CHAPTER 6

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

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ABSTRACT

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

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

INTRODUCTION

Mining activities along the West Coast of South Africa will destroy the topography, vegetation, animal life and chemical and physical characteristics of the soil. Mining companies are, however, compelled by law (Mining Rights Act No. 20 of 1967, Hoogervorst, 1990) to rehabilitate mined areas. The specific requirement that has to be met is the revegetation of the area with indigenous plant species, to obtain a vegetation cover that conforms to the pre-mining vegetation as soon as possible after mining has been completed (Environmental Evaluation Unit, 1990). To restore the mined area as close as possible to its pre-mining natural condition, a pre-mining vegetation survey can serve as a benchmark to measure the success of the rehabilitation process. A complete description of the plant communities must also include the buried viable seeds, because they are as much part of the species composition as is the aboveground components (Major & Pyott, 1966; Fenner, 1985; Thompson, 1992).

The soil seed bank of most plant communities represents a vast pool of regenerative potential (Henderson *et al.*, 1988) as well as a 'memory' of previous conditions (Coffin & Lauenroth, 1989). Ecologists and evolutionary biologists have become increasingly aware of the role that seed banks can play in maintaining ecological (species) and genetic diversity in populations and communities (Gross, 1990). For the applied biologist in particular, the aspect of greatest significance is the role of the seed bank in determining the future vegetation, especially after natural or deliberate perturbation (Roberts, 1981; Coffin & Lauenroth, 1989).

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

MATERIAL AND METHODS

The study area covers approximately 9 400 ha and is situated in the vicinity of Brand-se-Baai (31°18' S, 17°54' E) on the arid West Coast, South Africa (De Villiers *et al.*, 1999). This area has a mean annual precipitation of 282 mm, of which rainfall constitutes 160 mm (De Villiers *et al.*, 1999). Advective sea fogs and heavy dewfalls supplement the low rainfall significantly. The mean daily temperature measured at the study site is 15.8°C.

According to Low & Rebelo (1998), the vegetation of the study area consists of Strandveld Succulent Karoo and Lowland Succulent Karoo, both of which are classified under the Succulent Karoo Biome. The Strandveld Succulent Karoo vegetation, containing many drought deciduous and succulent species, is associated with areas of calcareous sand. The vegetation varies in height according to the depth of the sand - the shortest vegetation growing on exposed calcrete and coastal rocks and the tallest being found in areas with deep calcareous sand (Boucher & Le Roux, 1990). Small patches of Lowland Succulent Karoo vegetation, characterized by a sparse cover of dwarf succulent-leaved shrubs which do not recover easily from disturbance, occur within the study area (Boucher & Le Roux, 1990).

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

At each of the 60 sampling locations (Figure 6.1), 15 soil samples were taken linearly at intervals of two meters. Each sample consisted of a soil core with a diameter of 65 mm taken to a depth of 100 mm, totaling a volume of approximately 246 cm^3. The soil samples were stored dry in soil sampling bags at ambient temperatures for approximately one week, before the seed content was estimated by means of the emergence method (De Villiers *et al.*, 1994). Sampling took place four times a year, for a total period of two years.

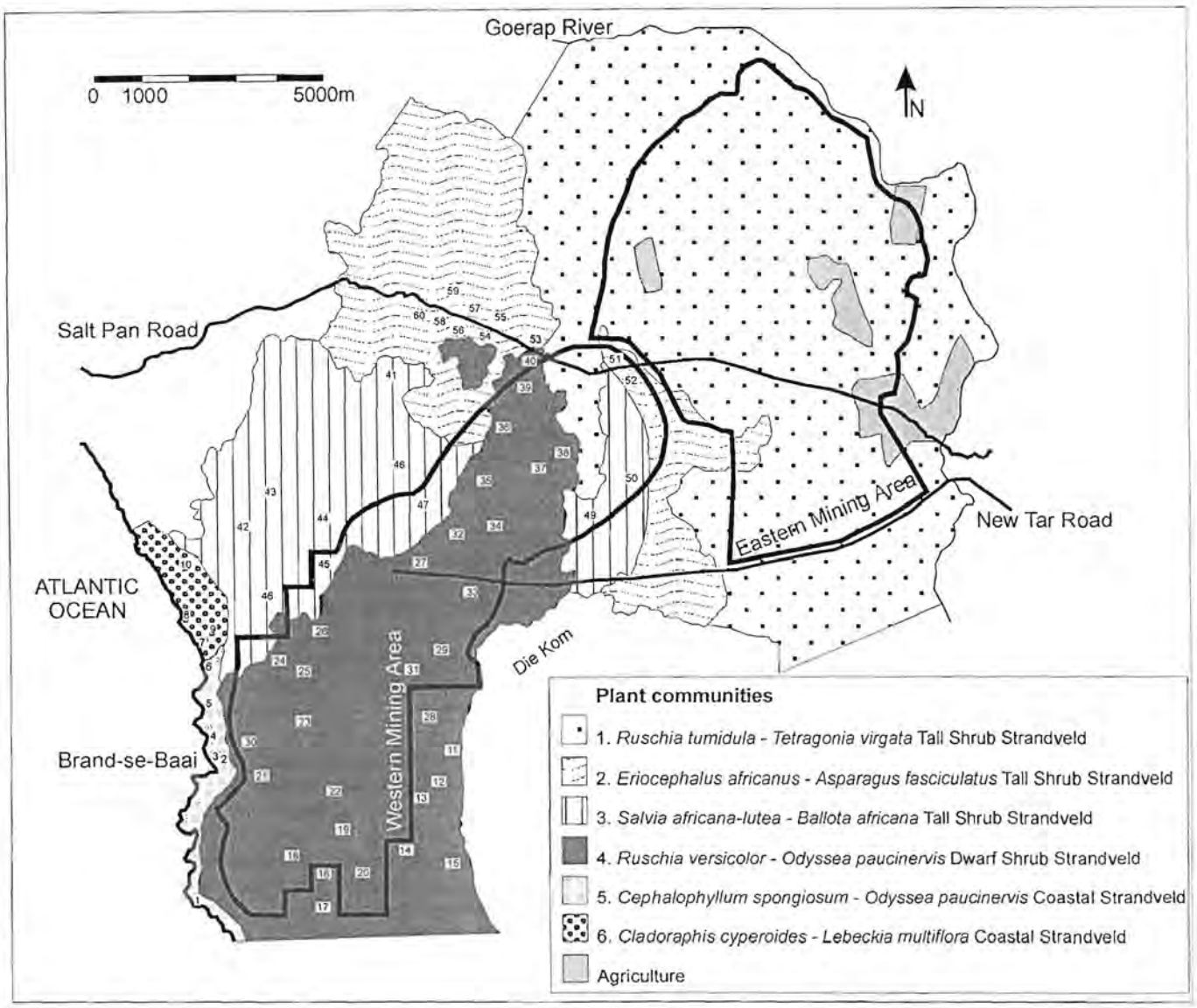

Figure 6.1. Vegetation map of the study area (De Villiers *et al.*, 1999), indicating 60 seed bank sampling locations.

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

Seed bank abundance data obtained during the eight sampling seasons were lumped. These lumped seed bank abundance values for each species (individuals m^{-2}) from each plot were transformed to a scale of 1 – 9, for classification purposes with the TURBOVEG (Hennekens, 1996a) and MEGATAB (Hennekens, 1996b) computer programs. The first classification of the seed bank, based on the total floristic set, was obtained by the application of the TWINSPAN classification algorithm (Hill, 1979). Using the Zürich-Montpellier (Braun-Blanquet) approach (Werger, 1974), the species and relevés in the matrix were assembled to produce a phytosociological table (Table 6.1) for the seed bank. The seed bank units obtained in the phytosociological table (Table 6.1) closely resembled the main vegetation units obtained in the standing vegetation of the study area (De Villiers *et al.*, 1999; Chapter 3). For this reason, seed bank units were numbered in accordance with the allocated community numbers in the standing vegetation.

Canonical Correspondence Analysis (CCA) was applied to the seed bank data with the computer program CANOCO version 3.15 (Ter Braak, 1997), to detect possible gradients in and between seed bank units and to detect possible habitat gradients associated with seed bank gradients.

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

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

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

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

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

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

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

Table 6.1. (Continued)

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

Table 6.1. (Continued)

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

Table 6.1. (Continued)

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

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

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

Table 6.1. (Continued)

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

* - species not recorded in the standing vegetation

A - annual

P - perennial

RESULTS AND DISCUSSION

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

1. *Ruschia tumidula - Tetragonia virgata* Tall Shrub Strandveld
2. *Eriocephalus africanus - Asparagus fasciculatus* Tall Shrub Strandveld
   - 2.1. *Othonna floribunda - Lebeckia lotonoides* Variant
   - 2.2. *Zygophyllum morgsana - Coelanthum semiquinquefidum* Variant
3. *Salvia africana-lutea - Ballota africana* Tall Shrub Strandveld
4. *Ruschia versicolor - Odyssea paucinervis* Dwarf Shrub Strandveld
   - 4.1. *Ruschia caroli - Aspalathus divaricata* Variant
   - 4.2. *Tripteris oppositifolia - Cissampelos capensis* Variant
   - 4.3. *Ehrharta calycina - Crassula expansa* Variant
5. *Cephalophyllum spongiosum - Odyssea paucinervis* Coastal Strandveld
6. *Cladoraphis cyperoides - Lebeckia multiflora* Coastal Strandveld

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

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

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

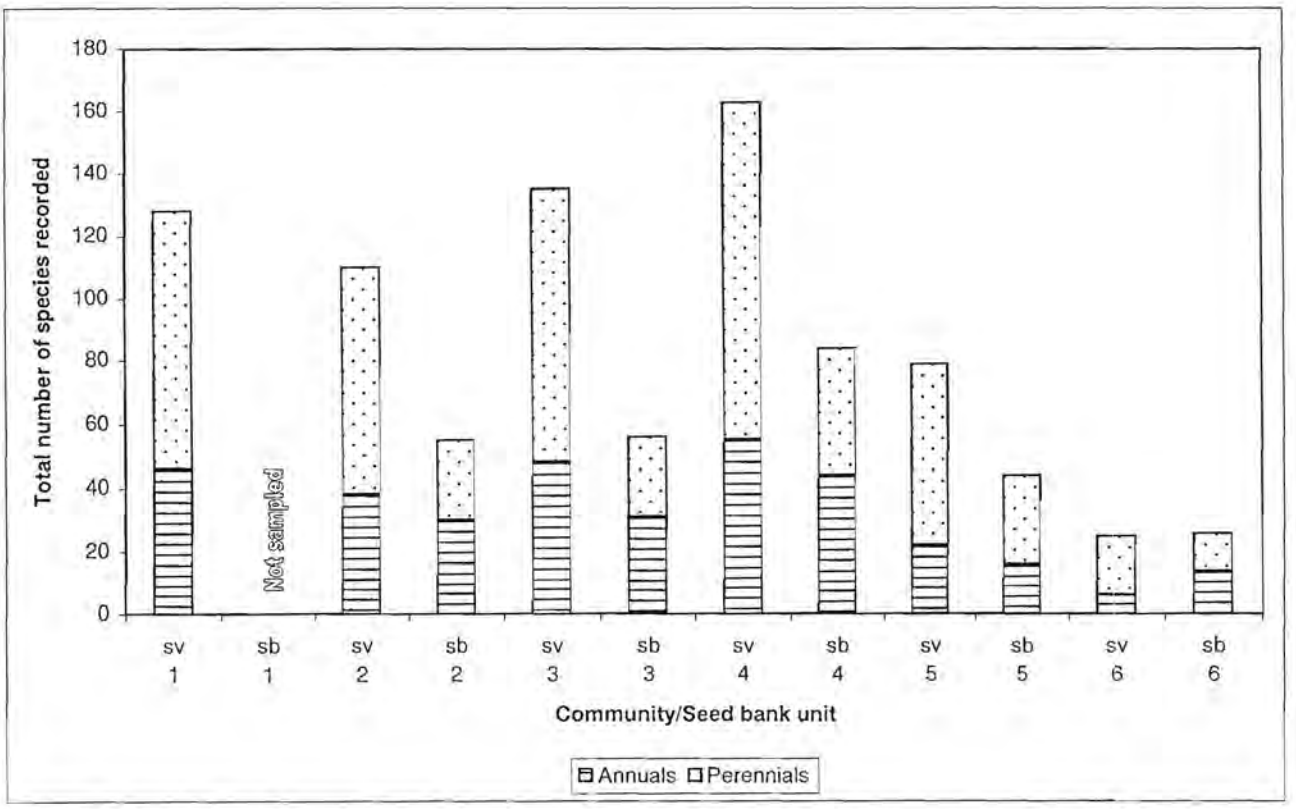

Figure 6.2. Total number of species recorded in the standing vegetation (sv) and the seed bank (sb) of six plant communities of the study area.

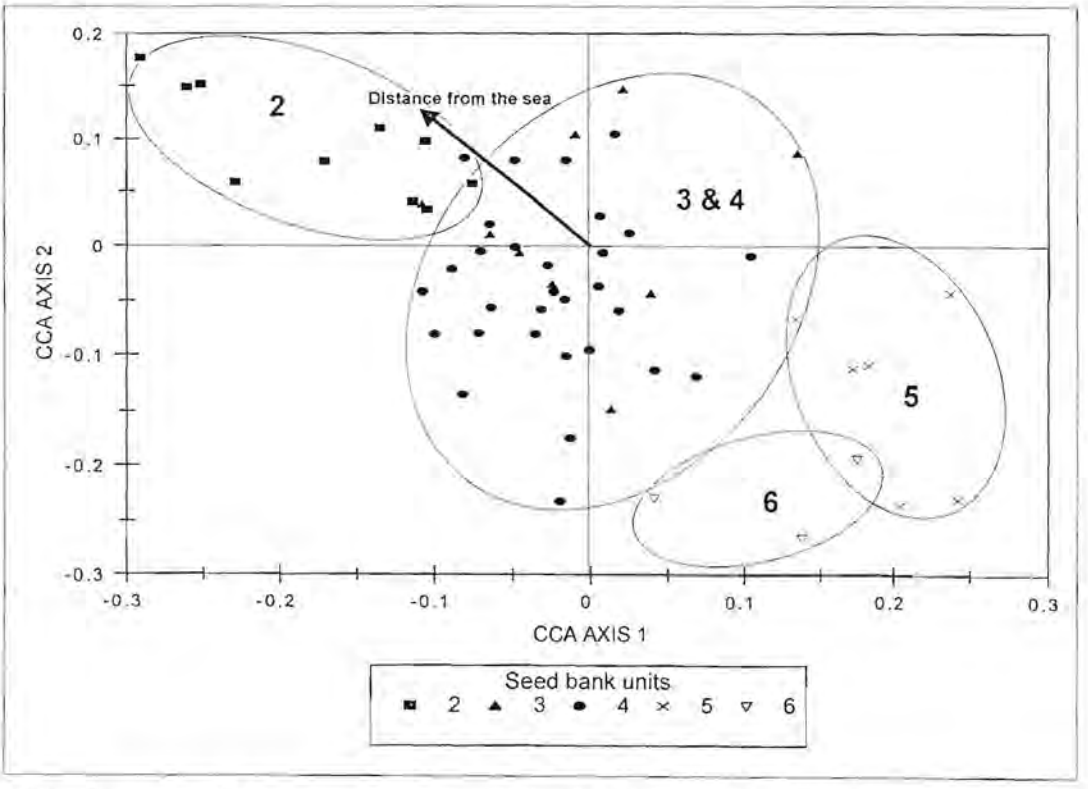

Figure 6.3. Canonical Correspondence Analysis (CCA) of floristic data of the soil seed bank along the first and second ordination axes (Eigen 1 = 0.195; eigen 2 = 0.101; scaling = 2).

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

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

- Communities for which the soil seed bank was not estimated

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

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

Seed bank unit 2

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

Seed bank unit 3

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

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

Seed bank unit 4

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

Seed bank unit 5

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

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

Seed bank unit 6

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

Ordination

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

CONCLUSIONS

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

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

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

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

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

Considering the dominance of perennial species in the standing vegetation, topsoil replacement alone will not be sufficient for the restoration of the mining area at the study site. However, mining of heavy minerals at the study site commences in a specific sequence, and topsoil is replaced directly to the adjacent preceded mined area (Environmental Evaluation Unit, 1990). Consequently, after revegetation by means of topsoil replacement, post-mining plant community boundaries may show little deviation from pre-mining plant community boundaries. The effectiveness of topsoil replacement for the restoration of a specific plant community will therefore depend mainly on the size and composition of the seed bank of that community.

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

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

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

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

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

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CHAPTER 7

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

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ABSTRACT

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

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

INTRODUCTION

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

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

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

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

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

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

MATERIAL AND METHODS

The study area covers approximately 9 400 ha and is situated in the vicinity of Brand-se-Baai (31°18' S, 17°54' E) on the Cape West Coast, South Africa (De Villiers *et al.*, 1999). The West Coast has a mediterranean-type climate with hot dry summers (November - January) and rain during the winter months (April - July). Rainfall increases from north to south with an average of 160 mm per annum (measured over a period of four years) at the study area. Fog is a characteristic feature of the Namaqualand coastal climate, occurring throughout the year. This advective sea fog (*c.* 100 days per annum at the study area) and the heavy dew-falls supplement the low rainfall significantly. The average annual precipitation (rainfall + fog) at the study area is 282 mm (De Villiers *et al.*, 1999). The average annual temperature is 15.8°C with a relatively small annual fluctuation due to the marine influence. The maximum average monthly temperature is 24.1°C in January (summer) and the minimum average monthly temperature is 7.5°C in July (winter) (De Villiers *et al.*, 1999). Frequent easterly berg winds, which blow from the interior, bring hot, dry conditions to the coast (Environmental Evaluation Unit, 1990).

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

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

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

Within each of these vegetation units, two sites were randomly selected using 1:50 000 aerial photographs. At each site, both the density and species richness of the standing vegetation and the soil seed bank were determined. During autumn 1995, 15 soil samples were collected linearly at intervals of two meters, at each site. Each sample consisted of a soil core with a diameter of 65 mm taken to a depth of 100 mm, totaling a volume of approximately 246 cm^3.

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

During early spring of 1995, an area of 10 m x 10 m at each site was divided into 100 quadrants measuring 1 m^2 each. Within each quadrant the number of all perennial and annual plant species (excluding grass species) were recorded. For grass species (Poaceae), percentage cover was estimated in each quadrant. In this paper, grass species are not included in the perennial and annual plant type categories, but are dealt with as a separate category. Species names conform to those of Arnold & De Wet (1999).

To compare species composition and density in the vegetation with that in the seed bank, data were ordinated by Principal Component Analysis (PCA) with the computer program CANOCO version 3.15 (Ter Braak, 1997). Before the analysis, the standing vegetation density/cover values for each species (individuals m^{-2}) from each plot were transformed to scores on a 1 – 9 abundance scale (Standing vegetation (excluding grasses): 1 = >0 – 0.05, 2 = >0.05 – 0.1, 3 = >0.1 – 0.5, 4 = >0.5 – 1, 5 = >1 – 2, 6 = >2 – 5, 7 = >5 – 10, 8 = >10 – 20, 9 = >20) (Grasses: 1 = >0 - 0.05, 2 = >0.05 – 0.1, 3 = >0.1 – 0.5, 4 = >0.5 – 1, 5 = >1 – 2, 6 = >2 – 3, 7 = >3 – 5, 8 = >5 – 10, 9 = >10). The seed bank data (emerged seedlings m^{-2}) were also transformed to scores on a 1 – 9 abundance scale (Seed bank: 1 = >0 - 100, 2 = >100 - 200, 3 = >200 - 300, 4 = >300 - 500, 5 = >500 - 750, 6 = >750 – 1 000, 7 = >1 000 – 1 500, 8 = >1 500 – 2 000, 9 = >2 000). These limits were chosen so that the density distribution of the nine classes would be similar for the vegetation and seed bank data.

For vegetation and soil seed bank, the density of individual m^{-2}, frequency (%) as well as the mean number of taxa per vegetation unit were calculated. Similarity in species composition between the standing vegetation and the soil seed bank was determined by means of Sorensen's index of similarity (*ISs*)(Mueller-Dombois & Ellenberg, 1974):

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

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

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

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

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

RESULTS

Standing vegetation

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

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

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

Seed bank

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

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

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

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

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

Table 7.1. (Continued)

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

P - perennial
A - annual

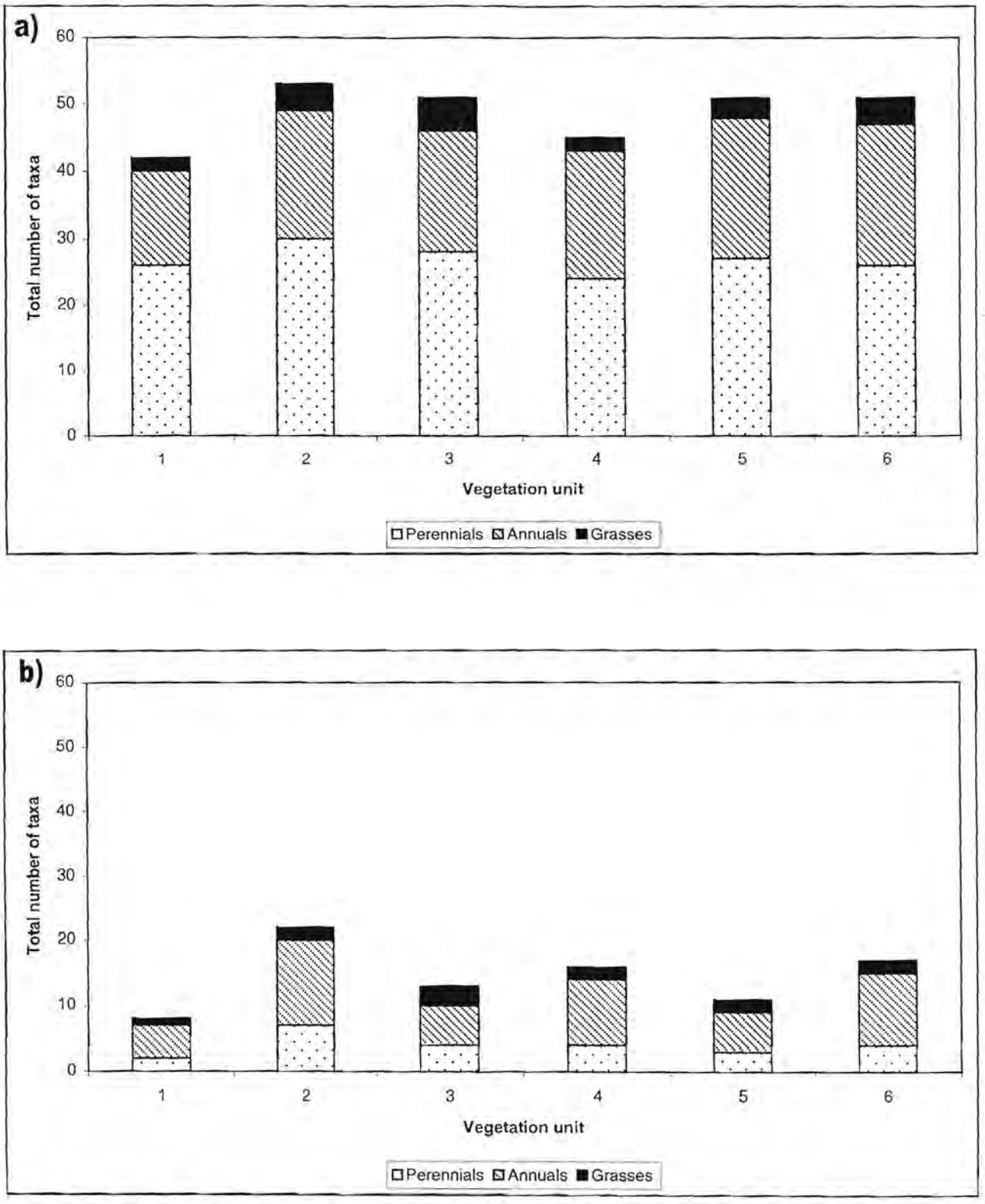

Figure 7.1. Total number of perennial, annual and grass taxa recorded in the a) standing vegetation and the b) seed bank, for six vegetation units of the Strandveld Succulent Karoo.

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

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

Standing vegetation *versus* seed bank

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

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

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

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

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

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

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

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

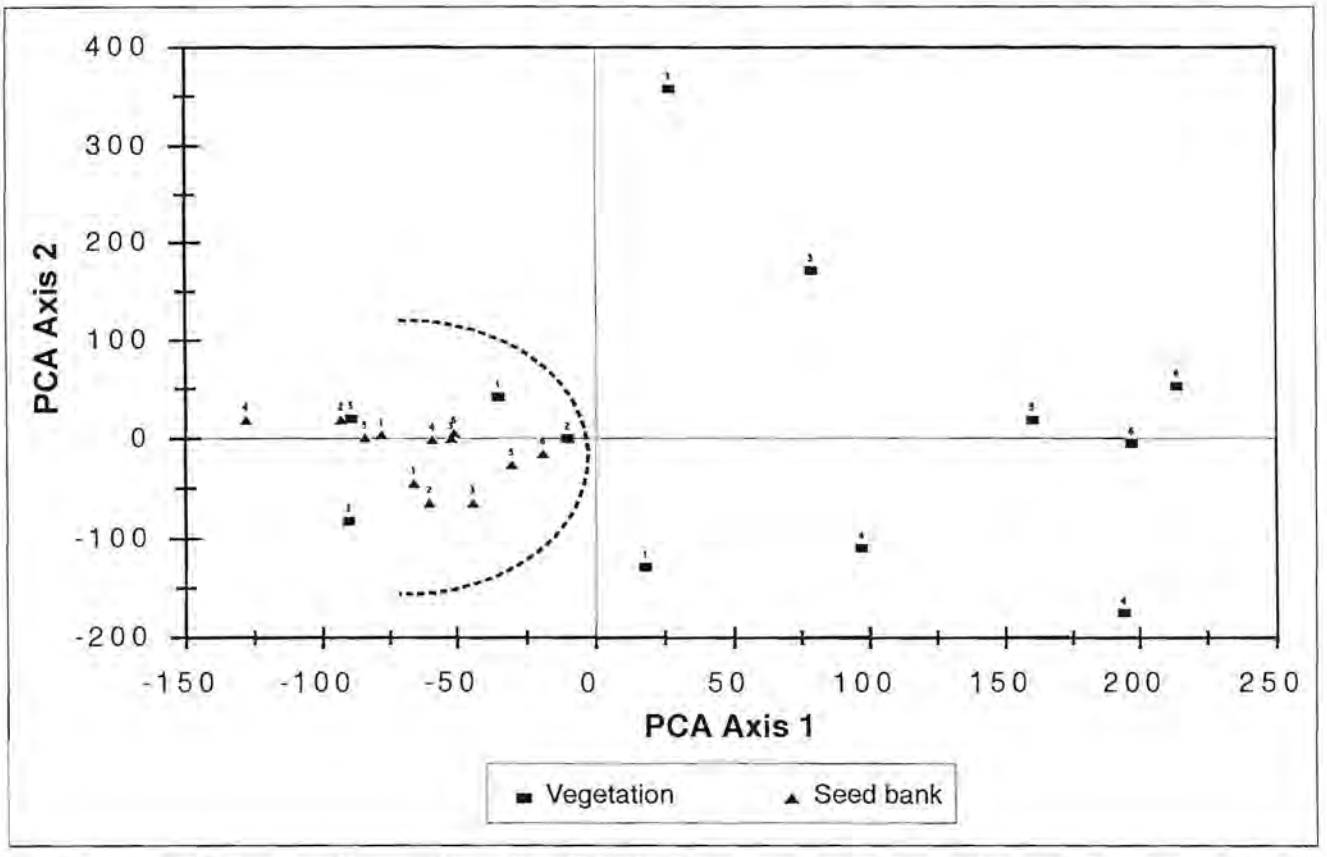

Figure 7.2. Ordination diagram based on Principal Component analysis of vegetation and seed bank density data, for six Strandveld Succulent Karoo vegetation units (Eigen1 = 0.153; eigen2 = 0.119; scaling = 2).

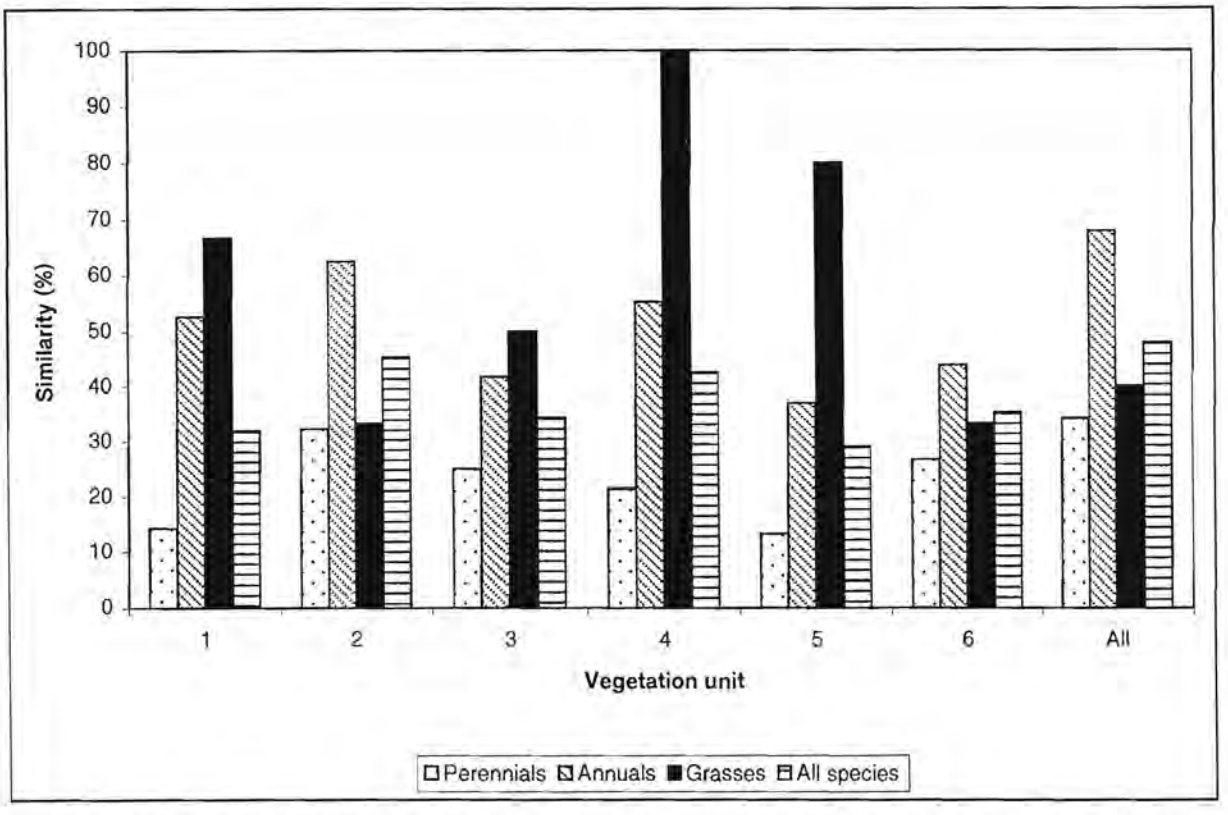

Figure 7.3. Similarity in number of taxa (%) according to Sorensen's Index of Similarity, between the standing vegetation and the seed bank, for different plant types in the Strandveld Succulent Karoo.

DISCUSSION

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

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

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

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

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

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

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

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

Revegetation

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

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

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

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

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

Topsoil replacement, sowing and transplanting should all be considered for the revegetation of mined areas in the Strandveld Succulent Karoo. Annual species will be recruited from the topsoil stored seed bank. However, all will depend on the period of stockpiling before being used in restoration, as this can negatively influence recruitment (Van der Valk *et al.*, 1992). Short-lived viable seeds may be lost if the soil is held too long, and environmental conditions, particularly temperatures, in the stockpiled soil may be so unfavourable that seeds are killed. Selected perennial species should be considered for transplanting and sowing.

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

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CHAPTER 8

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

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ABSTRACT

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

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

INTRODUCTION

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

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

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

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

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

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

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

MATERIAL AND METHODS

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

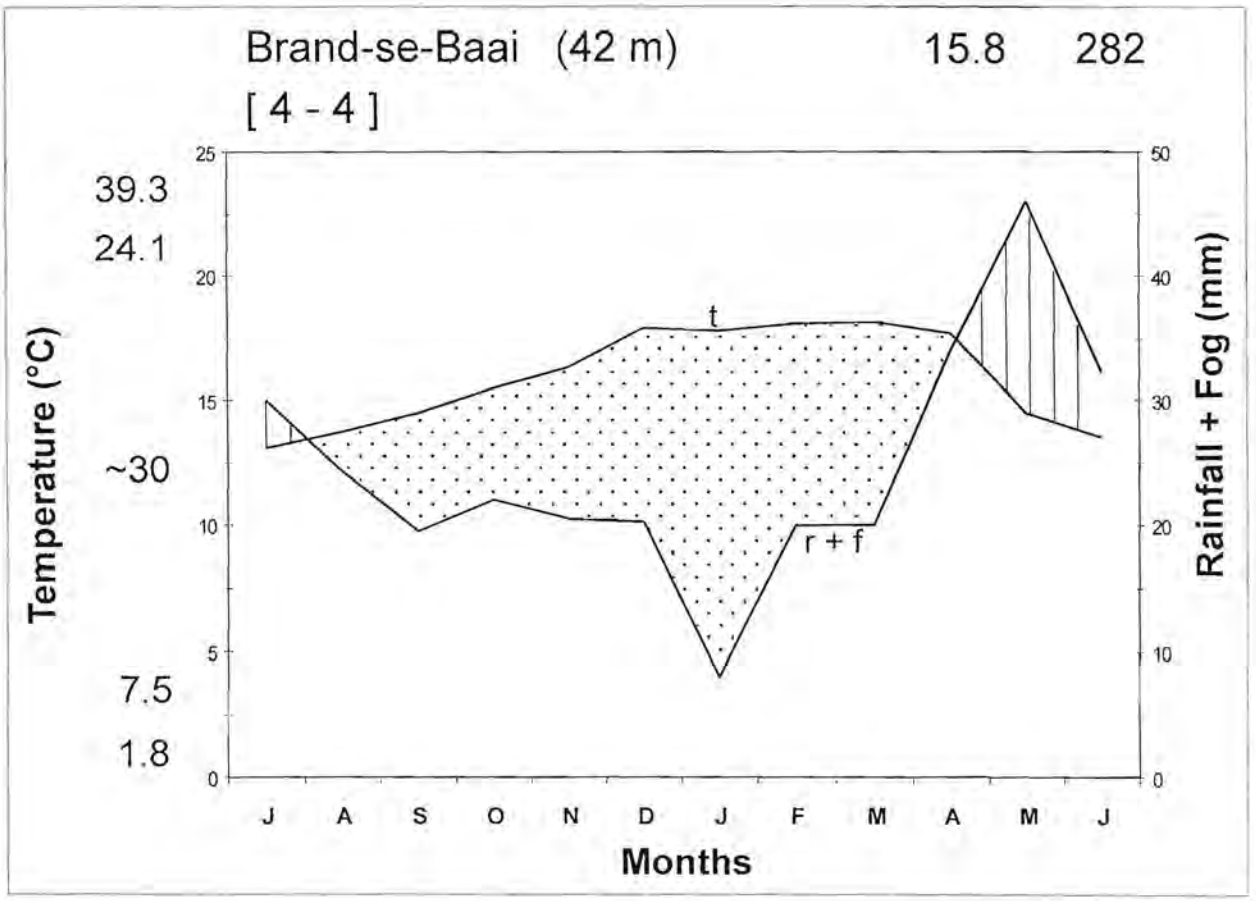

Figure 8.1. Climate diagram (following Walter & Lieth, 1960) of the Brand-se-Baai station for the period March 1993 – February 1997.

7.5°C and 24.1°C respectively (Figure 8.1). Collected seeds were air-dried at room temperature for a period of two weeks, whereafter seeds were stored in brown paper bags under ambient conditions at the University of Pretoria, for 28 weeks.

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

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

Seeds were germinated in Petri dishes with a diameter of either 90 mm or 50 mm (depending on the seed size), containing two layers of filter paper (Schleicher & Schüll, no. 595, Dassel, Germany) to which approximately 6 cm^3 or 4 cm^3 distilled water was added respectively. Germination tests were conducted in germination cabinets and each treatment consisted of five replicates of 50 seeds for each species. To determine the optimum light and temperature requirements for germination, tests were conducted in the light (under constant fluorescent light with a photosynthetic photon flux density of 9.3 µmol m^{-2} s^{-1}) and dark at six constant temperatures (7°C; 12°C; 17°C; 22°C; 27°C and 32°C) and one alternating temperature regime (12°C/22°C; 12h/12h). Petri dishes of the dark treatments were placed in cardboard boxes and sealed with aluminium foil to eliminate light. Germination of dark replicates was determined under a green safety light (Baskin & Baskin, 1998).

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

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

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

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

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

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

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

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

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

RESULTS

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

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

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

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

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

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

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

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

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

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

P - Perennial
A - Annual

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

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

-- No optimum temperature as all germination percentages were 0

P - Perennial

A - Annual

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

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

P - Perennial
A - Annual

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

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

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

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

DISCUSSION

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

Light requirements

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

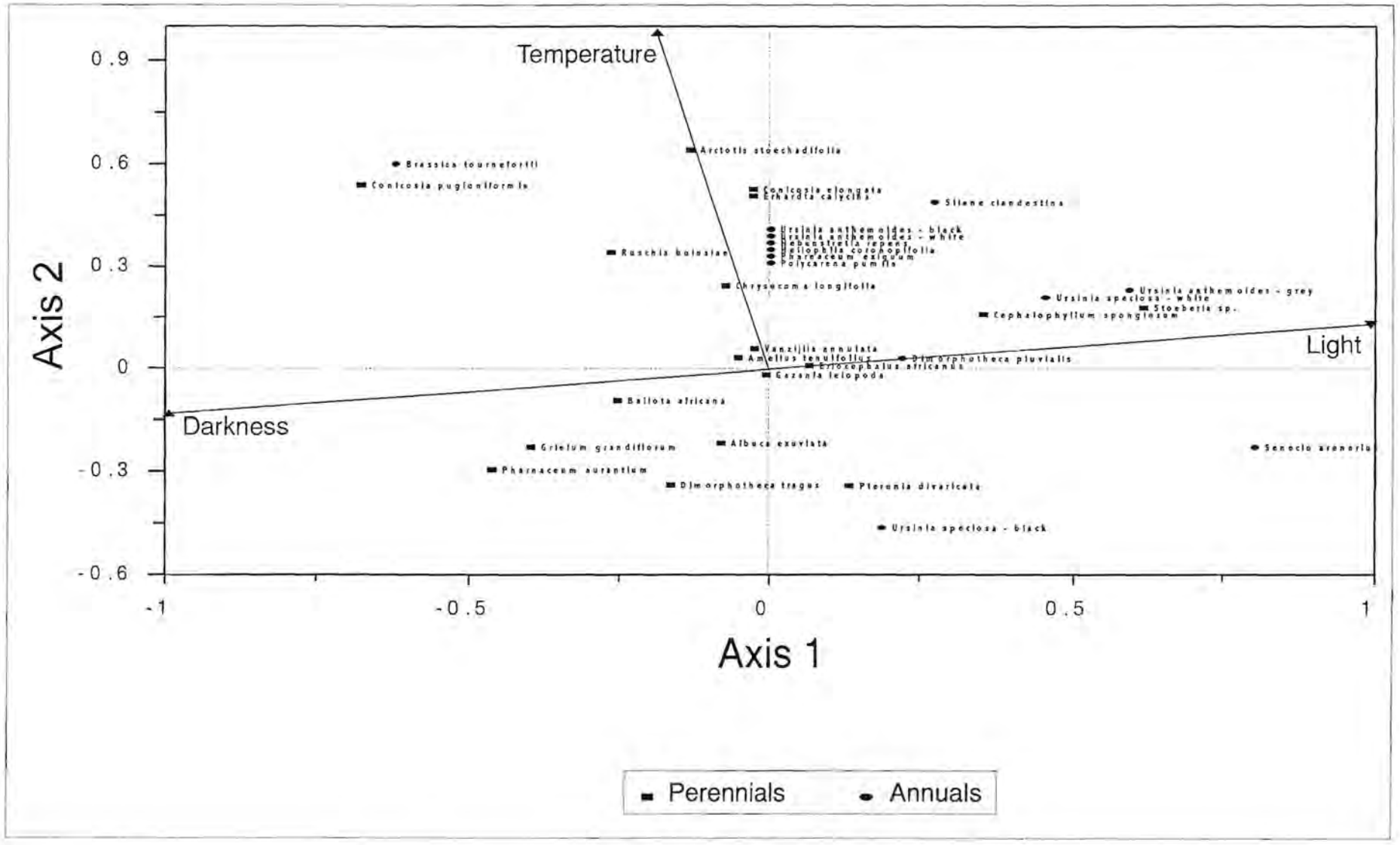

Figure 8.2. Ordination diagram based on Canonical Correspondence Analysis of the species germination percentage data with respect to three environmental variables (temperature, light & darkness). The species/environment correlation of the first two axes is 0.936 and 0.839 respectively. (Eigen1 = 0.094;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

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

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

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

Temperature requirements

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

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

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

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

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

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

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

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

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

Effect on revegetation

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

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

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

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

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

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

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CHAPTER 9

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

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ABSTRACT

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

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

INTRODUCTION

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

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

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

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

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

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

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

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

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

MATERIAL AND METHODS

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

Collected seeds were air-dried at *c.* 20°C for a period of two weeks (henceforth referred to as fresh seeds) before dormancy-breaking experiments commenced. Seeds were germinated in Petri dishes with a diameter of either 90 mm or 50 mm (depending on the seed size), containing two layers of filter paper (Schleicher & Schüll, no. 595, Dassel, Germany) to which approximately 6 cm^3 or 4 cm^3 distilled water was added respectively. Germination tests were conducted in germination cabinets and radicle protrusion was the germination criterion.

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

After-ripening

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

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

To determine the requirement for an after-ripening period, freshly collected seeds of each species were divided into three sets. The first set was used to determine the germination percentage of fresh seeds (stored for 2 weeks at *c.* 20°C). The second and third sets were stored dry in paper bags at ambient temperatures at the University of Pretoria, for six weeks or 28 weeks respectively, before conducting germination tests.

Germination tests were conducted in the light (under constant fluorescent light with a photosynthetic photon flux density of 9.3 µmol m^{-2} s^{-1}) at a constant temperature of 17°C. This temperature was found to be optimal for the germination of seeds of several Namaqualand plant species (Van Rensburg, 1978; Beneke *et al.*, 1993; De Villiers *et al.*, 1994; Visser, 1993). Each treatment consisted of five replicates of 50 seeds per replicate, for each species. The Petri dishes were examined every second day for a period of 30 days, and germinated seeds counted and removed.

Endogenous germination patterns

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

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

Alternative dormancy-breaking treatments

Seeds used in these experiments were collected during spring 1995 and included the following species: *Albuca exuviata* Bak., *Amellus tenuifolius* Burm., *Brassica tournefortii* Gouan, *Conicosia pugioniformis* (L.) N.E.Br., *Dimorphotheca pluvialis* (L.) Moench. (disc & ray achenes), *Ehrharta* calycina J.E.Sm., *Senecio arenarius* Thunb., *Tetragonia microptera* Fenzl, *Tripteris oppositifolia* (Ait.) T.Norl., and *Ursinia speciosa* DC. (white achenes).

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

1) Seeds were scarified mechanically by pricking the seed coat, whereafter they were germinated directly or leached in distilled water for four hours prior to conducting germination tests. Seeds of *Conicosia pugioniformis* were not pricked, but scarified with sandpaper. Both sandpaper or pricking of the seed coat were used for mechanical scarification of the seeds of *Brassica tournefortii.*
2) Chemical scarification entailed the submergence of the seeds in 98% sulphuric acid for periods of 0.5, 1, 2, 4, 8 or 16 minutes. Untreated seeds of *Tetragonia microptera* and *Brassica tournefortii* were also submerged for periods of 32 minutes and 32 or 64 minutes, respectively. After the period of submergence, seeds were rinsed with running distilled water for five minutes.
3) In hydration/dehydration treatments, seeds were submerged in 50 cm^3 distilled water for periods of 1, 2, 4, 8 or 16 hours. The water containing the submerged seeds was disturbed as little as possible. After hydration, seeds were air-dried at room temperature for 24 hours.
4) Seeds of the heat and/or cold pre-treatments were stored dry for one week at constant temperatures of 45°C or 5°C respectively. The seeds of the heat+cold treatment were stored dry for one week at a temperature of 45°C, followed by a one week dry storage period at 5°C. The seeds of the cold+heat treatment were treated in the reverse order.
5) In the "leaching" experiment, seeds were submerged in 50 cm^3 distilled water for periods of 1, 2, 4, 8 or 16 hours. The water containing the submerged seeds was stirred every 30 minutes, and was replaced with fresh distilled water every 60 minutes.

Germination tests were conducted at optimum temperature and light conditions for the germination of seeds of each species (Chapter 8). Seeds of *Amellus tenuifolius, Dimorphotheca pluvialis* (disc & ray achenes), *Senecio arenarius, Tetragonia microptera, Tripteris oppositifolia* and *Ursinia speciosa* (white achenes) were germinated in the light (under constant fluorescent light with a photosynthetic photon flux density of 9.3 µmol m^{-2} s^{-1}) at a constant temperature of 17°C. Seeds of *Albuca exuviata* and *Ehrharta calycina* were germinated in darkness at a constant temperature of 17°C. Seeds of *Brassica tournefortii* and *Conicosia pugioniformis* were germinated in darkness at a constant temperature of 22°C. The Petri dishes of the dark treatments were placed in cardboard boxes and sealed with aluminium foil to eliminate light. Each treatment consisted of five replicates of 50 seeds per replicate, for each species. The Petri dishes were examined every second day for a period of 30 days, and germinated seeds counted and removed. Germination of dark replicates was determined under a green safety light.

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

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

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

RESULTS

After-ripening

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

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

Endogenous germination patterns

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

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

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

A - annual
P - perennial

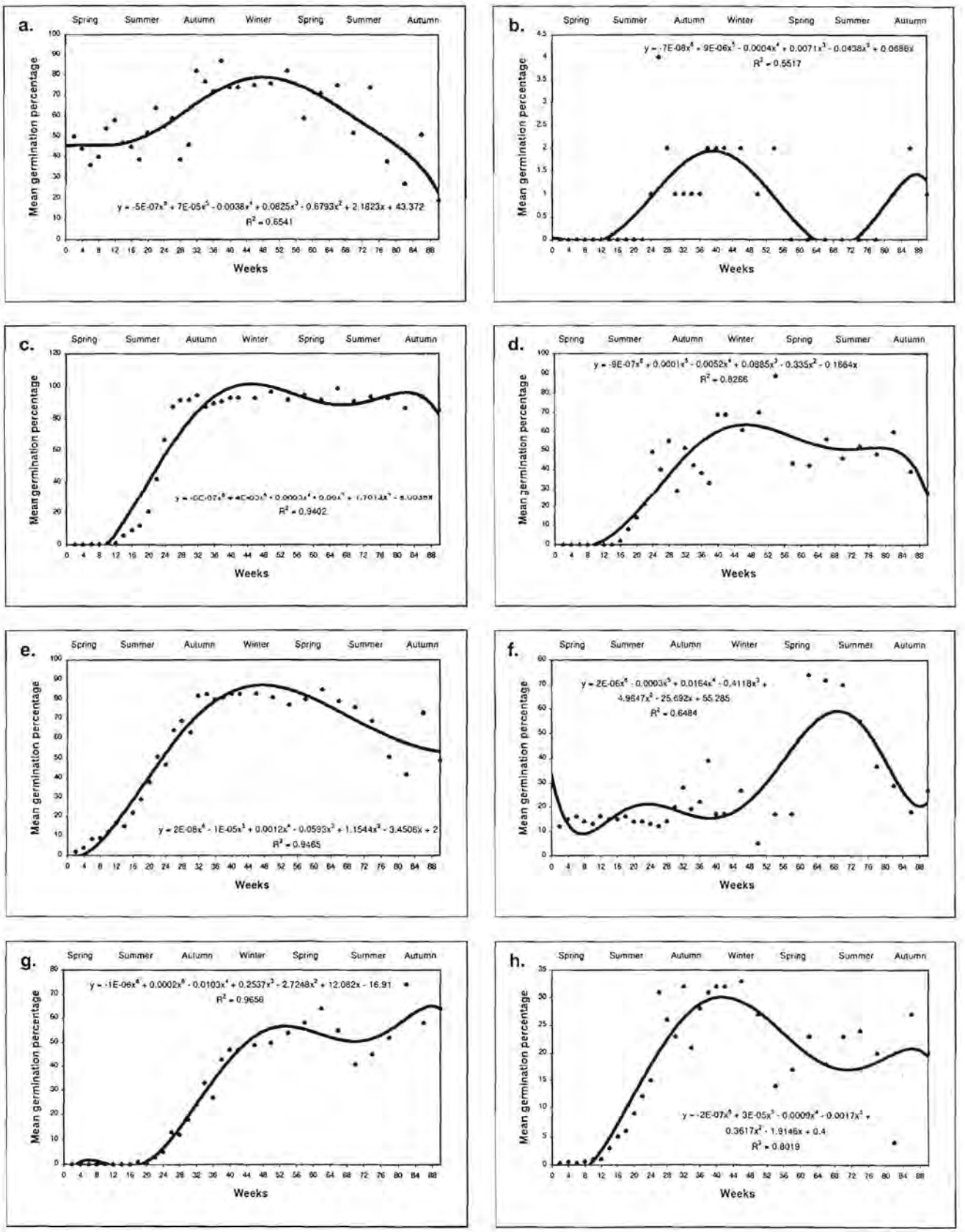

Figure 9.1. Sixth order polynomial functions fitted to mean germination percentages of a) *Amellus tenuifolius* (perennial), b) *Conicosia pugioniformis* (annual), c) *Dimorphotheca pluvialis* disc floret seeds (annual), d) *Dimorphotheca pluvialis* ray floret seeds (annual), e) *Gazania leiopoda* (perennial),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

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

Alternative dormancy-breaking treatments

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

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

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

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

DISCUSSION

After-ripening

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

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

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

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

- Treatment not used for this species

P - Perennial

A - Annual

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

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

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

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

- Treatment not used for this species

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

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

P - Perennial

A - Annual

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

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

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

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

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

Endogenous germination patterns

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

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

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

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

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

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

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

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

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

Alternative dormancy-breaking treatments

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

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

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

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

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

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

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

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

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

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

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

Revegetation

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

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

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

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

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

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

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

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

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

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

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