CHAPTER 13

THE ROLE OF FACILITATION IN SEEDLING RECRUITMENT AND SURVIVAL PATTERNS, IN THE STRANDVELD SUCCULENT KAROO, SOUTH AFRICA

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ABSTRACT

Adult plant distribution may be determined by processes operating during regeneration. Seedling emergence and survival beneath as well as in open spaces between selected perennial shrub species were investigated at five localities in the Strandveld Succulent Karoo, each dominated by a different shrub species. Seedling emergence and survival were also examined at three localities dominated by annual species. In general, species richness and seedling numbers were significantly higher in open areas than underneath shrubs, while seedling survival percentages did not differ significantly between microhabitats. None of the shrub species investigated seem to facilitate recruitment and survival of other species. The pattern of seedling distribution partly conformed to the model of Succulent Karoo vegetation dynamics. Knowledge on factors such as seedling recruitment and survival, underneath and in open areas between the canopies of selected shrub species, provided a predictive basis for assessing possible methods for revegetation of mined areas in the Strandveld Succulent Karoo.

Key words: Mining; Namaqualand; revegetation; seedling survival; shrub canopies; topsoil replacement; transplanting

INTRODUCTION

Events occurring during the seed and seedling stages are the primary determinants of the distribution of adult plants (Grubb, 1977; De Jong & Klinkhamer, 1988; Mustart & Cowling, 1993). A knowledge of the dynamics of germination and early seedling growth is important for an understanding of the structure and dynamics of communities (Valiente-Banuet & Ezcurra, 1991).

In most arid ecosystems, vegetation displays a heterogeneous spatial array consisting of vegetation patches alternating with areas of bare soil (Bertiller, 1998). Studies on arid ecosystems have demonstrated that seedling establishment and survival may depend on the shelter provided by shrub species (Carlsson & Callaghan, 1991; Hobbie, 1992; Yeaton & Esler, 1990). The communities of shrubs and their understoreys may maintain diversity in areas where otherwise only poor vegetation of stress-tolerant species would survive (Pugnaire *et al.*, 1996a).

An understanding of seedling responses to environmental differences provides some insight into restoration management problems. For example, information on differential survival characteristics of seedlings can be used to assist in the selection of species for reintroduction into disturbed vegetation. Furthermore, an understanding of the mechanisms and rates of recruitment is important for managers, since these processes influence population turnover and therefore maintenance of cover (Esler & Phillips, 1994).

The mining of heavy minerals along the arid West Coast of South Africa involves the total destruction of the existing vegetation (Environmental Evaluation Unit, 1990). Successful seedling establishment and survival will be crucial during the revegetation of these mined areas, irrespective of the method of revegetation *i.e.* sowing or topsoil replacement.

This study focused on seedling recruitment and survival underneath and in open areas between each of five shrub species dominant in the pre-mining standing vegetation of the Strandveld Succulent Karoo. An experimental analysis of seedling recruitment and survival at three localities predominated by annual species is also described. We predicted that these reproductive processes of the plant life-cycle would yield higher values underneath the canopies of Strandveld Succulent Karoo shrub species, since the amelioration of the physical environment produced by such shrub species is important in the patch-structured population dynamics of many communities of desert plants. Knowledge on these processes may also indicate local species and methods best suited for achieving post-mining revegetation goals.

MATERIAL AND METHODS

During the winter of 1995, eight localities were selected in the vicinity of Brand-se-Baai (31°18'S, 17°54'E), South Africa. The vegetation at each locality was predominated by a different perennial shrub (P) or annual (A) plant species *i.e. Eriocephalus africanus* L. (P), *Othonna floribunda* Schltr. (P), *Salvia africana-lutea* L. (P), *Senecio arenarius* Thunb. (A), *Tripteris oppositifolia* (Aiton) B.Nord. (P), *Ursinia speciosa* DC. (A), *Zygophyllum morgsana* L. (P) and a community with a number of dominant annual species.

At localities dominated by perennial species, a 1 m x 0.5 m metal frame was randomly placed either directly under the canopy or in open areas between shrubs of the dominant species. Ten replicates were used for each microhabitat and species. At localities dominated by annual species, ten replicates were used in total and the metal frame was randomly placed within each locality.

The position of each frame was marked semi-permanently with 150 mm long plastic pegs. Within each frame, all seedlings were identified and counted. For some seedlings, identification to species level was not possible and these seedlings have been grouped according to taxa or plant types, *e.g.* Mesembryanthemaceae, *Babiana* spp. and geophytes.

After three months (spring 1995), the surveys were repeated. Seedlings that emerged after the initial winter count were not incorporated in the calculation of seedling survival percentages. Nomenclature follows that of Arnold & De Wet (1999).

The least significant difference (LSD) one-way and multi-factor analyses of variance (ANOVA) as well as the multiple range test (Statgraphics 5.0, 1989, STSC, Inc., U.S.A.) were used to determine significant differences ($P \leq 0.05$) in seedling numbers, species richness and seedling survival, between treatments.

RESULTS AND DISCUSSION

Localities dominated by shrub species

Fifty-four percent of the taxa recorded at the five shrub dominated localities occurred both underneath and in open areas between shrubs (Group 1, Table 13.1). Taxa recorded only underneath (Group 2) or between shrubs (Group 3) constituted 23% each. Seedlings of annuals predominated in open areas (58%), while areas underneath shrub canopies were not dominated by any specific plant type (annuals 52%, perennials 48%) (Table 13.1).

Seedling numbers recorded underneath shrub canopies ranged from 0.2 m^{-2} to 50.4 m^{-2}, while that in open areas ranged from 0.2 m^{-2} to 227.0 m^{-2} (Table 13.1). The size of any germination event is directly related to the availability of seed, which can be influenced by a number of factors, such as the size, duration and timing of the rainfall event (Esler, 1999).

Annuals represented only 27% of the taxa unique to areas beneath shrub canopies (Group 2), in contrast to 47% in open areas (Group 3) (Table 13.1). Perennial species therefore predominated the taxa unique to areas beneath shrub canopies. The seeds of several shrub species from the Strandveld Succulent Karoo were found to be larger than those of most annual and perennial herb species in this area (Chapter 11), and did not require light for germination (Chapter 8). Larger seeds tend to be found in species whose seedlings establish in shaded environments (Westoby *et al.*, 1992) such as beneath the canopies of shrubs. Seedlings from larger seeds may in general be able to emerge successfully from greater depths in the soil, or from under larger accumulations of litter (Molofsky & Augspurger, 1992). Seedlings that have large cotyledons tend to be more vulnerable, and establishment below canopies possibly provides them with an added advantage against herbivory and/or water stress (Esler, 1999). Seed dispersal strategies will also influence species distribution between microhabitats, *e.g.* the large seeds (> 5 mm) of *Salvia africana-lutea* have no telechoric mechanisms, which may explain the absence of this species' seedlings in open areas (Table 13.1); the seeds of *Othonna floribunda* are anemochorous and seedlings were recorded at both microhabitats.

Species recorded at both microhabitats (Group 1, Table 13.1), as well as those unique to open areas (Group 3), were well represented in the soil seed bank of the study area (Chapters 4 & 5) and topsoil replacement will be sufficient for the recruitment of these species during revegetation efforts. Most of the species unique to areas underneath shrub canopies (Group 2) were not well represented in the soil seed bank of the study area (Chapters 4 & 5) and should be reintroduced to revegetation areas by means of sowing and/or transplanting. Also, these species may have a greater chance of survival when sown underneath rather than between transplanted shrub species.

Table 13.1. Mean number of seedlings m^{-2} for species recorded underneath or in open areas between shrubs during winter. Mean number of plants, recorded during the following spring, is indicated between brackets. Data were recorded at five locations, each dominated by a different shrub species

Microsite	Underneath plants					Open areas between plants				
Shrub species (location)	*Eriocephalus africanus*	*Othonna floribunda*	*Salvia africana-lutea*	*Tripteris oppositifolia*	*Zygophyllum morgsana*	*Eriocephalus africanus*	*Othonna floribunda*	*Salvia africana-lutea*	*Tripteris oppositifolia*	*Zygophyllum morgsana*
Species										
Group 1: Species recorded underneath and in open areas between shrubs										
Geophyte spp. (P)	0.2 (0.0)	1.2 (1.6)	0.4 (0.8)	1.2 (0.8)	1.0 (1.8)	0.8 (0.2)	0.4 (0.0)	0.4 (0.4)	0.4 (0.0)	1.6 (0.2)
Nemesia bicornis (A)	1.6 (1.2)	2.4 (1.2)	1.2 (0.0)	0.8 (0.0)	0.2 (0.0)	5.8 (1.0)	0.8 (0.8)	8.4 (0.8)	7.4 (1.0)	0.4 (0.0)
Ehrharta calycina (P)	2.4 (4.0)	5.6 (7.2)	4.8 (1.2)	2.0 (2.6)	2.8 (4.0)	2.6 (5.0)	7.6 (5.2)	7.2 (4.4)	6.6 (11.2)	0.8 (0.6)
Zaluzianskya villosa (A)	0.0 (0.2)	0.4 (0.0)		1.0 (0.0)		0.0 (0.4)	1.2 (0.0)	14.8 (0.0)	1.6 (0.4)	
Senecio arenarius (A)	1.2 (1.0)			1.0 (0.0)		6.2 (0.2)	0.4 (0.0)	3.2 (0.0)	2.4 (0.4)	
Wahlenbergia paniculata (A)		4.4 (0.8)				0.2 (0.0)		0.4 (0.4)	0.6 (0.6)	0.2 (0.0)
Karroochloa schismoides (A)	0.2 (0.2)	2.8 (0.4)		4.0 (1.8)		1.0 (1.0)	4.4 (4.0)		25.0 (16.8)	
Pharnaceum exiguum (A)		2.8 (0.4)		0.6 (0.6)	0.2 (0.2)		2.4 (1.6)		35.6 (12.2)	
Dimorphotheca pluvialis (A)	0.2 (0.2)				13.0 (4.0)	8.4 (4.0)		5.6 (3.6)		227.0 (96.4)
Oncosiphon suffruticosum (A)	0.0 (0.2)					0.2 (0.6)	0.4 (0.0)		1.0 (1.4)	
Helichrysum marmarolepis (A)				0.2 (0.2)		0.0 (0.4)		55.2 (22.8)	1.2 (0.6)	
Grielum grandiflorum (P)				0.2 (0.2)				0.8 (0.0)	2.8 (0.8)	0.4 (0.0)
Arctotheca calendula (A)	0.2 (0.2)			0.2 (0.0)		2.6 (2.2)				
Silene clandestina (A)	0.0 (0.6)			1.2 (1.2)		0.4 (0.8)			0.8 (1.0)	
Coelanthum semiquinquefidum (A)		1.2 (0.8)		0.6 (0.6)			8.8 (4.4)		1.0 (0.6)	
Oxalis spp. (P)		50.4 (45.6)		0.4 (0.0)			48.0 (42.8)		1.8 (1.4)	
Pelargonium senecioides (A)		0.0 (0.4)		0.4 (0.0)			0.8 (0.6)		1.8 (2.2)	
Arctotis hirsuta (A)		0.4 (0.4)					2.0 (0.0)		0.8 (0.2)	
Polycarena pumila (A)		0.8 (0.0)					0.4 (0.0)		8.0 (1.0)	
Heliophila coronopifolia (A)	0.2 (0.0)					0.8 (2.4)				
Chaetobromus dregeanus (P)	0.6 (0.2)					0.0 (0.2)				
Hermannia amoena (P)	0.2 (0.2)					0.0 (0.2)				
Babiana spp. (P)	0.0 (0.2)					0.4 (0.4)				
Crassula umbellata (A)	0.0 (2.2)								0.0 (0.4)	
Pharnaceum aurantium (P)	0.0 (0.6)					0.8 (1.2)				
Nestlera biennis (P)		0.4 (0.0)					41.2 (15.6)			
Hebenstretia repens (A)		0.8 (0.4)							0.0 (2.8)	
Othonna floribunda (P)		0.4 (0.4)					0.4 (0.0)			
Manulea altissima (A)		0.0 (0.4)					2.4 (2.4)			
Limeum africanum (A)				0.2 (0.0)					4.0 (2.6)	
Adenogramma littoralis (A)				2.4 (0.2)					101.4 (43.0)	
Mesembryanthemaceae (P)				0.0 (0.2)		0.4 (0.0)				
Tripteris oppositifolia (P)				0.0 (0.2)					1.2 (0.2)	
Convolvulus sp. (P)					15.6 (6.0)					11.2 (4.0)
Tetragonia microptera (A)					1.4 (0.6)					1.0 (0.8)
Group 2: Species recorded only underneath shrubs										
Asparagus spp. (P)	0.2 (0.0)									
Zygophyllum morgsana (P)	0.2 (0.4)			0.2 (0.0)						
Crassula expansa (A)	0.0 (0.2)									
Mesembryanthemum crystallinum (A)	0.0 (0.8)									
Moraea spp. (P)	0.0 (0.2)									
Amellus tenuifolius (P)		0.4 (0.0)								
Hermannia spp. (P)		0.4 (0.0)								
Asparagus fasciculatus (P)		0.8 (0.4)								
Euphorbia spp. (P)		0.8 (0.4)								
Tripteris clandestinum (A)		3.2 (1.6)								
Pharnaceum lanatum (P)		0.0 (1.2)								
Salvia africana-lutea (P)			0.4 (0.8)		0.0 (0.2)					
Ballota africana (P)			0.0 (0.8)							
Lessertia benguellensis (A)					0.2 (0.2)					
Lycium ferocissimum (P)					0.0 (0.2)					
Group 3: Species recorded only in open areas between shrubs										
Foveolina tenella (A)						0.4 (0.0)				
Brassica tournefortii (A)						1.4 (1.2)				
Arctotis stoechadifolia (P)						0.2 (0.2)				
Pelargonium gibbosum (P)						0.2 (0.2)				
Trachyandra divaricata (P)						0.2 (0.2)		0.4 (0.4)		
Sonderina tenuis (A)						0.0 (0.4)				
Felicia dregei (P)							0.4 (0.4)			
Isolepis marginata (A)							1.6 (2.8)			
Conicosia pugioniformis (P)								0.4 (0.0)		
Manulea pusilla (A)								0.8 (0.0)		
Tetragonia virgata (P)								2.4 (0.0)	0.2 (0.0)	
Wahlenbergia sonderi (P)								0.0 (1.2)		
Hermannia cernua (P)									0.0 (0.2)	
Hermannia scordifolia (A)									0.2 (0.4)	
Senecio breviscapus (A)										0.2 (0.0)

P - perennial
A - annual

The facilitation of seedling recruitment of some species by the presence of others (nurse-plant phenomenon) has been described for a variety of arid and semi-arid environments (McAuliffe, 1988; Valiente-Banuet & Ezcurra, 1991) including the Succulent Karoo (Beukman, 1991; Dean & Yeaton, 1992; Esler, 1999). The occurrence of seedlings under nurse-plants is considered primarily a method of avoiding abiotic stress at the seedling stage (Dean & Yeaton, 1992). In arid ecosystems, seedling establishment and survival may depend on the shelter provided by shrub species (Carlsson & Callaghan, 1991; Hobbie, 1992; Wiegand *et al.*, 1995), which protect seedlings from high irradiance, temperature (Vetaas, 1992), rates of transpiration (Moro *et al.*, 1997) and predation (Turner *et al.*, 1966; Nobel, 1980; Noy-Meir, 1980; McAuliffe, 1988; Franco & Nobel, 1989; Yeaton & Esler, 1990; Carlsson & Callaghan, 1991; Valiente-Banuet & Ezcurra, 1991; Keeley, 1992; Moro *et al.*, 1997). Shrubs may also cause an accumulation of mineral nutrients (Chapin *et al.*, 1994) and water (De Jong & Klinkhamer, 1988; Gutiérrez *et al.*, 1993; Moro *et al.*, 1997), leading to a local increase in fertility (Miles, 1985; Garner & Steinberger, 1989; Schomberg *et al.*, 1994; Pugnaire *et al.*, 1996a; Stock *et al.*, 1999). However, herbs rather than shrubs are directly responsible for the accumulation of nutrients under the canopy (Vetaas, 1992). Retention of seeds by the litter layer beneath shrubs may also influence the spatial distribution of vegetation (Redbo-Torstensson & Telenius, 1995).

Shrubs may also benefit from the effect of understorey plants, for example, protecting the soil from erosion, direct insolation, and over-heating (Fowler, 1986; Pugnaire *et al.*, 1996b).

In general, a higher number of seedlings (Figure 13.1) and species richness (Figure 13.2) were recorded during winter than plants during spring, irrespective of microhabitat and locality (Table 13.2). Open areas yielded higher seedling numbers (Figure 13.1) and species richness' (Figure 13.2) than areas underneath shrub canopies (Table 13.2). Therefore, none of the shrub species investigated seemed to act as "nurse-plants", which is consistent with the Succulent Karoo vegetation dynamics model described by Yeaton & Esler (1990). According to this model, open areas are colonised by species of the Mesembryanthemaceae (mesembs), which later serve as sites of establishment for seedlings of woody shrub species. The latter species eventually replace the mesembs through interspecific competition and persist in the community until they reach senescence and die or are removed through overgrazing. Also, seedlings in supposedly more favourable microhabitats or safe sites may not be nursed but rather trapped (Esler, 1999). According to Wiegand *et al.* (1995), colonizer species of the Succulent Karoo establish in safe sites on bare ground in areas not shaded by plants. To avoid competition for water from neighbouring plants, seedlings of these colonizer species require gaps of minimum sizes. Shaded sites within or under the edge of the canopy of established colonizer species' plants provide safe sites for seedlings of secondary succession species.

Seedling survival percentages ranged from 37% to 78% and did not differ significantly between microhabitats for any of the localities investigated (Table 13.3), which supports the view that seedling recruitment of most species was not facilitated by the presence of others, *i.e.* shrubs. The number of seedlings that survived until spring was generally higher in open areas. Few seedlings reach reproductive maturity in undisturbed Karoo shrublands where long-lived species dominate (Milton, 1994), and seedling survival ranged from 1 - 5% of emergent seedlings in average years to 20 – 30% in years with ample post-germination rain (Milton, 1995). Because of markedly higher seedling survival percentages, population turnover in this part of the Strandveld Succulent Karoo should be faster than that reported for the southern Succulent Karoo.

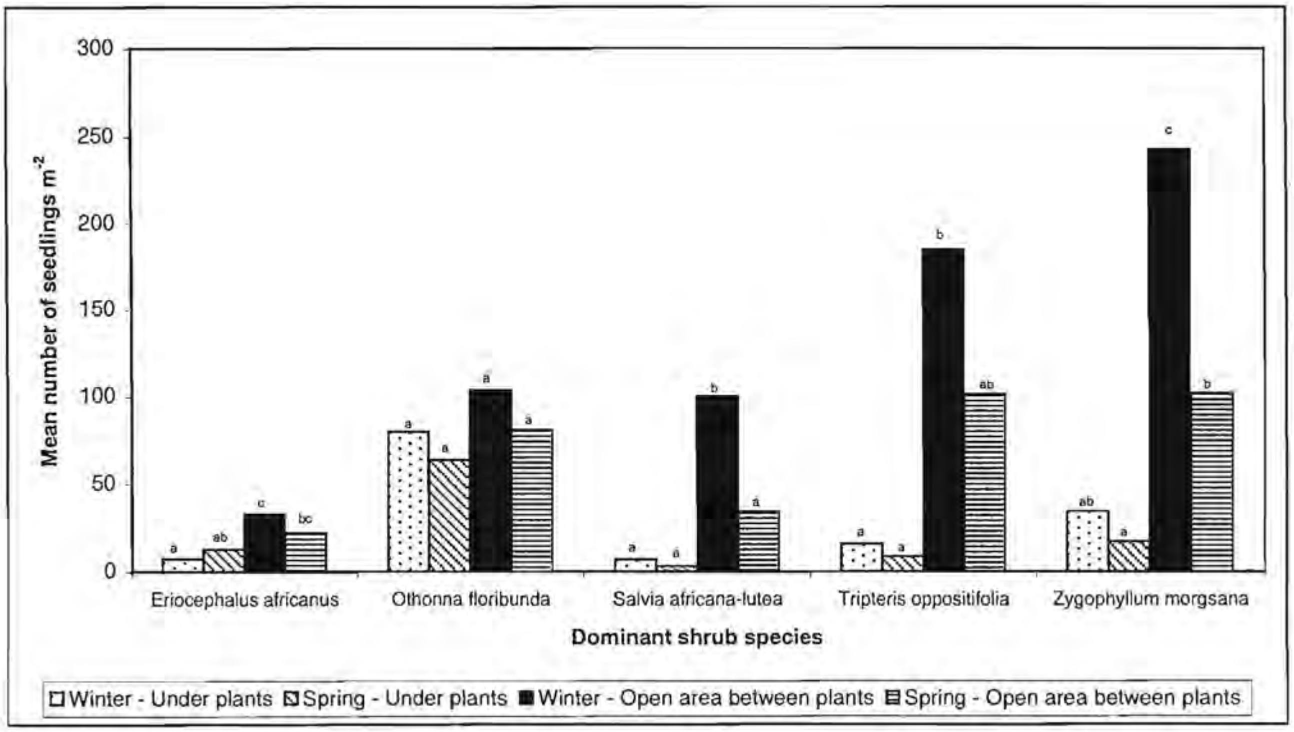

Figure 13.1. Mean number of seedlings m^{-2} recorded underneath and between shrubs. Data were recorded in five locations, each dominated by a different shrub species.

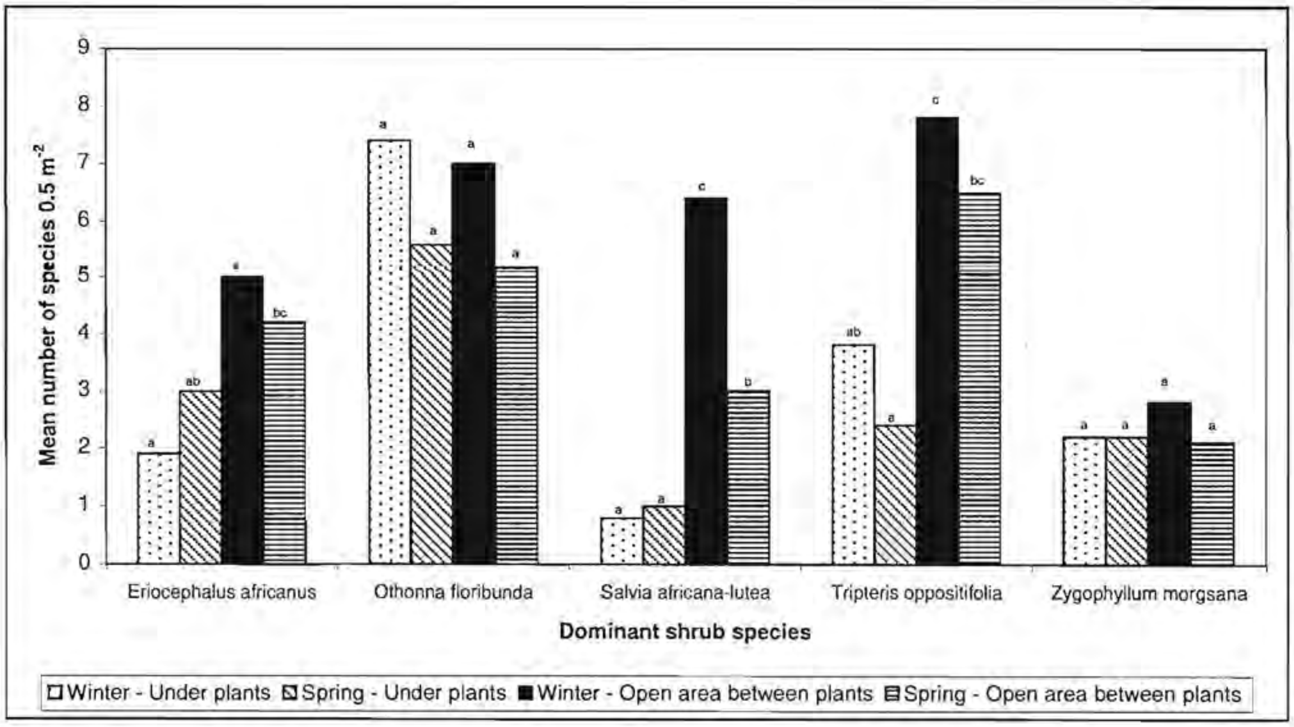

Figure 13.2. Mean number of species 0.5 m^{-2} recorded underneath and between shrubs. Data were recorded in five locations, each dominated by a different shrub species.

Table 13.2 Multi-factor analysis of variance ($P \leq 0.05$) for number of seedlings, species richness and seedling survival, recorded during two seasons (winter and spring) at two microhabitats (underneath and between shrubs) in five localities (each dominated by a different shrub species) of the Strandveld Succulent Karoo

Source of variation	Significance level ($P \leq 0.05$)		
	Number of seedlings	Species richness	Seedling survival
Main factors			
Locality (L)	0.0001 *	0.0000 *	0.0055 *
Microhabitat (MH)	0.0000 *	0.0000 *	0.0857 NS
Season (S)	0.0011 *	0.0221 *	
2-Factor interaction			
L x MH	0.0006 *	0.0001 *	0.9604 NS
L x S	0.3133 NS	0.3417 NS	
MH x S	0.0114 *	0.1312 NS	

* Significant at $P \leq 0.05$.

NS Not significant at $P \leq 0.05$.

Table 13.3. Seedling survival (%) recorded in eight localities of the Strandveld Succulent Karoo. In localities dominated by perennial species, seedling survival was recorded underneath and in open areas between the dominant shrubs, and significant differences between these two microhabitats were determined for each locality. In localities predominated by annual species, values followed by different letters indicate significant differences between localities. Seedlings that emerged after the initial winter count were not included in the survival percentages

Dominant species (locality)		Microhabitat		Significance level ($P \leq 0.05$)
		Underneath dominant species	Between dominant species	
Shrubs	*Eriocephalus africanus*	78.4	47.3	0.4136
	Othonna floribunda	74.9	64.4	0.7828
	Salvia africana-lutea	56.3	36.6	0.9592
	Tripteris oppositifolia	48.2	46.5	0.1854
	Zygophyllum morgsana	44.2	42.0	0.3971
Annuals	*Senecio arenarius*		47.0 a	0.0066
	Ursinia speciosa		64.8 b	
	Various annual species		45.3 a	

Although attempts to reseed degraded Karoo vegetation are generally not successful, the impact of seedling mortality on revegetation efforts at the study site would probably be negligible provided the availability of sufficient moisture (Esler, 1999), the exclusion of herbivores as well as the presence of wind-breaks (pers. obs.). The timing of recruitment will be of vital importance for seedling survival and to assure successful revegetation. In the Karoo, follow-up rain in the six months after emergence is crucial for seedling establishment (Milton, 1995; Esler, 1999).

Interfering effects of perennial shrubs on seedling survival and establishment in their understorey community may be through light deprivation (Goldberg & Werner, 1983; Franco & Nobel, 1989), mechanical effects caused by litter (Kitajima & Tilman, 1996), competition for water and nutrients (Carlsson & Callaghan, 1991; Yeaton *et al.*, 1993; Esler & Phillips, 1994; Esler, 1999), or leaching of allelopathic compounds (Moro *et al.*, 1997). The magnitude of reduction in seedling growth caused by any of these factors depends on seedling size and location under the shrub (Franco & Nobel, 1989).

Localities predominated by annual species

Of the 34 taxa recorded at the three locations predominated by annual species, only one annual species, *i.e.* *Zaluzianskya villosa*, was common to all locations (Table 13.4). Six taxa (4 annuals, 2 perennials) occurred at two of the locations. Seedling numbers ranged from 0.4 m^{-2} to 660.0 m^{-2} (Table 13.4), which are markedly lower than germinable seed bank density values recorded during autumn for the study area, *i.e.* 7771.7 seedlings m^{-2} recorded in 1994 and 5584.9 seedlings m^{-2} in 1995. This large difference in observed seedling numbers can be attributed to various factors, of which the size, duration and timing of the rainfall/watering events are the most obvious.

In general, a higher number of seedlings (Figure 13.3) were recorded during winter than plants during spring, irrespective of locality. Winter examination yielded mean seedling numbers of more than 100 seedlings m^{-2} at all locations, and more than 50 seedlings m^{-2} survived until spring. Seasonal differences in mean species richness was only significant at the locality predominated by *Senecio arenarius* (Figure 13.4), and was possibly due to low species richness' recorded.

Annual species constituted 74% of all seedling taxa recorded at locations predominated by annuals (Table 13.4). Topsoil replacement should therefore be sufficient for the recruitment of these species during revegetation efforts. Seedling survival (Table 13.3) ranged from 45% to 65% and differed significantly between localities. Seedlings of short-lived and ephemeral species have high probabilities of survival (Gutterman, 1993; Esler, 1999). In the Upland Succulent Karoo, recorded survival rates of annuals were highly variable within and between species at different sites and ranged from 47% to 74% of emerging seedlings (Van Rooyen *et al.*, 1979).

Table 13.4. Mean number of seedlings m^{-2} for species recorded during winter, at three locations, each pre-dominated in previous years by different annual species. Mean number of plants recorded during the following spring, is indicated between brackets

	Annual species (location)	*Senecio arenarius*	*Ursinia speciosa*	Various annual species
Species	**Group A: Species recorded at 3 locations**			
	Zaluzianskya villosa (A)	7.2 (2.8)	2.0 (0.4)	424.0 (252.0)
	Group B: Species recorded at 2 locations			
	Polycarena pumila (A)	0.4 (0.0)	0.8 (0.0)	
	Foveolina tenella (A)	2.0 (0.0)		126.0 (126.0)
	Senecio arenarius (A)	49.6 (15.2)	2.0 (2.0)	
	Mesembryanthemum crystallinum (A)	37.2 (21.2)		8.0 (6.0)
	Ehrharta calycina (P)	12.4 (26.0)	2.8 (1.6)	
	Oxalis spp. (P)		3.2 (1.2)	2.0 (6.0)
	Group C: Species recorded at single locations			
	Arctotheca calendula (A)	2.8 (0.4)		
	Galenia sarcophylla (P)	0.4 (0.4)		
	Oncosiphon suffruticosum (A)	0.4 (0.8)		
	Amellus microglossus (A)	0.0 (0.8)		
	Arctotis hirsuta (A)		1.6 (0.0)	
	Heliophila coronopifolia (A)		0.4 (0.0)	
	Nemesia bicornis (A)		0.8 (0.0)	
	Wahlenbergia paniculata (A)		10.0 (0.4)	
	Rumex spp. (A)		1.6 (0.4)	
	Limeum africanum (A)		1.2 (0.4)	
	Lapeirousia spp. (P)		0.8 (0.4)	
	Ursinia speciosa (A)		132.4 (92.0)	
	Nestlera biennis (P)		14.0 (10.0)	
	Adenogramma littoralis (A)		12.8 (9.2)	
	Cotula thunbergii (A)		4.0 (6.4)	
	Geophyte spp. (P)		3.2 (4.4)	
	Pelargonium senecioides (A)		0.8 (1.2)	
	Hebenstretia dentata (A)		0.0 (2.4)	
	Isolepis marginata (A)		0.0 (1.2)	
	Stipagrostis zeyheri (P)		0.0 (0.8)	
	Pharnaceum exiguum (A)			42.0 (0.0)
	Karroochloa schismoides (A)			660.0 (132.0)
	Tetragonia virgata (P)			352.0 (154.0)
	Tripteris clandestinum (A)			10.0 (8.0)
	Chenopodium opulifolium (A)			124.0 (104.0)
	Convolvulus spp. (P)			6.0 (6.0)
	Brassica tournefortii (A)			0.0 (4.0)

P - perennial

A - annual

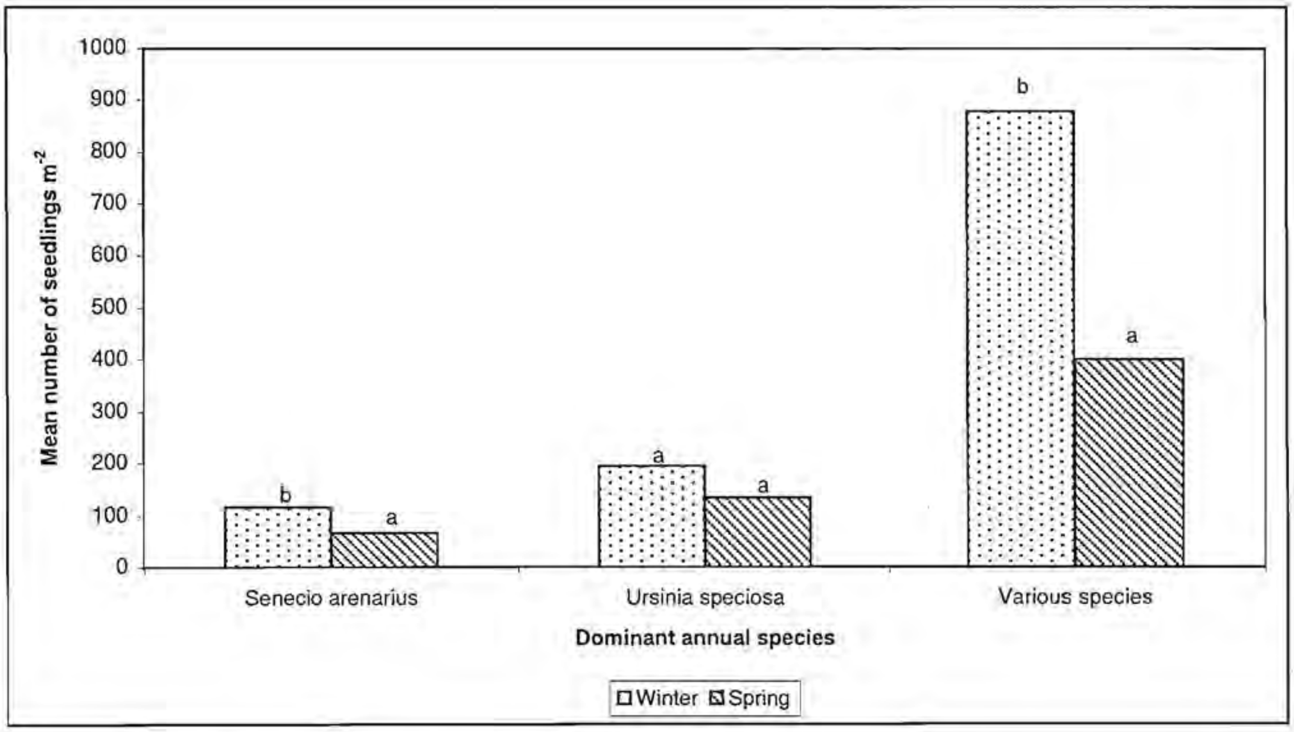

Figure 13.3. Mean number of seedlings m^{-2} recorded in three Strandveld Succulent Karoo communities predominated by annual species.

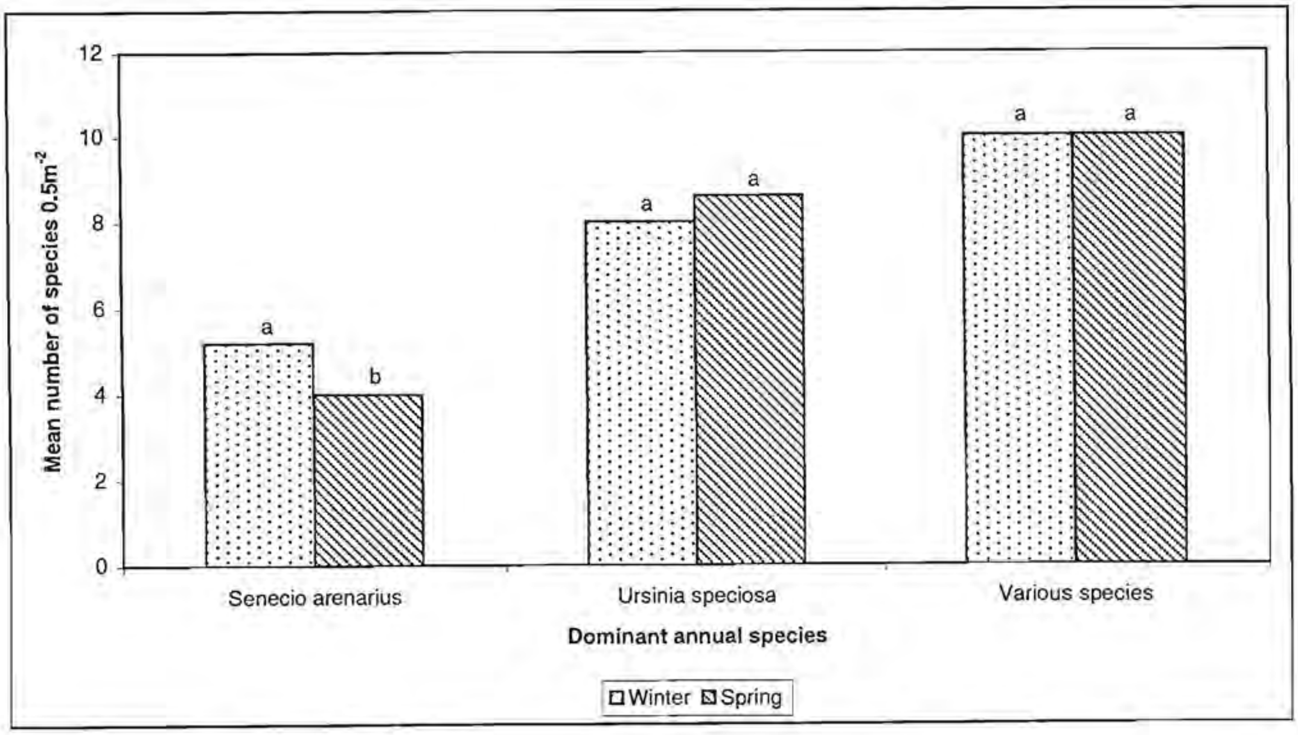

Figure 13.4. Mean number of species 0.5 m^{-2} recorded in three Strandveld Succulent Karoo communities predominated by annual species.

Few perennial shrub species' seedlings were recorded at localities predominated by annuals (Table 13.4), and those perennial shrub seedlings that did occur in these open areas, yielded high seedling numbers. Low seed availability, due to the transient nature of shrub species' seed banks as well as to seed dispersal characteristics, was probably the main reason for the few shrub seedlings recorded at localities predominated by annual species. These species will have to be reintroduced to post-mining areas by sowing and/or transplanting as a means to increase the species richness' of the areas. Transplanted shrubs may act as wind-breaks, thereby contributing to seedling survival of species recruited from replaced topsoil or which were sown. Transplanting of shrub species may also reduce the period between initial revegetation and seed production in these species.

CONCLUSIONS

Poor seed germination and seedling mortality, due to environmental constraints like water stress, soil salinity, high temperature and pathogens will limit the success of revegetation efforts in the Strandveld Succulent Karoo. One of the goals of post-mining revegetation efforts at Brand-se-Baai is to revegetate the area with at least 60% of the plant species present in the area prior to the start of mining activities (Environmental Evaluation Unit, 1990). Shrub species dominate the pre-mining standing vegetation at the study area (De Villiers *et al.*, 1999), and reintroduction of these species should be a priority during revegetation efforts. The seeds, of many of these shrub species, can germinate soon after dispersal, are probably not long-lived, and consequently produce transient seed banks (Chapters 4, 5 & 11). These shrubs can probably not be recruited from replaced topsoil, but transplanting or sowing of these species will benefit revegetation efforts due to increased species richness.

Both seedling numbers and species richness were higher in open areas than underneath shrub canopies, while seedling survival did not differ significantly between microhabitats. Therefore, none of the five shrub species investigated seem to facilitate the recruitment and survival of other species. In fact, seedling numbers and species richness were negatively affected by such shrub species. The negative effects of shrubs on seedling survival and establishment in their understorey community are usually through light deprivation, mechanical effects caused by litter, competition for water and nutrients, or leaching of allelopathic compounds (Cunliffe *et al.*, 1990; Yeaton & Esler, 1990; Yeaton *et al.*, 1993; Moro *et al.*, 1997; Esler, 1999).

Although seedlings of the dominant shrub *Salvia africana-lutea* were restricted to areas underneath the canopies of this species, the specific dispersal strategy seems more likely to be responsible for the recruitment pattern observed in this species. However, this aspect needs further investigation. Higher seedling survival underneath the canopies of shrub species, in arid regions such as the Strandveld Succulent Karoo, is chiefly the result of differential survival in shaded microsites with less direct solar radiation, and consequently, with lower daytime temperatures and lower evaporative demand (Valiente-Banuet & Ezcurra, 1991). Competition for water and shading by the nurse-plant may reduce the growth of the associated seedlings compared with exposed seedlings, as well as the eventual seed yield (Cunliffe *et al.*, 1990; Beukman, 1991; Dean & Yeaton, 1992; Yeaton *et al.*, 1993). Shrubs may also provide a microhabitat with higher soil nitrogen levels, which can partially offset the reduced seedling growth caused by shading and competition for soil water (Franco & Nobel, 1989). Differences in soil fertility under shrubs may therefore be of secondary importance, but restoration of mined areas along the West Coast of South Africa should also consider soil fertilization schemes.

Seedlings of annuals and perennial herb species will establish in the absence of transplanted shrubs at the study site. Most of these species accumulate persistent seed banks (Chapters 4, 5 & 11) and can be recruited from replaced topsoil and/or by sowing. However, in mined areas, high wind speeds during the period of seedling recruitment and establishment (Environmental Evaluation Unit, 1990) may result in high seedling mortality due to a sand blasting effect (pers. obs.). Shrubs present in these post-mining areas may aid in reducing wind speeds and therefore contribute to the survival of species in open areas. Additionally, vegetation patches established from transplanted shrubs may also act as sources of seeds that may eventually reach other patch types or patches of bare soil (Bertiller, 1998).

Results obtained in this study partly conform to the model for Succulent Karoo vegetation dynamics (Yeaton & Esler, 1990). Woody shrubs are the climax species in the succession sequence and therefore do not act as nurse-plants themselves. In this study, shrubs influenced recruitment, rather than survival, of seedlings derived from seeds that were "trapped" beneath the canopies of the shrubs. The Karoo vegetation dynamics model was based on southern Succulent Karoo vegetation, where Mesembryanthemaceae species are abundant. These species are less prominent in Strandveld Succulent Karoo vegetation, where annual precipitation, especially fog, is more predictable (Desmet & Cowling, 1999). It is therefore questioned whether these species act as nurse-plants for woody shrub species. The high number of perennial herb species present in Strandveld Succulent Karoo vegetation (pers. obs.) may indicate the functioning of these species as nurse-plants or sites for seed "trapping". In conclusion, further investigation of these aspects will prove invaluable for understanding the processes and dynamics of seed and seedling ecology in the Strandveld Succulent Karoo. In turn, these dynamic processes will contribute towards the formulation of appropriate post-mining revegetation strategies.

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CHAPTER 14

SEED PRODUCTION OF FOUR NAMAQUALAND PIONEER PLANT SPECIES GROWN ON SALINE SOIL

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ABSTRACT

The mining of heavy minerals along the west coast of South Africa will destroy all the standing vegetation, and will also lead to the salinization of the soil as sea-water will eventually be used in the mining process. Local, salt tolerant species should be selected for the revegetation of the area, and it is essential that the selected species should be able to reproduce to ensure growth of the population. Survival and seed production of four pioneer plant species were determined along a salinity gradient. None of the four species survived at the moderate and high salinities. Seed production of the ephemeral species was reduced at the low salinity, while that of the perennial species did not differ significantly.

Key words: Mining; Namaqualand; pioneer plant species; salinity; seed production

INTRODUCTION

The high accumulation of salts in soils which could be caused by any of several factors (eg. saline irrigation water, inadequate leaching, poor drainage, naturally saline soils) may hinder germination, seedling and vegetative growth as well as the yield and quality of plants (Mamo *et al.*, 1996). Two major effects have been identified as the probable causes of the detrimental effect of salinity on plant growth: the ionic effect and the osmotic effect (Lewis *et al.*, 1989; Banuls *et al,*. 1991; Leidi *et al.*, 1991).

Even though saline environments are unfavourable for most plant species, some plants, namely the halophytes, seem to flourish under these conditions. These plants have adapted to living under these harsh conditions by either avoiding salt uptake through osmoregulation; excreting the salts by means of salt glands and bladders; or tolerating the high salt concentration as euhalophytes or succulents (Larcher, 1995). Interspecific differences in response to salinity and differential responses resulting from interaction of salinity with other environmental factors occur. Variables such as irradiance and calcium content (Hyder & Greenway, 1965; Bogemans *et al.*, 1989), ecotypic variation within species (Tiku & Snaydon, 1971), soils (Venables & Wilkins, 1978; Watt, 1983), nitrogen levels and temperature (Kemp & Cunningham, 1981), species (Kingsbury & Epstein, 1986), CO_2 -

concentrations (Munns & Termaat, 1986) and humidity (Salim, 1989), can all affect plant responses to salinity. Several investigations showed that salt tolerance can vary with the phenological stage and that the effects of saline stress change with its duration (Gutierrez Boem *et al.*, 1997).

Along the western coast of South Africa, the sandy soils are rich in heavy minerals. Not only will the mining activities in the area destroy the topography, vegetation, soil chemical and physical characteristics and alter the animal life, but the process whereby the heavy minerals are extracted will eventually involve the use of sea-water and therefore the salinity of the mined soil will be increased to levels where plants will find it difficult to grow (Environmental Evaluation Unit, 1990). Although several local species are able to tolerate high salinities (De Villiers, 1993), it does not mean that they will produce seeds under these conditions. The aim of this study was to determine if selected plant species growing on saline soil are able to survive and reproduce by means of seeds, and thus contribute towards the growth of the population and the successful revegetation of the area.

MATERIAL AND METHODS

Seeds of natural populations of *Gazania leiopoda* (DC.) Rössl. (perennial), *Tetragonia microptera* Fenzl (ephemeral), *Dimorphotheca pluvialis* (L.) Moench (ephemeral) and *Senecio arenarius* Thunb. (ephemeral), were collected at Brand-se-Baai (31°18'S, 17°54'E), South Africa. Although members of the Asteraceae have achenes and *Tetragonia microptera* produces a samara, the term seed will be used throughout this paper. These species were chosen because they are abundant and native to the area and/or seem to be acting as pioneer species in surrounding areas (De Villiers, 1993). Seeds were sown in 1 dm^3 pots, containing fine sand (0.5 -1.1 mm particle size), and irrigated daily with tap water, under free-draining conditions, for a period of two weeks. Thereafter the plants were irrigated daily under free draining conditions, with 250 cm^3 solution having a sodium chloride (NaCl) concentration of either 1%, 2% or 3%. Distilled water was used as a control. The chemicals of half strength Arnon and Hoagland's nutrient solution (Hewitt, 1952) were added to all dilutions. Salts, that might have accumulated in the soil, were leached from the soil by giving each pot 500 cm^3 distilled water twice a week, before the saline solution was applied. A randomized blockless design was used. One plant was grown in each pot and ten replicates of each treatment (control; 1% NaCl, 2% NaCl and 3% NaCl) were used for each of the four species. Inflorescences / flowers and mature seeds were harvested and counted before dispersal. Results were analysed statistically as a blockless design using the one-way analysis of variance and LSD (Least Significant Difference) multiple range test of the Statgraphics 5.0[1] computer program, to test for significant differences at a 95% confidence level.

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

RESULTS AND DISCUSSION

None of the four species survived at salinities higher than 1% NaCl (Table 14.1). Although most of the plants of the four species survived at the 1% NaCl treatment, the ephemeral species showed signs of chlorosis. The mortality rate of the four species increased as the salinity increased. The plants of the 3% NaCl treatment died first (after three weeks), followed by the plants of the 2% NaCl treatment (after nine weeks). De Villiers *et al.* (1997) found several perennial species of this area to be moderately salt tolerant. Although *Gazania leiopoda* is a perennial species, it did not survive at the moderate and high salinities as expected.

In the case of *Gazania leiopoda* (perennial), the mean number of inflorescences produced per plant did not differ significantly between the 1% NaCl and the control treatment (Figure 14.1). The mean number of seed bearing inflorescences were significantly lower than those not bearing seeds, for both the control and 1% NaCl treatment. Although the mean number of seed bearing inflorescences decreased when this species was grown on saline soil, the total number of inflorescences produced did not differ. The mean number of inflorescences produced per plant decreased significantly with increasing salinity, for both *Senecio arenarius* and *Dimorphotheca pluvialis* (Figure 14.1). In the control treatment, both these ephemeral species produced a significantly greater number of seed bearing inflorescences than non-seed bearing inflorescences. In the 1% NaCl treatment, the number of seed bearing inflorescences were less than the inflorescences not bearing seeds, but this was only significant in the case of *Dimorphotheca pluvialis*. Therefore, the ephemeral species not only produce less inflorescences when grown on saline soil, but the inflorescences that are produced bear less or no seeds.

The mean number of seeds produced per plant are given in Table 14.2. Although not significantly, *Gazania leiopoda* produced a greater number of seeds per plant in the 1% NaCl treatment than in the control treatment, mainly because of the greater number of seeds produced per inflorescence. A low salinity therefore seems to enhance the number of seeds produced by this species. Francois & Kleiman (1990) reported that *Crambe abyssinica* showed a 6.5% reduction of seed yield for each unit increase in soil salinity above 2.0 dS m^{-1}, but no significant reduction of seed yield below this concentration. The mean number of seeds produced per plant decreased with increasing salinity for all three ephemeral species (Table 14.2). In the cases of *Dimorphotheca pluvialis* and *Senecio arenarius*, this decrease is due to a reduction in both the number of inflorescences produced per plant and the number of seeds produced per inflorescence, with increasing salinity. A decrease in yield with increasing salinity has been reported for many species (Abdul-Halim *et al.*, 1988; Francois *et al.*, 1988; Francois *et al.*, 1989; Jones *et al.*, 1989; Francois & Kleiman, 1990; Ashraf & Tufail, 1995; Ashraf & O'Leary, 1996; Mamo *et al.*, 1996; Gutierrez Boem *et al.*, 1997). Abdul-Halim *et al.* (1988) found that at a low soil salinity level (< 8.0 dS m^{-1}), and maintaining the available soil water above a specified percentage during the growth period, would effect a small reduction on wheat yield.

Table 14.1. Survival percentages of four pioneer species grown at different soil salinities

Species	Treatment			
	Control	1% NaCl	2% NaCl	3% NaCl
Gazania leiopoda (perennial)	100	100	0	0
Senecio arenarius (ephemeral)	90	60	0	0
Tetragonia microptera (ephemeral)	100	80	0	0
Dimorphotheca pluvialis (ephemeral)	90	70	0	0

Table 14.2. Seed production (seeds/plant) of four pioneer species grown at different soil salinities. For each species, values followed by the same letter do not differ significantly at $P \leq 0.05$

Species	Treatment	
	Control	1% NaCl
Gazania leiopoda (perennial)	9.1 [a]	15.0 [a]
Senecio arenarius (ephemeral)	807.8 [a]	12.4 [b]
Tetragonia microptera (ephemeral)	96.9 [a]	21.9 [b]
Dimorphotheca pluvialis (ephemeral)	77.2 [a]	0.0 [b]

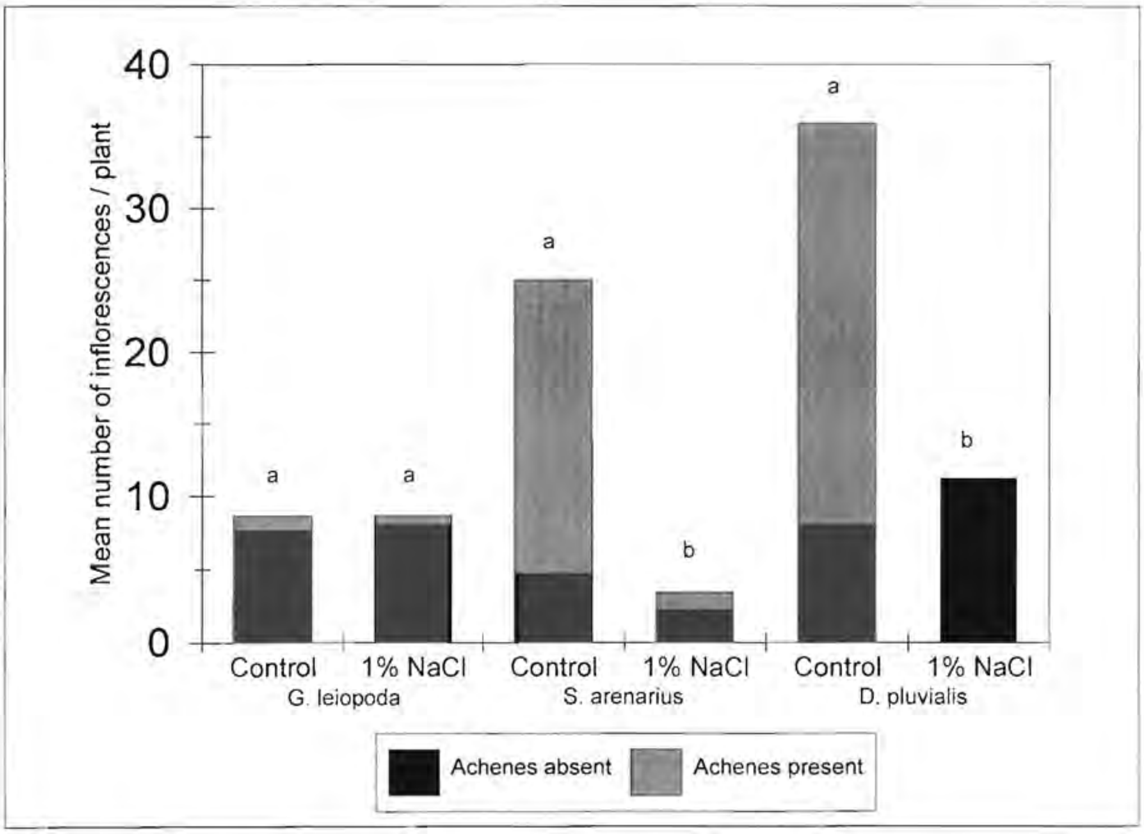

Figure 14.1. The mean number of inflorescences produced per plant, of *Gazania leiopoda, Senecio arenarius* and *Dimorphotheca pluvialis* grown on saline soil. Bars with the same letter are not significantly different at the $P \leq 0.05$ level.

CONCLUSIONS

Although most ephemeral species survive when grown on soil with low salinities, these species yield almost no seeds. As seeds are ephemeral species' only means of reproduction, these species will have to be revegetated from seed sources outside the mined area, or from replaced topsoil. Fortunately, populations of representative ephemeral species occur outside the mined area, and the seeds of most of these species are wind dispersed. If the salinity of the mined soil can be kept at a low concentration, perennial species will be able to survive and in some cases seed production may even be enhanced. Studies comparing the viability, longevity and germinability of seeds, produced by plants grown on soils with different salinities, are now essential. Future studies should also include emergence, seedling survival, plant growth, yield, etc. of plants derived from seeds produced at different soil salinities.

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CHAPTER 15

SEEDLING EMERGENCE AND SURVIVAL OF THREE NAMAQUALAND PIONEER PLANT SPECIES GROWN UNDER SALINE SOIL CONDITIONS

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ABSTRACT

The effects of salinity (NaCl) on emergence and seedling survival of three Namaqualand pioneer plant species, were investigated. In the perennial species (*Gazania leiopoda*), seedlings did emerge in the 1% NaCl treatment (although the maximum mean percentage of emerged seedlings was only 2%), but not at the higher salinities. Seedlings of the two ephemeral species only emerged in the control treatment. Increased salinity resulted in an increased mortality rate of seedlings. Perennial species are recommended for revegetation of saline soils in this area. To ensure successful restoration of mined areas in Namaqualand, soil salinity should be at a minimum.

Key words: Emergence; mined soil; NaCl; salinity; seedling survival

INTRODUCTION

Along the western coast of South Africa, the sandy soils are rich in heavy minerals. The mining process whereby the heavy minerals are extracted, involves the use of sea-water and therefore the salinity of the mined soil can be so high that plants will find it difficult to grow under these conditions (Environmental Evaluation Unit, 1990). Although mature plants of several local species are able to tolerate high salinities (De Villiers *et al.*, 1997), it does not mean that they will germinate, emerge and survive the seedling stage under these conditions.

Salinity, whether natural or induced, is a widespread environmental stress that can limit growth and development of salt-sensitive plants (Rodriguez *et al.*, 1997). Although the germination of seeds in saline environments has been examined in various studies (McMillan, 1959; Ungar, 1962; Younis & Hatata, 1971; Williams & Ungar, 1972; Ahmed, 1985; Mariko *et al.*, 1992; Yokoishi & Tanimoto, 1994; Ungar, 1995, 1996; Baskin *et al.*, 1998; Gul & Weber, 1998; Masuda *et al.*, 1999), only a few studies examined the effect of salinity on emergence and seedling survival/growth of plant species (Seneca, 1972; Singh, 1990; Van Hoorn, 1991; Azaizeh *et al.*, 1992; Evlagon *et al.*, 1992; Zhong & Läuchli, 1993; Chartzoulakis & Loupassaki, 1997; Franco *et al.*, 1997; Rodriguez *et al.*, 1997; Katembe *et al.*, 1998). On saline soil, the plant encounters more problems during germination, emergence and early seedling growth than during later growth stages and may fail to establish. Early seedling growth of some species appears to be less salt tolerant than during germination and later growth (Van Hoorn, 1991; Chartzoulakis & Loupassaki, 1997).

Interspecific differences in response to salinity and differential responses resulting from interaction of salinity with other environmental factors occur. Variables such as irradiance and calcium content (Hyder & Greenway, 1965; Bogemans *et al.*, 1989; Volkmar *et al.*, 1998), ecotypic variation within species (Tiku & Snaydon, 1971), soils (Venables & Wilkins, 1978; Watt, 1983), nitrogen levels and temperature (Kemp & Cunningham, 1981; Khan & Ungar, 1996; Masuda *et al.*, 1999), species (Kingsbury & Epstein, 1986), CO_2 concentration (Munns & Termaat, 1986; Yeo, 1999) and humidity (Salim, 1989), can all affect plant responses to salinity.

Several studies in the Karoo, South Africa, have focused on factors affecting seedling establishment and survival (Esler & Phillips, 1994; Milton, 1995), but plant responses to salinity has been a neglected area of study in this arid environment (Theron, 1964; Lloyd, 1985; De Villiers *et al.*, 1994a, 1994b, 1995, 1996, 1997, 1999).

The present study was undertaken to improve understanding of the responses of three Namaqualand pioneer species to different levels of salinity during emergence and the seedling stage. Information about salinity tolerance at the seedling stage would also provide a predictive basis for assessing the suitability of different plant types and local species for post-mining revegetation.

MATERIAL AND METHODS

Seeds (achenes) of three local species, *Gazania leiopoda* (DC.) Rössl., *Senecio arenarius* Thunb. and *Senecio elegans* L., were sown in 8 dm^3 trays, containing fine sand (0.5 - 1.1 mm particle size), and irrigated daily under free-draining conditions with 2 dm^3 solution depending on the treatment. In the emergence experiment, solutions with salinities of 1%, 2% or 3% NaCl were applied from the start (salt shock). In the seedling survival experiment, seeds in the trays were irrigated with distilled water for four weeks, whereafter the salinity of the solutions applied was raised gradually (0.5% NaCl per day) until the correct salinity was reached *i.e.* 1%, 2% or 3% NaCl (salt acclimation). Distilled water was used as a control. Half strength Arnon and Hoagland's nutrient solution (Hewitt, 1952) was added to all dilutions. Salts, that might have accumulated, were leached from the soil by giving each tray 2 dm^3 distilled water twice a week, before the saline solution was applied.

Trays were placed in a Phytotron room with a glass roof, and maintained at a constant temperature of 20°C. A randomized blockless design was used. Each tray contained 20 seeds/seedlings and five replicates of each salinity treatment (control; 1% NaCl, 2% NaCl and 3% NaCl) were used for each of the experiments and three species. The number of emerged and surviving seedlings was noted weekly.

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

RESULTS AND DISCUSSION

Salinity had a negative effect on seedling emergence of all three species (Table 15.1). Seedling emergence of the perennial species *Gazania leiopoda* reached a maximum of 74% after three weeks in the control, while that in the 1% NaCl treatment was 2%. In the 2% NaCl and 3% NaCl treatments, no seedlings emerged. In the control treatment, seedlings of the two ephemeral species, *Senecio arenarius* and *Senecio elegans*, reached maximum mean emergence percentages, of 19% and 87% respectively, after three weeks. No seedlings of the two *Senecio* species emerged in the 1% NaCl, 2% NaCl or 3% NaCl treatments. This reduction in the number of emerged seedlings with increasing salinity may be due to a reduction and/or delay in germination, as reported for both halophyte and glycophyte seeds (Chartzoulakis & Loupassaki, 1997; Katembe *et al.*, 1998). However, De Villiers *et al.* (1994) found that *Senecio elegans* had a mean germination percentage of 19% at a salinity of 1/3 sea-water, when germinated in Petri dishes at an optimum temperature of 15°C under light conditions. Sodium-chloride salinity was therefore inhibitory to germination and pre-emergence seedling survival, but seedlings were more sensitive to external salinity than seed germination. The reduction in emerged seedling numbers with increasing salinity could be a combined effect of osmotic stress (Greenway & Munns, 1980), which is more harmful to plants during the seedling stage and the higher ion uptake (Dumbroff & Cooper, 1974). Some plants are generally relatively salt tolerant during germination, but become more sensitive during emergence and the early seedling stage (Chartzoulakis & Loupassaki, 1997). This seems to be the case for *Senecio elegans*, and thus any failure in these stages will reduce the plant stand, and potential yields will be reduced far more than predicted by salt tolerance data (De Villiers *et al.*, 1997). Elevated salinity has been reported to slow down water uptake by seeds, thereby inhibiting their germination and root elongation (Werner & Finkelstein, 1995). The inability of *Senecio elegans*' seedlings to emerge at the 1% NaCl treatment indicated the necessity of salinity experiments at all growth stages, as well as this species' unsuitability for revegetation on saline soil.

In the survival experiment, salinity had a negative effect on the seedling survival percentages of all three species (Figures 15.1a, b and c), with *Senecio arenarius* showing the lowest salt tolerance. At the start of the salinity treatment (after four weeks), the percentage of surviving seedlings of all three species rapidly decreased at the 3% NaCl treatment, followed by that of the 2% NaCl treatment about a week later and the 1% NaCl treatment thereafter. An increase in salinity therefore resulted in an increased mortality rate of the seedlings. De Villiers *et al.* (1997) reported that the mortality rate of adult Namaqualand ephemeral species increased as salinity was increased. Numerous authors reported on increasing mortality and a reduction in growth rate in seedlings exposed to high salinity stress (Wagner, 1964; Tsonev *et al.*, 1998).

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

Table 15.1. The mean percentage of emerged seedlings for the three pioneer species at different salinities. Within each species, values followed by the same letter do not differ significantly at $P \leq 0.05$

Species	Treatment			
	Control	1% NaCl	2% NaCl	3% NaCl
Gazania leiopoda (perennial)	74[a]	2[b]	0[b]	0[b]
Senecio arenarius (annual)	19[a]	0[b]	0[b]	0[b]
Senecio elegans (annual)	87[a]	0[b]	0[b]	0[b]

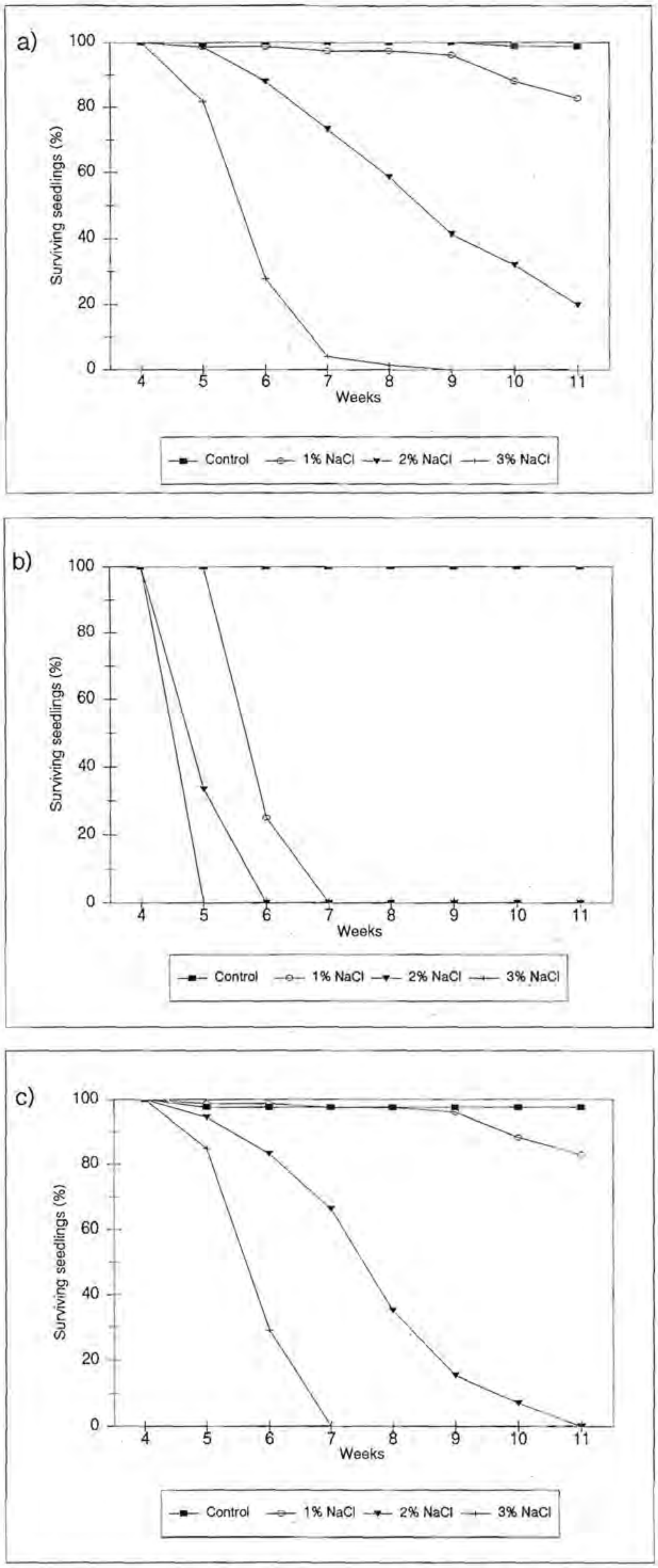

Figure 15.1. The mean seedling survival as a percentage of the original emergence percentage of a) *Gazania leiopoda*, b) *Senecio arenarius*, and c) *Senecio elegans*, at different soil salinities.

In all NaCl treatments, seedlings of the three Namaqualand pioneer species showed typical symptoms of salinity stress - the tips of the outer leaves became yellowish (chlorosis), and then necrosis set in from the tips downward. Yellowish leaves are indicative of many metabolic abnormalities, one of which is salt toxicity brought about by the decolouration of chlorophyll (Strogonov, 1964; Seneca, 1972).

Mortality during the first growth stages is not solely due to lower salt tolerance during this period, although some salt tolerant crops like barley, wheat, safflower and sugarbeets are reported to be less saline-tolerant at this point (Maas & Hoffman, 1977; Van Hoorn, 1991). The problem appears to be the high salinity in the top layer of the soil, exposing the germinating seed and seedlings to a higher salt concentration than at later growth stages. During the young seedling stage the root system is still shallow and water uptake by the plant is mainly limited to the top layer. Water loss from the top layer causes a high salt concentration, partly through a sharply reduced moisture content and partly through an increase of the salt content due to capillary transport from the underlying layers (Van Hoorn, 1991).

CONCLUSIONS

Both interspecific and intraspecific differences occurred, during seedling emergence and survival in saline soil, for the three species examined. The perennial species (*Gazania leiopoda*) showed a low maximum mean emergence percentage (2%) at the 1% NaCl treatment, while no seedlings of the two ephemeral species (*Senecio* spp.) emerged at this treatment. These results support the conclusion drawn by Seneca (1972), that seeds do not germinate (seedling emergence in this case) in salinities above those that young seedlings can tolerate, and that this mechanism is of great survival value to the species. In the case of *Senecio elegans*, however, seeds may germinate at a soil salinity of 1% NaCl (De Villiers *et al.*, 1994b), but the seedlings will probably not survive. Germination experiments will determine if the same is true for the other two species examined. The mortality rate of *Gazania leiopoda* and *Senecio elegans* seedlings was also slower than that of *Senecio arenarius*. However, this perennial species will be better suited for revegetation on saline soil than the ephemeral species examined, when both germination and emergence are considered. Between the two *Senecio* species, differences were observed for mean emergence percentages, emergence rates as well as for the mortality rate at different salinities. The negative effect of salinity on the emergence and survival of these species implies that the salinity of the soil should be very low for successful seedling emergence, and the soil salinity should be kept relatively low for better seedling survival.

In practice the effect of salinity on germination and emergence may be much worse than in laboratory experiments, and will differ according to soil and season (Van Hoorn, 1991). High temperature will increase evaporation and capillary rise of salts, while low temperature may delay germination and emergence to such an extent that the seedlings are caught in the crust formed in the meantime. Rainfall will decrease the salinity of the top layer but may also induce harmful crusting. In general, it is unwise to transfer results obtained with saline water irrigation from the laboratory to the field or from one region to another without carefully considering the conditions of soil and weather during germination and emergence (Van Hoorn, 1991). Field experiments are therefore essential and together with mean precipitation levels will give insight into emergence and seedling survival *in situ*, as well as to the extent to which irrigation should be used.

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CHAPTER 16

CONCLUSIONS

Seed bank studies in the Succulent Karoo Biome previously focused on annual plant populations (Van Rooyen & Grobbelaar, 1982), "heuweltjies" in the Southern Succulent Karoo (Esler, 1993) and seed bank estimation methods (De Villiers *et al.*, 1994a). In general, very little attention has been given to the role of seed banks in restoration and revegetation processes (Levassor *et al.*, 1990; Moll, 1992; Aerts *et al.*, 1995; Bakker *et al.*, 1996; Kotanen, 1996). This thesis represents a first attempt to incorporate data on seed bank dynamics in the planning phase of post-mining revegetation processes in the Strandveld Succulent Karoo, South Africa.

The aim of the rehabilitation program along this coast is to restore mined areas as closely as possible to their pre-mining, natural condition, as soon as possible after mining has been completed (Environmental Evaluation Unit, 1990). The goal of revegetation at the Brand-se-Baai mining area (31°18'S, 17°54'E) is to obtain a vegetation cover, which contains plant species from all the pre-mining communities of the mined area. Six main plant communities were identified, described and mapped. Such descriptions of plant communities, together with the vegetation map, can serve as a basis in the final formulation of the rehabilitation plan for the area being mined. An understanding of the pre-mining plant communities and their associated habitats is of fundamental importance for devising sound rehabilitation, management and conservation strategies.

The floristic classification of the vegetation prior to mining activities served as a benchmark, and indicated species with which the greatest success, *i.e.* plant community composition and structure, would be achieved in the rehabilitation of the area. It is recommended that this program should concentrate on the perennial species, as these species dominate the pre-mining standing vegetation and will help to stabilize the mined sand during the windy, dry and hot summer months. Also, revegetating these species should restore the physiognomic structural appearance of the vegetation. It should be possible to revegetate the entire area with species abundant in almost all pre-mining communities. These constitute 28% of the total species richness of the area. Therefore, a realistic revegetation goal will be 30% of the total number of 230 plant species present prior to mining. Establishment of the grass species *Odyssea paucinervis* should be a priority in the western mining area.

Due to the high concentration of heavy minerals in the upper soil layers, topsoil replacement is not favoured for revegetation purposes by the mining company at Brand-se-Baai. However, results on the size and composition of the soil seed bank, as well as comparisons thereof with the standing vegetation, indicated that topsoil replacement will be vital for successful revegetation of the study area.

The soil seed bank of the Strandveld Succulent Karoo yielded a mean of 2 725 emerged seedlings m^{-2}, which belonged to 109 species. Annual species dominated the soil seed bank in terms of numbers, but in terms of species richness, the seed bank was not dominated by any specific plant type. The size of annual species' soil seed banks was large in comparison with annual inputs and losses, indicating the persistent nature of seed banks in these species. Seed banks of perennial species were small compared to annual inputs and losses, and are therefore of a transient nature.

The spatial pattern of soil seed bank density and composition was not as pronounced as that of the temporal pattern. Between vegetation units, variation in soil seed bank density, composition and species richness was relatively low. Mining of heavy minerals at the study site commences in a specific sequence, and topsoil is to be replaced directly to the adjacent preceding mined area (Environmental Evaluation Unit, 1990). Consequently, after revegetation by means of topsoil replacement, post-mining plant community boundaries may show little deviation from pre-mining boundaries. The effectiveness of topsoil replacement for the restoration of a specific plant community will therefore depend mainly on the size and composition of the seed bank of that community.

Seasonal variation in seed bank size and composition was relatively high at the study site. Samples collected during autumn and summer did not differ significantly from each other in terms of seed bank size, and include both the transient and persistent fractions of the soil seed bank. However, summer and autumn collected samples did differ significantly from each other in terms of emerged seedling density and species richness directly after sampling, which was probably due to unfavourable environmental conditions for germination during summer. When samples were examined directly after sampling, the highest mean number of emerged seedlings and species richness occurred in samples collected during autumn. Winter sampling indicated the presence of a large persistent seed bank, constituting *c.* 50% of the total soil seed bank species richness of the study area. Seedling recruitment from replaced topsoil and sowing should be restricted to the period of natural field emergence, *i.e.* autumn. Transplanting of selected species should commence during the winter months. During these periods, both moisture and temperature are usually non-limiting for the germination and survival of local species. In areas where topsoil replacement and sowing have been completed, irrigation should commence at the start of the rainy season, as many seeds present in the replaced topsoil will be in a state of dormancy during spring and summer. Also, temperatures during spring and summer may be too high for the seeds of most species to germinate. Although some seeds may germinate, the resulting seedlings will probably not survive during the hot seasons. Although the usefulness of annual species in the revegetation program will mainly be restricted to the wet and cool winter months, remaining plant debris may act as wind-breaks for the control of wind erosion. Irrigation, during the hot seasons following initial emergence events in autumn and/or winter, will be beneficial for the survival of perennial species' seedlings and adult plants.

The general dissimilarity between the seed bank and its associated vegetation was manifested by dissimilarities in species composition, plant/seedling densities and frequencies. The standing vegetation at the study site was not well represented in the seed bank samples, but the seed bank species were well represented in the standing vegetation. Those species recorded only in the seed bank were mainly annuals with relatively low densities and frequencies.

As in most arid ecosystems, the frequency distribution of seeds in the seed bank was highly kurtotic, since most samples had a few or no seeds and only a minor proportion had a large number of seeds. This general spatial pattern may in part be the result of the relatively short seed dispersal distances that characterise the majority of desert plants (Ellner & Shmida, 1981), or the consequence of directed dispersal by ants or rodents (Van Rheede van Oudtshoorn & Van Rooyen, 1999).

Species that were abundant in the seed bank of almost all plant communities constituted 15% of the total species richness of the standing vegetation. Species abundant in the seed bank of several communities made up another 4% to the species richness of the study area. Perennial species abundant in the seed bank of almost all communities will contribute 6% to the restored species richness of the study area.

In general, total, annual and perennial species' richness of all communities to be mined was higher in the standing vegetation than in the seed bank. According to Sorensens' index, similarity in total species composition between the standing vegetation and the soil seed bank was 54.3%. Higher similarity in annual than perennial species composition was obtained between the standing vegetation and the soil seed bank. An increase in species richness generally correlated with an increase in species composition similarity between the standing vegetation and the soil seed bank.

The seed bank contained in replaced topsoil will probably be a good predictor of the future vegetation. This is true for at least the early stages of succession in the mined area. Topsoil replacement alone will not be sufficient for reaching revegetation goals, as species abundant in the seed bank of most communities totalled only 19% of the total standing vegetation species richness. Considering only perennial species, this percentage decreased to 8%. Also, species dominant in the standing vegetation do not produce persistent seed banks. Even with a revegetation goal of 30%, sowing and transplanting of selected species will be indispensable.

Perennial taxa, which could be recruited in sufficient numbers from the soil seed bank include: *Nestlera biennis, Ruschia bolusiae, Ehrharta calycina,* Geophyte spp., *Tetragonia virgata, Manochlamys albicans, Ruschia brevicyma, Hypertelis salsoloides, Hermannia* spp. and *Zygophyllum morgsana*. Annual species abundant in the standing vegetation and the seed bank were *Senecio arenarius, Oncosiphon suffruticosum, Crassula expansa, Ficinia argyropa, Crassula umbellata, Manulea altissima, Isolepis marginata, Cotula thunbergii, Karroochloa schismoides, Pentaschistis patula* and *Helichrysum marmarolepis*.

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

The presence of species in a seed bank disposes of many of the revegetation problems associated with collecting, storing, and sowing seeds or transplanting individuals, but it does not eliminate uncertainties associated with seed germination and seedling survival (Van der Valk & Pederson, 1989). Most annual species in this study obtained highest germination percentages and shortest mean times to germination at intermediate temperatures in the light. The perennial species in this study obtained highest germination percentages and shortest mean times to germination at a wide range of temperatures, in the absence of light. Revegetation efforts must therefore ensure that after sowing, seeds of perennial species are not merely left on top of the soil. A solution to some of these problems may be the replacement of topsoil after sowing, ensuring that the light requirements for germination of both perennial and annual species are met.

Another factor that influences the timing of germination is seed dormancy. The requirement of an after-ripening period by seeds indicates a delay in germination until the probability of seedling survival and plant growth is high (Baskin & Baskin, 1998). In the Strandveld Succulent Karoo, this germination strategy ensures that newly shed seeds do not germinate during occasional summer precipitation, as few seedlings will survive during the hot season. Of the species investigated, 52% required an after-ripening period, most of which were annuals or perennial herb species. Moisture and temperature probably control the timing of germination in most of the species from this area.

Mechanical scarification, short period chemical scarification, leaching, hydration/dehydration, heat, and/or cold treatments increased the germination of some species investigated. These artificial dormancy-breaking treatments may prove to be viable for species to be sown. However, most species exhibiting seed dormancy were found to be annuals, which also predominate the soil seed bank and will therefore be reintroduced to mined areas by means of topsoil replacement. Species to be sown are mainly perennial and exhibited less dormancy, rendering artificial dormancy-breaking treatments impractical.

An increase in relative humidity generally resulted in a decrease in seed viability. Seeds remained viable for longer periods under low temperature conditions in the laboratory, than under fluctuating temperatures in the field. Irrigation during summer after topsoil replacement in spring/summer may solve seedling recruitment problems related to low moisture, but the dormancy status of most annual species in the seed bank will prevent their germination. Also, the increase in relative humidity due to irrigation may result in increased seed moisture contents. Prevailing high summer temperatures and high relative humidities will enhance seed deterioration and consequently, seed viability and longevity will be reduced. Irrigation during the summer following topsoil replacement in spring/summer would result in the germination of many of the perennial shrub species, but seeds of annual species may be lost. Irrigation during the second summer after topsoil replacement in spring/summer will be beneficial for the survival of these perennial species, and many annual species would already have been recruited, matured and reproduced during the preceding winter.

Collected seeds of perennial shrub species should not be stored for too long, as they are probably not as long-lived as seeds of the annual species investigated. Recruitment of these species should occur during autumn, as germination during this season should provide sufficient time for seedling establishment and growth.

Species recruitment from replaced topsoil will be influenced by the period that seeds of different species remain viable in the seed bank. Because detailed studies could not be performed on all species present at the study site, the grouping of species with high abundancies, according to their expected seed bank strategies provided a means for determining the revegetation method best suited for each group or seed bank type. The key with laboratory characteristics of seeds to predict seed bank types seems to be well suited for the classification of seed banks of the Strandveld Succulent Karoo. Modifications to the original key (after Grime & Hillier, 1981) included: a dry heat pre-treatment rather than cold stratification, mean germination percentages of fresh and stored seeds (20°C for one month) were considered for both large and small seeds, some categories were subdivided due to the large number of species with persistent seed banks, and the time taken by seeds stored dry at 20°C for one month to reach 50% germination was not incorporated as a means of distinguishing between seed bank types.

Of the 37 species investigated, 32% have seeds with a transient seed bank strategy, while 68% exhibited persistent seed bank strategies. Five percent of the species produce small persistent seed banks, while 22% and 49% of the species have seed types which accumulate small short-term persistent seed banks and large persistent seed banks respectively. Predicted seed bank strategies should, however, be examined and checked in the field for each species.

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

Seed dispersal distance and seed bank formation form only part of the total reproductive strategy of a species. Reproduction by seeds integrates a variety of critical life history processes, which are often separated far from each other in place and time of occurrence: these are pollination, seed development, dispersal, germination and seedling establishment (Van Rheede van Oudtshoorn & Van Rooyen, 1999). Successful regeneration depends on trade-offs between the often conflicting pressures and constraints imposed by these processes. However, because these multiple functions interact, they evolve as co-adapted syndromes. It is therefore impossible to evaluate the adaptive value of a particular dispersal mode without taking the constraints imposed by other life history functions into account. Factors such as flowering, seed production, predation, seed release time and duration, timing of germination, seedling survival and, after establishment, clonal and sexual reproduction speed may be equally important in restoration.

In the perennial species investigated, seed yield ranged from 9.1 to 27 444.1 seeds plant^{-1}, while that of annual species ranged from 77.2 to 807.8 seeds plant^{-1}. The mean number of seeds entering the seed pool ranged between 9.0 and 4851.8 seeds plant^{-1} for perennials and between 74.8 and 510.5 seeds plant^{-1} for annual species. The relationship between seed production and pre-dispersal seed predation appeared to be density-dependent at the between species level. Pre-dispersal seed predators may have the potential to regulate species recruitment, especially in species that do not accumulate a persistent seed bank.

Seedling recruitment during the peak germination season (autumn) following dispersal was largely unaffected by post-dispersal predators. Since most perennials had low seed densities in the soil, plant recruitment may be reduced by seed predation. On the other hand, soil seed densities of most annual species were high. This may result in intense competition for access to suitable recruitment microsites and as a consequence, seed predation is unlikely to have any impact on mature plant density.

Seed-borne fungi will not affect seed numbers in the soil to a great extent, under natural environmental conditions. In the Strandveld Succulent Karoo, low seed mortality due to fungal attack could be ascribed to the combination of low occurrence (< 2%) and unfavourable environmental conditions for growth (low moisture during summer, low temperature during moist winters). Although irrigation in the hot, dry seasons may induce seed decay due to fungal attack, irrigation during the seasons following initial emergence in autumn, will be beneficial for the survival of seedlings of many species.

Poor seed germination and seedling mortality, due to environmental constraints like water stress, soil salinity, high temperature and pathogens will limit the success of revegetation efforts in the Strandveld Succulent Karoo. Transplanting of selected shrub species will increase species richness and therefore be beneficial for the restoration process. Apart from their role as wind-breaks, transplanted adult perennial plants may also reduce the period between revegetation and reproduction. Shrub species investigated did not act as nurse-plants, *i.e.* seedling numbers and species richness were higher in open areas than beneath shrub canopies. Seedling survival did not differ between these microhabitats. Seedlings of most annuals and perennial herb species will establish and survive in open areas at the study site. These species can be recruited from replaced topsoil and/or by sowing.

Sea-water is used in the mining process, leading to soil salinities few plants will be able to tolerate. The selection of local salt-tolerant species will therefore be advantageous to the revegetation of the area. When both germination and emergence are considered, perennial species will be better suited for revegetation on saline soil than annual species. The negative effect of salinity on the emergence and survival of the annual species investigated implies that the salinity of the soil should be very low for successful seedling emergence, and the soil salinity should be kept relatively low for better seedling survival. Also, annual species that do survive on soil with low salinities, yield almost no seeds. As seeds are annual species' only means of reproduction, these species will have to be revegetated from seed sources outside the mined area, or by sowing. If the salinity of the mined soil can be kept at a minimum concentration, perennial species will be able to survive and in some cases seed production may even be enhanced.

In practice the effect of salinity on germination and emergence may be much worse than in laboratory experiments, and will differ according to soil and season. High temperature will increase evaporation and capillary rise of salts, and may delay germination and emergence to such an extent that the seedlings are caught in the crust formed in the meantime.

It is very important to realise that the dynamics of the seed bank constitutes many processes influencing inputs and outputs to the seed bank, *e.g.* seed production, predation, dispersal, dormancy, germination, seed-borne pathogens and environmental conditions. Differential shifts in the relative importance of these processes can account for much of the differences observed in seed banks. Temporally, seed banks differentiate clearly into two fundamental types, transient and persistent. Whenever risk is high, persistent seed banks are favoured. At one level climate is of overriding importance; beyond that, factors including predation, dispersal, seed longevity, and biotic interference dictate seed bank and alternative regeneration diversity within a community.

In conclusion, these factors and processes will determine the revegetation method (topsoil replacement, sowing and transplanting) best suited for individual species. Taking all these factors into account, mining authorities should achieve great success in revegetating mined areas. Also, knowledge obtained from this seed bank study will aid plant ecologists to gain a better understanding of the processes contributing to reproductive strategies and plant population and community dynamics in the Strandveld Succulent Karoo.

SUMMARY

SEED BANK DYNAMICS OF THE STRANDVELD SUCCULENT KAROO

by

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Seed banks are influenced by many factors and processes related to more than one field of ecology. It is therefore necessary to consider all these components when assessing seed bank dynamics, which constitutes many processes influencing inputs and outputs to the seed bank. Apart from describing the seed bank dynamics of the Strandveld Succulent Karoo in terms of spatial and temporal variation in seed bank size and composition, factors such as seed production, predation, dispersal, dormancy, germination, seed-borne fungi and environmental conditions were investigated. This information was incorporated in the development of suitable post-mining revegetation strategies at a management level.

In the Strandveld Succulent Karoo, viable methods for the compulsory revegetation of post-mining areas include topsoil replacement, sowing and transplanting of selected species. An understanding of the pre-mining plant communities and their associated habitats is of fundamental importance to devise sound rehabilitation, management and conservation strategies.

Phytosociological benchmark studies on the pre-mining vegetation and seed bank indicated that in this species rich area, a realistic revegetation goal will be to return 30% of the total number of 230 plant species recorded. The soil seed bank of the study area yielded a mean of 2 725 seedlings m^{-2}, belonging to 109 species. Spatial variation in seed bank size and composition was not as pronounced as temporal variation. The general dissimilarity between the seed bank and its associated vegetation was manifested by dissimilarities in species composition, plant/seed densities and frequencies. The seed bank species were

well represented in the standing vegetation, but standing vegetation species were uncommon in the seed bank. Few species were unique to the seed bank.

Topsoil replacement, sowing and transplanting of selected species were found to be essential for the rehabilitation of this area after mining has been completed. Seeds of annual species were abundant and of a persistent nature in the soil seed bank, required a summer after-ripening period, germinated to higher percentages at intermediate temperatures in the light, and generally had lower seed yields than perennial species. Also, seed predation is unlikely to have any impact on mature plant density of annuals, their seedlings will establish in open microsites and they can be recruited from replaced topsoil during revegetation efforts.

Seeds of perennial herb species were less abundant and of both a persistent and transient nature in the seed bank, depending on the species. Revegetation using these species should involve sowing. Large seeded perennial shrub species were uncommon and of a transient nature in the seed bank. Transplanting will be a viable means for reestablishment of these species. In general, seeds of perennial species obtained highest germination percentages and shortest mean times to germination at a wide range of temperatures in the absence of light, and seed predators have the potential to regulate species recruitment of these species. Perennial species also yielded higher survival percentages and seed production under saline conditions.

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

OPSOMMING

SAADBANKDINAMIKA VAN DIE STRANDVELD SUKKULENTE KAROO

deur

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Medeleier: Prof. G.K. Theron

DEPARTEMENT PLANTKUNDE

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'n Saadbank word deur verskeie faktore en prosesse, wat verband hou met meer as een veld van ekologie, beïnvloed. Dit is daarom noodsaaklik om al hierdie komponente in ag te neem indien die saadbankdinamika ondersoek word. Laasgenoemde is saamgestel uit verskeie prosesse wat toevoegings en verliese tot die saadbank beïnvloed. Buiten die beskrywing van die saadbankdinamika van die Strandveld Sukkulente Karoo in terme van ruimtelike en temporele variasie in saadbank grootte en samestelling, is faktore soos saadproduksie, predasie, saadverspreiding, dormansie, ontkieming, saadswamme en omgewingstoestande, ook ondersoek. Hierdie inligting is op bestuursvlak geïnkorporeer in die ontwikkeling van geskikte plantegroeihervestiging strategieë vir gebruik in rehabilitasie van gemynde areas.

Die terugplaas van bogrond, saai en oorplant van geselekteerde spesies word as lewensvatbare metodes beskou vir die verpligte hervestiging van plantegroei na mynbou-aktiwiteite in die Strandveld Sukkulente Karoo. Kennis van plantgemeenskappe en hul geassosieerde habitatte, voordat mynbou-aktiwiteite 'n aanvang neem, is van kardinale belang vir die daarstelling van goeie rehabilitasie-, bestuurs- en bewaringstrategieë.

Fitososiologiese studies van die staande plantegroei en saadbank, voor die aanvang van mynbou-aktiwiteite, het aangetoon dat 'n hervestigingsdoelwit van 30% van die 230 plantspesies aangeteken, realisties sal wees. Die saadbank van die studiegebied het gemiddeld 2 725 saailinge m^{-2} opgelewer, wat tot 109 spesies behoort het. Ruimtelike variasie in die grootte en samestelling van die saadbank was nie so opvallend soos

variasie in tyd nie. Die verskil tussen die saadbank en die geassosieerde bogrondse plantegroei is weerspieël deur verskille in spesiesamestelling, digtheid en frekwensie. Saadbank spesies was goed verteenwoordig in die bogrondse plantegroei, terwyl spesies van die staande plantegroei nie volop in die saadbank was nie. Min spesies het slegs in die saadbank voorgekom.

Nadat mynbou-aktiwiteite voltooi is, sal die terugplaas van bogrond, saai en oorplant van spesies noodsaaklik wees om plantegroei te hervestig. Sade van eenjarige spesies was volop en van 'n blywende aard in die saadbank, benodig 'n somer-narypingsperiode, het hoër ontkiemingspersentasies by intermediêre temperature in die lig, en het in die algemeen laer saadopbrengste as meerjarige spesies getoon. Verder is dit onwaarskynlik dat saadpredasie 'n inpak op die digtheid van volwasse eenjarige plante sal hê. Saailinge van eenjarige spesies kan vestig in onbeskutte mikrolokaliteite en gedurende plantegroeihervestiging kan hulle gewerf word vanuit teruggeplaasde bogrond.

Sade van meerjarige kruide was minder volop en beide blywend en kortstondig van aard in die saadbank, afhangend van die spesie. Hervestiging van hierdie spesies moet saai insluit. Die groot sade van meerjarige struikspesies was skaars en van kortstondige aard in die saadbank. Oorplanting sal 'n geskikte metode wees vir die hervestiging van hierdie spesies. In die algemeen het sade van meerjarige spesies hoër ontkiemingspersentasies en korter ontkiemingstempo's getoon by 'n wye reeks temperature in die afwesigheid van lig. Saadpredatore het die potensiaal om die werwing van hierdie spesies te reguleer. Meerjarige spesies het ook hoër oorlewingspersentasies en saadproduksie onder souttoestande getoon.

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

APPENDIX 1

PLANT TAXA STUDIED AND/OR ENCOUNTERED IN THIS STUDY

Plant specimens are housed in the H.G.W.J. Schweickerd Herbarium,
University of Pretoria, Pretoria, South Africa

TAXON	REFERENCE	PLANT TYPE
Aizoaceae		
Adenogramma littoralis Adamson	A.J. de Villiers 305	Annual (A)
Coelanthum semiquinquefidum (Hook.f.) Druce	A.J. de Villiers 306	A
Galenia africana L. var. *africana*	A.J. de Villiers 7	Perennial (P)
Galenia sarcophylla Fenzl	Le Roux *et al.* (1997)	P
Hypertelis salsoloides (Burch.) Adamson var. *salsoloides*	M.W. van Rooyen 2229	P
Limeum africanum L. ssp. *africanum*	M.W. van Rooyen 2036	A
Pharnaceum aurantium (DC.) Druce	A.J. de Villiers 343, 344	P
Pharnaceum exiguum Adamson	A.J. de Villiers 230, 304	A
Pharnaceum lanatum Bartl.	A.J. de Villiers 200	P
Pharnaceum microphyllum L.f.	A.J. de Villiers 285	P
Psammotropha quadrangularis (L.f.) Fenzl	A.J. de Villiers 102	A
Tetragonia microptera Fenzl	Le Roux *et al.* (1997)	A
Tetragonia pillansii Adamson	M.W. van Rooyen 2158	P
Tetragonia virgata Schltr.	A.J. de Villiers 222	P
Aloaceae		
Aloe framesii L.Bol.	Le Roux *et al.* (1997)	P
Amaryllidaceae		
Boophane sp.	Manning & Goldblatt (1996)	P
Brunsvigia orientalis (L.) Ait. ex Eckl.	A.J. de Villiers 61	P
Gethyllis sp.	Le Roux *et al.* (1997)	P
Haemanthus amarylloides Jacq. ssp. *polyanthus* Snijman	A.J. de Villiers 25	P
Anacardiaceae		
Rhus longispina Eckl. & Zeyh.	A.J. de Villiers 294	P
Apiaceae		
Annesorhiza macrocarpa Eckl. & Zeyh.	A.J. de Villiers 250	P
Sonderina tenuis (Sond.) H.Wolff	A.J. de Villiers 127	A
Asclepiadaceae		
Cynanchum africanum R.Br. var. *africanum*	A.J. de Villiers 301	P
Microloma sagittatum (L.) R.Br.	M.W. van Rooyen 2162	A
Asphodelaceae		
Bulbine sp.	Le Roux *et al.* (1997)	P
Trachyandra divaricata (Jacq.) Kunth	A.J. de Villiers 38	P
Trachyandra falcata (L.f.) Kunth.	M.W. van Rooyen 2601	P
Asteraceae		
Amellus microglossus DC.	A.J. de Villiers 238	A
Amellus tenuifolius Burm.	A.J. de Villiers 14, 88	P
Arctotheca calendula (L.) Levyns	A.J. de Villiers 249	A
Arctotis auriculata Jacq.	M.W. van Rooyen 2045	P
Arctotis hirsuta (Harv.) Beauv.	A.J. de Villiers 137, 189	A
Arctotis scullyi R.A.Dummer	M.W. van Rooyen 2140, 2248	P
Arctotis stoechadifolia Berg.	A.J. de Villiers 280, 283	P
Arctotis sp.	A.J. de Villiers 213	P
Arctotis sp. (ADV220)	A.J. de Villiers 220	A
Arctotis spp.	Le Roux *et al.* (1997)	P
Berkheya fruticosa (L.) Ehrh.	A.J. de Villiers 197, 247	P
Berkheya spinosa (L.f.) Druce	Van Breda & Barnard (1991)	P
Chrysanthemoides monilifera (L.) T.Norl. ssp. *pisifera* (L.) T.Norl.	A.J. de Villiers 12, 288	P
Chrysocoma longifolia DC.	M.W. van Rooyen 2150	P
Cotula thunbergii Harv.	A.J. de Villiers 147, 161, 191	A
Didelta carnosa (L.f.) Ait. var. *carnosa*	M.W. van Rooyen 2011	A

Didelta spinosa (L.f.) Ait.	M.W. van Rooyen 2293	P
Dimorphotheca nudicaulis (L.) DC.	Van Rooyen *et al.* (1999)	P
Dimorphotheca pluvialis (L.) Moench	M.W. van Rooyen 2201	A
Dimorphotheca sinuata DC.	H. Rosch 25	A
Eriocephalus africanus L.	M.W. van Rooyen 2161, 2419, 2533	P
Felicia dregei DC.	A.J. de Villiers 327	P
Felicia merxmuelleri Grau	A.J. de Villiers 226, 328	A
Foveolina tenella (DC.) Kallersjo	A.J. de Villiers 194	A
Gazania leiopoda (DC.) Roessl.	A.J. de Villiers 252	P
Gymnodiscus capillaris (L.f.) DC.	A.J. de Villiers 86	A
Helichrysum hebelepis DC.	M.W. van Rooyen 2179, 2440	P
Helichrysum incarnatum DC.	A.J. de Villiers 204	A
Helichrysum kraussii Sch.Bip.	Van Wyk & Malan (1988)	P
Helichrysum marmarolepis S.Moore	A.J. de Villiers 133, 146, 86	A
Helichrysum revolutum (Thunb.) Less.	M.W. van Rooyen 2252, 2442, 2564	A
Hirpicium alienatum (Thunb.) Druce	A.J. de Villiers 89	P
Leysera gnaphalodes (L.) L.	A.J. de Villiers 176	P
Nestlera biennis (Jacq.) Spreng.	A.J. de Villiers 111, 195, 281	P
Oncosiphon suffruticosum (L.) Kallersjo	H. Rosch 3	A
Othonna cuneata DC.	Le Roux *et al.* (1997)	P
Othonna floribunda Schltr.	A.J. de Villiers 196, 271, 9	P
Othonna sp1.	Le Roux *et al.* (1997)	P
Othonna sp2.	Le Roux *et al.* (1997)	P
Othonna sp3.	Le Roux *et al.* (1997)	P
Othonna sp4.	Le Roux *et al.* (1997)	P
Pteronia divaricata (Berg.) Less.	A.J. de Villiers 216, 279, 324	P
Pteronia onobromoides DC.	A.J. de Villiers 55, 91	P
Pteronia ovalifolia DC.	A.J. de Villiers 248	P
Pteronia paniculata Thunb.	A.J. de Villiers 319, 56	P
Pteronia spp.	Le Roux *et al.* (1997)	P
Senecio arenarius Thunb.	A.J. de Villiers 338	A
Senecio bulbinifolius DC.	M.W. van Rooyen 2114	P
Senecio cardaminefolius DC.	Le Roux *et al.* (1997)	A
Senecio niveus (Thunb.) Willd.	A.J. de Villiers 109	P
Stoebe nervigera (DC.) Sch.Bip.	A.J. de Villiers 110, 46	P
Trichogyne ambigua (L.) Druce	A.J. de Villiers 114	P
Tripteris clandestina Less.	A.J. de Villiers 333, 97	A
Tripteris oppositifolia (Aiton) B.Nord.	M.W. van Rooyen 2137, 2497	P
Tripteris sinuata DC.	Le Roux *et al.* (1997)	P
Ursinia nana DC.	Le Roux *et al.* (1997)	A
Ursinia speciosa DC.	A.J. de Villiers 126, 334, 74	A
Brassicaceae		
Brassica tournefortii Gouan	A.J. de Villiers 205	A
Cardamine hirsuta L.	A.J. de Villiers 232	A
Heliophila coronopifolia L.	A.J. de Villiers, H. Steyn & M. Nel 2	A
Campanulaceae		
Wahlenbergia androsacea A.DC.	A.J. de Villiers 75	A
Wahlenbergia paniculata (Thunb.) A.DC.	A.J. de Villiers 174, 184, 302, 310, 335	A
Wahlenbergia schlechteri V.Brehm.	A.J. de Villiers 227	A
Wahlenbergia sonderi Lammers	A.J. de Villiers 274	P
Caryophyllaceae		
Silene clandestina Jacq.	A.J. de Villiers 221	A
Celastraceae		
Gloveria integrifolia (L.f.) M.Jordaan	A.J. de Villiers 293	P
Maytenus sp.	M.W. van Rooyen 2213	P
Chenopodiaceae		
Atriplex lindleyi Moq. ssp. *inflata* (F.Mull.) P.G.Wilson	Le Roux *et al.* (1997)	P
Atriplex semibaccata R.Br.	Manning & Goldblatt (1996)	P
Chenopodium opulifolium Schrad. ex Koch & Ziz	A.J. de Villiers 167	A
Exomis microphylla (Thunb.) Aell. var. *microphylla*	Shearing & Van Heerden (1997)	P
Manochlamys albicans (Ait.) Aell.	A.J. de Villiers 18, 21, 51	P
Colchicaceae		
Ornithoglossum sp.	Le Roux *et al.* (1997)	P
Convolvulaceae		
Convolvulus sp.	M.W. van Rooyen 2190	P
Crassulaceae		
Crassula dichotoma L.	A.J. de Villiers 115	A
Crassula expansa Dryand. ssp. *expansa*	A.J. de Villiers 149, 33	A
Crassula muscosa L. var. *muscosa*	A.J. de Villiers 257, 40	P
Crassula nudicaulis L.	Mustart *et al.* (1997)	P
Crassula sp.1	A.J. de Villiers 22	P
Crassula tomentosa Thunb.	M.W. van Rooyen 2227	P
Crassula umbellata Thunb.	A.J. de Villiers 239	A
Tylecodon sp.	A.J. de Villiers 59	P

Cyperaceae		
Ficinia argyropa Nees	A.J. de Villiers 312	A
Isolepis marginata (Thunb.) Dietr.	A.J. de Villiers 225, 99	A
Scirpus dioecus (Kunth) Boeck.	A.J. de Villiers 136	P
Willdenowia incurvata (Thunb.) Linder	A.J. de Villiers 152	P
Ebenaceae		
Euclea racemosa Murray	A.J. de Villiers 260	P
Euphorbiaceae		
Clutia alaternoides L. var. *alaternoides*	A.J. de Villiers 94	P
Euphorbia burmannii E.Mey. ex Boiss.	M.W. van Rooyen 2258	P
Euphorbia caput-medusae L.	Manning & Goldblatt (1996)	P
Euphorbia decussata E.Mey. ex Boiss.	Le Roux *et al.* (1997)	P
Euphorbia filiflora Marloth	Leach (1986)	P
Euphorbia sp.	Le Roux *et al.* (1997)	P
Fabaceae		
Aspalathus divaricata Thunb. ssp. *divaricata*	A.J. de Villiers 262	P
Crotalaria humilis Eckl. & Zeyh.	A.J. de Villiers 223	A
Indigofera amoena Ait.	M.W. van Rooyen 2012	A
Indigofera intermedia Harv.	A.J. de Villiers 317	A
Lebeckia lotonoides Schltr.	A.J. de Villiers 188, 261	P
Lebeckia multiflora E.Mey.	Le Roux *et al.* (1997)	P
Lessertia benguellensis Bak.f.	A.J. de Villiers 308	A
Melolobium exudans Harv.	A.J. de Villiers 309	P
Wiborgia monoptera E.Mey.	A.J. de Villiers 81	P
Wiborgia obcordata (Berg.) Thunb.	A.J. de Villiers 85	P
Frankeniaceae		
Frankenia pulverulenta L.	A.J. de Villiers 138	A
Fumariaceae		
Cysticapnos cracca (Cham. & Schlechtd.) Liden	M.W. van Rooyen 2254	A
Geraniaceae		
Pelargonium dipetalum L'Hérit.	Bohnen (1986)	P
Pelargonium fulgidum (L.) L'Hérit.	A.J. de Villiers 132	P
Pelargonium gibbosum (L.) L'Hérit.	M.W. van Rooyen 2166	P
Pelargonium senecioides L'Hérit.	A.J. de Villiers 330	A
Pelargonium sp.1	H.M. Steyn 12	P
Pelargonium sp.2	M.W. van Rooyen 2243	P
Pelargonium spp.	Le Roux *et al.* (1997)	P
Sarcocaulon sp.	M.W. van Rooyen 2173	P
Hyacinthaceae		
Albuca exuviata Bak.	M.W. van Rooyen 2226	P
Albuca spp.	Le Roux *et al.* (1997)	P
Lachenalia spp.	A.J. de Villiers 129, Le Roux *et al.* (1997)	P
Iridaceae		
Babiana brachystachys (Bak.) G.J.Lewis	A.J. de Villiers 122	P
Babiana spp.	Manning & Goldblatt (1996)	P
Babiana thunbergii Ker-Gawl., Konig & Sims	M.W. van Rooyen 2138	P
Lapeirousia spp.	Le Roux *et al.* (1997)	P
Moraea spp.	Le Roux *et al.* (1997)	P
Lamiaceae		
Ballota africana (L.) Benth.	A.J. de Villiers 69	P
Ocimum canum Sims	A.J. de Villiers 171	A
Salvia africana-lutea L.	A.J. de Villiers 16, 54	P
Liliaceae		
Asparagus aethiopicus L.	A.J. de Villiers 295	P
Asparagus asparagoides (L.) W.Wight	A.J. de Villiers 296	P
Asparagus capensis L. var. *capensis*	A.J. de Villiers 303	P
Asparagus fasciculatus Thunb.	A.J. de Villiers 315	P
Asparagus retrofractus L.	A.J. de Villiers 313	P
Asparagus undulatus (L.f.) Thunb.	A.J. de Villiers 292	P
Melianthaceae		
Melianthus minor L.	A.J. de Villiers 66	P
Menispermaceae		
Cissampelos capensis L.f.	A.J. de Villiers 325, 77	P
Mesembryanthemaceae		
Aridaria sp. (RDV273)	A.J. de Villiers 273	P
Cephalophyllum spongiosum (L.Bol.) L.Bol.	A.J. de Villiers 5	P
Cephalophyllum sp.	A.J. de Villiers 282	P
Conicosia elongata N.E.Br.	Le Roux *et al.* (1997)	P
Conicosia pugioniformis (L.) N.E.Br. ssp. *alborosea* (L.Bol.) Ihlenfeldt & Gerbaulet	A.J. de Villiers 177, 318	P

Dorotheanthus bellidiformis (Burm.f.) N.E.Br. ssp. *hestermalanensis* Ihlenf. & Struck	M.W. van Rooyen 2321	A
Drosanthemum calycinum (Haw.) Schwant.	A.J. de Villiers 43	P
Drosanthemum spp.	A.J. de Villiers 182, 201, 277, 336	P
Drosanthemum sp. (RDV277)	A.J. de Villiers 277	P
Drosanthemum sp. (RDV336)	A.J. de Villiers 336	P
Lampranthus godmaniae (L.Bol.) L.Bol. var. *godmaniae*	A.J. de Villiers 278	P
Lampranthus lanatus (Willd.) N.E.Br.	A.J. de Villiers 103	P
Leipoldtia jacobeniana Schwant.	A.J. de Villiers 266, 267	P
Mesembryanthemaceae spp.	Smith *et al.* (1998)	P
Mesembryanthemum crystallinum L.	A.J. de Villiers B11	A
Monilaria chrysoleuca (Schltr.) Schwant. var. *chrysoleuca*	A.J. de Villiers 90	P
Prenia pallens (Ait.) N.E.Br.	A.J. de Villiers 264	P
Psilocaulon spp.	A.J. de Villiers 15, 19, 32, 36	P
Rhinephyllum frithii (L.Bol.) L.Bol.	A.J. de Villiers 290	P
Ruschia bolusiae Schwant.	A.J. de Villiers 300	P
Ruschia brevicyma L.Bol.	M.W. van Rooyen 2117	P
Ruschia caroli (L.Bol.) Schwant.	M.W. van Rooyen 2116	P
Ruschia cymosa (L.Bol.) Schwant.	M.W. van Rooyen 2086	P
Ruschia extensa L.Bol.	A.J. de Villiers 155	P
Ruschia firma L.Bol.	A.J. de Villiers 178	P
Ruschia namaquana L.Bol.	Smith *et al.* (1998)	P
Ruschia sp.1	Smith *et al.* (1998)	P
Ruschia sp. (GVR2245)	M.W. van Rooyen 2245	P
Ruschia subpaniculata L.Bol.	A.J. de Villiers 180	P
Ruschia tecta L.Bol.	A.J. de Villiers 246, 291	P
Ruschia tumidula (Haw.) Schwant.	A.J. de Villiers 105	P
Ruschia versicolor L.Bol.	H.M. Steyn 8	P
Species x4(RDV268)(Mesembryanthemaceae)	A.J. de Villiers 268	P
Species x7 (Mesembryanthemaceae)	A.J. de Villiers 270	P
Sphalmanthus sp. (RDV270)	A.J. de Villiers 270	P
Stoeberia sp.	A.J. de Villiers 179; Smith *et al.* (1998)	P
Vanzijlia annulata (Berger) L.Bol.	A.J. de Villiers 3	P
Oxalidaceae		
Oxalis pardalis Sond.	A.J. de Villiers 254	P
Oxalis spp.	A.J. de Villiers 151, Le Roux *et al.* (1997)	P
Plumbaginaceae		
Limonium perigrinum (Berg.) R.A.Dyer	A.J. de Villiers 13, 28	P
Limonium sp.	M.W. van Rooyen 2230	P
Poaceae		
Bromus pectinatus Thunb.	A.J. de Villiers 119, 210	A
Chaetobromus dregeanus Nees	A.J. de Villiers 112, 311	P
Chloris pycnothrix Trin.	A.J. de Villiers 168	A
Cladoraphis cyperoides (Thunb.) S.M.Phillips	M.W. van Rooyen 2228	P
Ehrharta brevifolia Schrad. var. *brevifolia*	A.J. de Villiers 145	A
Ehrharta calycina J.E.Sm.	A.J. de Villiers 251	P
Karroochloa schismoides (Stapf ex Conert) Conert & Tuerpe	A.J. de Villiers 162	A
Odyssea paucinervis (Nees) Stapf	M.W. van Rooyen 2223	P
Pentaschistis patula (Nees) Stapf	A.J. de Villiers 331	A
Species x2(Poaceae)	Van Oudtshoorn (1991)	A
Species x3(RDV286)(Poaceae)	A.J. de Villiers 286	P
Stipagrostis zeyheri (Nees) De Winter ssp. *macropus* (Nees) De Winter	A.J. de Villiers 106, 209, 307	P
Polygonaceae		
Emex australis Steinh.	A.J. de Villiers 206	A
Rumex spp.	Le Roux *et al.* (1997)	A
Portulacaceae		
Portulaca quadrifida L.	A.J. de Villiers 229	A
Rosaceae		
Grielum grandiflorum (L.) Druce	M.W. van Rooyen 2013	P
Grielum humifusum Thunb. var. *humifusum*	A.J. de Villiers 192	A
Rubiaceae		
Galium tomentosum Thunb.	A.J. de Villiers 326	P
Santalaceae		
Thesium spinosum L.f.	M.W. van Rooyen 2122	P
Scropulariaceae		
Diascia sp.	A.J. de Villiers 329	A
Hemimeris racemosa (Houtt.) Merrill	A.J. de Villiers 186	A
Lyperia tristis (L.f.) Benth.	A.J. de Villiers 337	A
Manulea altissima L.f. ssp. *altissima*	M.W. van Rooyen 2203	A
Manulea cinerea Hilliard	A.J. de Villiers 284	P
Manulea pusilla E.Mey. ex Benth.	A.J. de Villiers 143	A
Nemesia bicornis (L.) Pers.	M.W. van Rooyen 2152	P
Nemesia ligulata E.Mey. ex Benth.	A.J. de Villiers 183	A
Polycarena pumila (Benth.) Levyns	A.J. de Villiers 235	A
Zaluzianskya villosa (Thunb.) F.W.Schmidt	M.W. van Rooyen 2005	A

Selaginaceae		
Hebenstretia dentata L.	A.J. de Villiers 207	A
Hebenstretia repens Jarosz	A.J. de Villiers 231, 236	A
Solanaceae		
Lycium ferocissimum Miers	A.J. de Villiers 245,258,287	P
Lycium sp.	A.J. de Villiers 259,323	P
Lycium spp.	Le Roux *et al.* (1997)	P
Solanum guineense L.	A.J. de Villiers 154, 71	P
Sterculiaceae		
Hermannia amoena Dinter ex M.Holzhammer	A.J. de Villiers 298	P
Hermannia cernua Thunb. ssp. *eroidioides*	M.W. van Rooyen 2159	P
Hermannia cuneifolia Jacq. var. *cuneifolia*	A.J. de Villiers 297	P
Hermannia modesta (Ehrenb.) Mast.	A.J. de Villiers 116	P
Hermannia scordifolia Jacq.	A. J. de Villiers 107, 203	A
Hermannia sp.	A.J. de Villiers 299	P
Hermannia spp.	Le Roux *et al.* (1997)	P
Tecophilaeaceae		
Ferraria densepunctulata De Vos	A.J. de Villiers 121	P
Ferraria divaricata Sweet ssp. *aurea* De Vos	A.J. de Villiers 130	P
Ferraria spp.	Le Roux *et al.* (1997)	P
Viscaceae		
Viscum capense L.f. ssp. *capense*	A.J. de Villiers 181	P
Zygophyllaceae		
Zygophyllum meyeri Sond.	Le Roux *et al.* (1997)	P
Zygophyllum morgsana L.	A.J. de Villiers 4	P
Zygophyllum pygmaeum Eckl. & Zeyh.	A.J. de Villiers 79	P

APPENDIX 2

CURRICULUM VITAE

Adriaan Jakobus De Villiers was born in Boksburg on the 10th of February 1967. He started his education in 1973 at the Baanbreker Primary School and matriculated in 1984 from Voortrekker High School, Boksburg.

In 1988 he obtained the B.Sc. degree with Botany and Zoology as main subjects, and in 1989 the B.Sc. Hons. (Botany) (*cum laude*) at the University of Pretoria.

During 1990 and 1991 he completed his South African military service with a rank of 1st Lieutenant in the Engineering Corps. During this period he also obtained a post-graduate diploma in Terrain Evaluation from the Potchefstroom University for Christian Higher Education.

In 1991 he enrolled for the M.Sc. (Botany) degree at the University of Pretoria, which he obtained *cum laude* in 1993 for his dissertation entitled: "Ecophysiological studies on several Namaqualand pioneer species, with special reference to the revegetation of saline mined soil".

During the period 1989 to 1998 he worked as academic assistant, research assistant, tutor and demonstrator in the Botany Department of the University of Pretoria. In 1997 he also worked as demonstrator for the Vista University. He is currently employed as a Senior Agricultural Product Technician by the National Department of Agriculture, in the Variety Control Division, Genetic Resources, Roodeplaat.

He was author or co-author of eight publications, four unpublished reports, and was involved in the presentation of ten scientific papers/posters. He also was the photographer of the field guide to the wild flowers of the Cederberg, which was published in 1999.

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