple range test (Statgraphics 5.0, 1989, STSC, Inc., U.S.A.) were used to determine significant differences ($P \leq 0.05$) in seedling numbers, species richness and seedling survival, between treatments.

RESULTS AND DISCUSSION

Localities dominated by shrub species

Fifty-four percent of the taxa recorded at the five shrub dominated localities occurred both underneath and in open areas between shrubs (Group 1, Table 13.1). Taxa recorded only underneath (Group 2) or between shrubs (Group 3) constituted 23% each. Seedlings of annuals predominated in open areas (58%), while areas underneath shrub canopies were not dominated by any specific plant type (annuals 52%, perennials 48%) (Table 13.1).

Seedling numbers recorded underneath shrub canopies ranged from 0.2 m^{-2} to 50.4 m^{-2}, while that in open areas ranged from 0.2 m^{-2} to 227.0 m^{-2} (Table 13.1). The size of any germination event is directly related to the availability of seed, which can be influenced by a number of factors, such as the size, duration and timing of the rainfall event (Esler, 1999).

Annuals represented only 27% of the taxa unique to areas beneath shrub canopies (Group 2), in contrast to 47% in open areas (Group 3) (Table 13.1). Perennial species therefore predominated the taxa unique to areas beneath shrub canopies. The seeds of several shrub species from the Strandveld Succulent Karoo were found to be larger than those of most annual and perennial herb species in this area (Chapter 11), and did not require light for germination (Chapter 8). Larger seeds tend to be found in species whose seedlings establish in shaded environments (Westoby *et al.*, 1992) such as beneath the canopies of shrubs. Seedlings from larger seeds may in general be able to emerge successfully from greater depths in the soil, or from under larger accumulations of litter (Molofsky & Augspurger, 1992). Seedlings that have large cotyledons tend to be more vulnerable, and establishment below canopies possibly provides them with an added advantage against herbivory and/or water stress (Esler, 1999). Seed dispersal strategies will also influence species distribution between microhabitats, *e.g.* the large seeds (> 5 mm) of *Salvia africana-lutea* have no telechoric mechanisms, which may explain the absence of this species' seedlings in open areas (Table 13.1); the seeds of *Othonna floribunda* are anemochorous and seedlings were recorded at both microhabitats.

Species recorded at both microhabitats (Group 1, Table 13.1), as well as those unique to open areas (Group 3), were well represented in the soil seed bank of the study area (Chapters 4 & 5) and topsoil replacement will be sufficient for the recruitment of these species during revegetation efforts. Most of the species unique to areas underneath shrub canopies (Group 2) were not well represented in the soil seed bank of the study area (Chapters 4 & 5) and should be reintroduced to revegetation areas by means of sowing and/or transplanting. Also, these species may have a greater chance of survival when sown underneath rather than between transplanted shrub species.

Table 13.1. Mean number of seedlings m^{-2} for species recorded underneath or in open areas between shrubs during winter. Mean number of plants, recorded during the following spring, is indicated between brackets. Data were recorded at five locations, each dominated by a different shrub species

Microsite	Underneath plants					Open areas between plants				
Shrub species (location)	*Eriocephalus africanus*	*Othonna floribunda*	*Salvia africana-lutea*	*Tripteris oppositifolia*	*Zygophyllum morgsana*	*Eriocephalus africanus*	*Othonna floribunda*	*Salvia africana-lutea*	*Tripteris oppositifolia*	*Zygophyllum morgsana*
Species										
Group 1: Species recorded underneath and in open areas between shrubs										
Geophyte spp. (P)	0.2 (0.0)	1.2 (1.6)	0.4 (0.8)	1.2 (0.8)	1.0 (1.8)	0.8 (0.2)	0.4 (0.0)	0.4 (0.4)	0.4 (0.0)	1.6 (0.2)
Nemesia bicornis (A)	1.6 (1.2)	2.4 (1.2)	1.2 (0.0)	0.8 (0.0)	0.2 (0.0)	5.8 (1.0)	0.8 (0.8)	8.4 (0.8)	7.4 (1.0)	0.4 (0.0)
Ehrharta calycina (P)	2.4 (4.0)	5.6 (7.2)	4.8 (1.2)	2.0 (2.6)	2.8 (4.0)	2.6 (5.0)	7.6 (5.2)	7.2 (4.4)	6.6 (11.2)	0.8 (0.6)
Zaluzianskya villosa (A)	0.0 (0.2)	0.4 (0.0)		1.0 (0.0)		0.0 (0.4)	1.2 (0.0)	14.8 (0.0)	1.6 (0.4)	
Senecio arenarius (A)	1.2 (1.0)			1.0 (0.0)		6.2 (0.2)	0.4 (0.0)	3.2 (0.0)	2.4 (0.4)	
Wahlenbergia paniculata (A)		4.4 (0.8)				0.2 (0.0)		0.4 (0.4)	0.6 (0.6)	0.2 (0.0)
Karroochloa schismoides (A)	0.2 (0.2)	2.8 (0.4)		4.0 (1.8)		1.0 (1.0)	4.4 (4.0)		25.0 (16.8)	
Pharnaceum exiguum (A)		2.8 (0.4)		0.6 (0.6)	0.2 (0.2)		2.4 (1.6)		35.6 (12.2)	
Dimorphotheca pluvialis (A)	0.2 (0.2)				13.0 (4.0)	8.4 (4.0)		5.6 (3.6)		227.0 (96.4)
Oncosiphon suffruticosum (A)	0.0 (0.2)					0.2 (0.6)	0.4 (0.0)		1.0 (1.4)	
Helichrysum marmarolepis (A)				0.2 (0.2)		0.0 (0.4)		55.2 (22.8)	1.2 (0.6)	
Grielum grandiflorum (P)				0.2 (0.2)				0.8 (0.0)	2.8 (0.8)	0.4 (0.0)
Arctotheca calendula (A)	0.2 (0.2)			0.2 (0.0)		2.6 (2.2)				
Silene clandestina (A)	0.0 (0.6)			1.2 (1.2)		0.4 (0.8)			0.8 (1.0)	
Coelanthum semiquinquefidum (A)		1.2 (0.8)		0.6 (0.6)			8.8 (4.4)		1.0 (0.6)	
Oxalis spp. (P)		50.4 (45.6)		0.4 (0.0)			48.0 (42.8)		1.8 (1.4)	
Pelargonium senecioides (A)		0.0 (0.4)		0.4 (0.0)			0.8 (0.8)		1.8 (2.2)	
Arctotis hirsuta (A)		0.4 (0.4)					2.0 (0.0)		0.8 (0.2)	
Polycarena pumila (A)		0.8 (0.0)					0.4 (0.0)		8.0 (1.0)	
Heliophila coronopifolia (A)	0.2 (0.0)					0.8 (2.4)				
Chaetobromus dregeanus (P)	0.6 (0.2)					0.0 (0.2)				
Hermannia amoena (P)	0.2 (0.2)					0.0 (0.2)				
Babiana spp. (P)	0.0 (0.2)					0.4 (0.4)				
Crassula umbellata (A)	0.0 (2.2)								0.0 (0.4)	
Pharnaceum aurantium (P)	0.0 (0.6)					0.8 (1.2)				
Nestlera biennis (P)		0.4 (0.0)					41.2 (15.6)			
Hebenstretia repens (A)		0.8 (0.4)							0.0 (2.8)	
Othonna floribunda (P)		0.4 (0.4)					0.4 (0.0)			
Manulea altissima (A)		0.0 (0.4)					2.4 (2.4)			
Limeum africanum (A)				0.2 (0.0)					4.0 (2.6)	
Adenogramma littoralis (A)				2.4 (0.2)					101.4 (43.0)	
Mesembryanthemaceae (P)				0.0 (0.2)		0.4 (0.0)				
Tripteris oppositifolia (P)				0.0 (0.2)					1.2 (0.2)	
Convolvulus sp. (P)					15.6 (6.0)					11.2 (4.0)
Tetragonia microptera (A)					1.4 (0.6)					1.0 (0.8)
Group 2: Species recorded only underneath shrubs										
Asparagus spp. (P)	0.2 (0.0)									
Zygophyllum morgsana (P)	0.2 (0.4)			0.2 (0.0)						
Crassula expansa (A)	0.0 (0.2)									
Mesembryanthemum crystallinum (A)	0.0 (0.8)									
Moraea spp. (P)	0.0 (0.2)									
Amellus tenuifolius (P)		0.4 (0.0)								
Hermannia spp. (P)		0.4 (0.0)								
Asparagus fasciculatus (P)		0.8 (0.4)								
Euphorbia spp. (P)		0.8 (0.4)								
Tripteris clandestinum (A)		3.2 (1.6)								
Pharnaceum lanatum (P)		0.0 (1.2)								
Salvia africana-lutea (P)			0.4 (0.8)		0.0 (0.2)					
Baliota africana (P)			0.0 (0.8)							
Lessertia benguellensis (A)					0.2 (0.2)					
Lycium ferocissimum (P)					0.0 (0.2)					
Group 3: Species recorded only in open areas between shrubs										
Foveolina tenella (A)						0.4 (0.0)				
Brassica tournefortii (A)						1.4 (1.2)				
Arctotis stoechadifolia (P)						0.2 (0.2)				
Pelargonium gibbosum (P)						0.2 (0.2)				
Trachyandra divaricata (P)						0.2 (0.2)		0.4 (0.4)		
Sonderina tenuis (A)						0.0 (0.4)				
Felicia dregei (P)							0.4 (0.4)			
Isolepis marginata (A)							1.6 (2.8)			
Conicosia pugioniformis (P)								0.4 (0.0)		
Manulea pusilla (A)								0.8 (0.0)		
Tetragonia virgata (P)								2.4 (0.0)	0.2 (0.0)	
Wahlenbergia sonderi (P)								0.0 (1.2)		
Hermannia cernua (P)									0.0 (0.2)	
Hermannia scordifolia (A)									0.2 (0.4)	
Senecio breviscapus (A)										0.2 (0.0)

P - perennial
A - annual

The facilitation of seedling recruitment of some species by the presence of others (nurse-plant phenomenon) has been described for a variety of arid and semi-arid environments (McAuliffe, 1988; Valiente-Banuet & Ezcurra, 1991) including the Succulent Karoo (Beukman, 1991; Dean & Yeaton, 1992; Esler, 1999). The occurrence of seedlings under nurse-plants is considered primarily a method of avoiding abiotic stress at the seedling stage (Dean & Yeaton, 1992). In arid ecosystems, seedling establishment and survival may depend on the shelter provided by shrub species (Carlsson & Callaghan, 1991; Hobbie, 1992; Wiegand *et al.*, 1995), which protect seedlings from high irradiance, temperature (Vetaas, 1992), rates of transpiration (Moro *et al.*, 1997) and predation (Turner *et al.*, 1966; Nobel, 1980; Noy-Meir, 1980; McAuliffe, 1988; Franco & Nobel, 1989; Yeaton & Esler, 1990; Carlsson & Callaghan, 1991; Valiente-Banuet & Ezcurra, 1991; Keeley, 1992; Moro *et al.*, 1997). Shrubs may also cause an accumulation of mineral nutrients (Chapin *et al.*, 1994) and water (De Jong & Klinkhamer, 1988; Gutiérrez *et al.*, 1993; Moro *et al.*, 1997), leading to a local increase in fertility (Miles, 1985; Garner & Steinberger, 1989; Schomberg *et al.*, 1994; Pugnaire *et al.*, 1996a; Stock *et al.*, 1999). However, herbs rather than shrubs are directly responsible for the accumulation of nutrients under the canopy (Vetaas, 1992). Retention of seeds by the litter layer beneath shrubs may also influence the spatial distribution of vegetation (Redbo-Torstensson & Telenius, 1995).

Shrubs may also benefit from the effect of understorey plants, for example, protecting the soil from erosion, direct insolation, and over-heating (Fowler, 1986; Pugnaire *et al.*, 1996b).

In general, a higher number of seedlings (Figure 13.1) and species richness (Figure 13.2) were recorded during winter than plants during spring, irrespective of microhabitat and locality (Table 13.2). Open areas yielded higher seedling numbers (Figure 13.1) and species richness' (Figure 13.2) than areas underneath shrub canopies (Table 13.2). Therefore, none of the shrub species investigated seemed to act as "nurse-plants", which is consistent with the Succulent Karoo vegetation dynamics model described by Yeaton & Esler (1990). According to this model, open areas are colonised by species of the Mesembryanthemaceae (mesembs), which later serve as sites of establishment for seedlings of woody shrub species. The latter species eventually replace the mesembs through interspecific competition and persist in the community until they reach senescence and die or are removed through overgrazing. Also, seedlings in supposedly more favourable microhabitats or safe sites may not be nursed but rather trapped (Esler, 1999). According to Wiegand *et al.* (1995), colonizer species of the Succulent Karoo establish in safe sites on bare ground in areas not shaded by plants. To avoid competition for water from neighbouring plants, seedlings of these colonizer species require gaps of minimum sizes. Shaded sites within or under the edge of the canopy of established colonizer species' plants provide safe sites for seedlings of secondary succession species.

Seedling survival percentages ranged from 37% to 78% and did not differ significantly between microhabitats for any of the localities investigated (Table 13.3), which supports the view that seedling recruitment of most species was not facilitated by the presence of others, *i.e.* shrubs. The number of seedlings that survived until spring was generally higher in open areas. Few seedlings reach reproductive maturity in undisturbed Karoo shrublands where long-lived species dominate (Milton, 1994), and seedling survival ranged from 1 - 5% of emergent seedlings in average years to 20 – 30% in years with ample post-germination rain (Milton, 1995). Because of markedly higher seedling survival percentages, population turnover in this part of the Strandveld Succulent Karoo should be faster than that reported for the southern Succulent Karoo.

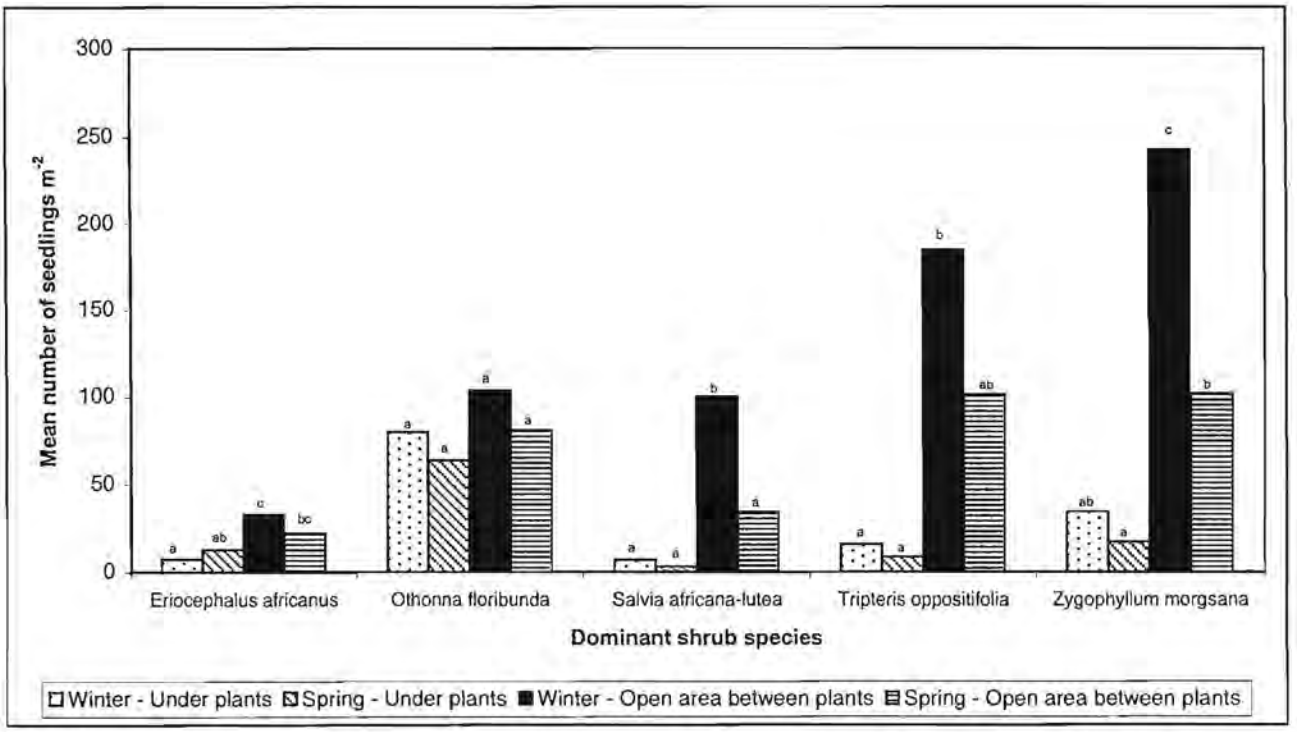

Figure 13.1. Mean number of seedlings m^{-2} recorded underneath and between shrubs. Data were recorded in five locations, each dominated by a different shrub species.

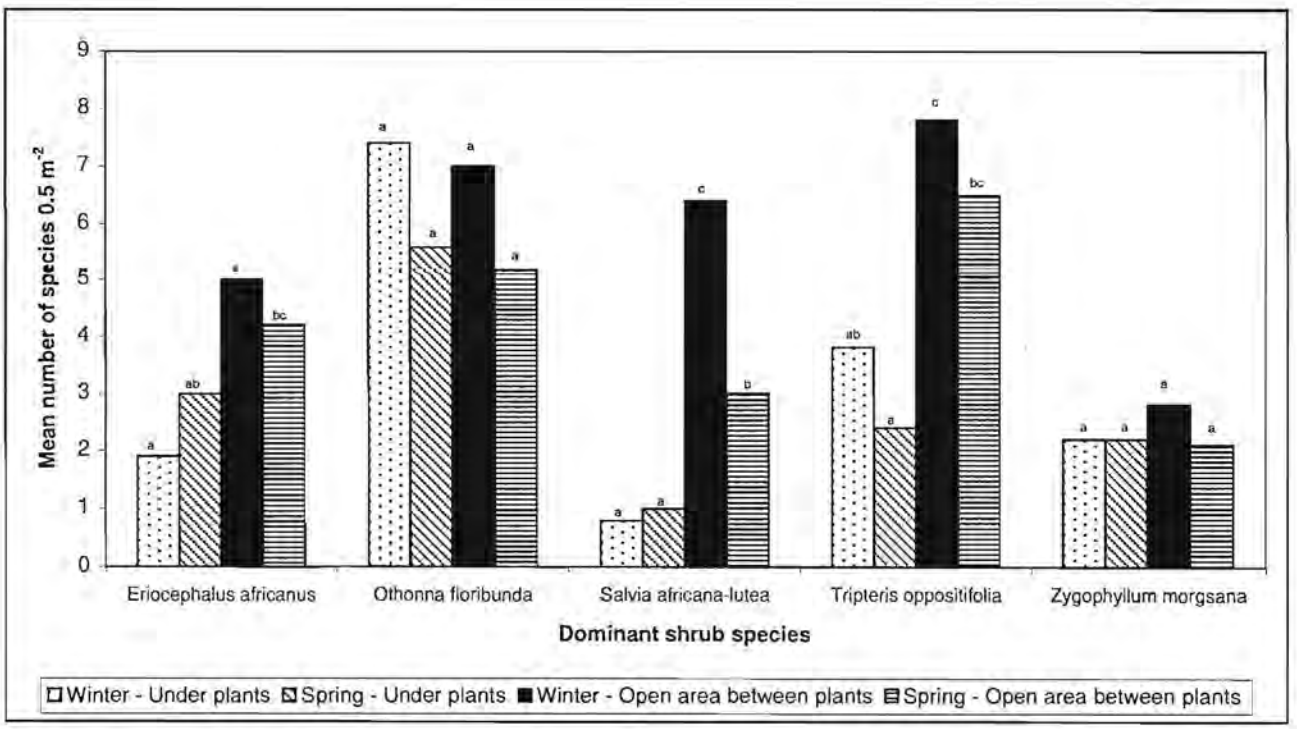

Figure 13.2. Mean number of species 0.5 m^{-2} recorded underneath and between shrubs. Data were recorded in five locations, each dominated by a different shrub species.

Table 13.2 Multi-factor analysis of variance ($P \leq 0.05$) for number of seedlings, species richness and seedling survival, recorded during two seasons (winter and spring) at two microhabitats (underneath and between shrubs) in five localities (each dominated by a different shrub species) of the Strandveld Succulent Karoo

Source of variation	Significance level ($P \leq 0.05$)		
	Number of seedlings	Species richness	Seedling survival
Main factors			
Locality (L)	0.0001 *	0.0000 *	0.0055 *
Microhabitat (MH)	0.0000 *	0.0000 *	0.0857 ^{NS}
Season (S)	0.0011 *	0.0221 *	
2-Factor interaction			
L x MH	0.0006 *	0.0001 *	0.9604 ^{NS}
L x S	0.3133 ^{NS}	0.3417 ^{NS}	
MH x S	0.0114 *	0.1312 ^{NS}	

* Significant at $P \leq 0.05$.
^{NS} Not significant at $P \leq 0.05$.

Table 13.3. Seedling survival (%) recorded in eight localities of the Strandveld Succulent Karoo. In localities dominated by perennial species, seedling survival was recorded underneath and in open areas between the dominant shrubs, and significant differences between these two microhabitats were determined for each locality. In localities predominated by annual species, values followed by different letters indicate significant differences between localities. Seedlings that emerged after the initial winter count were not included in the survival percentages

	Dominant species (locality)	Microhabitat		Significance level ($P \leq 0.05$)
		Underneath dominant species	Between dominant species	
Shrubs	*Eriocephalus africanus*	78.4	47.3	0.4136
	Othonna floribunda	74.9	64.4	0.7828
	Salvia africana-lutea	56.3	36.6	0.9592
	Tripteris oppositifolia	48.2	46.5	0.1854
	Zygophyllum morgsana	44.2	42.0	0.3971
Annuals	*Senecio arenarius*		47.0 a	0.0066
	Ursinia speciosa		64.8 b	
	Various annual species		45.3 a	

Although attempts to reseed degraded Karoo vegetation are generally not successful, the impact of seedling mortality on revegetation efforts at the study site would probably be negligible provided the availability of sufficient moisture (Esler, 1999), the exclusion of herbivores as well as the presence of wind-breaks (pers. obs.). The timing of recruitment will be of vital importance for seedling survival and to assure successful revegetation. In the Karoo, follow-up rain in the six months after emergence is crucial for seedling establishment (Milton, 1995; Esler, 1999).

Interfering effects of perennial shrubs on seedling survival and establishment in their understorey community may be through light deprivation (Goldberg & Werner, 1983; Franco & Nobel, 1989), mechanical effects caused by litter (Kitajima & Tilman, 1996), competition for water and nutrients (Carlsson & Callaghan, 1991; Yeaton *et al.*, 1993; Esler & Phillips, 1994; Esler, 1999), or leaching of allelopathic compounds (Moro *et al.*, 1997). The magnitude of reduction in seedling growth caused by any of these factors depends on seedling size and location under the shrub (Franco & Nobel, 1989).

Localities predominated by annual species

Of the 34 taxa recorded at the three locations predominated by annual species, only one annual species, *i.e. Zaluzianskya villosa*, was common to all locations (Table 13.4). Six taxa (4 annuals, 2 perennials) occurred at two of the locations. Seedling numbers ranged from 0.4 m^{-2} to 660.0 m^{-2} (Table 13.4), which are markedly lower than germinable seed bank density values recorded during autumn for the study area, *i.e.* 7771.7 seedlings m^{-2} recorded in 1994 and 5584.9 seedlings m^{-2} in 1995. This large difference in observed seedling numbers can be attributed to various factors, of which the size, duration and timing of the rainfall/watering events are the most obvious.

In general, a higher number of seedlings (Figure 13.3) were recorded during winter than plants during spring, irrespective of locality. Winter examination yielded mean seedling numbers of more than 100 seedlings m^{-2} at all locations, and more than 50 seedlings m^{-2} survived until spring. Seasonal differences in mean species richness was only significant at the locality predominated by *Senecio arenarius* (Figure 13.4), and was possibly due to low species richness' recorded.

Annual species constituted 74% of all seedling taxa recorded at locations predominated by annuals (Table 13.4). Topsoil replacement should therefore be sufficient for the recruitment of these species during revegetation efforts. Seedling survival (Table 13.3) ranged from 45% to 65% and differed significantly between localities. Seedlings of short-lived and ephemeral species have high probabilities of survival (Gutterman, 1993; Esler, 1999). In the Upland Succulent Karoo, recorded survival rates of annuals were highly variable within and between species at different sites and ranged from 47% to 74% of emerging seedlings (Van Rooyen *et al.*, 1979).

Table 13.4. Mean number of seedlings m^{-2} for species recorded during winter, at three locations, each pre-dominated in previous years by different annual species. Mean number of plants recorded during the following spring, is indicated between brackets

Species	Annual species (location)	*Senecio arenarius*	*Ursinia speciosa*	Various annual species
	Group A: Species recorded at 3 locations			
	Zaluzianskya villosa (A)	7.2 (2.8)	2.0 (0.4)	424.0 (252.0)
	Group B: Species recorded at 2 locations			
	Polycarena pumila (A)	0.4 (0.0)	0.8 (0.0)	
	Foveolina tenella (A)	2.0 (0.0)		126.0 (126.0)
	Senecio arenarius (A)	49.6 (15.2)	2.0 (2.0)	
	Mesembryanthemum crystallinum (A)	37.2 (21.2)		8.0 (6.0)
	Ehrharta calycina (P)	12.4 (26.0)	2.8 (1.6)	
	Oxalis spp. (P)		3.2 (1.2)	2.0 (6.0)
	Group C: Species recorded at single locations			
	Arctotheca calendula (A)	2.8 (0.4)		
	Galenia sarcophylla (P)	0.4 (0.4)		
	Oncosiphon suffruticosum (A)	0.4 (0.8)		
	Amellus microglossus (A)	0.0 (0.8)		
	Arctotis hirsuta (A)		1.6 (0.0)	
	Heliophila coronopifolia (A)		0.4 (0.0)	
	Nemesia bicornis (A)		0.8 (0.0)	
	Wahlenbergia paniculata (A)		10.0 (0.4)	
	Rumex spp. (A)		1.6 (0.4)	
	Limeum africanum (A)		1.2 (0.4)	
	Lapeirousia spp. (P)		0.8 (0.4)	
	Ursinia speciosa (A)		132.4 (92.0)	
	Nestlera biennis (P)		14.0 (10.0)	
	Adenogramma littoralis (A)		12.8 (9.2)	
	Cotula thunbergii (A)		4.0 (6.4)	
	Geophyte spp. (P)		3.2 (4.4)	
	Pelargonium senecioides (A)		0.8 (1.2)	
	Hebenstretia dentata (A)		0.0 (2.4)	
	Isolepis marginata (A)		0.0 (1.2)	
	Stipagrostis zeyheri (P)		0.0 (0.8)	
	Pharnaceum exiguum (A)			42.0 (0.0)
	Karroochloa schismoides (A)			660.0 (132.0)
	Tetragonia virgata (P)			352.0 (154.0)
	Tripteris clandestinum (A)			10.0 (8.0)
	Chenopodium opulifolium (A)			124.0 (104.0)
	Convolvulus spp. (P)			6.0 (6.0)
	Brassica tournefortii (A)			0.0 (4.0)

P - perennial

A - annual

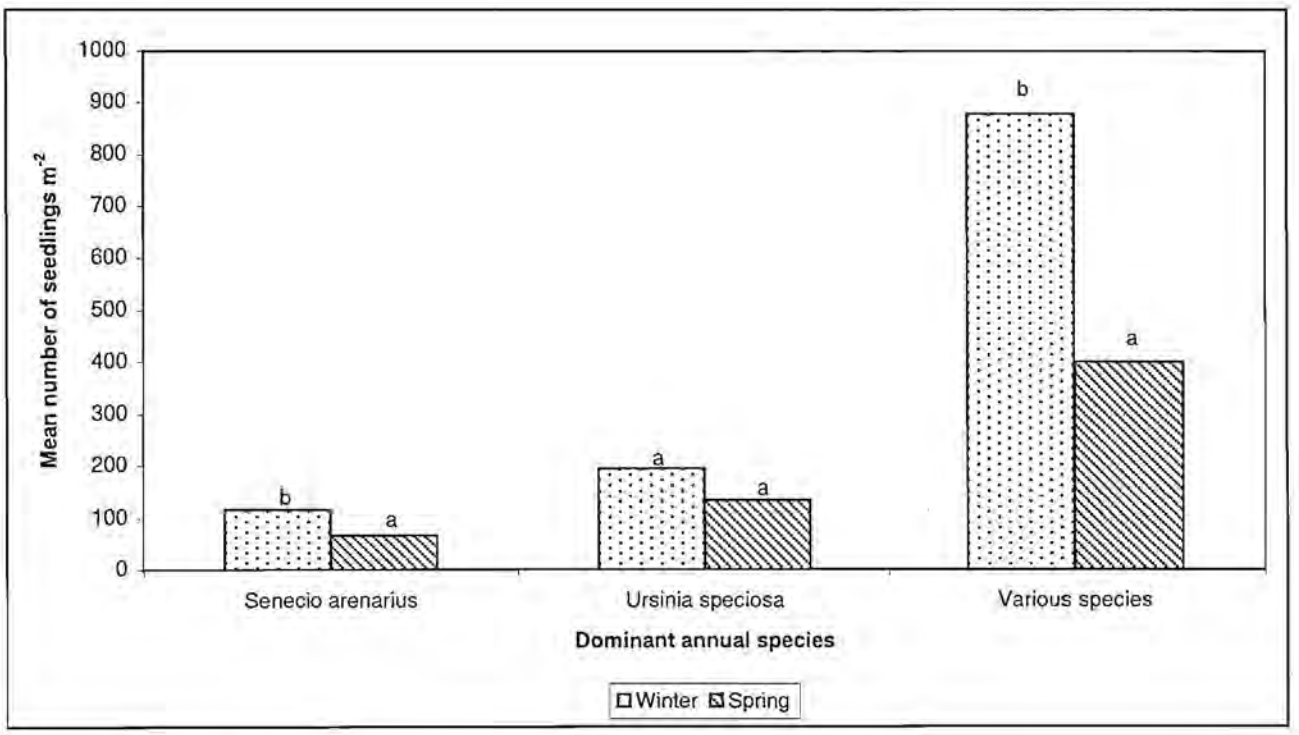

Figure 13.3. Mean number of seedlings m^{-2} recorded in three Strandveld Succulent Karoo communities predominated by annual species.

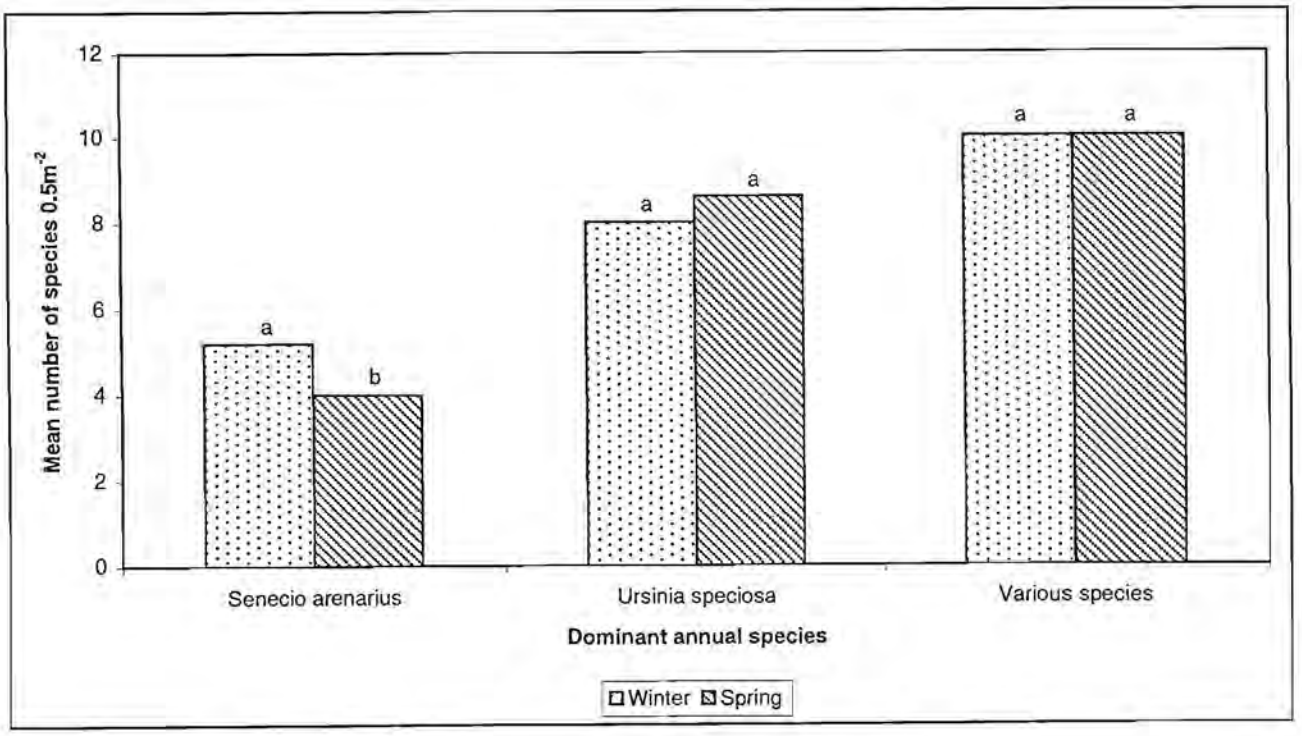

Figure 13.4. Mean number of species 0.5 m^{-2} recorded in three Strandveld Succulent Karoo communities predominated by annual species.

Few perennial shrub species' seedlings were recorded at localities predominated by annuals (Table 13.4), and those perennial shrub seedlings that did occur in these open areas, yielded high seedling numbers. Low seed availability, due to the transient nature of shrub species' seed banks as well as to seed dispersal characteristics, was probably the main reason for the few shrub seedlings recorded at localities predominated by annual species. These species will have to be reintroduced to post-mining areas by sowing and/or transplanting as a means to increase the species richness' of the areas. Transplanted shrubs may act as wind-breaks, thereby contributing to seedling survival of species recruited from replaced topsoil or which were sown. Transplanting of shrub species may also reduce the period between initial revegetation and seed production in these species.

CONCLUSIONS

Poor seed germination and seedling mortality, due to environmental constraints like water stress, soil salinity, high temperature and pathogens will limit the success of revegetation efforts in the Strandveld Succulent Karoo. One of the goals of post-mining revegetation efforts at Brand-se-Baai is to revegetate the area with at least 60% of the plant species present in the area prior to the start of mining activities (Environmental Evaluation Unit, 1990). Shrub species dominate the pre-mining standing vegetation at the study area (De Villiers *et al.*, 1999), and reintroduction of these species should be a priority during revegetation efforts. The seeds, of many of these shrub species, can germinate soon after dispersal, are probably not long-lived, and consequently produce transient seed banks (Chapters 4, 5 & 11). These shrubs can probably not be recruited from replaced topsoil, but transplanting or sowing of these species will benefit revegetation efforts due to increased species richness.

Both seedling numbers and species richness were higher in open areas than underneath shrub canopies, while seedling survival did not differ significantly between microhabitats. Therefore, none of the five shrub species investigated seem to facilitate the recruitment and survival of other species. In fact, seedling numbers and species richness were negatively affected by such shrub species. The negative effects of shrubs on seedling survival and establishment in their understorey community are usually through light deprivation, mechanical effects caused by litter, competition for water and nutrients, or leaching of allelopathic compounds (Cunliffe *et al.*, 1990; Yeaton & Esler, 1990; Yeaton *et al.*, 1993; Moro *et al.*, 1997; Esler, 1999).

Although seedlings of the dominant shrub *Salvia africana-lutea* were restricted to areas underneath the canopies of this species, the specific dispersal strategy seems more likely to be responsible for the recruitment pattern observed in this species. However, this aspect needs further investigation. Higher seedling survival underneath the canopies of shrub species, in arid regions such as the Strandveld Succulent Karoo, is chiefly the result of differential survival in shaded microsites with less direct solar radiation, and consequently, with lower daytime temperatures and lower evaporative demand (Valiente-Banuet & Ezcurra, 1991). Competition for water and shading by the nurse-plant may reduce the growth of the associated seedlings compared with exposed seedlings, as well as the eventual seed yield (Cunliffe *et al.*, 1990; Beukman, 1991; Dean & Yeaton, 1992; Yeaton *et al.*, 1993). Shrubs may also provide a

microhabitat with higher soil nitrogen levels, which can partially offset the reduced seedling growth caused by shading and competition for soil water (Franco & Nobel, 1989). Differences in soil fertility under shrubs may therefore be of secondary importance, but restoration of mined areas along the West Coast of South Africa should also consider soil fertilization schemes.

Seedlings of annuals and perennial herb species will establish in the absence of transplanted shrubs at the study site. Most of these species accumulate persistent seed banks (Chapters 4, 5 & 11) and can be recruited from replaced topsoil and/or by sowing. However, in mined areas, high wind speeds during the period of seedling recruitment and establishment (Environmental Evaluation Unit, 1990) may result in high seedling mortality due to a sand blasting effect (pers. obs.). Shrubs present in these post-mining areas may aid in reducing wind speeds and therefore contribute to the survival of species in open areas. Additionally, vegetation patches established from transplanted shrubs may also act as sources of seeds that may eventually reach other patch types or patches of bare soil (Bertiller, 1998).

Results obtained in this study partly conform to the model for Succulent Karoo vegetation dynamics (Yeaton & Esler, 1990). Woody shrubs are the climax species in the succession sequence and therefore do not act as nurse-plants themselves. In this study, shrubs influenced recruitment, rather than survival, of seedlings derived from seeds that were "trapped" beneath the canopies of the shrubs. The Karoo vegetation dynamics model was based on southern Succulent Karoo vegetation, where Mesembryanthemaceae species are abundant. These species are less prominent in Strandveld Succulent Karoo vegetation, where annual precipitation, especially fog, is more predictable (Desmet & Cowling, 1999). It is therefore questioned whether these species act as nurse-plants for woody shrub species. The high number of perennial herb species present in Strandveld Succulent Karoo vegetation (pers. obs.) may indicate the functioning of these species as nurse-plants or sites for seed "trapping". In conclusion, further investigation of these aspects will prove invaluable for understanding the processes and dynamics of seed and seedling ecology in the Strandveld Succulent Karoo. In turn, these dynamic processes will contribute towards the formulation of appropriate post-mining revegetation strategies.

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REFERENCES

ARNOLD, T.H. & DE WET, B.C. 1999. Plants of southern Africa: names and distribution. Electronic data-base, National Botanical Institute, Pretoria.

BERTILLER, M.B. 1998. Spatial patterns of the germinable soil seed bank in northern Patagonia. *Seed Science Research*, **8**: 39-45.

BEUKMAN, R.P. 1991. The role of nurse plants in the vegetation dynamics of the succulent karoo. M.Sc. dissertation, University of Cape Town, Cape Town.

CARLSSON, B.A. & CALLAGHAN, T.V. 1991. Positive plant interactions in Tundra vegetation and the importance of shelter. *Journal of Ecology*, **79**: 973-983.

CHAPIN, F.S., WALKER, R.L., FASTIE, C.L. & SHARMAN, L.C. 1994. Mechanisms of primary succession following deglaciation at Glacier Bay, Alaska. *Ecological Monographs*, **64**: 149-175.

CUNLIFFE, R.N., JARMAN, M.L., MOLL, E.J. & YEATON R.I. 1990. Competitive interactions between the perennial shrub *Leipoldtia constricta* and an annual forb, *Gorteria diffusa*. *South African Journal of Botany*, **56**: 34-38.

DEAN, W.R.J. & YEATON, R.I. 1992. The importance of harvester ant *Messor capensis* nest mounds as germination sites in the southern Karoo, South Africa. *African Journal of Ecology*, **30**: 335-345.

DE JONG, T.J. & KLINKHAMER, P.G.L. 1988. Seedling establishment of the biennials *Cirsium vulgare* and *Cynoglossum officinale* in a sand-dune area: The importance of water for differential survival and growth. *Journal of Ecology*, **76**: 393-402.

DESMET, P.G. & COWLING, R.M . 1999. The climate of the karoo – a functional approach. In: Dean, W.R.J. & Milton, S.J. (eds). *The Karoo – Ecological patterns and processes*. Cambridge University Press, Cambridge. pp. 3-16.

DE VILLIERS, A.J., VAN ROOYEN, M.W., THERON, G.K. & VAN ROOYEN, N. 1999. Vegetation diversity of the Brand-se-Baai coastal dune area, West Coast, South Africa: A pre-mining benchmark survey for rehabilitation. *Land Degradation & Development*, **10**: 207-224.

ENVIRONMENTAL EVALUATION UNIT. 1990. *Anglo American Corporation: West Coast heavy mineral sands project*. Unpublished report. University of Cape Town, Cape Town.

ESLER, K.J. 1999. Plant reproductive ecology. In: Dean, W.R.J. & Milton, S.J. (eds). *The Karoo – Ecological patterns and processes*. Cambridge University Press, Cambridge. pp. 123-144.

ESLER, K.J. & PHILLIPS, N. 1994. Experimental effects of water stress on semi-arid Karoo seedlings: implications for field seedling survivorship. *Journal of Arid Environments*, **26**: 325-337.

FOWLER, N. 1986. The role of competition in plant communities in arid and semiarid regions. *Annual Review of Ecology and Systematics*, **17**: 89-110.

FRANCO, A.C. & NOBEL, P.S. 1989. Effect of nurse plants on the microhabitat and growth of Cacti. *Journal of Ecology*, **77**: 870-886.

GARNER, W. & STEINBERGER, Y. 1989. A proposed mechanism for the formation of 'Fertile Islands' in the desert ecosystem. *Journal of Arid Environments*, **16**: 257-262.

GOLDBERG, D.E. & WERNER, P.A. 1983. The effects of size of opening in vegetation and litter cover on seedling establishment of goldenrods (*Solidago* spp.). *Oecologia*, **60**: 149-155.

GRUBB, P.J. 1977. The maintenance of species-richness in plant communities, the importance of the regeneration niche. *Biological Reviews*, **52**: 107-145.

GUTIÉRREZ, J.R., MESERVE, P.L., CONTRERAS, L.C., VáSQUEZ, H. & JAKSIC, F.M. 1993. Spatial distribution of soil nutrients and ephemeral plants underneath and outside the canopy of *Porlieria chilensis* shrubs (Zygophyllaceae) in arid coastal Chile. *Oecologia*, **95**: 347-352.

GUTTERMAN, Y. 1993. *Seed germination in desert plants*. Springer-Verlag, Berlin.

HOBBIE, S. 1992. Effects of plant species on nutrient cycling. *Trends in Ecology and Evolution*, **7**: 336-339.

KEELEY, J.E. 1992. Recruitment of seedlings and vegetative sprouts in unburned Chaparral. *Ecology*, **73**: 1194-1208.

KITAJIMA, K. & TILMAN, D. 1996. Seed banks and seedling establishment on an experimental productivity gradient. *Oikos*, **76**: 381-391.

McAULIFFE, J.R. 1988. Markovian dynamics of simple and complex desert plant communities. *American Naturalist*, **131**: 459-490.

MILES, J. 1985. The pedogenic effects of different species and vegetation types and the implications of succession. *Journal of Soil Science*, **36**: 571-584.

MILTON, S.J. 1994. Growth, flowering and recruitment of shrubs in grazed and in protected rangeland in the arid Karoo, South Africa. *Vegetatio*, **111**: 17-27.

MILTON, S.J. 1995. Spatial and temporal patterns in the emergence and survival of seedlings in arid Karoo shrubland. *Journal of Applied Ecology*, **32**: 145-156.

MOLOFSKY, J. & AUGSPURGER, C.K. 1992. The effect of leaf litter on early seedling establishment in a tropical forest. *Ecology*, **73**: 68-77.

MORO, M.J., PUGNAIRE, F.I., HAASE, P. & PUIGDEFáBREGAS, J. 1997. Mechanisms of interaction between a leguminous shrub and its understorey in a semi-arid environment. *Ecography*, **20**: 175-184.

MUSTART, P.J. & COWLING, R.M. 1993. The role of regeneration stages in the distribution of edaphically restricted fynbos Proteaceae. *Ecology*, **74**: 1490-1499.

NOBEL, P.S. 1980. Morphology, nurse plants, and minimum apical temperatures for young *Carnegiea gigantea*. *Botanical Gazette*, **141**: 188-191.

NOY-MEIR, I. 1980. Structure and function of desert ecosystems. *Israel Journal of Botany*, **28**: 1-19.

PUGNAIRE, F.I., HAASE, P., PUIGDEFáBREGAS, J., CUETO, M., CLARK, S.C. & INCOLL, L.D. 1996a. Facilitation and succession under the canopy of a leguminous shrub, *Retama sphaerocarpa*, in a semi-arid environment in south-east Spain. *Oikos*, **76**: 455-464.

PUGNAIRE, F.I., HAASE, P. & PUIGDEFáBREGAS, J. 1996b. Facilitation between higher plant species in a semiarid environment. *Ecology*, **77**: 1420-1426.

REDBO-TORSTENSSON, P. & TELENIUS, A. 1995. Primary and secondary seed dispersal by wind and water in *Spergularia salina*. *Ecography*, **18**: 230-237.

SCHOMBERG, H.H., STEINER, J.L. & UNGER, P.W. 1994. Decomposition and nitrogen dynamics of crop residues: residue quality and water effects. *Soil Science Society of America Journal*, **58**: 372-381.

STOCK, W.D., DLAMINI, T.S. & COWLING, R.M. 1999. Plant induced fertile islands as possible indicators of desertification in a succulent desert ecosystem in northern Namaqualand, South Africa. *Plant Ecology*, **142**: 161-167.

TURNER, R.M., ALCORN, S.M., OLIN, G. & BOOTH, J.A. 1966. The influence of shade, soil and water on saguaro seedling establishment. *Botanical Gazette*, **127**: 95-102.

VALIENTE-BANUET, A. & EZCURRA, E. 1991. Shade as a cause of the association between the cactus *Neobuxbaumia tetetzo* and the nurse plant *Mimosa luisana* in the Tehuacán Valley, Mexico. *Journal of Ecology*, **79**: 961-971.

VAN ROOYEN, M.W., GROBBELAAR, N. & THERON, G.K. 1979. Phenology of the vegetation in the Hester Malan Nature Reserve in the Namaqualand Broken Veld. 2. The therophyte population. *Journal of South African Botany*, **45**: 433-452.

VETAAS, O.R. 1992. Micro-site effects of trees and shrubs in dry savannas. *Journal of Vegetation Science*, **3**: 337-344.

WESTOBY, M., JURADO, E. & LEISHMAN, M. 1992. Comparative evolutionary ecology of seed size. *Tree*, **7**: 368-372.

WIEGAND, T., MILTON, S.J. & WISSEL, C. 1995. A simulation model for a shrub ecosystem in the semiarid Karoo, South Africa. *Ecology*, **76**: 2205-2221.

YEATON, R.I. & ESLER, K.J. 1990. The dynamics of a succulent Karoo vegetation: a study of species association and recruitment. *Vegetatio*, **88**: 103-113.

YEATON, R.I., MOLL, E.J., JARMAN, M.L. & CUNLIFFE, R.N. 1993. The impact of competition on the structure of early successional plant species of the Atlantic Coast of South Africa. *Journal of Arid Environments*, **25**: 211-219.

CHAPTER 14

SEED PRODUCTION OF FOUR NAMAQUALAND PIONEER PLANT SPECIES GROWN ON SALINE SOIL

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ABSTRACT

The mining of heavy minerals along the west coast of South Africa will destroy all the standing vegetation, and will also lead to the salinization of the soil as sea-water will eventually be used in the mining process. Local, salt tolerant species should be selected for the revegetation of the area, and it is essential that the selected species should be able to reproduce to ensure growth of the population. Survival and seed production of four pioneer plant species were determined along a salinity gradient. None of the four species survived at the moderate and high salinities. Seed production of the ephemeral species was reduced at the low salinity, while that of the perennial species did not differ significantly.

Key words: Mining; Namaqualand; pioneer plant species; salinity; seed production

INTRODUCTION

The high accumulation of salts in soils which could be caused by any of several factors (eg. saline irrigation water, inadequate leaching, poor drainage, naturally saline soils) may hinder germination, seedling and vegetative growth as well as the yield and quality of plants (Mamo *et al.*, 1996). Two major effects have been identified as the probable causes of the detrimental effect of salinity on plant growth: the ionic effect and the osmotic effect (Lewis *et al.*, 1989; Banuls *et al,.* 1991; Leidi *et al.*, 1991).

Even though saline environments are unfavourable for most plant species, some plants, namely the halophytes, seem to flourish under these conditions. These plants have adapted to living under these harsh conditions by either avoiding salt uptake through osmoregulation; excreting the salts by means of salt glands and bladders; or tolerating the high salt concentration as euhalophytes or succulents (Larcher, 1995). Interspecific differences in response to salinity and differential responses resulting from interaction of salinity with other environmental factors occur. Variables such as irradiance and calcium content (Hyder & Greenway, 1965; Bogemans *et al.*, 1989), ecotypic variation within species (Tiku & Snaydon, 1971), soils (Venables & Wilkins, 1978; Watt, 1983), nitrogen levels and temperature (Kemp & Cunningham, 1981), species (Kingsbury & Epstein, 1986), CO_2 -

concentrations (Munns & Termaat, 1986) and humidity (Salim, 1989), can all affect plant responses to salinity. Several investigations showed that salt tolerance can vary with the phenological stage and that the effects of saline stress change with its duration (Gutierrez Boem *et al.*, 1997).

Along the western coast of South Africa, the sandy soils are rich in heavy minerals. Not only will the mining activities in the area destroy the topography, vegetation, soil chemical and physical characteristics and alter the animal life, but the process whereby the heavy minerals are extracted will eventually involve the use of sea-water and therefore the salinity of the mined soil will be increased to levels where plants will find it difficult to grow (Environmental Evaluation Unit, 1990). Although several local species are able to tolerate high salinities (De Villiers, 1993), it does not mean that they will produce seeds under these conditions. The aim of this study was to determine if selected plant species growing on saline soil are able to survive and reproduce by means of seeds, and thus contribute towards the growth of the population and the successful revegetation of the area.

MATERIAL AND METHODS

Seeds of natural populations of *Gazania leiopoda* (DC.) Rössl. (perennial), *Tetragonia microptera* Fenzl (ephemeral), *Dimorphotheca pluvialis* (L.) Moench (ephemeral) and *Senecio arenarius* Thunb. (ephemeral), were collected at Brand-se-Baai (31°18'S, 17°54'E), South Africa. Although members of the Asteraceae have achenes and *Tetragonia microptera* produces a samara, the term seed will be used throughout this paper. These species were chosen because they are abundant and native to the area and/or seem to be acting as pioneer species in surrounding areas (De Villiers, 1993). Seeds were sown in 1 dm^3 pots, containing fine sand (0.5 -1.1 mm particle size), 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 250 cm^3 solution 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. A randomized blockless design was used. One plant was grown in each pot and ten replicates of each treatment (control; 1% NaCl, 2% NaCl and 3% NaCl) were used for each of the four species. Inflorescences / flowers and mature seeds were harvested and counted before dispersal. Results were analysed statistically as a blockless design using the one-way analysis of variance and LSD (Least Significant Difference) multiple range test of the Statgraphics 5.0[1] computer program, to test for significant differences at a 95% confidence level.

[1] Statgraphics 5.0, 1989. STSC, Inc., U.S.A.

RESULTS AND DISCUSSION

None of the four species survived at salinities higher than 1% NaCl (Table 14.1). Although most of the plants of the four species survived at the 1% NaCl treatment, the ephemeral species showed signs of chlorosis. The mortality rate of the four species increased as the salinity increased. The plants of the 3% NaCl treatment died first (after three weeks), followed by the plants of the 2% NaCl treatment (after nine weeks). De Villiers *et al.* (1997) found several perennial species of this area to be moderately salt tolerant. Although *Gazania leiopoda* is a perennial species, it did not survive at the moderate and high salinities as expected.

In the case of *Gazania leiopoda* (perennial), the mean number of inflorescences produced per plant did not differ significantly between the 1% NaCl and the control treatment (Figure 14.1). The mean number of seed bearing inflorescences were significantly lower than those not bearing seeds, for both the control and 1% NaCl treatment. Although the mean number of seed bearing inflorescences decreased when this species was grown on saline soil, the total number of inflorescences produced did not differ. The mean number of inflorescences produced per plant decreased significantly with increasing salinity, for both *Senecio arenarius* and *Dimorphotheca pluvialis* (Figure 14.1). In the control treatment, both these ephemeral species produced a significantly greater number of seed bearing inflorescences than non-seed bearing inflorescences. In the 1% NaCl treatment, the number of seed bearing inflorescences were less than the inflorescences not bearing seeds, but this was only significant in the case of *Dimorphotheca pluvialis*. Therefore, the ephemeral species not only produce less inflorescences when grown on saline soil, but the inflorescences that are produced bear less or no seeds.

The mean number of seeds produced per plant are given in Table 14.2. Although not significantly, *Gazania leiopoda* produced a greater number of seeds per plant in the 1% NaCl treatment than in the control treatment, mainly because of the greater number of seeds produced per inflorescence. A low salinity therefore seems to enhance the number of seeds produced by this species. Francois & Kleiman (1990) reported that *Crambe abyssinica* showed a 6.5% reduction of seed yield for each unit increase in soil salinity above 2.0 dS m^{-1}, but no significant reduction of seed yield below this concentration. The mean number of seeds produced per plant decreased with increasing salinity for all three ephemeral species (Table 14.2). In the cases of *Dimorphotheca pluvialis* and *Senecio arenarius*, this decrease is due to a reduction in both the number of inflorescences produced per plant and the number of seeds produced per inflorescence, with increasing salinity. A decrease in yield with increasing salinity has been reported for many species (Abdul-Halim *et al.*, 1988; Francois *et al.*, 1988; Francois *et al.*, 1989; Jones *et al.*, 1989; Francois & Kleiman, 1990; Ashraf & Tufail, 1995; Ashraf & O'Leary, 1996; Mamo *et al.*, 1996; Gutierrez Boem *et al.*, 1997). Abdul-Halim *et al.* (1988) found that at a low soil salinity level (< 8.0 dS m^{-1}), and maintaining the available soil water above a specified percentage during the growth period, would effect a small reduction on wheat yield.

Table 14.1. Survival percentages of four pioneer species grown at different soil salinities

Species	Treatment			
	Control	1% NaCl	2% NaCl	3% NaCl
Gazania leiopoda (perennial)	100	100	0	0
Senecio arenarius (ephemeral)	90	60	0	0
Tetragonia microptera (ephemeral)	100	80	0	0
Dimorphotheca pluvialis (ephemeral)	90	70	0	0

Table 14.2. Seed production (seeds/plant) of four pioneer species grown at different soil salinities. For each species, values followed by the same letter do not differ significantly at $P \leq 0.05$

Species	Treatment	
	Control	1% NaCl
Gazania leiopoda (perennial)	9.1 [a]	15.0 [a]
Senecio arenarius (ephemeral)	807.8 [a]	12.4 [b]
Tetragonia microptera (ephemeral)	96.9 [a]	21.9 [b]
Dimorphotheca pluvialis (ephemeral)	77.2 [a]	0.0 [b]

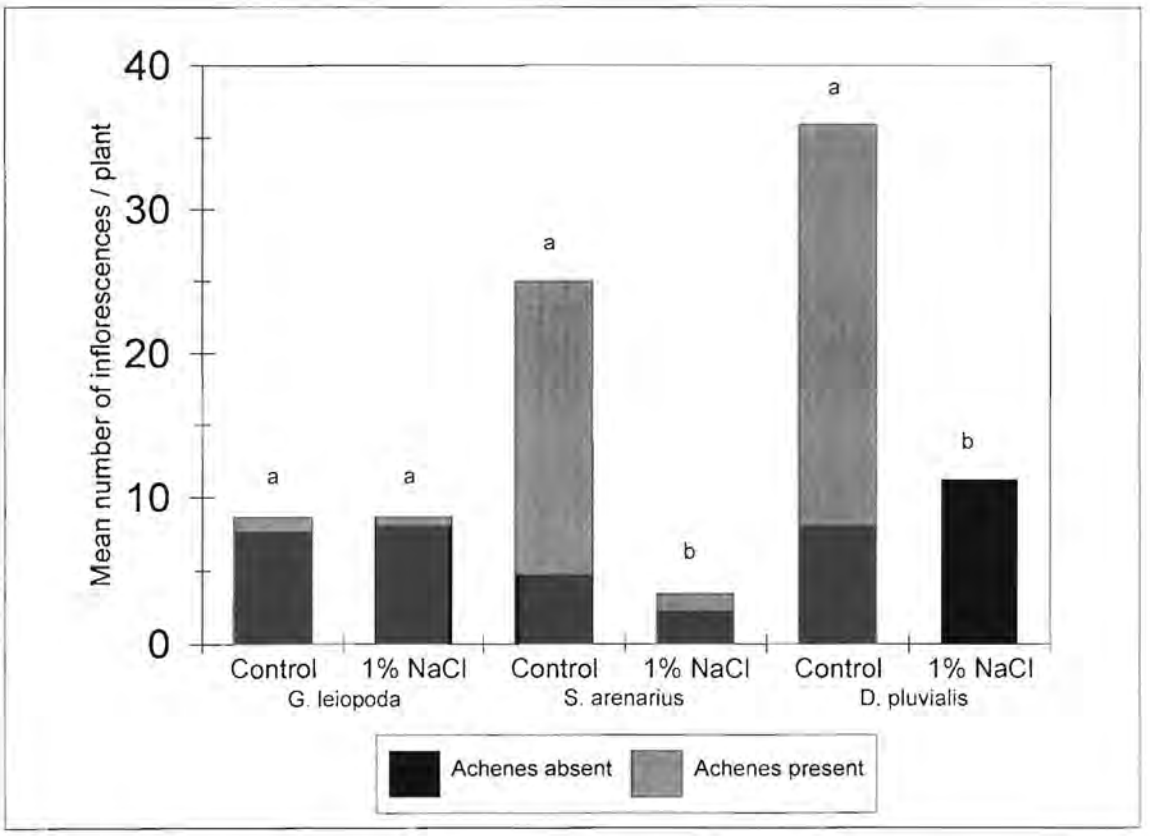

Figure 14.1. The mean number of inflorescences produced per plant, of *Gazania leiopoda*, *Senecio arenarius* and *Dimorphotheca pluvialis* grown on saline soil. Bars with the same letter are not significantly different at the $P \leq 0.05$ level.

CONCLUSIONS

Although most ephemeral species survive when grown on soil with low salinities, these species yield almost no seeds. As seeds are ephemeral species' only means of reproduction, these species will have to be revegetated from seed sources outside the mined area, or from replaced topsoil. Fortunately, populations of representative ephemeral species occur outside the mined area, and the seeds of most of these species are wind dispersed. If the salinity of the mined soil can be kept at a low concentration, perennial species will be able to survive and in some cases seed production may even be enhanced. Studies comparing the viability, longevity and germinability of seeds, produced by plants grown on soils with different salinities, are now essential. Future studies should also include emergence, seedling survival, plant growth, yield, etc. of plants derived from seeds produced at different soil salinities.

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REFERENCES

ABDUL-HALIM, R.K., SALIH, H.M., AHMED, A.A. & ABDUL-RAHEM, A.M. 1988. Growth and development of maxipak wheat as affected by soil salinity and moisture levels. *Plant and Soil,* **112**: 255-259.

ASHRAF, M. & O'LEARY, J.W. 1996. Responses of some newly developed salt-tolerant genotypes of spring wheat to salt stress: 1. Yield components and ion distribution. *Journal of Agronomy and Crop Science,* **176**: 91-101.

ASHRAF, M. & TUFAIL, M. 1995. Variation in salinity tolerance in sunflower (*Helianthus annuus* L.). *Journal of Agronomy and Crop Science,* **174**: 361-362.

BANULS, J., LEGAZ, F. & PRIMO-MILLO, E. 1991. Salinity-calcium interactions on growth and ionic concentration of Citrus plants. *Plant and Soil,* **133**: 39-46.

BOGEMANS, J., NEIRINCKX, L. & STASSART, J.M. 1989. Effect of deicing NaCl and $CaCl_2$ on spruce (*Picea abies* (L.) sp.). *Plant and Soil,* **120**: 203-211.

DE VILLIERS, A.J. 1993. Ecophysiological studies on several Namaqualand pioneer species, with special reference to the revegetation of saline mined soil. MSc. dissertation, University of Pretoria, Pretoria.

DE VILLIERS, A.J., VAN ROOYEN, M.W., THERON, G.K. & CLAASSENS, A.S. 1997. Tolerance of six Namaqualand pioneer species to saline soil conditions. *South African Journal of Plant and Soil,* **14**: 38-42.

ENVIRONMENTAL EVALUATION UNIT 1990. *Anglo American Corporation: West Coast heavy mineral sands project.* Unpublished report. University of Cape Town, Cape Town.

FRANCOIS, L.E., DONOVAN, T.J., LORENZ, K. & MAAS, E.V. 1989. Salinity effects on rye grain yield, quality, vegetative growth, and emergence. *Agronomy Journal*, **81**: 707-712.

FRANCOIS, L.E., DONOVAN, T.J., MAAS, E.V. & RUBENTHALER, G.L. 1988. Effect of salinity on grain yield and quality, vegetative growth, and germination of triticale. *Agronomy Journal*, **80**: 642-647.

FRANCOIS, L.E. & KLEIMAN, R. 1990. Salinity effects on vegetative growth, seed yield, and fatty acid composition of crambe. *Agronomy Journal*, **82**: 1110-1114.

GUTIERREZ BOEM, F.H., LAVADO, R.S. & PORCELLI, C.A. 1997. Effects of waterlogging followed by a salinity peak on rapeseed (*Brassica napus* L.). *Journal of Agronomy and Crop Science*, **178**: 135-140.

HEWITT, E.J. 1952. *Sand and water culture methods used in the study of plant nutrition.* Farnham Royal, Bucks, Commonwealth Agricultural Bureau.

HYDER, S.Z. & GREENWAY, H. 1965. Effects of Ca^{2+} on plant sensitivity to high NaCl concentrations. *Plant and Soil*, **23**: 258-260.

JONES, R.W. Jr., PIKE, L.M. & YOURMAN, L.F. 1989. Salinity influences cucumber growth and yield. *Journal of the American Society for Horticultural Science*, **114**: 547-551.

KEMP, P.R. & CUNNINGHAM, G.L. 1981. Light, temperature and salinity effects on growth, leaf anatomy and photosynthesis of *Distichlis spicata* (L.) Greene. *American Journal of Botany*, **68**: 507-516.

KINGSBURY, R.W. & EPSTEIN, E. 1986. Salt sensitivity in wheat. *Plant Physiology*, **80**: 651-654.

LARCHER, W. 1995. *Physiological plant ecology : ecophysiology and stress physiology of functional groups.* Springer-Verlag, Berlin.

LEIDI, E.O., NOGALES, R. & LIPS, S.H. 1991. Effect of salinity on cotton plants grown under nitrate or ammonium nutrition at different calcium levels. *Field Crops Research*, **26**: 35-44.

LEWIS, O.A.M., LEIDI, E.O. & LIPS, S.H. 1989. Effect of nitrogen source on growth response to salinity stress in maize and wheat. *New Phytologist*, **111**: 155-160.

MAMO, T., RICHTER, C. & HEILIGTAG, B. 1996. Salinity effects on the growth and ion contents of some chickpea (*Cicer arietinum* L.) and lentil (*Lens culinaris* Medic.) varieties. *Journal of Agronomy and Crop Science*, **176**: 235-247.

MUNNS, R. & TERMAAT, A. 1986. Whole-plant responses to salinity. *Australian Journal of Plant Physiology*, **13**: 143-160.

SALIM, M. 1989. Effects of salinity and relative humidity on growth and ionic relations of plants. *New Phytologist*, **113**: 13-20.

TIKU, B.L. & SNAYDON, R.W. 1971. Salinity tolerance in the grass species *Agrostis stolonifera* L.. *Plant and Soil*, **35**: 421-431.

VENABLES, A.V. & WILKINS, D.A. 1978. Salt tolerance in pasture grasses. *New Phytologist*, **80**: 613-622.

WATT, T.A. 1983. The effects of salt water and soil type upon the germination, establishment and vegetative growth of *Holcus lanatus* L. and *Lolium perenne* L.. *New Phytologist*, **94**: 275-291.

CHAPTER 15

SEEDLING EMERGENCE AND SURVIVAL OF THREE NAMAQUALAND PIONEER PLANT SPECIES GROWN UNDER SALINE SOIL CONDITIONS

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ABSTRACT

The effects of salinity (NaCl) on emergence and seedling survival of three Namaqualand pioneer plant species, were investigated. In the perennial species (*Gazania leiopoda*), seedlings did emerge in the 1% NaCl treatment (although the maximum mean percentage of emerged seedlings was only 2%), but not at the higher salinities. Seedlings of the two ephemeral species only emerged in the control treatment. Increased salinity resulted in an increased mortality rate of seedlings. Perennial species are recommended for revegetation of saline soils in this area. To ensure successful restoration of mined areas in Namaqualand, soil salinity should be at a minimum.

Key words: Emergence; mined soil; NaCl; salinity; seedling survival

INTRODUCTION

Along the western coast of South Africa, the sandy soils are rich in heavy minerals. The mining process whereby the heavy minerals are extracted, involves the use of sea-water and therefore the salinity of the mined soil can be so high that plants will find it difficult to grow under these conditions (Environmental Evaluation Unit, 1990). Although mature plants of several local species are able to tolerate high salinities (De Villiers *et al.*, 1997), it does not mean that they will germinate, emerge and survive the seedling stage under these conditions.

Salinity, whether natural or induced, is a widespread environmental stress that can limit growth and development of salt-sensitive plants (Rodriguez *et al.*, 1997). Although the germination of seeds in saline environments has been examined in various studies (McMillan, 1959; Ungar, 1962; Younis & Hatata, 1971; Williams & Ungar, 1972; Ahmed, 1985; Mariko *et al.*, 1992; Yokoishi & Tanimoto, 1994; Ungar, 1995, 1996; Baskin *et al.*, 1998; Gul & Weber, 1998; Masuda *et al.*, 1999), only a few studies examined the effect of salinity on emergence and seedling survival/growth of plant species (Seneca, 1972; Singh, 1990; Van Hoorn, 1991; Azaizeh *et al.*, 1992; Evlagon *et al.*, 1992; Zhong & Läuchli, 1993; Chartzoulakis & Loupassaki, 1997; Franco *et al.*, 1997; Rodriguez *et al.*, 1997; Katembe *et al.*, 1998). On saline soil, the plant encounters more problems during germination, emergence and early seedling growth than during later growth stages and may fail to establish. Early seedling

growth of some species appears to be less salt tolerant than during germination and later growth (Van Hoorn, 1991; Chartzoulakis & Loupassaki, 1997).

Interspecific differences in response to salinity and differential responses resulting from interaction of salinity with other environmental factors occur. Variables such as irradiance and calcium content (Hyder & Greenway, 1965; Bogemans *et al.*, 1989; Volkmar *et al.*, 1998), ecotypic variation within species (Tiku & Snaydon, 1971), soils (Venables & Wilkins, 1978; Watt, 1983), nitrogen levels and temperature (Kemp & Cunningham, 1981; Khan & Ungar, 1996; Masuda *et al.*, 1999), species (Kingsbury & Epstein, 1986), CO_2 concentration (Munns & Termaat, 1986; Yeo, 1999) and humidity (Salim, 1989), can all affect plant responses to salinity.

Several studies in the Karoo, South Africa, have focused on factors affecting seedling establishment and survival (Esler & Phillips, 1994; Milton, 1995), but plant responses to salinity has been a neglected area of study in this arid environment (Theron, 1964; Lloyd, 1985; De Villiers *et al.*, 1994a, 1994b, 1995, 1996, 1997, 1999).

The present study was undertaken to improve understanding of the responses of three Namaqualand pioneer species to different levels of salinity during emergence and the seedling stage. Information about salinity tolerance at the seedling stage would also provide a predictive basis for assessing the suitability of different plant types and local species for post-mining revegetation.

MATERIAL AND METHODS

Seeds (achenes) of three local species, *Gazania leiopoda* (DC.) Rössl., *Senecio arenarius* Thunb. and *Senecio elegans* L., were sown in 8 dm^3 trays, containing fine sand (0.5 - 1.1 mm particle size), 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 (salt shock). 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 (salt acclimation). 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, were leached from the soil by giving each tray 2 dm^3 distilled water twice a week, before the saline solution was applied.

Trays were placed in a Phytotron room with a glass roof, and maintained at a constant temperature of 20°C. A randomized blockless design was used. Each tray contained 20 seeds/seedlings and five replicates of each salinity treatment (control; 1% NaCl, 2% NaCl and 3% NaCl) were used for each of the experiments and three species. The number of emerged and surviving seedlings was noted weekly.

Results were analysed statistically using the least significant difference one-way analysis of variance and multiple range test of the Statgraphics 5.0[1] computer program, to test for significant differences at a 95% confidence level.

RESULTS AND DISCUSSION

Salinity had a negative effect on seedling emergence of all three species (Table 15.1). Seedling emergence of the perennial species *Gazania leiopoda* reached a maximum of 74% after three weeks in the control, while that in the 1% NaCl treatment was 2%. In the 2% NaCl and 3% NaCl treatments, no seedlings emerged. In the control treatment, seedlings of the two ephemeral species, *Senecio arenarius* and *Senecio elegans,* reached maximum mean emergence percentages, of 19% and 87% respectively, after three weeks. No seedlings of the two *Senecio* species emerged in the 1% NaCl, 2% NaCl or 3% NaCl treatments. This reduction in the number of emerged seedlings with increasing salinity may be due to a reduction and/or delay in germination, as reported for both halophyte and glycophyte seeds (Chartzoulakis & Loupassaki, 1997; Katembe *et al.*, 1998). However, De Villiers *et al.* (1994) found that *Senecio elegans* had a mean germination percentage of 19% at a salinity of 1/3 sea-water, when germinated in Petri dishes at an optimum temperature of 15°C under light conditions. Sodium-chloride salinity was therefore inhibitory to germination and pre-emergence seedling survival, but seedlings were more sensitive to external salinity than seed germination. The reduction in emerged seedling numbers with increasing salinity could be a combined effect of osmotic stress (Greenway & Munns, 1980), which is more harmful to plants during the seedling stage and the higher ion uptake (Dumbroff & Cooper, 1974). Some plants are generally relatively salt tolerant during germination, but become more sensitive during emergence and the early seedling stage (Chartzoulakis & Loupassaki, 1997). This seems to be the case for *Senecio elegans*, and thus any failure in these stages will reduce the plant stand, and potential yields will be reduced far more than predicted by salt tolerance data (De Villiers *et al.*, 1997). Elevated salinity has been reported to slow down water uptake by seeds, thereby inhibiting their germination and root elongation (Werner & Finkelstein, 1995). The inability of *Senecio elegans*' seedlings to emerge at the 1% NaCl treatment indicated the necessity of salinity experiments at all growth stages, as well as this species' unsuitability for revegetation on saline soil.

In the survival experiment, salinity had a negative effect on the seedling survival percentages of all three species (Figures 15.1a, b and c), with *Senecio arenarius* showing the lowest salt tolerance. At the start of the salinity treatment (after four weeks), the percentage of surviving seedlings of all three species rapidly decreased at the 3% NaCl treatment, followed by that of the 2% NaCl treatment about a week later and the 1% NaCl treatment thereafter. An increase in salinity therefore resulted in an increased mortality rate of the seedlings. De Villiers *et al.* (1997) reported that the mortality rate of adult Namaqualand ephemeral species increased as salinity was increased. Numerous authors reported on increasing mortality and a reduction in growth rate in seedlings exposed to high salinity stress (Wagner, 1964; Tsonev *et al.*, 1998).

[1] Statgraphics 5.0, 1989. STSC, Inc., U.S.A.

Table 15.1. The mean percentage of emerged seedlings for the three pioneer species at different salinities. Within each species, values followed by the same letter do not differ significantly at $P \leq 0.05$

Species	Treatment			
	Control	1% NaCl	2% NaCl	3% NaCl
Gazania leiopoda (perennial)	74[a]	2[b]	0[b]	0[b]
Senecio arenarius (annual)	19[a]	0[b]	0[b]	0[b]
Senecio elegans (annual)	87[a]	0[b]	0[b]	0[b]

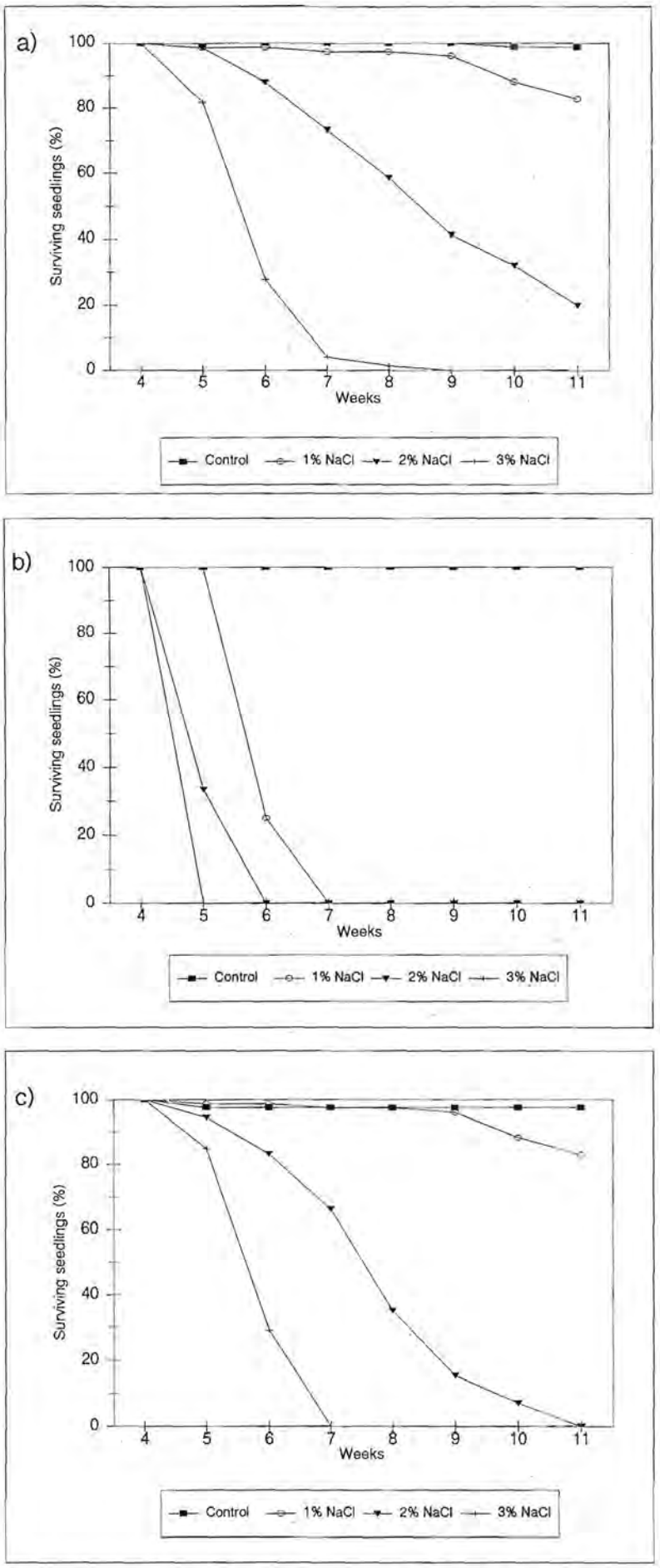

Figure 15.1. The mean seedling survival as a percentage of the original emergence percentage of a) *Gazania leiopoda*, b) *Senecio arenarius*, and c) *Senecio elegans*, at different soil salinities.

In all NaCl treatments, seedlings of the three Namaqualand pioneer species showed typical symptoms of salinity stress - the tips of the outer leaves became yellowish (chlorosis), and then necrosis set in from the tips downward. Yellowish leaves are indicative of many metabolic abnormalities, one of which is salt toxicity brought about by the decolouration of chlorophyll (Strogonov, 1964; Seneca, 1972).

Mortality during the first growth stages is not solely due to lower salt tolerance during this period, although some salt tolerant crops like barley, wheat, safflower and sugarbeets are reported to be less saline-tolerant at this point (Maas & Hoffman, 1977; Van Hoorn, 1991). The problem appears to be the high salinity in the top layer of the soil, exposing the germinating seed and seedlings to a higher salt concentration than at later growth stages. During the young seedling stage the root system is still shallow and water uptake by the plant is mainly limited to the top layer. Water loss from the top layer causes a high salt concentration, partly through a sharply reduced moisture content and partly through an increase of the salt content due to capillary transport from the underlying layers (Van Hoorn, 1991).

CONCLUSIONS

Both interspecific and intraspecific differences occurred, during seedling emergence and survival in saline soil, for the three species examined. The perennial species (*Gazania leiopoda*) showed a low maximum mean emergence percentage (2%) at the 1% NaCl treatment, while no seedlings of the two ephemeral species (*Senecio* spp.) emerged at this treatment. These results support the conclusion drawn by Seneca (1972), that seeds do not germinate (seedling emergence in this case) in salinities above those that young seedlings can tolerate, and that this mechanism is of great survival value to the species. In the case of *Senecio elegans*, however, seeds may germinate at a soil salinity of 1% NaCl (De Villiers *et al.*, 1994b), but the seedlings will probably not survive. Germination experiments will determine if the same is true for the other two species examined. The mortality rate of *Gazania leiopoda* and *Senecio elegans* seedlings was also slower than that of *Senecio arenarius*. However, this perennial species will be better suited for revegetation on saline soil than the ephemeral species examined, when both germination and emergence are considered. Between the two *Senecio* species, differences were observed for mean emergence percentages, emergence rates as well as for the mortality rate at different salinities. The negative effect of salinity on the emergence and survival of these species implies that the salinity of the soil should be very low for successful seedling emergence, and the soil salinity should be kept relatively low for better seedling survival.

In practice the effect of salinity on germination and emergence may be much worse than in laboratory experiments, and will differ according to soil and season (Van Hoorn, 1991). High temperature will increase evaporation and capillary rise of salts, while low temperature may delay germination and emergence to such an extent that the seedlings are caught in the crust formed in the meantime. Rainfall will decrease the salinity of the top layer but may also induce harmful crusting. In general, it is unwise to transfer results obtained with saline water irrigation from the laboratory to the field or from one region to another without carefully considering the conditions of soil and weather during germination and emergence (Van Hoorn, 1991). Field

experiments are therefore essential and together with mean precipitation levels will give insight into emergence and seedling survival *in situ*, as well as to the extent to which irrigation should be used.

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REFERENCES

AHMED, S.U. 1985. Germination and seedling growth characteristics of some cultivated and wild selections of wheat cultured in sea water. *Journal of Arid Environments*, **8**: 133-139.

AZAIZEH, H., GUNSE, B. & STEUDLE, E. 1992. Effects of NaCl an $CaCl_2$ on water transport across root cells of maize (*Zea mays* L.) seedlings. *Plant Physiology*, **99**: 886-894.

BASKIN, J.M., TYNDALL, R.W., CHAFFINS, M. & BASKIN, C.C. 1998. Effect of salinity on germination and viability of nondormant seeds of the federal-threatened species *Aeschynomene virginica* (Fabaceae). *Journal of the Torrey Botanical Society*, **125**: 246-248.

BOGEMANS, J., NEIRINCKX, L. & STASSART, J.M. 1989. Effect of deicing NaCl and $CaCl_2$ on spruce (*Picea abies* (L.) sp.). *Plant and Soil*, **120**: 203-211.

CHARTZOULAKIS, K.S. & LOUPASSAKI, M.H. 1997. Effects of NaCl salinity on germination, growth, gas exchange and yield of greenhouse eggplant. *Agricultural Water Management*, **32**: 215-225.

DE VILLIERS, A.J., VAN ROOYEN, M.W. & THERON, G.K. 1994a. Removal of sodium and chloride from a saline soil by *Mesembryanthemum barklyi*. *Journal of Arid Environments*, **29**: 325-330.

DE VILLIERS, A.J., VAN ROOYEN, M.W. & THERON, G.K. 1999. Seed production of four Namaqualand pioneer plant species grown on saline soil. *South African Journal of Botany*, **65**: 110-112.

DE VILLIERS, A.J., VAN ROOYEN, M.W., THERON, G.K. & CLAASSENS, A.S. 1995. The effect of leaching and irrigation on the growth of *Atriplex semibaccata*. *Land Degradation and Rehabilitation*, **6**: 125-131.

DE VILLIERS, A.J., VAN ROOYEN, M.W., THERON, G.K. & CLAASSENS, A.S. 1997. Tolerance of six Namaqualand pioneer species to saline soil conditions. *South African Journal of Plant and Soil*, **14**: 38-42.

DE VILLIERS, A.J., VAN ROOYEN, M.W., THERON, G.K. & VAN DE VENTER, H.A. 1994b. Germination of three Namaqualand pioneer species, as influenced by salinity, temperature and light. *Seed Science and Technology*, **22**: 427-433.

DE VILLIERS, A.J., VON TEICHMAN, I., VAN ROOYEN, M.W. & THERON, G.K. 1996. Salinity-induced changes in anatomy, stomatal counts and photosynthetic rate of *Atriplex semibaccata* R. Br.. *South African Journal of Botany*, **62**: 270-276.

DUMBROFF, E.B. & COOPER, A. 1974. Effects of salt stress applied in balanced nutrient solutions at several stages during growth of tomato. *Botanical Gazette*, **135**: 219-224.

ENVIRONMENTAL EVALUATION UNIT. 1990. *Anglo American Corporation: West Coast heavy mineral sands project.* Unpublished report. University of Cape Town, Cape Town.

ESLER, K.J. & PHILLIPS, N. 1994. Experimental effects of water stress on semi-arid Karoo seedlings: implications for field seedling survivorship. *Journal of Arid Environments*, **26**: 325-337.

EVLAGON, D., RAVINA, I. & NEUMANN, P.M. 1992. Effects of salinity stress and calcium on hydraulic conductivity and growth in maize seedling roots. *Journal of Plant Nutrition*, **15**: 795-803.

FRANCO, J.A., FERNáNDEZ, J.A. & BAÑóN, S. 1997. Relationship between the effects of salinity on seedling leaf area and fruit yield of six Muskmelon cultivars. *Hortscience*, **32**: 642-644.

GREENWAY, H. & MUNNS, R. 1980. Mechanisms of salt tolerance in non-halophytes. *Annual Review of Plant Physiology*, **31**: 149-190.

GUL, B. & WEBER, D.J. 1998. Effect of dormancy relieving compounds on the seed germination of non-dormant *Allenrolfea occidentalis* under salinity stress. *Annals of Botany*, **82**: 555-560.

HEWITT, E.J. 1952. *Sand and water culture methods used in the study of plant nutrition.* Farnham Royal, Bucks, Commonwealth Agricultural Bureau.

HYDER, S.Z. & GREENWAY, H. 1965. Effects of Ca^{2+} on plant sensitivity to high NaCl concentrations. *Plant and Soil*, **23**: 258-260.

KATEMBE, W.J., UNGAR, I.A. & MITCHELL, J.P. 1998. Effect of salinity on germination and seedling growth of two *Atriplex* species (Chenopodiaceae). *Annals of Botany*, **82**: 167-175.

KEMP, P.R. & CUNNINGHAM, G.L. 1981. Light, temperature and salinity effects on growth, leaf anatomy and photosynthesis of *Distichlis spicata* (L.) Greene. *American Journal of Botany*, **68**: 507-516.

KHAN, M.A. & UNGAR, I.A. 1996. Influence of salinity and temperature on the germination of *Haloxylon recurvum* Bunge ex Boiss.. *Annals of Botany*, **78**: 547-551.

KINGSBURY, R.W. & EPSTEIN, E. 1986. Salt sensitivity in wheat. *Plant Physiology*, **80**: 651-654.

LLOYD, J.W. 1985. A plant ecological study of the farm 'Vaalputs', Bushmanland, with special reference to edaphic factors. M.Sc. dissertation, University of Cape Town, Cape Town.

MAAS, E.V. & HOFFMAN, G.J. 1977. Crop salt tolerance - current assessment. *Journal of the Irrigation and Drainage Division, ASCE*, **103**: 115-134.

MARIKO, S., KACHI, N., ISHIKAWA, S. & FURUKAWA, A. 1992. Germination ecology of coastal plants in relation to salt environment. *Ecological Research*, **7**: 225-233.

MASUDA, M., MAKI, M. & YAHARA, T. 1999. Effects of salinity and temperature on seed germination in a Japanese endangered halophyte *Triglochin maritimum* (Juncaginaceae). *Journal of Plant Research*, **112**: 457-461.

McMILLAN, C. 1959. Salt tolerance within a *Typha* population. *American Journal of Botany*, **46**: 521-526.

MILTON, S.J. 1995. Spatial and temporal patterns in the emergence and survival of seedlings in arid Karoo shrubland. *Journal of Applied Ecology*, **32**: 145-156.

MUNNS, R. & TERMAAT, A. 1986. Whole-plant responses to salinity. *Australian Journal of Plant Physiology*, **13**: 143-160.

RODRIGUEZ, H.G., ROBERTS, J.K.M., JORDAN, W.R. & DREW, M.C. 1997. Growth, water relations, and accumulation of organic and inorganic solutes in roots of maize seedlings during salt stress. *Plant Physiology*, **113**: 881-893.

SALIM, M. 1989. Effects of salinity and relative humidity on growth and ionic relations of plants. *New Phytologist*, **113**: 13-20.

SENECA, E.D. 1972. Seedling response to salinity in four dune grasses from the outer banks of North Carolina. *Ecology*, **53**: 465-471.

SINGH, K. 1990. Effect of soil salinity and sodicity on seedling growth and mineral composition of *Pongamia pinnata* and *Araucaria cunningamii*. *Tropical Ecology*, **31**: 124-130.

STROGONOV, B.P. 1964. *Physiological bases of salt tolerance of plants.* Israel Program for Scientific Translations, Jerusalem.

THERON, G.K. 1964. 'n Outekologiese studie van *Plinthus karooicus* Verdoorn. M.Sc. dissertation, University of Pretoria, Pretoria.

TIKU, B.L. & SNAYDON, R.W. 1971. Salinity tolerance in the grass species *Agrostis stolonifera* L.. *Plant and Soil*, **35**: 421-431.

TSONEV, T.D., LAZOVA, G.N., STOINOVA, Z.G. & POPOVA, L.P. 1998. A possible role for Jasmonic Acid in adaptation of barley seedlings to salinity stress. *Journal of Plant Growth Regulation*, **17**: 153-159.

UNGAR, I.A. 1962. Influence of salinity on seed germination in succulent halophytes. *Ecology*, **43**: 763-764.

UNGAR, I.A. 1995. Seed germination and seed-bank ecology in halophytes. In: Kigel, J. & Galilli, G. (eds). *Seed development and germination.* Marcel Dekker, New York. pp. 599-628.

UNGAR, I.A. 1996. Effect of salinity on seed germination, growth, and ion accumulation of *Atriplex patula* (Chenopodiaceae). *American Journal of Botany*, **83**: 604-607.

VAN HOORN, J.W. 1991. Development of soil salinity during germination and early seedling growth and its effect on several crops. *Agricultural Water Management*, **20**: 17-28.

VENABLES, A.V. & WILKINS, D.A. 1978. Salt tolerance in pasture grasses. *New Phytologist*, **80**: 613-622.

VOLKMAR, K.M., HU, Y. & STEPPUHN, H. 1998. Physiological responses of plants to salinity: a review. *Canadian Journal of Plant Science*, **78**: 19-27.

WAGNER, R.H. 1964. The ecology of *Uniola paniculata* L. in the dune-strand habitat of North Carolina. *Ecological Monographs*, **34**: 79-96.

WATT, T.A. 1983. The effects of salt water and soil type upon the germination, establishment and vegetative growth of *Holcus lanatus* L. and *Lolium perenne* L.. *New Phytologist*, **94**: 275-291.

WERNER, J.E. & FINKELSTEIN, R.R. 1995. *Arabidopsis* mutants with reduced response to NaCl and osmotic stress. *Physiologia Plantarum*, **93**: 659-666.

WILLIAMS, M.D. & UNGAR, I.A. 1972. The effect of environmental parameters on the germination, growth, and development of *Suaeda depressa* (Pursh) Wats. *American Journal of Botany*, **59**: 912-918.

YEO, A. 1999. Predicting the interaction between the effects of salinity and climate change on crop plants. *Scientia Horticulturae*, **78**: 159-174.

YOKOISHI, T. & TANIMOTO, S. 1994. Seed germination of the halophyte *Suaeda japonica* under salt stress. *Journal of Plant Research*, **107**: 385-388.

YOUNIS, A.F & HATATA, M.A. 1971. Studies on the effects of certain salts on germination, on growth of root, and on metabolism. I. Effects of chlorides and sulphates of sodium, potassium and magnesium on germination of wheat grains. *Plant and Soil*, **34**: 183-200.

ZHONG, H. & LÄUCHLI, A. 1993. Spatial and temporal aspects of growth in the primary root of cotton seedlings: effects of NaCl and $CaCl_2$. *Journal of Experimental Botany*, **44**: 763-771.

CHAPTER 16

CONCLUSIONS

Seed bank studies in the Succulent Karoo Biome previously focused on annual plant populations (Van Rooyen & Grobbelaar, 1982), "heuweltjies" in the Southern Succulent Karoo (Esler, 1993) and seed bank estimation methods (De Villiers *et al.*, 1994a). In general, very little attention has been given to the role of seed banks in restoration and revegetation processes (Levassor *et al.*, 1990; Moll, 1992; Aerts *et al.*, 1995; Bakker *et al.*, 1996; Kotanen, 1996). This thesis represents a first attempt to incorporate data on seed bank dynamics in the planning phase of post-mining revegetation processes in the Strandveld Succulent Karoo, South Africa.

The aim of the rehabilitation program along this coast is to restore mined areas as closely as possible to their pre-mining, natural condition, as soon as possible after mining has been completed (Environmental Evaluation Unit, 1990). The goal of revegetation at the Brand-se-Baai mining area (31°18'S, 17°54'E) is to obtain a vegetation cover, which contains plant species from all the pre-mining communities of the mined area. Six main plant communities were identified, described and mapped. Such descriptions of plant communities, together with the vegetation map, can serve as a basis in the final formulation of the rehabilitation plan for the area being mined. An understanding of the pre-mining plant communities and their associated habitats is of fundamental importance for devising sound rehabilitation, management and conservation strategies.

The floristic classification of the vegetation prior to mining activities served as a benchmark, and indicated species with which the greatest success, *i.e.* plant community composition and structure, would be achieved in the rehabilitation of the area. It is recommended that this program should concentrate on the perennial species, as these species dominate the pre-mining standing vegetation and will help to stabilize the mined sand during the windy, dry and hot summer months. Also, revegetating these species should restore the physiognomic structural appearance of the vegetation. It should be possible to revegetate the entire area with species abundant in almost all pre-mining communities. These constitute 28% of the total species richness of the area. Therefore, a realistic revegetation goal will be 30% of the total number of 230 plant species present prior to mining. Establishment of the grass species *Odyssea paucinervis* should be a priority in the western mining area.

Due to the high concentration of heavy minerals in the upper soil layers, topsoil replacement is not favoured for revegetation purposes by the mining company at Brand-se-Baai. However, results on the size and composition of the soil seed bank, as well as comparisons thereof with the standing vegetation, indicated that topsoil replacement will be vital for successful revegetation of the study area.

The soil seed bank of the Strandveld Succulent Karoo yielded a mean of 2 725 emerged seedlings m^{-2}, which belonged to 109 species. Annual species dominated the soil seed bank in terms of numbers, but in terms of species richness, the seed bank was not dominated by any specific plant type. The size of annual species' soil seed banks was large in comparison with annual inputs and losses, indicating the persistent nature of seed banks in these species. Seed banks of perennial species were small compared to annual inputs and losses, and are therefore of a transient nature.

The spatial pattern of soil seed bank density and composition was not as pronounced as that of the temporal pattern. Between vegetation units, variation in soil seed bank density, composition and species richness was relatively low. Mining of heavy minerals at the study site commences in a specific sequence, and topsoil is to be replaced directly to the adjacent preceding mined area (Environmental Evaluation Unit, 1990). Consequently, after revegetation by means of topsoil replacement, post-mining plant community boundaries may show little deviation from pre-mining boundaries. The effectiveness of topsoil replacement for the restoration of a specific plant community will therefore depend mainly on the size and composition of the seed bank of that community.

Seasonal variation in seed bank size and composition was relatively high at the study site. Samples collected during autumn and summer did not differ significantly from each other in terms of seed bank size, and include both the transient and persistent fractions of the soil seed bank. However, summer and autumn collected samples did differ significantly from each other in terms of emerged seedling density and species richness directly after sampling, 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 and species richness occurred in samples collected during autumn. Winter sampling indicated the presence of a large persistent seed bank, constituting *c.* 50% of the total soil seed bank species richness of the study area. Seedling recruitment from replaced topsoil and sowing should be restricted to the period of natural field emergence, *i.e.* autumn. Transplanting of selected species should commence during the winter months. During these periods, both moisture and temperature are usually non-limiting for the germination and survival of local species. In areas where topsoil replacement and sowing have been completed, irrigation should commence at the start of the rainy season, as many seeds present in the replaced topsoil will be in a state of dormancy during spring and summer. Also, temperatures during spring and summer may be too high for the seeds of most species to germinate. Although some seeds may germinate, the resulting seedlings will probably not survive during the hot seasons. Although the usefulness of annual species in the revegetation program will mainly be restricted to the wet and cool winter months, remaining plant debris may act as wind-breaks for the control of wind erosion. Irrigation, during the hot seasons following initial emergence events in autumn and/or winter, will be beneficial for the survival of perennial species' seedlings and adult plants.

The general dissimilarity between the seed bank and its associated vegetation was manifested by dissimilarities in species composition, plant/seedling densities and frequencies. The standing vegetation at the study site was not well represented in the seed bank samples, but the seed bank species were well represented in the standing vegetation. Those species recorded only in the seed bank were mainly annuals with relatively low densities and frequencies.

As in most arid ecosystems, the frequency distribution of seeds in the seed bank was highly kurtotic, since most samples had a few or no seeds and only a minor proportion had a large number of seeds. This general spatial pattern may in part be the result of the relatively short seed dispersal distances that characterise the majority of desert plants (Ellner & Shmida, 1981), or the consequence of directed dispersal by ants or rodents (Van Rheede van Oudtshoorn & Van Rooyen, 1999).

Species that were abundant in the seed bank of almost all plant communities constituted 15% of the total species richness of the standing vegetation. Species abundant in the seed bank of several communities made up another 4% to the species richness of the study area. Perennial species abundant in the seed bank of almost all communities will contribute 6% to the restored species richness of the study area.

In general, total, annual and perennial species' richness of all communities to be mined was higher in the standing vegetation than in the seed bank. According to Sorensens' index, similarity in total species composition between the standing vegetation and the soil seed bank was 54.3%. Higher similarity in annual than perennial species composition was obtained between the standing vegetation and the soil seed bank. An increase in species richness generally correlated with an increase in species composition similarity between the standing vegetation and the soil seed bank.

The seed bank contained in replaced topsoil will probably be a good predictor of the future vegetation. This is true for at least the early stages of succession in the mined area. Topsoil replacement alone will not be sufficient for reaching revegetation goals, as species abundant in the seed bank of most communities totalled only 19% of the total standing vegetation species richness. Considering only perennial species, this percentage decreased to 8%. Also, species dominant in the standing vegetation do not produce persistent seed banks. Even with a revegetation goal of 30%, sowing and transplanting of selected species will be indispensable.

Perennial taxa, which could be recruited in sufficient numbers from the soil seed bank include: *Nestlera biennis, Ruschia bolusiae, Ehrharta calycina,* Geophyte spp., *Tetragonia virgata, Manochlamys albicans, Ruschia brevicyma, Hypertelis salsoloides, Hermannia* spp. and *Zygophyllum morgsana.* Annual species abundant in the standing vegetation and the seed bank were *Senecio arenarius, Oncosiphon suffruticosum, Crassula expansa, Ficinia argyropa, Crassula umbellata, Manulea altissima, Isolepis marginata, Cotula thunbergii, Karroochloa schismoides, Pentaschistis patula* and *Helichrysum marmarolepis.*

Shrub species such as *Lycium ferocissimum, Asparagus retrofractus, Rhus longispina, Othonna floribunda* and *Lebeckia multiflora* were abundant in almost all communities in the standing vegetation, but were absent or less abundant in the soil seed bank, and should probably be reintroduced to mined areas by means of transplanting and sowing. Annuals and perennial herb species that were abundant in the standing vegetation but absent or less abundant in the seed bank, should be reintroduced by means of sowing, *e.g. Limeum africanum, Lyperia tristis, Grielum grandiflorum, Microloma sagittatum, Hebenstretia dentata* and *Heliophila coronopifolia.*

The presence of species in a seed bank disposes of many of the revegetation problems associated with collecting, storing, and sowing seeds or transplanting individuals, but it does not eliminate uncertainties associated with seed germination and seedling survival (Van der Valk & Pederson, 1989). Most annual species in this study obtained highest germination percentages and shortest mean times to germination at intermediate temperatures in the light. The perennial species in this study obtained highest germination percentages and shortest mean times to germination at a wide range of temperatures, in the absence of light. Revegetation efforts must therefore ensure that after sowing, seeds of perennial species are not merely left on top of the soil. A solution to some of these problems may be the replacement of topsoil after sowing, ensuring that the light requirements for germination of both perennial and annual species are met.

Another factor that influences the timing of germination is seed dormancy. The requirement of an after-ripening period by seeds indicates a delay in germination until the probability of seedling survival and plant growth is high (Baskin & Baskin, 1998). In the Strandveld Succulent Karoo, this germination strategy ensures that newly shed seeds do not germinate during occasional summer precipitation, as few seedlings will survive during the hot season. Of the species investigated, 52% required an after-ripening period, most of which were annuals or perennial herb species. Moisture and temperature probably control the timing of germination in most of the species from this area.

Mechanical scarification, short period chemical scarification, leaching, hydration/dehydration, heat, and/or cold treatments increased the germination of some species investigated. These artificial dormancy-breaking treatments may prove to be viable for species to be sown. However, most species exhibiting seed dormancy were found to be annuals, which also predominate the soil seed bank and will therefore be reintroduced to mined areas by means of topsoil replacement. Species to be sown are mainly perennial and exhibited less dormancy, rendering artificial dormancy-breaking treatments impractical.

An increase in relative humidity generally resulted in a decrease in seed viability. Seeds remained viable for longer periods under low temperature conditions in the laboratory, than under fluctuating temperatures in the field. Irrigation during summer after topsoil replacement in spring/summer may solve seedling recruitment problems related to low moisture, but the dormancy status of most annual species in the seed bank will prevent their germination. Also, the increase in relative humidity due to irrigation may result in increased seed moisture contents. Prevailing high summer temperatures and high relative humidities will enhance seed deterioration and consequently, seed viability and longevity will be reduced. Irrigation during the summer following topsoil replacement in spring/summer would result in the germination of many of the perennial shrub species, but seeds of annual species may be lost. Irrigation during the second summer after topsoil replacement in spring/summer will be beneficial for the survival of these perennial species, and many annual species would already have been recruited, matured and reproduced during the preceding winter.

Collected seeds of perennial shrub species should not be stored for too long, as they are probably not as long-lived as seeds of the annual species investigated. Recruitment of these species should occur during autumn, as germination during this season should provide sufficient time for seedling establishment and growth.

Species recruitment from replaced topsoil will be influenced by the period that seeds of different species remain viable in the seed bank. Because detailed studies could not be performed on all species present at the study site, the grouping of species with high abundancies, according to their expected seed bank strategies provided a means for determining the revegetation method best suited for each group or seed bank type. The key with laboratory characteristics of seeds to predict seed bank types seems to be well suited for the classification of seed banks of the Strandveld Succulent Karoo. Modifications to the original key (after Grime & Hillier, 1981) included: a dry heat pre-treatment rather than cold stratification, mean germination percentages of fresh and stored seeds (20°C for one month) were considered for both large and small seeds, some categories were subdivided due to the large number of species with persistent seed banks, and the time taken by seeds stored dry at 20°C for one month to reach 50% germination was not incorporated as a means of distinguishing between seed bank types.

Of the 37 species investigated, 32% have seeds with a transient seed bank strategy, while 68% exhibited persistent seed bank strategies. Five percent of the species produce small persistent seed banks, while 22% and 49% of the species have seed types which accumulate small short-term persistent seed banks and large persistent seed banks respectively. Predicted seed bank strategies should, however, be examined and checked in the field for each species.

Species of all five seed bank types identified will be important during the revegetation of mined areas at Brand-se-Baai. The anemochorous seeds of seed bank types 1, 2, 3b and 4 species may disperse into the post-mining revegetation areas from surrounding vegetation, but this would not be sufficient for revegetation purposes. During revegetation, species with types 3a, 3b and 4 seed bank strategies should originate from replaced topsoil. Seeds of species with the seed bank type 3a strategy should also be sown in selected areas, as these species have a restricted spatial distribution. Seeds of herb species with types 1 and 2 seed bank strategies should be reintroduced to post-mining areas by means of sowing, while adult plants of seed bank type 1 shrub species should be transplanted.

Seed dispersal distance and seed bank formation form only part of the total reproductive strategy of a species. Reproduction by seeds integrates a variety of critical life history processes, which are often separated far from each other in place and time of occurrence: these are pollination, seed development, dispersal, germination and seedling establishment (Van Rheede van Oudtshoorn & Van Rooyen, 1999). Successful regeneration depends on trade-offs between the often conflicting pressures and constraints imposed by these processes. However, because these multiple functions interact, they evolve as co-adapted syndromes. It is therefore impossible to evaluate the adaptive value of a particular dispersal mode without taking the constraints imposed by other life history functions into account. Factors such as flowering, seed production, predation, seed release time and duration, timing of germination, seedling survival and, after establishment, clonal and sexual reproduction speed may be equally important in restoration.

In the perennial species investigated, seed yield ranged from 9.1 to 27 444.1 seeds plant^{-1}, while that of annual species ranged from 77.2 to 807.8 seeds plant^{-1}. The mean number of seeds entering the seed pool ranged between 9.0 and 4851.8 seeds plant^{-1} for perennials and between 74.8 and 510.5 seeds plant^{-1} for annual species. The relationship between seed production and pre-dispersal seed predation appeared to be

density-dependent at the between species level. Pre-dispersal seed predators may have the potential to regulate species recruitment, especially in species that do not accumulate a persistent seed bank.

Seedling recruitment during the peak germination season (autumn) following dispersal was largely unaffected by post-dispersal predators. Since most perennials had low seed densities in the soil, plant recruitment may be reduced by seed predation. On the other hand, soil seed densities of most annual species were high. This may result in intense competition for access to suitable recruitment microsites and as a consequence, seed predation is unlikely to have any impact on mature plant density.

Seed-borne fungi will not affect seed numbers in the soil to a great extent, under natural environmental conditions. In the Strandveld Succulent Karoo, low seed mortality due to fungal attack could be ascribed to the combination of low occurrence (< 2%) and unfavourable environmental conditions for growth (low moisture during summer, low temperature during moist winters). Although irrigation in the hot, dry seasons may induce seed decay due to fungal attack, irrigation during the seasons following initial emergence in autumn, will be beneficial for the survival of seedlings of many species.

Poor seed germination and seedling mortality, due to environmental constraints like water stress, soil salinity, high temperature and pathogens will limit the success of revegetation efforts in the Strandveld Succulent Karoo. Transplanting of selected shrub species will increase species richness and therefore be beneficial for the restoration process. Apart from their role as wind-breaks, transplanted adult perennial plants may also reduce the period between revegetation and reproduction. Shrub species investigated did not act as nurse-plants, *i.e.* seedling numbers and species richness were higher in open areas than beneath shrub canopies. Seedling survival did not differ between these microhabitats. Seedlings of most annuals and perennial herb species will establish and survive in open areas at the study site. These species can be recruited from replaced topsoil and/or by sowing.

Sea-water is used in the mining process, leading to soil salinities few plants will be able to tolerate. The selection of local salt-tolerant species will therefore be advantageous to the revegetation of the area. When both germination and emergence are considered, perennial species will be better suited for revegetation on saline soil than annual species. The negative effect of salinity on the emergence and survival of the annual species investigated implies that the salinity of the soil should be very low for successful seedling emergence, and the soil salinity should be kept relatively low for better seedling survival. Also, annual species that do survive on soil with low salinities, yield almost no seeds. As seeds are annual species' only means of reproduction, these species will have to be revegetated from seed sources outside the mined area, or by sowing. If the salinity of the mined soil can be kept at a minimum concentration, perennial species will be able to survive and in some cases seed production may even be enhanced.

In practice the effect of salinity on germination and emergence may be much worse than in laboratory experiments, and will differ according to soil and season. High temperature will increase evaporation and capillary rise of salts, and may delay germination and emergence to such an extent that the seedlings are caught in the crust formed in the meantime.

It is very important to realise that the dynamics of the seed bank constitutes many processes influencing inputs and outputs to the seed bank, *e.g.* seed production, predation, dispersal, dormancy, germination, seed-borne pathogens and environmental conditions. Differential shifts in the relative importance of these processes can account for much of the differences observed in seed banks. Temporally, seed banks differentiate clearly into two fundamental types, transient and persistent. Whenever risk is high, persistent seed banks are favoured. At one level climate is of overriding importance; beyond that, factors including predation, dispersal, seed longevity, and biotic interference dictate seed bank and alternative regeneration diversity within a community.

In conclusion, these factors and processes will determine the revegetation method (topsoil replacement, sowing and transplanting) best suited for individual species. Taking all these factors into account, mining authorities should achieve great success in revegetating mined areas. Also, knowledge obtained from this seed bank study will aid plant ecologists to gain a better understanding of the processes contributing to reproductive strategies and plant population and community dynamics in the Strandveld Succulent Karoo.

SUMMARY

SEED BANK DYNAMICS OF THE STRANDVELD SUCCULENT KAROO

by

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Seed banks are influenced by many factors and processes related to more than one field of ecology. It is therefore necessary to consider all these components when assessing seed bank dynamics, which constitutes many processes influencing inputs and outputs to the seed bank. Apart from describing the seed bank dynamics of the Strandveld Succulent Karoo in terms of spatial and temporal variation in seed bank size and composition, factors such as seed production, predation, dispersal, dormancy, germination, seed-borne fungi and environmental conditions were investigated. This information was incorporated in the development of suitable post-mining revegetation strategies at a management level.

In the Strandveld Succulent Karoo, viable methods for the compulsory revegetation of post-mining areas include topsoil replacement, sowing and transplanting of selected species. An understanding of the pre-mining plant communities and their associated habitats is of fundamental importance to devise sound rehabilitation, management and conservation strategies.

Phytosociological benchmark studies on the pre-mining vegetation and seed bank indicated that in this species rich area, a realistic revegetation goal will be to return 30% of the total number of 230 plant species recorded. The soil seed bank of the study area yielded a mean of 2 725 seedlings m^{-2}, belonging to 109 species. Spatial variation in seed bank size and composition was not as pronounced as temporal variation. The general dissimilarity between the seed bank and its associated vegetation was manifested by dissimilarities in species composition, plant/seed densities and frequencies. The seed bank species were

well represented in the standing vegetation, but standing vegetation species were uncommon in the seed bank. Few species were unique to the seed bank.

Topsoil replacement, sowing and transplanting of selected species were found to be essential for the rehabilitation of this area after mining has been completed. Seeds of annual species were abundant and of a persistent nature in the soil seed bank, required a summer after-ripening period, germinated to higher percentages at intermediate temperatures in the light, and generally had lower seed yields than perennial species. Also, seed predation is unlikely to have any impact on mature plant density of annuals, their seedlings will establish in open microsites and they can be recruited from replaced topsoil during revegetation efforts.

Seeds of perennial herb species were less abundant and of both a persistent and transient nature in the seed bank, depending on the species. Revegetation using these species should involve sowing. Large seeded perennial shrub species were uncommon and of a transient nature in the seed bank. Transplanting will be a viable means for reestablishment of these species. In general, seeds of perennial species obtained highest germination percentages and shortest mean times to germination at a wide range of temperatures in the absence of light, and seed predators have the potential to regulate species recruitment of these species. Perennial species also yielded higher survival percentages and seed production under saline conditions.

Taking all factors involved in seed bank dynamics into account, mining authorities should achieve great success in revegetating mined areas. Furthermore, knowledge obtained from this seed bank study will aid plant ecologists in gaining a better understanding of the processes contributing to reproductive strategies and plant population and community dynamics in the Strandveld Succulent Karoo.

OPSOMMING

SAADBANKDINAMIKA VAN DIE STRANDVELD SUKKULENTE KAROO

deur

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Medeleier: Prof. G.K. Theron

DEPARTEMENT PLANTKUNDE

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'n Saadbank word deur verskeie faktore en prosesse, wat verband hou met meer as een veld van ekologie, beïnvloed. Dit is daarom noodsaaklik om al hierdie komponente in ag te neem indien die saadbankdinamika ondersoek word. Laasgenoemde is saamgestel uit verskeie prosesse wat toevoegings en verliese tot die saadbank beïnvloed. Buiten die beskrywing van die saadbankdinamika van die Strandveld Sukkulente Karoo in terme van ruimtelike en temporele variasie in saadbank grootte en samestelling, is faktore soos saadproduksie, predasie, saadverspreiding, dormansie, ontkieming, saadswamme en omgewingstoestande, ook ondersoek. Hierdie inligting is op bestuursvlak geïnkorporeer in die ontwikkeling van geskikte plantegroeihervestiging strategieë vir gebruik in rehabilitasie van gemynde areas.

Die terugplaas van bogrond, saai en oorplant van geselekteerde spesies word as lewensvatbare metodes beskou vir die verpligte hervestiging van plantegroei na mynbou-aktiwiteite in die Strandveld Sukkulente Karoo. Kennis van plantgemeenskappe en hul geassosieerde habitatte, voordat mynbou-aktiwiteite 'n aanvang neem, is van kardinale belang vir die daarstelling van goeie rehabilitasie-, bestuurs- en bewaringstrategieë.

Fitososiologiese studies van die staande plantegroei en saadbank, voor die aanvang van mynbou-aktiwiteite, het aangetoon dat 'n hervestigingsdoelwit van 30% van die 230 plantspesies aangeteken, realisties sal wees. Die saadbank van die studiegebied het gemiddeld 2 725 saailinge m^{-2} opgelewer, wat tot 109 spesies behoort het. Ruimtelike variasie in die grootte en samestelling van die saadbank was nie so opvallend soos

variasie in tyd nie. Die verskil tussen die saadbank en die geassosieerde bogrondse plantegroei is weerspieël deur verskille in spesiesamestelling, digtheid en frekwensie. Saadbank spesies was goed verteenwoordig in die bogrondse plantegroei, terwyl spesies van die staande plantegroei nie volop in die saadbank was nie. Min spesies het slegs in die saadbank voorgekom.

Nadat mynbou-aktiwiteite voltooi is, sal die terugplaas van bogrond, saai en oorplant van spesies noodsaaklik wees om plantegroei te hervestig. Sade van eenjarige spesies was volop en van 'n blywende aard in die saadbank, benodig 'n somer-narypingsperiode, het hoër ontkiemingspersentasies by intermediêre temperature in die lig, en het in die algemeen laer saadopbrengste as meerjarige spesies getoon. Verder is dit onwaarskynlik dat saadpredasie 'n inpak op die digtheid van volwasse eenjarige plante sal hê. Saailinge van eenjarige spesies kan vestig in onbeskutte mikrolokaliteite en gedurende plantegroeihervestiging kan hulle gewerf word vanuit teruggeplaasde bogrond.

Sade van meerjarige kruide was minder volop en beide blywend en kortstondig van aard in die saadbank, afhangend van die spesie. Hervestiging van hierdie spesies moet saai insluit. Die groot sade van meerjarige struikspesies was skaars en van kortstondige aard in die saadbank. Oorplanting sal 'n geskikte metode wees vir die hervestiging van hierdie spesies. In die algemeen het sade van meerjarige spesies hoër ontkiemingspersentasies en korter ontkiemingstempo's getoon by 'n wye reeks temperature in die afwesigheid van lig. Saadpredatore het die potensiaal om die werwing van hierdie spesies te reguleer. Meerjarige spesies het ook hoër oorlewingspersentasies en saadproduksie onder souttoestande getoon.

Mynbou-instansies behoort groot sukses te behaal in die hervestiging van plantegroei op gemynde areas, indien hulle alle faktore betrokke by saadbankdinamika in ag neem. Verder sal die kennis ingewin deur hierdie saadbankstudie plantekoloë help om die prosesse wat bydra tot voortplantingstrategieë asook plantpopulasie- en gemeenskapsdinamika van die Strandveld Sukkulente Karoo beter te verstaan.

APPENDIX 1

PLANT TAXA STUDIED AND/OR ENCOUNTERED IN THIS STUDY

Plant specimens are housed in the H.G.W.J. Schweickerd Herbarium,
University of Pretoria, Pretoria, South Africa

TAXON	REFERENCE	PLANT TYPE
Aizoaceae		
Adenogramma littoralis Adamson	A.J. de Villiers 305	Annual (A)
Coelanthum semiquinquefidum (Hook.f.) Druce	A.J. de Villiers 306	A
Galenia africana L. var. *africana*	A.J. de Villiers 7	Perennial (P)
Galenia sarcophylla Fenzl	Le Roux *et al.* (1997)	P
Hypertelis salsoloides (Burch.) Adamson var. *salsoloides*	M.W. van Rooyen 2229	P
Limeum africanum L. ssp. *africanum*	M.W. van Rooyen 2036	A
Pharnaceum aurantium (DC.) Druce	A.J. de Villiers 343, 344	P
Pharnaceum exiguum Adamson	A.J. de Villiers 230, 304	A
Pharnaceum lanatum Barti.	A.J. de Villiers 200	P
Pharnaceum microphyllum L.f.	A.J. de Villiers 285	P
Psammotropha quadrangularis (L.f.) Fenzl	A.J. de Villiers 102	A
Tetragonia microptera Fenzl	Le Roux *et al.* (1997)	A
Tetragonia pillansii Adamson	M.W. van Rooyen 2158	P
Tetragonia virgata Schltr.	A.J. de Villiers 222	P
Aloaceae		
Aloe framesii L.Bol.	Le Roux *et al.* (1997)	P
Amaryllidaceae		
Boophane sp.	Manning & Goldblatt (1996)	P
Brunsvigia orientalis (L.) Ait. ex Eckl.	A.J. de Villiers 61	P
Gethyllis sp.	Le Roux *et al.* (1997)	P
Haemanthus amarylloides Jacq. ssp. *polyanthus* Snijman	A.J. de Villiers 25	P
Anacardiaceae		
Rhus longispina Eckl. & Zeyh.	A.J. de Villiers 294	P
Apiaceae		
Annesorhiza macrocarpa Eckl. & Zeyh.	A.J. de Villiers 250	P
Sonderina tenuis (Sond.) H.Wolff	A.J. de Villiers 127	A
Asclepiadaceae		
Cynanchum africanum R.Br. var. *africanum*	A.J. de Villiers 301	P
Microloma sagittatum (L.) R.Br.	M.W. van Rooyen 2162	A
Asphodelaceae		
Bulbine sp.	Le Roux *et al.* (1997)	P
Trachyandra divaricata (Jacq.) Kunth	A.J. de Villiers 38	P
Trachyandra falcata (L.f.) Kunth.	M.W. van Rooyen 2601	P
Asteraceae		
Amellus microglossus DC.	A.J. de Villiers 238	A
Amellus tenuifolius Burm.	A.J. de Villiers 14, 88	P
Arctotheca calendula (L.) Levyns	A.J. de Villiers 249	A
Arctotis auriculata Jacq.	M.W. van Rooyen 2045	P
Arctotis hirsuta (Harv.) Beauv.	A.J. de Villiers 137, 189	A
Arctotis scullyi R.A.Dummer	M.W. van Rooyen 2140, 2248	P
Arctotis stoechadifolia Berg.	A.J. de Villiers 280, 283	P
Arctotis sp.	A.J. de Villiers 213	P
Arctotis sp. (ADV220)	A.J. de Villiers 220	A
Arctotis spp.	Le Roux *et al.* (1997)	P
Berkheya fruticosa (L.) Ehrh.	A.J. de Villiers 197, 247	P
Berkheya spinosa (L.f.) Druce	Van Breda & Barnard (1991)	P
Chrysanthemoides monilifera (L.) T.Norl. ssp. *pisifera* (L.) T.Norl.	A.J. de Villiers 12, 288	P
Chrysocoma longifolia DC.	M.W. van Rooyen 2150	P
Cotula thunbergii Harv.	A.J. de Villiers 147, 161, 191	A
Didelta carnosa (L.f.) Ait. var. *carnosa*	M.W. van Rooyen 2011	A

Didelta spinosa (L.f.) Alt.	M.W. van Rooyen 2293	P
Dimorphotheca nudicaulis (L.) DC.	Van Rooyen *et al.* (1999)	P
Dimorphotheca pluvialis (L.) Moench	M.W. van Rooyen 2201	A
Dimorphotheca sinuata DC.	H. Rosch 25	A
Eriocephalus africanus L.	M.W. van Rooyen 2161, 2419, 2533	P
Felicia dregei DC.	A.J. de Villiers 327	P
Felicia merxmuelleri Grau	A.J. de Villiers 226, 328	A
Foveolina tenella (DC.) Kallersjo	A.J. de Villiers 194	A
Gazania leiopoda (DC.) Roessl.	A.J. de Villiers 252	P
Gymnodiscus capillaris (L.f.) DC.	A.J. de Villiers 86	A
Helichrysum hebelepis DC.	M.W. van Rooyen 2179, 2440	P
Helichrysum incarnatum DC.	A.J. de Villiers 204	A
Helichrysum kraussii Sch.Bip.	Van Wyk & Malan (1988)	P
Helichrysum marmarolepis S.Moore	A.J. de Villiers 133, 146, B6	A
Helichrysum revolutum (Thunb.) Less.	M.W. van Rooyen 2252, 2442, 2564	A
Hirpicium alienatum (Thunb.) Druce	A.J. de Villiers 89	P
Leysera gnaphalodes (L.) L.	A.J. de Villiers 176	P
Nestlera biennis (Jacq.) Spreng.	A.J. de Villiers 111, 195, 281	P
Oncosiphon suffruticosum (L.) Kallersjo	H. Rosch 3	A
Othonna cuneata DC.	Le Roux *et al.* (1997)	P
Othonna floribunda Schltr.	A.J. de Villiers 196, 271, 9	P
Othonna sp1.	Le Roux *et al.* (1997)	P
Othonna sp2.	Le Roux *et al.* (1997)	P
Othonna sp3.	Le Roux *et al.* (1997)	P
Othonna sp4.	Le Roux *et al.* (1997)	P
Pteronia divaricata (Berg.) Less.	A.J. de Villiers 216, 279, 324	P
Pteronia onobromoides DC.	A.J. de Villiers 55, 91	P
Pteronia ovalifolia DC.	A.J. de Villiers 248	P
Pteronia paniculata Thunb.	A.J. de Villiers 319, 56	P
Pteronia spp.	Le Roux *et al.* (1997)	P
Senecio arenarius Thunb.	A.J. de Villiers 338	A
Senecio bulbinifolius DC.	M.W. van Rooyen 2114	P
Senecio cardaminefolius DC.	Le Roux *et al.* (1997)	A
Senecio niveus (Thunb.) Willd.	A.J. de Villiers 109	P
Stoebe nervigera (DC.) Sch.Bip.	A.J. de Villiers 110, 46	P
Trichogyne ambigua (L.) Druce	A.J. de Villiers 114	P
Tripteris clandestina Less.	A.J. de Villiers 333, 97	A
Tripteris oppositifolia (Aiton) B.Nord.	M.W. van Rooyen 2137, 2497	P
Tripteris sinuata DC.	Le Roux *et al.* (1997)	P
Ursinia nana DC.	Le Roux *et al.* (1997)	A
Ursinia speciosa DC.	A.J. de Villiers 126, 334, 74	A
Brassicaceae		
Brassica tournefortii Gouan	A.J. de Villiers 205	A
Cardamine hirsuta L.	A.J. de Villiers 232	A
Heliophila coronopifolia L.	A.J. de Villiers, H. Steyn & M. Nel 2	A
Campanulaceae		
Wahlenbergia androsacea A.DC.	A.J. de Villiers 75	A
Wahlenbergia paniculata (Thunb.) A.DC.	A.J. de Villiers 174, 184, 302, 310, 335	A
Wahlenbergia schlechteri V.Brehm.	A.J. de Villiers 227	A
Wahlenbergia sonderi Lammers	A.J. de Villiers 274	P
Caryophyllaceae		
Silene clandestina Jacq.	A.J. de Villiers 221	A
Celastraceae		
Gloveria integrifolia (L.f.) M.Jordaan	A.J. de Villiers 293	P
Maytenus sp.	M.W. van Rooyen 2213	P
Chenopodiaceae		
Atriplex lindleyi Moq. ssp. *inflata* (F.Mull.) P.G.Wilson	Le Roux *et al.* (1997)	P
Atriplex semibaccata R.Br.	Manning & Goldblatt (1996)	P
Chenopodium opulifolium Schrad. ex Koch & Ziz	A.J. de Villiers 167	A
Exomis microphylla (Thunb.) Aell. var. *microphylla*	Shearing & Van Heerden (1997)	P
Manochlamys albicans (Ait.) Aell.	A.J. de Villiers 18, 21, 51	P
Colchicaceae		
Ornithoglossum sp.	Le Roux *et al.* (1997)	P
Convolvulaceae		
Convolvulus sp.	M.W. van Rooyen 2190	P
Crassulaceae		
Crassula dichotoma L.	A.J. de Villiers 115	A
Crassula expansa Dryand. ssp. *expansa*	A.J. de Villiers 149, 33	A
Crassula muscosa L. var. *muscosa*	A.J. de Villiers 257, 40	P
Crassula nudicaulis L.	Mustart *et al.* (1997)	P
Crassula sp.1	A.J. de Villiers 22	P
Crassula tomentosa Thunb.	M.W. van Rooyen 2227	P
Crassula umbellata Thunb.	A.J. de Villiers 239	A
Tylecodon sp.	A.J. de Villiers 59	P

Cyperaceae		
Ficinia argyropa Nees	A.J. de Villiers 312	A
Isolepis marginata (Thunb.) Dietr.	A.J. de Villiers 225, 99	A
Scirpus dioecus (Kunth) Boeck.	A.J. de Villiers 136	P
Willdenowia incurvata (Thunb.) Linder	A.J. de Villiers 152	P
Ebenaceae		
Euclea racemosa Murray	A.J. de Villiers 260	P
Euphorbiaceae		
Clutia alaternoides L. var. *alaternoides*	A.J. de Villiers 94	P
Euphorbia burmannii E.Mey. ex Boiss.	M.W. van Rooyen 2258	P
Euphorbia caput-medusae L.	Manning & Goldblatt (1996)	P
Euphorbia decussata E.Mey. ex Boiss.	Le Roux *et al.* (1997)	P
Euphorbia filiflora Marloth	Leach (1986)	P
Euphorbia sp.	Le Roux *et al.* (1997)	P
Fabaceae		
Aspalathus divaricata Thunb. ssp. *divaricata*	A.J. de Villiers 262	P
Crotalaria humilis Eckl. & Zeyh.	A.J. de Villiers 223	A
Indigofera amoena Ait.	M.W. van Rooyen 2012	A
Indigofera intermedia Harv.	A.J. de Villiers 317	A
Lebeckia lotonoides Schltr.	A.J. de Villiers 188, 261	P
Lebeckia multiflora E.Mey.	Le Roux *et al.* (1997)	P
Lessertia benguellensis Bak.f.	A.J. de Villiers 308	A
Melolobium exudans Harv.	A.J. de Villiers 309	P
Wiborgia monoptera E.Mey.	A.J. de Villiers 81	P
Wiborgia obcordata (Berg.) Thunb.	A.J. de Villiers 85	P
Frankeniaceae		
Frankenia pulverulenta L.	A.J. de Villiers 138	A
Fumariaceae		
Cysticapnos cracca (Cham. & Schlechtd.) Liden	M.W. van Rooyen 2254	A
Geraniaceae		
Pelargonium dipetalum L'Hérit.	Bohnen (1986)	P
Pelargonium fulgidum (L.) L'Hérit.	A.J. de Villiers 132	P
Pelargonium gibbosum (L.) L'Hérit.	M.W. van Rooyen 2166	P
Pelargonium senecioides L'Hérit.	A.J. de Villiers 330	A
Pelargonium sp.1	H.M. Steyn 12	P
Pelargonium sp.2	M.W. van Rooyen 2243	P
Pelargonium spp.	Le Roux *et al.* (1997)	P
Sarcocaulon sp.	M.W. van Rooyen 2173	P
Hyacinthaceae		
Albuca exuviata Bak.	M.W. van Rooyen 2226	P
Albuca spp.	Le Roux *et al.* (1997)	P
Lachenalia spp.	A.J. de Villiers 129, Le Roux *et al.* (1997)	P
Iridaceae		
Babiana brachystachys (Bak.) G.J.Lewis	A.J. de Villiers 122	P
Babiana spp.	Manning & Goldblatt (1996)	P
Babiana thunbergii Ker-Gawl., Konig & Sims	M.W. van Rooyen 2138	P
Lapeirousia spp.	Le Roux *et al.* (1997)	P
Moraea spp.	Le Roux *et al.* (1997)	P
Lamiaceae		
Ballota africana (L.) Benth.	A.J. de Villiers 69	P
Ocimum canum Sims	A.J. de Villiers 171	A
Salvia africana-lutea L.	A.J. de Villiers 16, 54	P
Liliaceae		
Asparagus aethiopicus L.	A.J. de Villiers 295	P
Asparagus asparagoides (L.) W.Wight	A.J. de Villiers 296	P
Asparagus capensis L. var. *capensis*	A.J. de Villiers 303	P
Asparagus fasciculatus Thunb.	A.J. de Villiers 315	P
Asparagus retrofractus L.	A.J. de Villiers 313	P
Asparagus undulatus (L.f.) Thunb.	A.J. de Villiers 292	P
Melianthaceae		
Melianthus minor L.	A.J. de Villiers 66	P
Menispermaceae		
Cissampelos capensis L.f.	A.J. de Villiers 325, 77	P
Mesembryanthemaceae		
Aridaria sp. (RDV273)	A.J. de Villiers 273	P
Cephalophyllum spongiosum (L.Bol.) L.Bol.	A.J. de Villiers 5	P
Cephalophyllum sp.	A.J. de Villiers 282	P
Conicosia elongata N.E.Br.	Le Roux *et al.* (1997)	P
Conicosia pugioniformis (L.) N.E.Br. ssp. *alborosea* (L.Bol.) Ihlenfeldt & Gerbaulet	A.J. de Villiers 177, 318	P

Dorotheanthus bellidiformis (Burm.f.) N.E.Br. ssp. *hestermalanensis* Ihlenf. & Struck	M.W. van Rooyen 2321	A
Drosanthemum calycinum (Haw.) Schwant.	A.J. de Villiers 43	P
Drosanthemum spp.	A.J. de Villiers 182, 201, 277, 336	P
Drosanthemum sp. (RDV277)	A.J. de Villiers 277	P
Drosanthemum sp. (RDV336)	A.J. de Villiers 336	P
Lampranthus godmaniae (L.Bol.) L.Bol. var. *godmaniae*	A.J. de Villiers 278	P
Lampranthus lanatus (Willd.) N.E.Br.	A.J. de Villiers 103	P
Leipoldtia jacobeniana Schwant.	A.J. de Villiers 266, 267	P
Mesembryanthemaceae spp.	Smith *et al.* (1998)	P
Mesembryanthemum crystallinum L.	A.J. de Villiers B11	A
Monilaria chrysoleuca (Schltr.) Schwant. var. *chrysoleuca*	A.J. de Villiers 90	P
Prenia pallens (Ait.) N.E.Br.	A.J. de Villiers 264	P
Psilocaulon spp.	A.J. de Villiers 15, 19, 32, 36	P
Rhinephyllum frithii (L.Bol.) L.Bol.	A.J. de Villiers 290	P
Ruschia bolusiae Schwant.	A.J. de Villiers 300	P
Ruschia brevicyma L.Bol.	M.W. van Rooyen 2117	P
Ruschia caroli (L.Bol.) Schwant.	M.W. van Rooyen 2116	P
Ruschia cymosa (L.Bol.) Schwant.	M.W. van Rooyen 2086	P
Ruschia extensa L.Bol.	A.J. de Villiers 155	P
Ruschia firma L.Bol.	A.J. de Villiers 178	P
Ruschia namaquana L.Bol.	Smith *et al.* (1998)	P
Ruschia sp.1	Smith *et al.* (1998)	P
Ruschia sp. (GVR2245)	M.W. van Rooyen 2245	P
Ruschia subpaniculata L.Bol.	A.J. de Villiers 180	P
Ruschia tecta L.Bol.	A.J. de Villiers 246, 291	P
Ruschia tumidula (Haw.) Schwant.	A.J. de Villiers 105	P
Ruschia versicolor L.Bol.	H.M. Steyn 8	P
Species x4(RDV268)(Mesembryanthemaceae)	A.J. de Villiers 268	P
Species x7 (Mesembryanthemaceae)	A.J. de Villiers 270	P
Sphalmanthus sp. (RDV270)	A.J. de Villiers 270	P
Stoeberia sp.	A.J. de Villiers 179; Smith *et al.* (1998)	P
Vanzijlia annulata (Berger) L.Bol.	A.J. de Villiers 3	P
Oxalidaceae		
Oxalis pardalis Sond.	A.J. de Villiers 254	P
Oxalis spp.	A.J. de Villiers 151, Le Roux *et al.* (1997)	P
Plumbaginaceae		
Limonium perigrinum (Berg.) R.A.Dyer	A.J. de Villiers 13, 28	P
Limonium sp.	M.W. van Rooyen 2230	P
Poaceae		
Bromus pectinatus Thunb.	A.J. de Villiers 119, 210	A
Chaetobromus dregeanus Nees	A.J. de Villiers 112, 311	P
Chloris pycnothrix Trin.	A.J. de Villiers 168	A
Cladoraphis cyperoides (Thunb.) S.M.Phillips	M.W. van Rooyen 2228	P
Ehrharta brevifolia Schrad. var. *brevifolia*	A.J. de Villiers 145	A
Ehrharta calycina J.E.Sm.	A.J. de Villiers 251	P
Karroochloa schismoides (Stapf ex Conert) Conert & Tuerpe	A.J. de Villiers 162	A
Odyssea paucinervis (Nees) Stapf	M.W. van Rooyen 2223	P
Pentaschistis patula (Nees) Stapf	A.J. de Villiers 331	A
Species x2(Poaceae)	Van Oudtshoorn (1991)	A
Species x3(RDV286)(Poaceae)	A.J. de Villiers 286	P
Stipagrostis zeyheri (Nees) De Winter ssp. *macropus* (Nees) De Winter	A.J. de Villiers 106, 209, 307	P
Polygonaceae		
Emex australis Steinh.	A.J. de Villiers 206	A
Rumex spp.	Le Roux *et al.* (1997)	A
Portulacaceae		
Portulaca quadrifida L.	A.J. de Villiers 229	A
Rosaceae		
Grielum grandiflorum (L.) Druce	M.W. van Rooyen 2013	P
Grielum humifusum Thunb. var. *humifusum*	A.J. de Villiers 192	A
Rubiaceae		
Galium tomentosum Thunb.	A.J. de Villiers 326	P
Santalaceae		
Thesium spinosum L.f.	M.W. van Rooyen 2122	P
Scropulariaceae		
Diascia sp.	A.J. de Villiers 329	A
Hemimeris racemosa (Houtt.) Merrill	A.J. de Villiers 186	A
Lyperia tristis (L.f.) Benth.	A.J. de Villiers 337	A
Manulea altissima L.f. ssp. *altissima*	M.W. van Rooyen 2203	A
Manulea cinerea Hilliard	A.J. de Villiers 284	P
Manulea pusilla E.Mey. ex Benth.	A.J. de Villiers 143	A
Nemesia bicornis (L.) Pers.	M.W. van Rooyen 2152	P
Nemesia ligulata E.Mey. ex Benth.	A.J. de Villiers 183	A
Polycarena pumila (Benth.) Levyns	A.J. de Villiers 235	A
Zaluzianskya villosa (Thunb.) F.W.Schmidt	M.W. van Rooyen 2005	A

Selaginaceae		
Hebenstretia dentata L.	A.J. de Villiers 207	A
Hebenstretia repens Jarosz	A.J. de Villiers 231, 236	A
Solanaceae		
Lycium ferocissimum Miers	A.J. de Villiers 245,258,287	P
Lycium sp.	A.J. de Villiers 259,323	P
Lycium spp.	Le Roux *et al.* (1997)	P
Solanum guineense L.	A.J. de Villiers 154, 71	P
Sterculiaceae		
Hermannia amoena Dinter ex M.Holzhammer	A.J. de Villiers 298	P
Hermannia cernua Thunb. ssp. *eroidioides*	M.W. van Rooyen 2159	P
Hermannia cuneifolia Jacq. var. *cuneifolia*	A.J. de Villiers 297	P
Hermannia modesta (Ehrenb.) Mast.	A.J. de Villiers 116	P
Hermannia scordifolia Jacq.	A. J. de Villiers 107, 203	A
Hermannia sp.	A.J. de Villiers 299	P
Hermannia spp.	Le Roux *et al.* (1997)	P
Tecophilaeaceae		
Ferraria densepunctulata De Vos	A.J. de Villiers 121	P
Ferraria divaricata Sweet ssp. *aurea* De Vos	A.J. de Villiers 130	P
Ferraria spp.	Le Roux *et al.* (1997)	P
Viscaceae		
Viscum capense L.f. ssp. *capense*	A.J. de Villiers 181	P
Zygophyllaceae		
Zygophyllum meyeri Sond.	Le Roux *et al.* (1997)	P
Zygophyllum morgsana L.	A.J. de Villiers 4	P
Zygophyllum pygmaeum Eckl. & Zeyh.	A.J. de Villiers 79	P

APPENDIX 2

CURRICULUM VITAE

Adriaan Jakobus De Villiers was born in Boksburg on the 10th of February 1967. He started his education in 1973 at the Baanbreker Primary School and matriculated in 1984 from Voortrekker High School, Boksburg.

In 1988 he obtained the B.Sc. degree with Botany and Zoology as main subjects, and in 1989 the B.Sc. Hons. (Botany) (*cum laude*) at the University of Pretoria.

During 1990 and 1991 he completed his South African military service with a rank of 1st Lieutenant in the Engineering Corps. During this period he also obtained a post-graduate diploma in Terrain Evaluation from the Potchefstroom University for Christian Higher Education.

In 1991 he enrolled for the M.Sc. (Botany) degree at the University of Pretoria, which he obtained *cum laude* in 1993 for his dissertation entitled: "Ecophysiological studies on several Namaqualand pioneer species, with special reference to the revegetation of saline mined soil".

During the period 1989 to 1998 he worked as academic assistant, research assistant, tutor and demonstrator in the Botany Department of the University of Pretoria. In 1997 he also worked as demonstrator for the Vista University. He is currently employed as a Senior Agricultural Product Technician by the National Department of Agriculture, in the Variety Control Division, Genetic Resources, Roodeplaat.

He was author or co-author of eight publications, four unpublished reports, and was involved in the presentation of ten scientific papers/posters. He also was the photographer of the field guide to the wild flowers of the Cederberg, which was published in 1999.

REFERENCES

ABDUL-HALIM, R.K., SALIH, H.M., AHMED, A.A. & ABDUL-RAHEM, A.M. 1988. Growth and development of maxipak wheat as affected by soil salinity and moisture levels. *Plant and Soil,* **112**: 255-259.

ACOCKS, J.P.H. 1988. Veld types of South Africa. 3rd ed. *Memoirs of the botanical Survey of South Africa*, **57**: 1-146.

ADAMS, R., ADAMS, M., WILLENS, A. & WILLENS, A. 1978. *Dry lands: Man and plants.* The Architectural Press, London.

AERTS, R., HUISZOON, A., VAN OOSTRUM, J.H.A., VAN DE VIJVER, C.A.D.M. & WILLEMS, J.H. 1995. The potential for heathland restoration on formerly arable land at a site in Drenthe, The Netherlands. *Journal of Applied Ecology*, **32**: 827-835.

AHMED, S.U. 1985. Germination and seedling growth characteristics of some cultivated and wild selections of wheat cultured in sea water. *Journal of Arid Environments*, **8**: 133-139.

ALBRECHT, H. & FORSTER, E.-M. 1996. The weed seed bank of soils in a landscape segment in southern Bavaria – I. Seed content, species composition and spatial variability. *Vegetatio*, **125**: 1-10.

ANDERSEN, A.N. 1988. Insect seed predators may cause far greater losses than they appear to. *Oikos*, **52**: 337-340.

ANDERSEN, A.N. 1989. How important is seed predation to recruitment in stable populations of long-lived perennials? *Oecologia*, **81**: 310-315.

ARCHIBOLD, O.W. 1981. Buried viable propagules in native prairie and adjacent agricultural sites in central Saskatchewan. *Canadian Journal of Botany*, **59**: 701-706.

ARNOLD, T.H. & DE WET, B.C. 1993. Plants of southern Africa: names and distribution. *Memoirs of the botanical Survey of South Africa*, **62**: 1-825.

ARNOLD, T.H. & DE WET, B.C. 1999. Plants of southern Africa: names and distribution. Electronic data-base, National Botanical Institute, Pretoria.

ASHRAF, M. & O'LEARY, J.W. 1996. Responses of some newly developed salt-tolerant genotypes of spring wheat to salt stress: 1. Yield components and ion distribution. *Journal of Agronomy and Crop Science,* **176**: 91-101.

ASHRAF, M. & TUFAIL, M. 1995. Variation in salinity tolerance in sunflower (*Helianthus annuus* L.). *Journal of Agronomy and Crop Science,* **174**: 361-362.

AZAIZEH, H., GUNSE, B. & STEUDLE, E. 1992. Effects of NaCl an $CaCl_2$ on water transport across root cells of maize (*Zea mays* L.) seedlings. *Plant Physiology*, **99**: 886-894.

AZIZ, S. & KHAN, M.A. 1996. Seed bank dynamics of a semi-arid coastal shrub community in Pakistan *Journal of Arid Environments*, **34**: 81-87.

BADGER, K.S. & UNGAR, I.A. 1989. The effects of salinity and temperature on the germination of the inland halophyte *Hordeum jubatum*. *Canadian Journal of Botany*, **67**: 1420-1425.

BADGER, K.S. & UNGAR, I.A. 1994. Seed bank dynamics in an inland salt marsh, with special emphasis on the halophyte *Hordeum jubatum* L.. *International Journal of Plant Science*, **155**: 66-72.

BAKKER, J. P. 1989. *Nature management by grazing and cutting.* Kluwer Academic, Dordrecht.

BAKKER, J.P., POSCHLOD, P., STRYKSTRA, R.J., BEKKER, R.M. & THOMPSON, K. 1996. Seed banks and seed dispersal: important topics in restoration ecology. *Acta Botanica Neerlandica*, **45**: 461-490.

BANULS, J., LEGAZ, F. & PRIMO-MILLO, E. 1991. Salinity-calcium interactions on growth and ionic concentration of Citrus plants. *Plant and Soil*, **133**: 39-46.

BARBERI, P., MACCHIA, M. & BONARI, E. 1998. Comparison between the seed extraction and seedling emergence methods for weed seedbank evaluation. *Aspects of Applied Biology*, **51**: 9-14.

BARBOUR, M.G. 1968. Germination requirements of the desert shrub *Larrea divaricata*. *Ecology*, **49**: 915-923.

BASKIN C.C. & BASKIN, J.M. 1998. *Seeds: Ecology, biogeography, and evolution of dormancy and germination*. Academic Press, London.

BASKIN, J.M. & BASKIN, C.C. 1976a. High temperature requirement for afterripening in seeds of winter annuals. *New Phytologist*, **77**: 619-624.

BASKIN, J.M. & BASKIN, C.C. 1976b. Effect of photoperiod on germination of *Cyperus inflexus* seeds. *Botanical Gazette*, **137**: 269-273.

BASKIN, J.M. & BASKIN, C.C. 1978. The seed bank in a population of an endemic plant species and its ecological significance. *Biological Conservation*, **14**: 125-130.

BASKIN, J.M & BASKIN, C.C. 1985. The annual dormancy cycle in buried weed seeds: A continuum. *BioScience*, **35**: 492-498.

BASKIN, J.M., TYNDALL, R.W., CHAFFINS, M. & BASKIN, C.C. 1998. Effect of salinity on germination and viability of nondormant seeds of the federal-threatened species *Aeschynomene virginica* (Fabaceae). *Journal of the Torrey Botanical Society*, **125**: 246-248.

BAUER, H.J. 1973. Ten years' studies of biocoenological succession in the excavated mines of the Cologne lignite district. In: Hutnik, R.J. & Davis, G. (eds). *Ecology and reclamation of devastated land*. Gordon & Breach, New York. pp. 271-283.

BECKSTEAD, J., MEYER, S.E. & ALLEN, P.S. 1996. *Bromus tectorum* seed germination: between-population and between-year variation. *Canadian Journal of Botany*, **74**: 875-882.

BELL, D.T., PLUMMER, J.A. & TAYLOR, S.K. 1993. Seed germination ecology in Southwestern Western Australia. *The Botanical Review*, **59**: 24-73.

BENEKE, K., VAN ROOYEN, M.W., THERON, G.K. & VAN DE VENTER, H.A. 1993. Fruit polymorphism in ephemeral species of Namaqualand: III. Germination differences between the polymorphic diaspores. *Journal of Arid Environments*, **24**: 333-344.

BENOIT, D.L., KENKEL, N.C. & CAVERS, P.B. 1989. Factors influencing the precision of soil seed bank estimates. *Canadian Journal of Botany*, **67**: 2833-2840.

BERGE, G. & HESTMARK, G. 1997. Composition of seed banks of roadsides, stream verges and agricultural fields in southern Norway. *Annales Botanici Fennici*, **34**: 77-90.

BERGER, A. 1985. Seed dimorphism and germination behaviour in *Salicornia patula*. *Vegetatio*, **61**: 137-143.

BERTILLER, M.B. 1998. Spatial patterns of the germinable soil seed bank in northern Patagonia. *Seed Science Research*, **8**: 39-45.

BEUKMAN, R.P. 1991. The role of nurse plants in the vegetation dynamics of the succulent karoo. M.Sc. dissertation, University of Cape Town, Cape Town.

BEWLEY, J.D. & BLACK, M. 1982. *Physiology and biochemistry of seeds*. Springer-Verlag, Heidelberg.

BEWLEY, J.D. & BLACK, M. 1994. *Seeds: Physiology of development and germination*. Plenum Press, London.

BEZUIDENHOUT, H. 1995. An ecological study of the major vegetation communities of the Vaalbos National Park, Northern Cape. 2. The Graspan-Holpan section. *Koedoe*, **38**: 65-83.

BIGWOOD, D.W. & INOUYE, D.W. 1988. Spatial pattern analysis of seed banks: an improved method and optimized sampling. *Ecology*, **69**: 497-507.

BLOMERUS, J.J. 1992. 'n Voorlopige outekologiese ondersoek na die seleksie van plante vir hervestiging in verbrakte omgewings in Suid-Afrika. M.Sc. dissertation. University of Stellenbosch, Stellenbosch.

BLUM, A. 1988. Plant breedings for stress environments. *CRC Critical Review in Plant Science*, **2**: 199-238.

BOGEMANS, J., NEIRINCKX, L. & STASSART, J.M. 1989. Effect of deicing NaCl and $CaCl_2$ on spruce (*Picea abies* (L.) sp.). *Plant and Soil*, **120**: 203-211.

BOHNEN, P. 1986. *Blomplante van Suid-Kaapland.* Die Stilbaai-trust, Stilbaai.

BOND, P. & GOLDBLATT, P. 1984. Plants of the Cape flora – A descriptive catalogue. *Journal of South African Botany*, Supplementary volume **13**: 1-455.

BORCHERT, M.I. & JAIN, S.K. 1978. The effect of rodent seed predation on four species of California annual grasses. *Oecologia*, **33**: 101-113.

BORTHWICK, H.A., HENDRICKS, S.B., TOOLE, E.H. & TOOLE, V.K. 1952. A reversible photoreaction controlling seed germination. *Proceedings of the National Academy of Science*, **38**: 662-666.

BOUCHER, C. & LE ROUX, A. 1990. Heavy mineral sand mining project assessment vegetation report. In: Environmental Evaluation Unit. *Anglo American Corporation: West Coast heavy mineral sands project - Supplementary Report.* Unpublished report. University of Cape Town, Cape Town. Section A5.

BOUCHER, C. & LE ROUX, A. 1993. Dry coastal ecosystems of the South African West Coast. *In:* Goodall, D.W. & Van der Maarel, E. (eds). *Ecosystems of the World. Volume 2B. Dry Coastal Ecosystems*, Elsevier, Amsterdam. pp. 75-88.

BOUWMEESTER, H.J. 1990. The effect of environmental conditions on the seasonal dormancy pattern and germination of weed seeds. Ph.D. thesis, Agricultural University in Wageningen, Wageningen.

BOUZA, P. & DEL VALLE, H.F. 1993. Micromorphological, physical, and chemical characteristics of soil crust types of the central Patagonia region, Argentina. *Arid Soil Research and Rehabilitation*, **7**: 355-368.

BOYD, R.S. & BRUM, G.D. 1983. Post-dispersal reproductive biology of Mojave desert population of *Larrea tridentata* (Zygophyllaceae). *American Midland Naturalist*, **110**: 25-36.

BRADBEER, J.W. 1988. *Seed dormancy and germination.* Chapman & Hall, London.

BRECK, S.W & JENKINS, S.H. 1997. Use of an ecotone to test the effects of soil and desert rodents on the distribution of Indian ricegrass. *Ecography*, **20**: 253-263.

BREDENKAMP G.J. & BEZUIDENHOUT, H. 1995. A proposed procedure for the analysis of large phytosociological data sets in the classification of South African grasslands. *Koedoe*, **38**: 33-39.

BROWN, R.F. 1987. Germination of *Aristida armata* under constant and alternating temperatures and its analysis with the accumulative Weibull distribution as a model. *Australian Journal of Botany*, **35**: 581-591.

BüNNING, E. 1965. Endogenous rhythmic activities. *Encyclopedia of Plant Physiology*, **15**: 879-907.

BURDON, J.J., MARSHALL, D.R. & BROWN, A.H.D. 1983. Demographic and genetic changes in populations of *Echium plantagineum*. *Journal of Ecology*, **71**: 667-679.

BURMAN, L., BEAN, A. & BURMAN, J. 1985. *Hottentots Holland to Hermanus. South African Wild Flower Guide 5.* Botanical Society of South Africa, Kirstenbosch.

BURROWS, C.J. 1989. Patterns of delayed germination in seeds. *New Zealand Natural Sciences*, **16**: 13-19.

BURROWS, C.J. 1994. The seeds always know best. *New Zealand Journal of Botany*, **32**: 349-363.

CAIXINHAS, M.L., JERONIMO, A., ROCHA, F. & LEITAO, A. 1998. Relationship between the seedbank and actual weed flora in one agricultural soil in the Tapada da Ajuda (Lisboa). *Aspects of Applied Biology*, **51**: 51-57.

CAPON, B. & VAN ASDALL, W. 1967. Heat pre-treatment as a means of increasing germination of desert annual seeds. *Ecology*, **48**: 305-306.

CARLSSON, B.A. & CALLAGHAN, T.V. 1991. Positive plant interactions in Tundra vegetation and the importance of shelter. *Journal of Ecology*, **79**: 973-983.

CASPER, B.B. 1988. Post-dispersal seed predation may select for wind dispersal but not seed number per dispersal unit in *Cryptantha flava*. *Oikos*, **52**: 27-30.

CAVERS, P. 1983. Seed demography. *Canadian Journal of Botany*, **61**: 3578-3590.

CHAMBERS, J.C. 1993. Seed and vegetation dynamics in an alpine herb field: effects of disturbance type. *Canadian Journal of Botany*, **71**: 471-485.

CHAPIN, F.S., WALKER, R.L., FASTIE, C.L. & SHARMAN, L.C. 1994. Mechanisms of primary succession following deglaciation at Glacier Bay, Alaska. *Ecological Monographs*, **64**: 149-175.

CHARTZOULAKIS, K.S. & LOUPASSAKI, M.H. 1997. Effects of NaCl salinity on germination, growth, gas exchange and yield of greenhouse eggplant. *Agricultural Water Management*, **32**: 215-225.

CHIPPINDALE, H.G. & MILTON, W.E.J. 1934. On the viable seeds present in the soil beneath pastures. *Journal of Ecology*, **22**: 508-531.

CHRISTENSEN, C.M. 1972. Microflora and seed deterioration. In: Roberts, E.H. (ed). *Viability of seeds*. Syracuse University Press, U.S.A. pp. 59-93.

CODD, L.E., DE WINTER, B., KILLICK, D.J.B. & RYCROFT, H.B. 1970. Brassica. *Flora of Southern Africa*, **13**: 5-7.

COFFIN, D.P. & LAUENROTH, W.K. 1989. Spatial and temporal variation in the seed bank of a semiarid grassland. *American Journal of Botany*, **76**: 53-58.

CONNER, L.N. & CONNER, A.J. 1988. Seed biology of *Chordospartium stevensonii*. *New Zealand Journal of Botany*, **26**: 473-475.

COPELAND, L.O. & McDONALD, M.B. 1995. *Principles of seed science and technology*. Chapman & Hall, New York.

CORBINEAU, F., BELAID, D. & COME, D. 1992. Dormancy of *Bromus rubens* L. seeds in relation to temperature, light and oxygen effects. *Weed Research*, **32**: 303-310.

COUNCIL FOR SCIENTIFIC AND INDUSTRIAL RESEARCH. 1997. Prints of climate statistics of the Brand-se-Baai Station from March 1993 up to February 1997. Pretoria.

COWLING, R.M. 1986. A description of the Karoo Biome Project. *South African National Scientific Programmes Report* No. 122, Council for Scientific and industrial Research, Pretoria.

COWLING, R.M. & HILTON-TAYLOR, C. 1999. Plant biogeography, endemism and diversity. In: Dean, W.R.J. & Milton, S.J. (eds). *The Karoo – Ecological patterns and processes*. Cambridge University Press, Cambridge. pp. 42-56.

COWLING, R.M., ESLER, K.J. & RUNDEL, P.W. 1999. Namaqualand, South Africa – an overview of a unique winter-rainfall desert ecosystem. *Plant Ecology*, **142**: 3-21.

CRAWFORD, R.M.M. 1989. *Studies in plant survival. Ecological case histories of plant adaptation to adversity.* Blackwell Scientific Publications, Oxford.

CRAWLEY, M.J. 1992. Seed predators and plant population dynamics. In: Fenner, M. (ed). *Seeds – The ecology of regeneration in plant communities.* CAB International, Wallingford. pp. 157-191.

CROCKER, W. & BARTON, L.V. 1957. *Physiology of seeds: An introduction to the experimental study of seed and germination problems.* Chronica Botany Company, Waltham, Massachusetts.

CUMMINGS, B.C. & WAGNER, E. 1968. Rhythmic processes in plants. *Annual Review of Plant Physiology*, **19**: 381-416.

CUNLIFFE, R.N., JARMAN, M.L., MOLL, E.J. & YEATON R.I. 1990. Competitive interactions between the perennial shrub *Leipoldtia constricta* and an annual forb, *Gorteria diffusa*. *South African Journal of Botany*, **56**: 34-38.

CURTIS, N.P. 1996. Germination and seedling survival studies of *Xanthorrhoea australis* in the Warby Range State Park, North-eastern Victoria, Australia. *Australian Journal of Botany*, **44**: 635-647.

DARWIN, C. 1859. *On the origin of species by means of natural selection.* J. Murray, London.

DATTA, S.C. 1965. Germination of seeds of two arid zone species. *Bulletin of the Botanical Society of Bengal*, **19**: 51-53.

DE JONG, T.J. & KLINKHAMER, P.G.L. 1988. Seedling establishment of the biennials *Cirsium vulgare* and *Cynoglossum officinale* in a sand-dune area: The importance of water for differential survival and growth. *Journal of Ecology*, **76**: 393-402.

DE STEVEN, D. 1983. Reproductive consequences of insect seed predation in *Hamamelis virginiana*. *Ecology*, **64**: 89-98.

DE VILLIERS, A.J. 1993. Ecophysiological studies on several Namaqualand pioneer species, with special reference to the revegetation of saline mined soil. MSc. dissertation, University of Pretoria, Pretoria.

DE VILLIERS, A.J., VAN ROOYEN, M.W. & THERON, G.K. 1994a. Comparison of two methods for estimating the size of the viable seed bank of two plant communities in the Strandveld of the west coast, South Africa. *South African Journal of Botany*, **60**: 81-84.

DE VILLIERS, A.J., VAN ROOYEN, M.W. & THERON, G.K. 1994b. Removal of sodium and chloride from a saline soil by *Mesembryanthemum barklyi*. *Journal of Arid Environments*, **29**: 325-330.

DE VILLIERS, A.J., VAN ROOYEN, M.W. & THERON, G.K. 1999b. Seed production of four Namaqualand pioneer plant species grown on saline soil. *South African Journal of Botany*, **65**: 110-112.

DE VILLIERS, A.J., VAN ROOYEN, M.W., THERON, G.K. & CLAASSENS, A.S. 1995. The effect of leaching and irrigation on the growth of *Atriplex semibaccata*. *Land Degradation and Rehabilitation*, **6**: 125-131.

DE VILLIERS, A.J., VAN ROOYEN, M.W., THERON, G.K. & CLAASSENS, A.S. 1997. Tolerance of six Namaqualand pioneer species to saline soil conditions. *South African Journal of Plant and Soil*, **14**: 38-42.

DE VILLIERS, A.J., VAN ROOYEN, M.W., THERON, G.K. & VAN DE VENTER, H.A. 1994c. Germination of three Namaqualand pioneer species, as influenced by salinity, temperature and light. *Seed Science & Technology*, **22**: 427-433.

DE VILLIERS, A.J., VAN ROOYEN, M.W., THERON, G.K. & VAN ROOYEN, N. 1999a. Vegetation diversity of the Brand-se-Baai coastal dune area, West Coast, South Africa: A pre-mining benchmark survey for rehabilitation. *Land Degradation & Development*, **10**: 207-224.

DE VILLIERS, A.J., VON TEICHMAN, I., VAN ROOYEN, M.W. & THERON, G.K. 1996. Salinity-induced changes in anatomy, stomatal counts and photosynthetic rate of *Atriplex semibaccata* R. Br.. *South African Journal of Botany*, **62**: 270-276.

DEAN, M.R.J., MILTON, S.J., WATKEYS, M.K. & HOCKEY, P.A.R. 1991. Distribution, habitat preference and conservation status of the Red Lark *Certhilauda burra* in Cape Province, South Africa. *Biological Conservation*, **58**: 257-274.

DEAN, W.R.J. & MILTON, S.J. 1999. Animal foraging and food. In: Dean, W.R.J. & Milton, S.J. (eds). *The Karoo – Ecological patterns and processes.* Cambridge University Press, Cambridge. pp. 164-177.

DEAN, W.R.J. & YEATON, R.I. 1992. The importance of harvester ant *Messor capensis* nest mounds as germination sites in the southern Karoo, South Africa. *African Journal of Ecology*, **30**: 335-345.

DERKX, M.P.M. & KARSSEN, C.M. 1994. Are seasonal dormancy patterns in *Arabidopsis thaliana* regulated by changes in seed sensitivity to light, nitrate and gibberellin ? *Annals of Botany*, **73**: 129-136.

DESMET, P.G. & COWLING, R.M . 1999. The climate of the karoo – a functional approach. In: Dean, W.R.J. & Milton, S.J. (eds). *The Karoo – Ecological patterns and processes.* Cambridge University Press, Cambridge. pp. 3-16.

DUMBROFF, E.B. & COOPER, A. 1974. Effects of salt stress applied in balanced nutrient solutions at several stages during growth of tomato. *Botanical Gazette*, **135**: 219-224.

DUTOIT, T. & ALARD, D. 1995. Permanent seed banks in chalk grassland under various management regimes: their role in the restoration of species-rich plant communities. *Biodiversity and Conservation*, **4**: 939-950.

EHRLÉN, J. 1996. Spatiotemporal variation in predispersal seed predation intensity. *Oecologia*, **108**: 708-713.

ELLIS, R.H. & ROBERTS, E.H. 1981. The quantification of ageing and survival in orthodox seeds. *Seed Science & Technology*, **9**: 373-409.

ELLIS, R.H., OSEI-BONSU, K. & ROBERTS, E.H. 1982. The influence of genotype, temperature and moisture on seed longevity in Chickpea, Cowpea and Soya bean. *Annals of Botany*, **50**: 69-82.

ELLNER, S. & SHMIDA, A. 1981. Why are adaptations for long-range seed dispersal rare in desert plants? *Oecologia*, **51**: 133-144.

EL-SHARKAWI, H.M., FARGALI, K.A. & SAYED, S.A. 1989. Interactive effects of water stress, temperature and nutrients in the seed germination of three desert plants. *Journal of Arid Environments*, **17**: 307-317.

ENVIRONMENTAL EVALUATION UNIT 1990. *Anglo American Corporation: West Coast heavy mineral sands project.* Unpublished report. University of Cape Town, Cape Town.

ESLER, K.J. 1993. Vegetation patterns and plant reproductive processes in the Succulent Karoo. Ph.D. thesis, University of Cape Town, Cape Town.

ESLER, K.J. 1999. Plant reproductive ecology. In: Dean, W.R.J. & Milton, S.J. (eds). *The Karoo – Ecological patterns and processes.* Cambridge University Press, Cambridge. pp. 123-144.

ESLER, K.J. & PHILLIPS, N. 1994. Experimental effects of water stress on semi-arid Karoo seedlings: implications for field seedling survivorship. *Journal of Arid Environments*, **26**: 325-337.

ESLER, K.J., COWLING, R.N. & IVEY, P. 1992. Seed biology of three species of Mesembryanthema in the Southern Succulent Karoo. *South African Journal of Botany*, **58**: 343-348.

EVENARI, M. 1965. Physiology of seed dormancy, after-ripening and germination. *Proceedings of the International Seed Testing Association*, **30**: 49-71.

EVLAGON, D., RAVINA, I. & NEUMANN, P.M. 1992. Effects of salinity stress and calcium on hydraulic conductivity and growth in maize seedling roots. *Journal of Plant Nutrition*, **15**: 795-803.

FEAST, P.M. & ROBERTS, H.A. 1973. Note on the estimation of viable weed seeds in soil samples. *Weed Research*, **13**: 110-113.

FENNER, M. 1985. *Seed ecology.* Chapman & Hall, London.

FENNER, M. 1987. Seedlings. *New Phytologist*, **106**: 35-47.

FOUNTAIN, D.W. & OUTRED, H.A. 1991. Germination requirements of New Zealand native plants: a review. *New Zealand Journal of Botany*, **29**: 311-316.

FOWLER, N. 1986. The role of competition in plant communities in arid and semiarid regions. *Annual Review of Ecology and Systematics*, **17**: 89-110.

FRANCO, A.C. & NOBEL, P.S. 1989. Effect of nurse plants on the microhabitat and growth of Cacti. *Journal of Ecology*, **77**: 870-886.

FRANCO, J.A., FERNáNDEZ, J.A. & BAÑóN, S. 1997. Relationship between the effects of salinity on seedling leaf area and fruit yield of six Muskmelon cultivars. *Hortscience*, **32**: 642-644.

FRANCOIS, L.E. & KLEIMAN, R. 1990. Salinity effects on vegetative growth, seed yield, and fatty acid composition of crambe. *Agronomy Journal*, **82**: 1110-1114.

FRANCOIS, L.E., DONOVAN, T.J., LORENZ, K. & MAAS, E.V. 1989. Salinity effects on rye grain yield, quality, vegetative growth, and emergence. *Agronomy Journal*, **81**: 707-712.

FRANCOIS, L.E., DONOVAN, T.J., MAAS, E.V. & RUBENTHALER, G.L. 1988. Effect of salinity on grain yield and quality, vegetative growth, and germination of triticale. *Agronomy Journal*, **80**: 642-647.

FREAS, K.E. & KEMP, P.R. 1983. Some relationships between environmental reliability and seed dormancy in desert annual plants. *Journal of Ecology*, **71**: 211-217.

FREEMAN, C.E., TIFFANY, R.S. & REID, W.H. 1977. Germination responses of *Agave lecheguilla*, *Agave parryi*, and *Fouquieria splendens*. *The Southwestern Naturalist*, **22**: 195-204.

GARNER, W. & STEINBERGER, Y. 1989. A proposed mechanism for the formation of 'Fertile Islands' in the desert ecosystem. *Journal of Arid Environments*, **16**: 257-262.

GARWOOD, N.C. 1989. Tropical soil seed banks: a review. In: Leck, M.A., Parker, V.T. & Simpson, R.L. (eds). *Ecology of soil seed banks.* Academic Press, London. pp. 149-209.

GEDGE, K.E. & MAUN, M.A. 1994. Compensatory response of two dune annuals to simulated browsing and fruit predation. *Journal of Vegetation Science*, **5**: 99-108.

GIBBS RUSSELL, G.E., WATSON, L., KOEKEMOER, M., SMOOK, L., BARKER, N.P., ANDERSON, H.M. & DALLWITZ, M.J. 1990. Grasses of southern Africa. *Memoirs of the botanical Survey of South Africa*, **58**: 1-437.

GOLDBERG, D.E. 1985. Effects of soil pH, competition, and seed predation on the distributions of two tree species. *Ecology*, **66**: 503-511.

GOLDBERG, D.E. & WERNER, P.A. 1983. The effects of size of opening in vegetation and litter cover on seedling establishment of goldenrods (*Solidago* spp.). *Oecologia*, **60**: 149-155.

GRAHAM, D.J. & HUTCHINGS, M.J. 1988. Estimation of the seed bank of a chalk grassland ley established on former arable land. *Journal of Applied Ecology*, **25**: 241-252.

GRANSTRöM, A. 1982. Seed banks in five boreal forest stands originating between 1810 and 1963. *Canadian Journal of Botany*, **60**: 1815-1821.

GRANSTRöM, A. 1988. Seed banks at six open and afforested heathland sites in southern Sweden. *Journal of Applied Ecology*, **25**: 297-306.

GREEN, T.W. & PALMBALD, I.G. 1975. Effects of insect seed predators on *Astragalus cibarius* and *Astragalus utahensis* (Leguminosae). *Ecology*, **56**: 1435-1440.

GREENWAY, H. & MUNNS, R. 1980. Mechanisms of salt tolerance in non-halophytes. *Annual Review of Plant Physiology*, **31**: 149-190.

GRIME, J.P. 1981. The role of seed dormancy in vegetation dynamics. *Annals of Applied Biology*, **98**: 555-558.

GRIME, J.P. & HILLIER, S.H. 1981. *Predictions based upon the laboratory characteristics of seeds.* Annual Report 1981, Unit of Comparative Plant Ecology (NERC), University of Sheffield, Sheffield.

GRIME, J.P., MASON, G., CURTIS, A.V., RODMAN, J., BAND, S.R., MOWFORTH, M.A.G., NEAL, A.M. & SHAW, S. 1981. A comparative study of germination characteristics in a local flora. *Journal of Ecology*, **69**: 1017-1059.

GRINDLEY, S. & BARBOUR, B. 1990. Conceptual rehabilitation plan. In: Anglo American Corporation. *West Coast heavy mineral sands project - Supplementary Report.* Unpublished report. University of Cape Town, Cape Town. Section A6.

GROSS, K.L. 1990. A comparison of methods for estimating seed numbers in the soil. *Journal of Ecology*, **78**: 1079-1093.

GRUBB, P.J. 1977. The maintenance of species-richness in plant communities, the importance of the regeneration niche. *Biological Reviews*, **52**: 107-145.

GRUBB, P.J. 1988. The uncoupling of disturbance and recruitment, two kinds of seed banks, and persistence of plant populations at the regional and local scales. *Annales Zoologici Fennici*, **25**: 23-36.

GUL, B. & WEBER, D.J. 1998. Effect of dormancy relieving compounds on the seed germination of non-dormant *Allenrolfea occidentalis* under salinity stress. *Annals of Botany*, **82**: 555-560.

GUTIERREZ BOEM, F.H., LAVADO, R.S. & PORCELLI, C.A. 1997. Effects of waterlogging followed by a salinity peak on rapeseed (*Brassica napus* L.). *Journal of Agronomy and Crop Science*, **178**: 135-140.

GUTIéRREZ, J.R., MESERVE, P.L., CONTRERAS, L.C., VáSQUEZ, H. & JAKSIC, F.M. 1993. Spatial distribution of soil nutrients and ephemeral plants underneath and outside the canopy of *Porlieria chilensis* shrubs (Zygophyllaceae) in arid coastal Chile. *Oecologia*, **95**: 347-352.

GUTTERMAN, Y. 1972. Delayed seed dispersal and rapid germination as survival mechanisms of the desert plant *blepharis persica* (Burm.) Kuntze. *Oecologia*, **10**: 145-149.

GUTTERMAN, Y. 1980. Annual rhythm and position effect in the germinability of *Mesembryanthemum nodiflorum*. *Israel Journal of Botany*, **29**: 93-97.

GUTTERMAN, Y. 1986. Are plants which germinate and develop during winter in the Negev Desert highlands of Israel, winter annuals ? *Environmental Quality and Ecosystem Stability*, **3**: 135-144.

GUTTERMAN, Y. 1992. Maternal effects on seed during development. In: Fenner, M. (ed). *Seeds: The ecology of regeneration in plant communities.* CAB International, Wallingford. pp. 145-162.

GUTTERMAN, Y. 1993. *Seed germination in desert plants.* Springer-Verlag, Berlin.

GUTTERMAN, Y. 1994. Strategies of seed dispersal and germination in plants inhabiting deserts. *The Botanical Review*, **60**: 373-425.

GUTTERMAN, Y., CORBINEAU, F. & COME, D. 1992. Interrelated effects of temperature, light and oxygen on *Amaranthus caudatus* L. seed germination. *Weed Research*, **32**: 111-117.

HAAS, R.H., MEYER, R.E., SCIFRIES, C.J. & BROCK, J.H. 1973. *Growth and development of mesquite.* Texas A&M Agr. Exp. Sta., Texas.

HARPER, J.L. 1977. *Population biology of plants.* Academic Press, London.

HARRINGTON, J.F. 1972. Seed storage and longevity. In: Kozlowski, T.T. (ed). *Seed biology.* Academic Press, New York. pp. 145-240.

HARRINGTON, J.F. 1973. Biochemical basis of seed longevity. *Seed Science and Technology*, **1**: 453-461.

HARTY, R.L. & McDONALD, T.J. 1972. Germination behaviour in beach spinifex (*Spinifex hirsutus* Labill.). *Australian Journal of Botany*, **20**: 241-251.

HAY, M.E. & FULLER, P.J. 1981. Seed escape from heteromyid rodents: the importance of microhabitat and seed preference. *Ecology*, **62**: 1395-1399.

HEDGE, S.G., LOKESHA, R. & GANESHAIAH, K.N. 1991. Seed size distribution in plants: an explanation based on fractal geometry. *Oikos*, **62**: 100-101.

HEGARTHY, T.W. 1978. The physiology of seed hydration and relation between water stress and control of germination: a review. *Plant, Cell and Environment*, **1**: 101-119.

HEITHAUS, E.R. 1981. Seed predation by rodents on three ant-dispersed plants. *Ecology*, **62**: 136-145.

HENDERSON, C.B., PETERSEN, K.E. & REDAK, R.A. 1988. Spatial and temporal patterns in the seed bank and vegetation of a desert grassland community. *Journal of Ecology*, **76**: 717-728.

HENNEKEN, S. 1996b. *MEGATAB - a visual editor for phytosociological tables.* Giesen & Geurts, Ulft.

HENNEKEN, S. 1996a. *TURBOVEG – software package for input, processing, and presentation of phytosociological data.* IBN-DLO, University of Lancaster, Lancaster.

HEWITT, E.J. 1952. *Sand and water culture methods used in the study of plant nutrition.* Farnham Royal, Bucks, Commonwealth Agricultural Bureau.

HILL, M.O. 1979b. *DECORANA - A Fortran program for detrended correspondence analysis and reciprocal averaging.* Cornell University, New York.

HILL, M.O. 1979a. *TWINSPAN - A Fortran program for arranging multivariate data in an ordered two-way table by classification of the individuals and attributes.* Cornell University, New York.

HILTON-TAYLOR, C. & LE ROUX, A. 1989. Conservation status of the Fynbos and Karoo biomes. In: Huntley, B.J. (ed). *Biotic diversity in southern Africa: concepts and conservation.* Oxford University Press, Cape Town. pp. 202-223.

HOBBIE, S. 1992. Effects of plant species on nutrient cycling. *Trends in Ecology and Evolution*, **7**: 336-339.

HODGSON, J.G. & THOMPSON, K. 1993. Seeds: Size. In: Hendry, G.A.F. & Grime, J.P. (eds). *Methods in comparative plant ecology.* Chapman & Hall, London. pp. 202-205.

HOFFMAN, M.T. & COWLING, R.M. 1987. Plant physiognomy, phenology and demography. In: Cowling, R.M. & Roux, P.W. (Eds). The Karoo biome: a preliminary synthesis. Part 2. – Vegetation and history. *South African National Scientific Programmes Report* No. 142, Council for Scientific and Industrial Research, Pretoria. pp. 1-34.

HOOGERVORST, A. 1990. Legislation identification & authorities' consultation study. In: Environmental Evaluation Unit. *Anglo American Corporation: West Coast heavy mineral sands project - Supplementary Report.* Unpublished report. University of Cape Town, Cape Town. Section C7.

HOWE, C.D. & CHANCELLOR, R.J. 1983. Factors affecting the viable seed content of soils beneath lowland pastures. *Journal of Applied Ecology*, **20**: 915-922.

HYDER, S.Z. & GREENWAY, H. 1965. Effects of Ca^{2+} on plant sensitivity to high NaCl concentrations. *Plant and Soil*, **23**: 258-260.

INOUYE, R.S., BYERS, G.S. & BROWN, J.H. 1980. Effects of predation and competition on survivorship, fecundity, and community structure of desert annuals. *Ecology*, **61**: 1344-1351.

JOHNSON, E.A. & FRYER, G.I. 1996. Why Engelmann spruce does not have a persistent seed bank. *Canadian Journal of Forestry Research*, **26**: 872-878.

JONES, N.E. 1998. The number of soil cores required to accurately estimate the seed bank on arable land. *Aspects of Applied Biology*, **51**: 1-8.

JONES, R.W. Jr., PIKE, L.M. & YOURMAN, L.F. 1989. Salinity influences cucumber growth and yield. *Journal of the American Society for Horticultural Science*, **114**: 547-551.

JÜRGENS, N. 1986. Contributions to the ecology of southern African succulent plants. *Mitteilungen aus dem Institut für Allgemeine Botanik*, **21**: 139-365.

KALISZ, S. 1991. Experimental determination of seed bank age structure in the winter annual *Collinsia verna*. *Ecology*, **72**: 575-585.

KARSSEN, C.M., HAIGH, A., VAN DER TOORN, P. & WEGES, R. 1989. Physiological mechanisms involved in seed priming. In: Taylorson, R.B. (ed). *Recent advances in the development and germination of seeds.* Plenum, New York. pp. 269-280.

KATEMBE, W.J., UNGAR, I.A. & MITCHELL, J.P. 1998. Effect of salinity on germination and seedling growth of two *Atriplex* species (Chenopodiaceae). *Annals of Botany*, **82**: 167-175.

KEDDY, P.A. 1981. Experimental demography of the sand-dune annual, *Cakile edentula*, growing along an environmental gradient in Nova Scotia. *Journal of Ecology*, **69**: 615-630.

KEELEY, J.E. 1992. Recruitment of seedlings and vegetative sprouts in unburned Chaparral. *Ecology*, **73**: 1194-1208.

KEELEY, J.E., KEELEY, S.C., SWIFT, C.C. & LEE, J. 1984. Seed predation due to the Yucca-moth symbiosis. *American Midland Naturalist*, **112**: 187-191.

KEMP, P.R. 1989. Seed banks and vegetation processes in deserts. In: Leck, M.A., Parker, V.T. & Simpson, R.L. (eds). *Ecology of soil seed banks.* Academic Press, London. pp. 257-281.

KEMP, P.R. & CUNNINGHAM, G.L. 1981. Light, temperature and salinity effects on growth, leaf anatomy and photosynthesis of *Distichlis spicata* (L.) Greene. *American Journal of Botany*, **68**: 507-516.

KEREN, A. & EVENARI, M. 1974. Some ecological aspects of distribution and germination of *Pancratium maritimum* L.. *Israel Journal of Botany*, **23**: 202-215.

KERLEY, G.I.H. 1991. Seed removal by rodents, birds and ants in the semi-arid Karoo, South Africa. *Journal of Arid Environments*, **20**: 63-69.

KERLEY, G.I.H. 1992. Small mammal seed consumption in the Karoo, South Africa, further evidence for divergence in desert biotic process. *Oecologia*, **89**: 471-475.

KERLEY, G.I.H. & WHITFORD, W.G. 1994. Desert-dwelling small mammals as granivores: intercontinental variations. *Australian Journal of Zoology*, **42**: 543-555.

KHAN, M.A. 1993. Relationship of seed bank to plant distribution in saline arid communities. *Pakistan Journal of Botany*, **25**: 73-82.

KHAN, M.A. & UNGAR, I.A. 1996. Influence of salinity and temperature on the germination of *Haloxylon recurvum* Bunge ex Boiss.. *Annals of Botany*, **78**: 547-551.

KINGSBURY, R.W. & EPSTEIN, E. 1986. Salt sensitivity in wheat. *Plant Physiology*, **80**: 651-654.

KIRKHAM, F.W. & KENT, M. 1997. Soil seed bank composition in relation to the standing vegetation in fertilized and unfertilized hay meadows on a Somerset peat moor. *Journal of Applied Ecology*, **34**: 889-902.

KITAJIMA, K. & TILMAN, D. 1996. Seed banks and seedling establishment on an experimental productivity gradient. *Oikos*, **76**: 381-391.

KJELLSSON, G. 1992. Seed banks in Danish deciduous forests: species composition, seed influx and distribution pattern in soil. *Ecography*, **15**: 86-100.

KLINKHAMER, P.G.L., DE JONG, T.J., METZ, J.A.J. & VAL, J. 1987. Life history tactics of annual organisms: the joint effects of dispersal and delayed germination. *Theoretical Population Biology*, **32**: 127-156.

KLINKHAMER, P.G.L., DE JONG, T.J. & VAN DER MEIJDEN, E. 1988. Production, dispersal and predation of seeds in the biennial *Cirsium vulgare*. *Journal of Ecology*, **76**: 403-414.

KOLLER, D. 1955. The regulation of germination in seeds. *Israel Research Council Bulletin*, **5**: 85-108.

KOTANEN, P.M. 1996. Revegetation following soil disturbance in a California meadow: the role of propagule supply. *Oecologia*, **108**: 652-662.

LARCHER, W. 1995. *Physiological plant ecology : ecophysiology and stress physiology of functional groups.* Springer-Verlag, Berlin.

LAVOREL, S., DEBUSSCHE, M., LEBRETON, J-D. & LEPART, J. 1993. Seasonal patterns in the seed bank of Mediterranean old-fields. *Oikos*, **67**: 114-128.

LE ROUX, A. 1984. 'n Fitososiologiese studie van die Hester Malan-natuurreservaat. M.Sc. dissertation, University of Pretoria, Pretoria.

LE ROUX, A., SCHELPE, T. & WAHL, Z. 1997. *Namaqualand. South African Wild Flower Guide 1.* Botanical Society of South Africa, Kirstenbosch.

LEACH, L.C. 1986. *Euphorbia filiflora* Marloth. *Flowering plants of Africa*, **49**: p. 1927.

LECK, M.A. & SIMPSON, R.L. 1993. Seeds and seedlings of the Hamilton marshes, a Delaware river tidal freshwater wetland. *Proceedings of The Academy of Natural Sciences of Philadelphia*, **144**: 267-281.

LECK, M.A., BASKIN, C.C. & BASKIN, J.M. 1994. Germination ecology of *Bidens laevis* (Asteraceae) from a tidal freshwater wetland. *Bulletin of the Torrey Botanical Club*, **121**: 230-239.

LECK, M.A., PARKER, V.T. & SIMPSON, R.L. 1989. *Ecology of soil seed banks.* Academic Press, London.

LEIDI, E.O., NOGALES, R. & LIPS, S.H. 1991. Effect of salinity on cotton plants grown under nitrate or ammonium nutrition at different calcium levels. *Field Crops Research,* **26**: 35-44.

LEVASSOR, C., ORTEGA, M. & PECO, B. 1990. Seed bank dynamics of Mediterranean pastures subjected to mechanical disturbance. *Journal of Vegetation Science*, **1**: 339-344.

LEVYNS, M.R. 1929. *Guide to the flora of the Cape Peninsula.* Juta & Co. Ltd., Cape Town.

LEWIS, O.A.M., LEIDI, E.O. & LIPS, S.H. 1989. Effect of nitrogen source on growth response to salinity stress in maize and wheat. *New Phytologist,* **111**: 155-160.

LIMONARD, T. 1968. Ecological aspects of seed health testing. *Proceedings of the International Seed Testing Association*, **33**: 343-513.

LLOYD, J.W. 1985. A plant ecological study of the farm 'Vaalputs', Bushmanland, with special reference to edaphic factors. M.Sc. dissertation, University of Cape Town, Cape Town.

LOUDA, S.M. 1982. Limitation of the recruitment of the shrub *Haplopappus squarrosus* (Asteraceae) by flower- and seed-feeding insects. *Journal of Ecology*, **70**: 43-53.

LOUDA, S.M. 1983. Seed predation and seedling mortality in the recruitment of a shrub, *Haplopappus venetus* (Asteraceae), along a climatic gradient. *Ecology*, **64**: 511-521.

LOW, A.B. & REBELO, A. 1996. *Vegetation of South Africa, Lesotho and Swaziland.* Department of Environmental Affairs & Tourism, Pretoria.

LOW, A.B. & REBELO, A. 1998. *Vegetation of South Africa, Lesotho and Swaziland.* Department of Environmental Affairs & Tourism, Pretoria.

LUNT, I.D. 1997. Germinable soil seed banks of anthropogenic native grasslands and grassy forest remnants in temperate south-eastern Australia. *Plant Ecology*, **130**: 21-34.

LYLE, E.S. Jr.. 1987. *Surface mine reclamation manual.* Elsevier, New York.

MAAS, E.V. & HOFFMAN, G.J. 1977. Crop salt tolerance - current assessment. *Journal of the Irrigation and Drainage Division, ASCE*, **103**: 115-134.

MACK, R.N. 1976. Survivorship of *Cerastium atrovirens* at Aberffraw, Anglesey. *Journal of Ecology*, **64**: 309-312.

MAGUIRE, J.D. 1969. Endogenous germination rhythms in seeds. *Proceedings of the Association of Official Seed Analysts*, **59**: 95-100.

MAJOR, J. & PYOTT, W.T. 1966. Buried, viable seeds in two California bunchgrass sites and their bearing on the definition of a flora. *Vegetatio*, **13**: 253-282.

MALO, J.E., JIMÉNEZ, B. & SUáREZ, F. 1995. Seed bank build-up in small disturbances in a Mediterranean pasture: the contribution of endozoochorous dispersal by rabbits. *Ecography*, **18**: 73-82.

MAMO, T., RICHTER, C. & HEILIGTAG, B. 1996. Salinity effects on the growth and ion contents of some chickpea (*Cicer arietinum* L.) and lentil (*Lens culinaris* Medic.) varieties. *Journal of Agronomy and Crop Science*, **176**: 235-247.

MANCHESTER, S.J. & SPARKS, T.H. 1998. Determining the seed bank of former flood meadow fields. *Aspects of Applied Biology*, **51**: 15-22.

MANNING, J. & GOLDBLATT, P. 1996. *West Coast. South African Wild Flower Guide 7.* Botanical Society of South Africa, Kirstenbosch.

MARIKO, S., KACHI, N., ISHIKAWA, S. & FURUKAWA, A. 1992. Germination ecology of coastal plants in relation to salt environment. *Ecological Research*, **7**: 225-233.

MARSHALL, H. & MOMMSEN, B. 1994. *Field guide to the West Coast – Environmental Resource Guides, Field guide series #1.* The National Botanical Institute, Claremont.

MASUDA, M., MAKI, M. & YAHARA, T. 1999. Effects of salinity and temperature on seed germination in a Japanese endangered halophyte *Triglochin maritimum* (Juncaginaceae). *Journal of Plant Research*, **112**: 457-461.

MATLACK, G.R. & GOOD, R.E. 1990. Spatial heterogeneity in the soil seed bank of a mature coastal plain forest. *Bulletin of the Torrey Botanical Club*, **117**: 143-152.

MAUDE, R.B. 1996. *Seedborne diseases and their control – Principles & Practice.* CAB International, Wallingford.

MAYER, A.M. & POLJAKOFF-MAYBER, A. 1975. *The germination of seeds.* Pergamon Press, Oxford.

McAULIFFE, J.R. 1988. Markovian dynamics of simple and complex desert plant communities. *American Naturalist*, **131**: 459-490.

McMILLAN, C. 1959. Salt tolerance within a *Typha* population. *American Journal of Botany*, **46**: 521-526.

MILBERG, P. 1994. Annual dark dormancy cycle in buried seeds of *Lychnis flos-cuculi*. *Annales Botanici Fennici*, **31**: 163-167.

MILBERG, P. & ANDERSSON, L. 1998. Dormancy dynamics in buried weed seeds. *Aspects of Applied Biology*, **51**: 153-158.

MILBERG, P. & PERSSON, T.S. 1994. Soil seed bank and species recruitment in road verge grassland vegetation. *Annales Botanici Fennici*, **31**: 155-162.

MILES, J. 1985. The pedogenic effects of different species and vegetation types and the implications of succession. *Journal of Soil Science*, **36**: 571-584.

MILTON, S.J. 1994a. Growth, flowering and recruitment of shrubs in grazed and in protected rangeland in the arid Karoo, South Africa. *Vegetatio*, **111**: 17-27.

MILTON, S.J. 1994b. Small-scale reseeding trials in arid rangelands: effects of rainfall, clearing and grazing on seedling survival. *African Journal of Range and Forage Science*, **11**: 54-58.

MILTON, S.J. 1995. Spatial and temporal patterns in the emergence and survival of seedlings in arid Karoo shrubland. *Journal of Applied Ecology*, **32**: 145-156.

MISRA, A.N., SAHU, S.M., MEERA, I., MOHAPATRA, P., DAS, N. & MISRA, M. 1997. Root growth of a salt susceptible and a salt resistant rice (*Oryza sativa* L.) during seedling establishment under NaCl salinity. *Journal of Agronomy & Crop Science*, **178**: 9-14.

MOLL, J.B. 1992. Studies on dune rehabilitation techniques for mined areas at Richards Bay, Natal. M.Sc. dissertation, Rhodes University, Grahamstown.

MOLOFSKY, J. & AUGSPURGER, C.K. 1992. The effect of leaf litter on early seedling establishment in a tropical forest. *Ecology*, **73**: 68-77.

MORGAN, W.C. & MYERS, B.A. 1989. Germination of the salt-tolerant grass *Diplachne fusca*. I. Dormancy and temperature responses. *Australian Journal of Botany*, **37**: 225-237.

MORO, M.J., PUGNAIRE, F.I., HAASE, P. & PUIGDEFáBREGAS, J. 1997. Mechanisms of interaction between a leguminous shrub and its understorey in a semi-arid environment. *Ecography*, **20**: 175-184.

MOTT, J.J. 1974. Factors affecting seed germination in three annual species from an arid region of western Australia. *Journal of Ecology*, **62**: 699-709.

MOTT, J.J. & GROVES, R.H. 1981. Germination strategies. In: Pate, J.S. & McComb, A.J. (eds). *The Biology of Australian Plants.* University of Western Australia Press, Nedlands. pp. 307-341.

MUELLER-DOMBOIS, D. & ELLENBERG, H. 1974. *Aims and methods of vegetation ecology.* Wiley, New York.

MUNNS, R. & TERMAAT, A. 1986. Whole-plant responses to salinity. *Australian Journal of Plant Physiology,* **13**: 143-160.

MURDOCH, A.J. & ELLIS, R.H. 1992. Longevity, viability and dormancy. In: Fenner, M. (ed). *Seeds: The ecology of regeneration in plant communities.* CAB International, Wallingford. pp. 193-229.

MUSTART, P.J. & COWLING, R.M. 1993. The role of regeneration stages in the distribution of edaphically restricted fynbos Proteaceae. *Ecology*, **74**: 1490-1499.

MUSTART, P., COWLING, R., ALBERTYN, J. & PATERSON-JONES, C. 1997. *Southern Overberg: South African Wild Flower Guide 8.* Botanical Society of South Africa, Kirstenbosch.

MYERS, B.A. & COUPER, D.I. 1989. Effects of temperature and salinity on the germination of *Puccinellia ciliata* (Bor) cv. Menemen. *Australian Journal of Agricultural Research*, **40**: 561-571.

NAUMOVA, N.A. 1972. *Testing of seeds for fungous and bacterial infections.* Israel Program for Scientific Translations, Jerusalem.

NIKOLAEVA, M.G. 1977. Factors controlling the seed dormancy pattern. In: Khan, A.A. (ed). *The physiology and biochemistry of seed dormancy and germination.* North-Holland, New York. pp. 51-74.

NOBEL, P.S. 1980. Morphology, nurse plants, and minimum apical temperatures for young *Carnegiea gigantea*. *Botanical Gazette*, **141**: 188-191.

NOY-MEIR, I. 1980. Structure and function of desert ecosystems. *Israel Journal of Botany*, **28**: 1-19.

O'CONNOR, T.G. 1997. Micro-site influence on seed longevity and seedling emergence of a bunchgrass (*Themeda triandra*) in a semi-arid savanna. *African Journal of Range & Forage Science*, **14**: 7-11.

O'DOWD, D.J. & HAY, M.E. 1980. Mutualism between harvester ants and a desert ephemeral: seed escape from rodents. *Ecology*, **61**: 531-540.

ODUM, E.P. 1971. *Fundamentals of ecology*. W.B. Saunders Company, London.

OHGA, N. 1991. Distribution patterns of buried seeds in the herbaceous lomas community over the entire plateau on Loma Ancon in the coastal desert of central Peru. *Journal of Arid Land Studies*, **1**: 41-51.

OHGA, N. 1992. Buried seed population in the herbaceous lomas on Loma Ancon in the coastal desert of central Peru. *Ecological Research*, **7**: 341-353.

OLFF, H., PEGTEL, D.M., VAN GROENENDAEL, J.M. & BAKKER, J.P. 1994. Germination strategies during grassland succession. *Journal of Ecology*, **82**: 69-77.

PAKE, C.E. & VENABLE, D.L. 1996. Seed banks in desert annuals: implications for persistence and coexistence in variable environments. *Ecology*, **77**: 1427-1435.

PARMENTER, R.R. & MACMAHON, J.A. 1983. Factors determining the abundance and distribution of rodents in a shrub-steppe ecosystem: the role of shrubs. *Oecologia*, **59**: 145-156.

PLANISEK, S.L. & PIPPEN, R.W. 1984. Do sand dunes have seed banks? *Michigan Botany*, **23**: 169-177.

POIANI, K.A. & JOHNSON, W.C. 1988. Evaluation of the emergence method in estimating seed bank composition of prairie wetlands. *Aquatic Botany*, **32**: 91-97.

PONS, T.L. 1991. Induction of dark dormancy in seeds: its importance for the seed bank in the soil. *Functional Ecology*, **5**: 669-675.

PONS, T.L. 1992. Seed responses to light. In: Fenner, M. (ed). *Seeds: The ecology of regeneration in plant communities.* CAB International, Wallingford. pp. 259-284.

POSCHLOD, P. 1995. Diaspore rain and diaspore bank in raised bogs and its implication for the restoration of peat mined sites. In: Wheeler, B.D., Shaw, S.C., Fojt, W.J. & Robertson, R.A. (eds). *Restoration of Temperate Wetlands.* Wiley, Chichester. pp. 471-494.

POSCHLOD, P. & JACKEL, A.K. 1993. Untersuchungen zur Dynamik von generativen Diasporenbanken von Samenpflanzen in Kalkmagerrasen. I. Jahreszeitliche Dynamik des Diasporenregens und der Diasporenbank auf zwei Kalkmagerrasenstandorten der Schwäbischen Alp. *Flora*, **188**: 49-71.

PRATT, D.W., BLACK, R.A. & ZAMORA, B.A. 1984. Buried viable seed in a ponderosa pine community. *Canadian Journal of Botany*, **62**: 44-52.

PRICE, M.V. & PODOLSKY, R.H. 1989. Mechanisms of seed harvest by heteromyid rodents: soil texture effects on harvest rate and seed size selection. *Oecologia*, **81**: 267-273.

PROBERT, T.L. 1992. The role of temperature in germination ecophysiology. In: Fenner, M. (ed). *Seeds: The ecology of regeneration in plant communities.* CAB International, Wallingford. pp. 285-325.

PUGNAIRE, F.I., HAASE, P. & PUIGDEFáBREGAS, J. 1996. Facilitation between higher plant species in a semiarid environment. *Ecology*, **77**: 1420-1426.

PUGNAIRE, F.I., HAASE, P., PUIGDEFáBREGAS, J., CUETO, M., CLARK, S.C. & INCOLL, L.D. 1996. Facilitation and succession under the canopy of a leguminous shrub, *Retama sphaerocarpa*, in a semi-arid environment in south-east Spain. *Oikos*, **76**: 455-464.

REDBO-TORSTENSSON, P. & TELENIUS, A. 1995. Primary and secondary seed dispersal by wind and water in *Spergularia salina*. *Ecography*, **18**: 230-237.

REICHMAN, O.J. 1984. Spatial and temporal variation of seed distributions in Sonoran desert soils. *Journal of Biogeography*, **11**: 1-11.

RISSING, S.W. 1986. Indirect effects of granivory by harvester ants: plant species composition and reproductive increase near ant nests. *Oecologia*, **68**: 231-234.

ROBERTS H.A. 1964. Emergence and longevity in cultivated soil of seeds of some annual weeds. *Weed Research*, **4**: 296-307.

ROBERTS, E.H. 1972. *Viability of seeds.* Syracuse University Press, Great Britain.

ROBERTS, H.A. 1981. Seed banks in soils. *Advances in Applied Biology*, **6**: 1-55.

ROBERTS, H.A. & STOKES, F.G. 1966. Studies on the weeds of vegetable crops. VI. Seed populations of soil under commercial cropping. *Journal of Applied Ecology*, **3**: 181-190.

RODRIGUEZ, H.G., ROBERTS, J.K.M., JORDAN, W.R. & DREW, M.C. 1997. Growth, water relations, and accumulation of organic and inorganic solutes in roots of maize seedlings during salt stress. *Plant Physiology*, **113**: 881-893.

SALIM, M. 1989. Effects of salinity and relative humidity on growth and ionic relations of plants. *New Phytologist*, **113**: 13-20.

SALONEN, V. 1987. Relationship between the seed rain and the establishment of vegetation in two areas abandoned after peat harvesting. *Holarctic Ecology*, **10**: 171-174.

SCHENKEVELD, A.J. & VERKLAAR, H.J. 1984. The ecology of short-lived forbs in chalk grasslands: distribution of germinative seeds and its significance for seedling emergence. *Journal of Biogeography*, **11**: 251-260.

SCHOMBERG, H.H., STEINER, J.L. & UNGER, P.W. 1994. Decomposition and nitrogen dynamics of crop residues: residue quality and water effects. *Soil Science Society of America Journal*, **58**: 372-381.

SENECA, E.D. 1972. Seedling response to salinity in four dune grasses from the outer banks of North Carolina. *Ecology*, **53**: 465-471.

SHARITZ, R.R. & McCORMICK, J.F. 1973. Population dynamics of two competing annual plant species. *Ecology*, **54**: 723-740.

SHEARING, D. & VAN HEERDEN, K. 1997. *Karoo: South African Wild Flower Guide 6.* Botanical Society of South Africa, Kirstenbosch.

SHELDON, J.C. 1973. The behaviour of seeds in soil. III. The influence of seed morphology and the behaviour of seedlings on the establishment of plants from surface-lying seeds. *Journal of Ecology*, **62**: 47-66.

SHELDON, J.C. & BURROWS, F.M. 1973. The effectiveness of the achene-pappus units of selected Compositae in steady winds with convection. *New Phytologist*, **72**: 665-675.

SILVERTOWN, J.W. & LOVETT-DOUST, J.L. 1995. *Introduction to plant population biology.* Blackwell Science Ltd., Oxford.

SIMPSON, G.M. 1990. *Seed dormancy in grasses.* Cambridge University Press, Cambridge.

SIMPSON, R.L., LECK, M.A. & PARKER, V.T. 1989. Seed bank: General concepts and methodological issues. In: Leck, M.A., Parker, V.T. & Simpson, R.L. (eds). *Ecology of soil seed banks.* Academic Press, London. pp. 257-281.

SINGH, K. 1990. Effect of soil salinity and sodicity on seedling growth and mineral composition of *Pongamia pinnata* and *Araucaria cunningamii*. *Tropical Ecology*, **31**: 124-130.

SKOGLUND, J. 1992. The role of seed banks in vegetation dynamics and restoration of dry tropical ecosystems. *Journal of Vegetation Science*, **3**: 357-360.

SMITH, G.F., CHESSELET, P., VAN JAARSVELD, E.J., HARTMANN, H., HAMMER, S., VAN WYK, B.-E., BURGOYNE, P., KLAK, C. & KURZWEIL, H. 1998. *Mesembs of the world – Illustrated guide to a remarkable succulent group.* Briza Publications, Pretoria.

SMITH, L.M. & KADLEC, J.A. 1983. Seed banks and their role during drawdown of a North American marsh. *Journal of Applied Ecology*, **20**: 673-684.

SOHOLT, L.F. 1973. Consumption of primary production by a population of kangaroo rats (*Dipodomys merriami*) in the Mojave desert. *Ecological Monographs*, **43**: 357-376.

SORK, V.L. & BOUCHER, D.H. 1977. Dispersal of sweet pignut hickory in a year of low fruit production, and the influence of predation by a Curculionid beetle. *Oecologia*, **28**: 289-299.

STOCK, W.D., DLAMINI, T.S. & COWLING, R.M. 1999. Plant induced fertile islands as possible indicators of desertification in a succulent desert ecosystem in northern Namaqualand, South Africa. *Plant Ecology*, **142**: 161-167.

STROGONOV, B.P. 1964. *Physiological bases of salt tolerance of plants.* Israel Program for Scientific Translations, Jerusalem.

TER BRAAK, C.J.F. 1997. *CANOCO – a Fortran program for canonical community ordination by [partial] [detrended] [canonical] correspondence analysis, principal component analysis and redundancy analysis (version 3.15).* Report LWA-88-02, Agricultural Mathematics Group, Wageningen.

TEVIS, L. Jr.. 1958. Germination and growth of ephemerals induced by sprinkling a sandy desert. *Ecology*, **39**: 681-688.

THERON, G.K. 1964. 'n Outekologiese studie van *Plinthus karooicus* Verdoorn. M.Sc. dissertation, University of Pretoria, Pretoria.

THISELTON-DYER, W.T. 1904. *Flora Capensis Vol. VI.* Reeve & Co., London.

THOMPSON, K. 1992. The functional ecology of seed banks. In: Fenner, M. (ed). *Seeds: The ecology of regeneration in plant communities.* CAB International, Wallingford. pp. 231-258.

THOMPSON, K. 1993. Persistence in soil. In: Hendry, G.A.F & Grime, J.P. (eds). *Methods in comparative plant ecology.* Chapman and Hall, London. pp. 199-202.

THOMPSON, K. & GRIME, J.P. 1979. Seasonal variation in the seed banks of herbaceous species in ten contrasting habitats. *Journal of Ecology*, **67**: 893-921.

THOMPSON, K., BAKKER, J.P. & BEKKER, R.M. 1996. *Soil seed banks of North-west Europe: Methodology, density and longevity.* Cambridge University Press, Cambridge.

THOMPSON, K., BAND, S.R. & HODGSON, J.G. 1993. Seed size and shape predict persistence in soil. *Functional Ecology*, **7**: 236-241.

THOMPSON, K., BEKKER, R.M. & BAKKER, J.P. 1998. Weed seed banks; evidence from the north-west European seed bank database. *Aspects of Applied Biology*, **51**: 105-112.

TIKU, B.L. & SNAYDON, R.W. 1971. Salinity tolerance in the grass species *Agrostis stolonifera* L.. *Plant and Soil*, **35**: 421-431.

TSONEV, T.D., LAZOVA, G.N., STOINOVA, Z.G. & POPOVA, L.P. 1998. A possible role for Jasmonic Acid in adaptation of barley seedlings to salinity stress. *Journal of Plant Growth Regulation*, **17**: 153-159.

TURNER, R.M., ALCORN, S.M., OLIN, G. & BOOTH, J.A. 1966. The influence of shade, soil and water on saguaro seedling establishment. *Botanical Gazette*, **127**: 95-102.

UNGAR, I.A. 1962. Influence of salinity on seed germination in succulent halophytes. *Ecology*, **43**: 763-764.

UNGAR, I.A. 1995. Seed germination and seed-bank ecology in halophytes. In: Kigel, J. & Galilli, G. (eds). *Seed development and germination.* Marcel Dekker, New York. pp. 599-628.

UNGAR, I.A. 1996. Effect of salinity on seed germination, growth, and ion accumulation of *Atriplex patula* (Chenopodiaceae). *American Journal of Botany*, **83**: 604-607.

VALIENTE-BANUET, A. & EZCURRA, E. 1991. Shade as a cause of the association between the cactus *Neobuxbaumia tetetzo* and the nurse plant *Mimosa luisana* in the Tehuacán Valley, Mexico. *Journal of Ecology*, **79**: 961-971.

VAN BREDA, P.A.B. & BARNARD, S.A. 1991. *Veld plants of the winter rainfall region.* Department of Agricultural Development, Pretoria.

VAN DER PIJL, L. 1982. *Principles of dispersal in higher plants.* Springer Verlag, Berlin.

VAN DER VALK, A.G. & PEDERSON, R.L. 1989. Seeds banks and the management and restoration of natural vegetation. In: Leck, M.A., Parker, V.T. & Simpson, R.L. (eds). *Ecology of soil seed banks.* Academic Press, New York. pp. 329-346.

VAN DER VALK, A.G., PEDERSON, R.L. & DAVIS, C.B. 1992. Restoration and creation of freshwater wetlands using seed banks. *Wetlands Ecology and Management*, **1**: 191-197.

VAN HOORN, J.W. 1991. Development of soil salinity during germination and early seedling growth and its effect on several crops. *Agricultural Water Management*, **20**: 17-28.

VAN OUDTSHOORN, F. 1991. *Gids tot grasse van Suid-Afrika.* Briza Publikasies Bk., Arcadia.

VAN RENSBURG, D.J. 1978. Fenologiese aspekte van enkele Namakwalandse spesies. B.Sc.(Hons.) project, University of Pretoria, Pretoria.

VAN RHEEDE VAN OUDTSHOORN, K. & VAN ROOYEN, M.W. 1999. *Dispersal biology of desert plants.* Springer-Verlag, Berlin.

VAN ROOYEN, G., STEYN, H. & DE VILLIERS, R. 1999. *Cederberg. South African Wild Flower Guide 10.* Botanical Society of South Africa, Cape Town.

VAN ROOYEN, M.W. 1999. Functional aspects of short-lived plants. In: Dean, W.R.J. & Milton, S.J. (eds). *The Karoo – Ecological patterns and processes.* Cambridge University Press, Cambridge. pp. 105-122.

VAN ROOYEN, M.W. & GROBBELAAR, N. 1982. Saadbevolkings in die grond van die Hester Malan-natuurreservaat in die Namakwalandse Gebrokeveld. *South African Journal of Botany*, **1**: 41-50.

VAN ROOYEN, M.W., GROBBELAAR, N. & THERON, G.K. 1979. Phenology of the vegetation in the Hester Malan Nature Reserve in the Namaqualand Broken Veld. 2. The therophyte population. *Journal of South African Botany*, **45**: 433-452.

VAN ROOYEN, M.W., THERON, G.K. & GROBBELAAR, N. 1990. Life form and dispersal spectra of the flora of Namaqualand, South Africa. *Journal of Arid Environments*, **19**: 133-145.

VAN WYK, B. & MALAN, S. 1988. *Field guide to the wild flowers of the Witwatersrand and Pretoria region, including the Magaliesberg and Suikerbosrand.* Struik, Cape Town.

VAUGHTON, G. 1998. Soil seed bank dynamics in the rare obligate seeding shrub, *Grevillea barklyana* (Proteaceae). *Australian Journal of Ecology*, **23**: 375-384.

VAVREK, M.C., McGRAW, J.B. & BENNINGTON, C.C. 1991. Ecological genetic variation in seed banks. III. Phenotypic and genetic differences between young and old seed populations of *Carex bigelowii*. *Journal of Ecology*, **79**: 645-662.

VAZQUEZ-YANES, C. & OROZCO-SEGOVIA, A. 1993. Patterns of seed longevity and germination in the tropical rainforest. *Annual Review of Ecology and Systematics*, **24**: 69-87.

VENABLE, D.L. 1985. The evolutionary ecology of seed heteromorphism. *American Naturalist*, **126**: 577-595.

VENABLE, D.L. & LAWLOR, L. 1980. Delayed germination and escape in desert annuals: escape in space and time. *Oecologia*, **46**: 272-282.

VENABLES, A.V. & WILKINS, D.A. 1978. Salt tolerance in pasture grasses. *New Phytologist*, **80**: 613-622.

VETAAS, O.R. 1992. Micro-site effects of trees and shrubs in dry savannas. *Journal of Vegetation Science*, **3**: 337-344.

VISSER, L. 1993. Saadontkiemingstudies van geselekteerde Namakwalandse efemeerspesies. M.Sc. dissertation, University of Pretoria, Pretoria.

VIVIAN-SMITH, G. & HANDEL, S.N. 1996. Freshwater wetland restoration of an abandoned sand mine: Seeds bank recruitment dynamics and plant colonization. *Wetlands*, **16**: 185-196.

VLEESHOUWERS, L.M., BOUWMEESTER, H.J. & KARSSEN, C.M. 1995. Redefining seed dormancy: an attempt to integrate physiology and ecology. *Journal of Ecology*, **83**: 1031-1037.

VOLKMAR, K.M., HU, Y. & STEPPUHN, H. 1998. Physiological responses of plants to salinity: a review. *Canadian Journal of Plant Science*, **78**: 19-27.

VON WILLERT, D.J., ELLER, B.M., WERGER, M.J.A., BRINCKMANN, E. & IHLENFELDT, H.D. 1992. *Life strategies of succulents in deserts: with special reference to the Namib desert*. Cambridge University Press, Cambridge.

WAGNER, R.H. 1964. The ecology of *Uniola paniculata* L. in the dune-strand habitat of North Carolina. *Ecological Monographs*, **34**: 79-96.

WALCK, J.L., BASKIN, J.M. & BASKIN, C.C. 1998. A comparative study of the seed germination biology of a narrow endemic and two geographically-widespread species of *Solidago* (Asteraceae). 6. Seed bank. *Seed Science Research*, **8**: 65-74.

WALTER, H. & LIETH, H. 1960. *Klimadiagramm - Weltatlas*. Fischer, Jena.

WARR, S.J., THOMPSON, K. & KENT, M. 1993. Seed banks as a neglected area of biogeographic research: a review of literature and sampling techniques. *Progress in Physical Geography*, **17**: 329-347.

WASHINGTON, R. 1990. Report on predicted wind patterns and sediment transfer at Brand-se-Baai on the West Cape coast. In: Environmental Evaluation Unit. *Anglo American Corporation: West coast heavy mineral sands project - Supplementary Report*. Unpublished report. University of Cape Town, Cape Town. Section B4.

WATT, T.A. 1983. The effects of salt water and soil type upon the germination, establishment and vegetative growth of *Holcus lanatus* L. and *Lolium perenne* L.. *New Phytologist*, **94**: 275-291.

WENT, F.W. 1955. The ecology of desert plants. *Science America*, **192**: 68-75.

WENT, F.W. 1961. Problems in seed viability and germination. *Proceedings of the International Seed Testing Association*, **26**: 674-685.

WERGER, M.J.A. 1974. On concepts and techniques applied in the Zürich-Montpellier method of vegetation survey. *Bothalia*, **11**: 309-323.

WERNER, J.E. & FINKELSTEIN, R.R. 1995. *Arabidopsis* mutants with reduced response to NaCl and osmotic stress. *Physiologia Plantarum*, **93**: 659-666.

WESTOBY, M., JURADO, E. & LEISHMAN, M. 1992. Comparative evolutionary ecology of seed size. *Tree*, **7**: 368-372.

WHITTAKER, R.H. 1980. *Classification of plant communities*. Dr. W. Junk bv Publishers, The Hague.

WIEGAND, T., MILTON, S.J. & WISSEL, C. 1995. A simulation model for a shrub ecosystem in the semiarid Karoo, South Africa. *Ecology*, **76**: 2205-2221.

WILLEMS, J.H. & HUIJSMANS, K.G.A. 1994. Vertical seed dispersal by earthworms: a quantitative approach. *Ecography*, **17**: 124-130.

WILLIAMS, M.D. & UNGAR, I.A. 1972. The effect of environmental parameters on the germination, growth, and development of *Suaeda depressa* (Pursh) Wats. *American Journal of Botany*, **59**: 912-918.

WILLIAMSON, J.C. & JOHNSON, D.B. 1990. Mineralisation of organic matter in topsoils subjected to stockpiling and restoration at opencast coal sites. *Plant and Soil*, **128**: 241-247.

WILLIS, A.J & GROVES, R.H. 1991. Temperature and light effects on the germination of seven native forbs. *Australian Journal of Botany*, **39**: 219-228.

WILSON, R.G., KERR, E.D. & NELSON, L.A. 1985. Potential for using weed seed content in the soil to predict future weed problems. *Weed Science*, **33**: 171-175.

WINSTON, P.W. & BATES, D.H. 1960. Saturated solutions for the control of humidity in biological research. *Ecology*, **41**: 232-237.

YEATON, R.I. & ESLER, K.J. 1990. The dynamics of a succulent Karoo vegetation: a study of species association and recruitment. *Vegetatio*, **88**: 103-113.

YEATON, R.I., MOLL, E.J., JARMAN, M.L. & CUNLIFFE, R.N. 1993. The impact of competition on the structure of early successional plant species of the Atlantic Coast of South Africa. *Journal of Arid Environments*, **25**: 211-219.

YEO, A. 1999. Predicting the interaction between the effects of salinity and climate change on crop plants. *Scientia Horticulturae*, **78**: 159-174.

YOKOISHI, T. & TANIMOTO, S. 1994. Seed germination of the halophyte *Suaeda japonica* under salt stress. *Journal of Plant Research*, **107**: 385-388.

YOUNIS, A.F & HATATA, M.A. 1971. Studies on the effects of certain salts on germination, on growth of root, and on metabolism. I. Effects of chlorides and sulphates of sodium, potassium and magnesium on germination of wheat grains. *Plant and Soil*, **34**: 183-200.

ZHONG, H. & LÄUCHLI, A. 1993. Spatial and temporal aspects of growth in the primary root of cotton seedlings: effects of NaCl and $CaCl_2$. *Journal of Experimental Botany*, **44**: 763-771.

ZIMMERMAN, M. 1980. Reproduction in *Polemonium*: pre-dispersal seed predation. *Ecology*, **61**: 502-506.