

## CHAPTER 10

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

Submitted for publication as:

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in:

*Seed Science & Technology*

### 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.) Röschl., *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%),  $K_2CO_3 \cdot H_2O$  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<sup>3</sup> 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<sup>-2</sup> s<sup>-1</sup>, 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* ≤ 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	
<i>Conicosia pugioniformis</i> (P; 17D)	32.5 <sub>b</sub>	74.0 <sub>c</sub>	97.0 <sub>a</sub>	89.0 <sub>d</sub>	2.0 <sub>a</sub>	-	-	-	0.0000
<i>Dimorphotheca pluvialis</i> - disc (A; 17L)	86.4 <sub>bc</sub>	77.0 <sub>b</sub>	83.0 <sub>bc</sub>	90.0 <sub>c</sub>	-	86.0 <sub>bc</sub>	53.0 <sub>a</sub>	-	0.0000
<i>Dimorphotheca pluvialis</i> - ray (A; 17L)	64.5 <sub>e</sub>	25.0 <sub>bc</sub>	18.0 <sub>b</sub>	41.0 <sub>d</sub>	0.0 <sub>a</sub>	44.0 <sub>d</sub>	35.0 <sub>cd</sub>	0.0 <sub>a</sub>	0.0000
<i>Gazania leiopoda</i> (P; 17D)	71.0 <sub>c</sub>	30.0 <sub>b</sub>	88.0 <sub>c</sub>	84.0 <sub>c</sub>	9.0 <sub>ab</sub>	30.0 <sub>b</sub>	16.0 <sub>ab</sub>	0.0 <sub>a</sub>	0.0000
<i>Tripteris oppositifolia</i> (P; 17L)	32.4 <sub>a</sub>	45.0 <sub>a</sub>	62.0 <sub>b</sub>	75.0 <sub>b</sub>	-	68.0 <sub>b</sub>	67.0 <sub>b</sub>	-	0.0000
<i>Senecio arenarius</i> (A; 17L)	50.5 <sub>abc</sub>	75.0 <sub>c</sub>	53.0 <sub>bc</sub>	41.0 <sub>ab</sub>	23.0 <sub>a</sub>	-	-	-	0.0196
<i>Ursinia speciosa</i> - white (A; 17L)	36.5 <sub>c</sub>	9.0 <sub>ab</sub>	27.0 <sub>c</sub>	31.0 <sub>c</sub>	14.0 <sub>b</sub>	30.0 <sub>c</sub>	2.0 <sub>ab</sub>	0.0 <sub>a</sub>	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	
<i>Conicosia pugioniformis</i> (P; 17D)	11.3 <sub>b</sub>	4.8 <sub>a</sub>	4.0 <sub>a</sub>	4.1 <sub>a</sub>	5.0 <sub>a</sub>	-	-	-	0.0000
<i>Dimorphotheca pluvialis</i> - disc (A; 17L)	4.0 <sub>ab</sub>	5.9 <sub>c</sub>	3.8 <sub>ab</sub>	4.8 <sub>bc</sub>	-	3.1 <sub>a</sub>	7.6 <sub>d</sub>	-	0.0000
<i>Dimorphotheca pluvialis</i> - ray (A; 17L)	5.5	5.9	5.8	4.6	--	4.6	5.1	--	0.6111
<i>Gazania leiopoda</i> (P; 17D)	9.0 <sub>b</sub>	19.4 <sub>e</sub>	6.1 <sub>a</sub>	6.0 <sub>a</sub>	14.0 <sub>d</sub>	10.6 <sub>bc</sub>	12.5 <sub>cd</sub>	--	0.0000
<i>Tripteris oppositifolia</i> (P; 17L)	9.0 <sub>b</sub>	9.1 <sub>b</sub>	14.3 <sub>c</sub>	5.8 <sub>a</sub>	-	8.0 <sub>b</sub>	7.3 <sub>ab</sub>	-	0.0000
<i>Senecio arenarius</i> (A; 17L)	8.7	9.5	8.4	8.7	11.0	-	-	-	0.6419
<i>Ursinia speciosa</i> - white (A; 17L)	5.2 <sub>a</sub>	8.0 <sub>ab</sub>	4.5 <sub>a</sub>	4.3 <sub>a</sub>	10.3 <sub>b</sub>	4.6 <sub>a</sub>	8.0 <sub>ab</sub>	--	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 hydrophilic 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	<i>Dimorphotheca pluvialis</i> - disc (A)	31.671	0.0000	18.521	0.0005	43.836	0.0000
	<i>Dimorphotheca pluvialis</i> - ray (A)	2.067	0.1634	25.364	0.0000	4.486	0.0221
	<i>Gazania leiopoda</i> (P)	34.747	0.0000	19.529	0.0000	5.703	0.0094
	<i>Tripteris oppositifolia</i> (P)	0.049	0.8303	1.756	0.2037	2.390	0.1416
	<i>Ursinia speciosa</i> - white (A)	12.308	0.0018	10.715	0.0005	5.915	0.0082
Mean time to germination	<i>Dimorphotheca pluvialis</i> - disc (A)	4.854	0.0426	32.626	0.0000	12.311	0.0029
	<i>Dimorphotheca pluvialis</i> - ray (A)	0.206	0.6611	0.258	0.6234	1.496	0.2390
	<i>Gazania leiopoda</i> (P)	77.338	0.0000	48.424	0.0000	2.729	0.1268
	<i>Tripteris oppositifolia</i> (P)	16.016	0.0010	61.126	0.0000	43.593	0.0000
	<i>Ursinia speciosa</i> - 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 & Ellis, 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.



## ACKNOWLEDGEMENTS

The authors would like to express their appreciation to Hester Steyn for her assistance during this experiment, the Mazda Wildlife Fund for transportation, the University of Pretoria for funding and facilities, and both the Anglo American Corporation and the National Research Foundation for financial assistance.

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## CHAPTER 11

# SEED BANK CLASSIFICATION OF THE STRANDVELD SUCCULENT KAROO, SOUTH AFRICA

Submitted for publication as:

De Villiers, A.J., Van Rooyen, M.W. & Theron, G.K.

in:

*Ecological Monographs*

### 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 & Hilliers' 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.) Röschl., *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 carnosus* (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  $\mu\text{mol m}^{-2} \text{s}^{-1}$ . 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 ( $T_{50}$ ) 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 not 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) Myxosperry – 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) Synaptosperry – 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

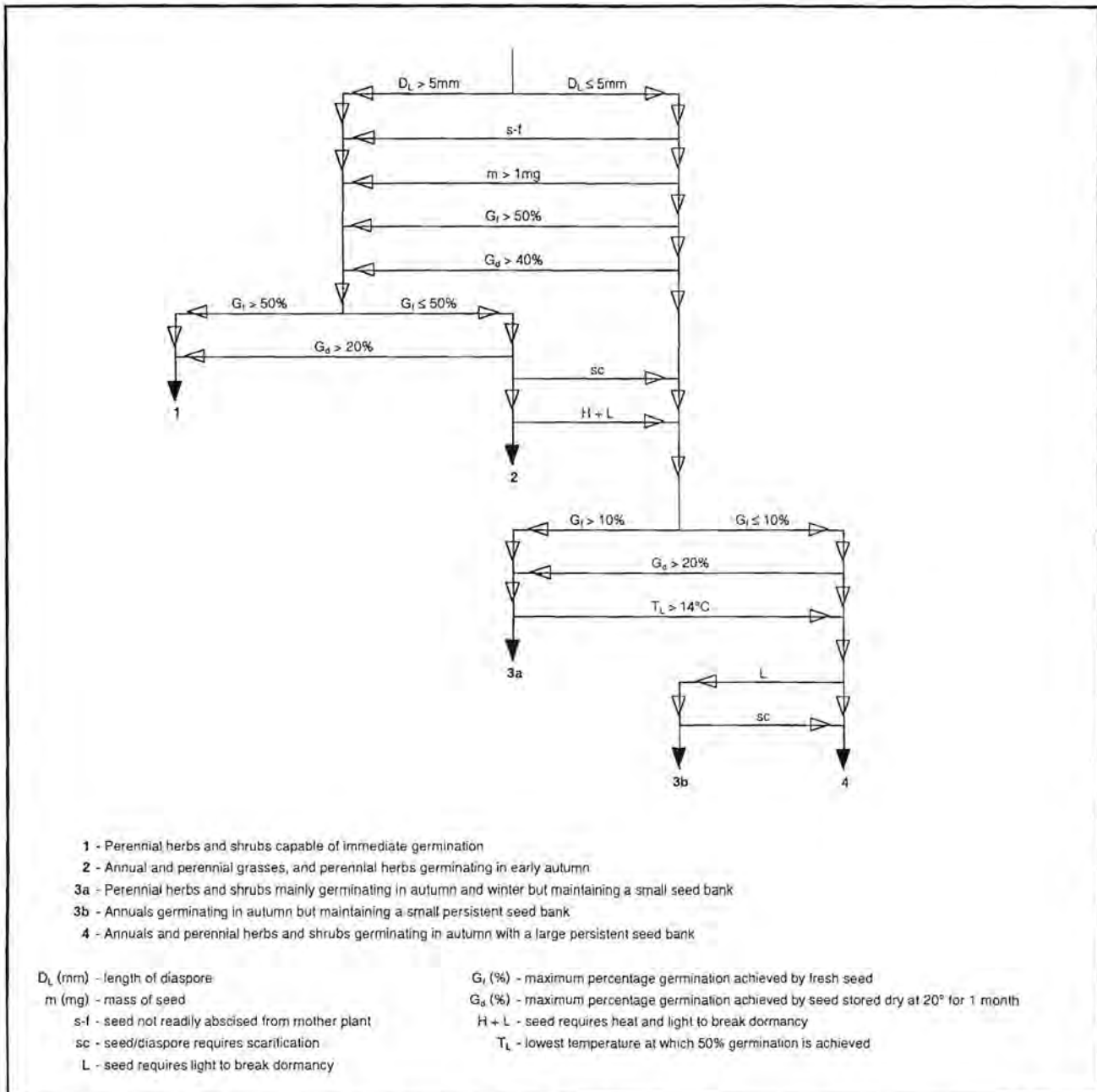


Figure 11.1. A key with laboratory characteristics of seeds developed to predict five seed bank types in the Strandveld Succulent Karoo (after Grime & Hillier, 1981).



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

 D<sub>L</sub> (mm) - length of diaspore

m (mg) - mass of seed

 G<sub>f</sub> (%) - maximum percentage germination achieved by fresh seed

 G<sub>s</sub> (%) - 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<sub>L</sub> - 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	<i>Albuca exuviata</i> (PH)	Anemochory	Atelechory  Myxospermy Atelechory/Synaptospermy
	<i>Amellus tenuifolius</i> (PS)	Anemochory	
	<i>Chrysocoma longifolia</i> (PS)	Anemochory	
	<i>Dimorphotheca tragus</i> (PH)	Anemochory	
	<i>Hypertelis salsoloides</i> (PH)	Anemoballistic	
	<i>Pteronia divaricata</i> (PS)	Anemochory	
	<i>Tripteris oppositifolia</i> (PS)	Anemochory	
	<i>Zygophyllum morgsana</i> (PS)	Anemochory	
2	<i>Arctotis acaulis</i> (PH)	Anemochory	Myxospermy
	<i>Arctotis stoechadiifolia</i> (PH)	Anemochory	
	<i>Ehrharta calycina</i> (PG)	Anemochory	
	<i>Gazania leiopoda</i> (PH)	Anemochory	
3a	<i>Cephalophyllum spongiosum</i> (PH)	Rain ballistic	Hygrochasy
	<i>Stoeberia</i> sp. (PS)	Rain ballistic	Hygrochasy
3b	<i>Arctotheca calendula</i> (A)	Anemochory	Myxospermy Heterodiaspory  Myxospermy Myxospermy/Heterodiaspory Myxospermy/Heterodiaspory
	<i>Cotula thunbergii</i> (A)	Anemochory	
	<i>Dimorphotheca pluvialis</i> (disc)(A)	Anemochory	
	<i>Nemesia bicornis</i> (A)	Anemochory	
	<i>Senecio arenarius</i> (A)	Anemochory	
	<i>Ursinia anthemoides</i> (grey)(A)	Anemochory	
	<i>Ursinia speciosa</i> (white)(A)	Anemochory	
<i>Wahlenbergia paniculata</i> (A)	Anemoballistic		
4	<i>Ballota africana</i> (PS)	Anemoballistic	Myxospermy
	<i>Conicosia pugioniformis</i> (PH)	Anemochory	Atelechory/Synaptospermy
	<i>Cysticapnos cracca</i> (A)	Anemochory	Atelechory/Synaptospermy
	<i>Didelta carnosia</i> (A)	Anemochory/Epizoochory	Synaptospermy
	<i>Dimorphotheca pluvialis</i> (ray)(A)		Heterodiaspory
	<i>Grielum grandiflorum</i> (PH)	Epizoochory	Synaptospermy
	<i>Hebenstretia dentata</i> (A)	Anemoballistic	Heterodiaspory
	<i>Hebenstretia repens</i> (A)		Atelechory
	<i>Heliophila coronopifolia</i> (A)	Anemochory	Myxospermy
	<i>Pharnaceum aurantium</i> (PH)	Anemochory	
	<i>Pharnaceum exiguum</i> (A)	Anemochory	
	<i>Pharnaceum lanatum</i> (PH)	Anemochory	
	<i>Polycarena pumila</i> (A)	Anemoballistic	Atelechory
	<i>Ruschia bolusiae</i> (PS)	Rain ballistic	Hygrochasy
	<i>Silene clandestina</i> (A)	Anemoballistic	
	<i>Tetragonia virgata</i> (PS)	Anemochory	Synaptospermy
	<i>Ursinia anthemoides</i> (black)(A)	Anemochory	Myxospermy/Heterodiaspory
<i>Ursinia anthemoides</i> (white)(A)	Anemochory	Myxospermy/Heterodiaspory	
<i>Ursinia speciosa</i> (black)(A)	Anemochory	Myxospermy/Heterodiaspory	

A - annual

PG - perennial grass

PH - perennial herb

PS - perennial shrub

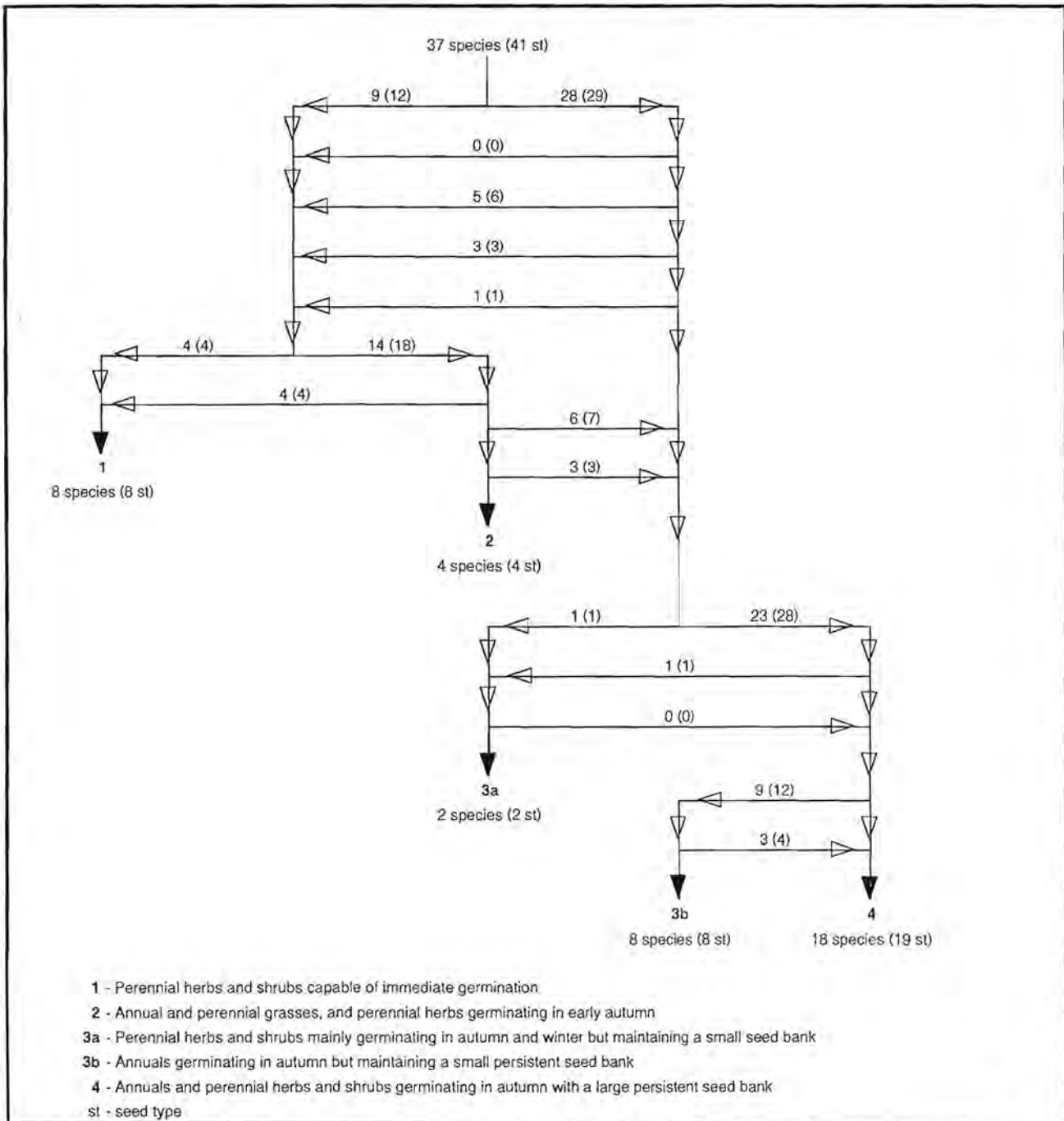


Figure 11.2. Distribution of 37 Strandveld Succulent Karoo species (41 seed types) between seed bank strategies predicted by using a modified key with laboratory characteristics of seeds.

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.

## ACKNOWLEDGEMENTS

The authors would like to express their appreciation to Hester Steyn for her assistance during this experiment, the Mazda Wildlife Fund for transportation, the University of Pretoria for funding and facilities, and both the Anglo American Corporation and the National Research Foundation for financial assistance.

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## 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

Submitted for publication as:

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in:

*Oikos*

### 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 Rhee de 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 enclosure 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		
	Field	Laboratory	Bagging	Inspection	Burial	Agar test	Burial
Method	1994	1993	1994	1994	1994	1995	1994
Year of seed collection	1994	1993	1994	1994	1994	1995	1994
Species							
<i>Albuca exuviata</i> (P)						X	
<i>Amellus tenuifolius</i> (P)						X	
<i>Arctotis stoechadifolia</i> (P)					X		
<i>Brassica tournefortii</i> (A)						X	
<i>Dimorphotheca pluvialis</i> (disc)(A)		X		X	X		
<i>Dimorphotheca pluvialis</i> (ray)(A)		X		X			X
<i>Eriocephalus africanus</i> (P)	X		X				
<i>Gazania leiopoda</i> (P)		X		X	X		
<i>Lebeckia multiflora</i> (P)	X		X				
<i>Pteronia divaricata</i> (P)							X
<i>Salvia africana-lutea</i> (P)	X		X				
<i>Senecio arenarius</i> (A)		X		X	X	X	
<i>Silene clandestina</i> (A)						X	
<i>Stoeberia</i> sp. (P)	X		X				
<i>Tetragonia microptera</i> (A)				X			
<i>Tripteris oppositifolia</i> (P)	X			X	X		X
<i>Ursinia speciosa</i> (white)(A)							X
<i>Zygophyllum morgsana</i> (P)	X		X				

P - perennial  
A - annual

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

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

P - perennial  
A - annual

## Post-dispersal seed predation

During spring 1994, 1 dm<sup>3</sup> 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 dishes 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<sup>-1</sup> for *Gazania leiopoda* to 27 444.1 seeds plant<sup>-1</sup> 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<sup>-1</sup>) occurred in *Stoeberia* sp.. Of the annual species investigated, *Senecio arenarius* had the highest seed production (807.8 seeds plant<sup>-1</sup>), level of pre-dispersal seed predation (36.8%) as well as number of seeds entering the seed pool (510.5 seeds plant<sup>-1</sup>) (Table 12.1). For the annual species, the lowest number of seeds produced (77.2 seeds plant<sup>-1</sup>), level of seed predation (3.1%) and number of seeds entering the seed pool (74.8 seeds plant<sup>-1</sup>) 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<sup>-1</sup> had a high fraction of seeds entering the seed pool, while in species producing high numbers of seeds plant<sup>-1</sup> 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<sup>-1</sup> (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 & Palmald, 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

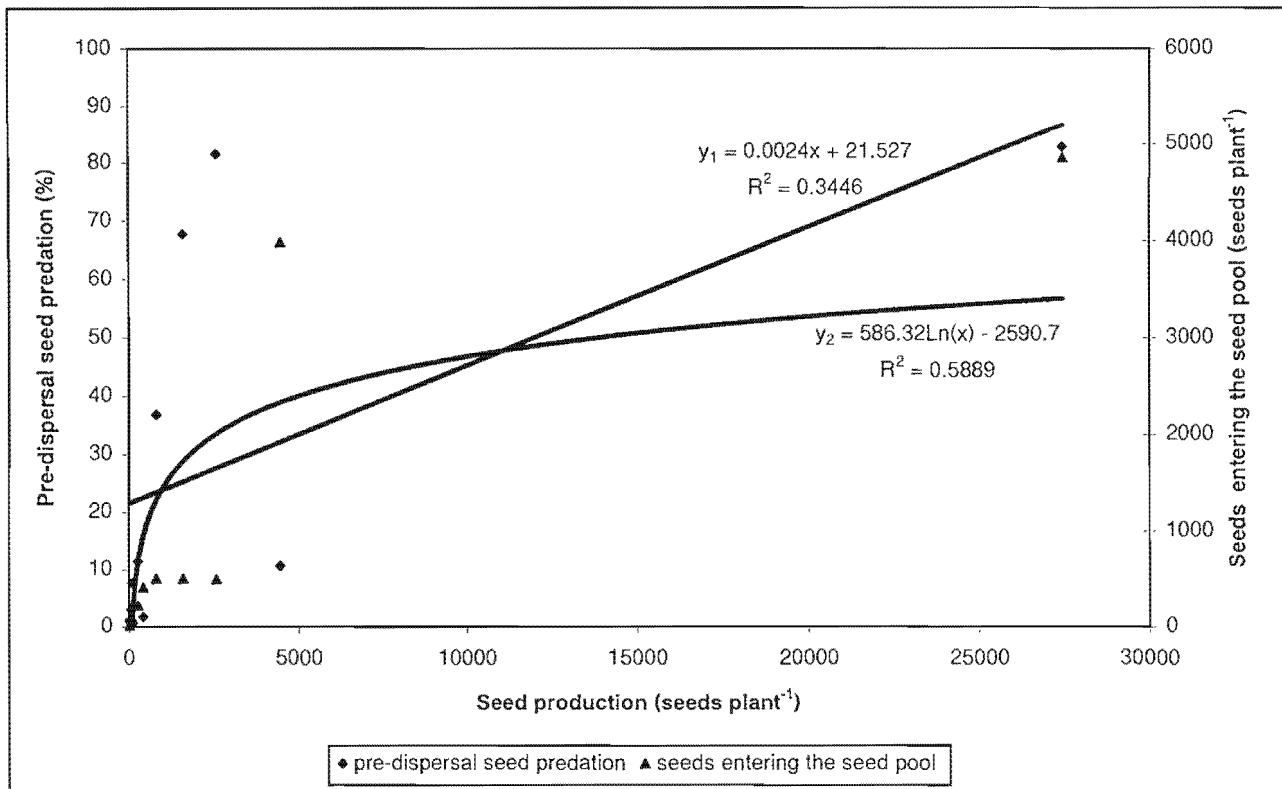


Figure 12.1. Interspecific regression analysis indicating the relationship between seed production and pre-dispersal seed predation ( $y_1$  – axis), as well as between seed production and the number of seeds entering the seed pool ( $y_2$  – axis).

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 (%)
<i>Arctotis stoechadifolia</i> (P)	Exclosure	70.0 c	3.6 a	73.6 b	50.6
	Open	22.4 b	0.6 a	23.0 a	
<i>Dimorphotheca pluvialis</i> (disc)(A)	Exclosure	62.8 b	15.0 a	77.8 b	41.0
	Open	22.0 a	14.8 a	36.8 a	
<i>Gazania leiopoda</i> (P)	Exclosure	77.2 c	10.6 a	87.8 b	42.4
	Open	36.8 b	8.6 a	45.4 a	
<i>Senecio arenarius</i> (A)	Exclosure	7.2 b	2.4 ab	9.6 b	9.6
	Open	0.0 a	0.0 a	0.0 a	
<i>Tripteris oppositifolia</i> (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 ( $\pm$  standard deviation) of seeds of five Strandveld Succulent Karoo plant species infected with seed-borne fungi**

Plant species	Fungus taxa			Total
	<i>Pithomyces</i> spp.	<i>Rhizopus</i> spp.	Other	
<i>Albuca exuviata</i> (P)	-	-	1.00 $\pm$ 1.70	1.00 $\pm$ 1.70
<i>Amellus tenuifolius</i> (P)	0.50 $\pm$ 0.90	-	0.75 $\pm$ 1.28	1.25 $\pm$ 1.88
<i>Brassica tournefortii</i> (A)	0.50 $\pm$ 0.90	0.25 $\pm$ 0.48	0.75 $\pm$ 1.28	1.50 $\pm$ 2.40
<i>Senecio arenarius</i> (A)	-	-	1.00 $\pm$ 1.60	1.00 $\pm$ 1.60
<i>Silene clandestina</i> (A)	0.50 $\pm$ 0.90	-	-	0.50 $\pm$ 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
<i>Dimorphotheca pluvialis</i> (ray)(A)	Exclosure	44.0 c	0.8 a
	Open	23.6 bc	3.2 ab
<i>Pteronia divaricata</i> (P)	Exclosure	0.0 a	1.2 b
	Open	0.0 a	0.0 a
<i>Tripteris oppositifolia</i> (P)	Exclosure	0.0 a	0.0 a
	Open	0.2 a	0.0 a
<i>Ursinia speciosa</i> (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 importance 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.

## ACKNOWLEDGEMENTS

The authors would like to express their appreciation to Hester Steyn, Marie Pretorius, Helena du Plessis, Jacqi Smith, Helga Rösch and Magda Nel for their assistance, the Mazda Wildlife Fund for transportation, the University of Pretoria for funding and facilities, and both the Anglo American Corporation and the National Research Foundation for financial assistance.

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