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Seed bank classification of the Strandveld Succulent Karoo, South Africa

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

Department of Botany, University of Pretoria, Pretoria, 0001, Republic of South Africa

Abstract

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

Keywords: mining, Namaqualand, persistent seed bank, revegetation, seed bank types, seed characteristics, seed dispersal, transient seed bank

Introduction

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

The seed bank of a plant community represents the 'memory' of previous conditions, and it is an important component of the potential of the community to respond to conditions in the present and future (Coffin and Lauenroth, 1989). For the applied biologist in particular, the aspect of greatest significance is the role of the seed bank in determining the future vegetation, especially after natural or deliberate disturbance (Roberts, 1981). The re-appearance of a plant species after disturbance may be the result of its persistence in the soil seed bank. If a species has been lost from the persistent soil seed bank, it must be transported by some vector, e.g. wind, water, animals or humans, and incorporated into the fresh seed bank. The re-appearance of a species either from the old seed bank or from the fresh seed bank depends on the availability of safe sites (Harper, 1977).

Thompson and Grime (1979) recognized two main seed bank strategies for temperate zones: transient types in which no seeds remain viable for more than 1 year, and persistent types in which some seeds remain viable for longer than 1 year. Bakker (1989) suggested the further division of Thompson and Grime's persistent seed bank into persistent, for species whose seeds survive in the soil for more than 1 year up to 5 years, and permanent, for species whose seeds persist for longer than 5 years. These two strategies have been renamed short-term persistent and long-term persistent, respectively (Thompson, 1993; Warr *et al.*, 1993), and they, together with the transient strategy, form a useful seed bank classification system (Thompson, 1993).

Grime and Hillier (1981) developed a key, based on laboratory characteristics of seeds, to predict seed

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*Correspondence
Fax: +27 012 8080364
Email: rdevil@global.co.za

bank types. Their key was compiled for the northwest European region, and modifications may be necessary for its successful use in other regions, especially as more than four seed bank strategies have already been reported for soil seed banks of other regions (Garwood, 1989; Baskin and Baskin, 1998).

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

During mining of heavy minerals along the arid western coast of South Africa, the topography, vegetation, soil chemical and physical characteristics and animal life are destroyed. The aim of the rehabilitation programme is to restore the area to its pre-mining state as soon as possible after mining. If topsoil of the area to be mined is to be removed and used in the revegetation process, knowledge of persistence of individual species present in the seed bank is essential. Data on seed bank strategies of individual species will also indicate local species that may not re-establish by means of topsoil replacement or dispersal from surrounding vegetation. These species will have to be reintroduced by seeding or transplanting.

The aim of this study was to develop an effective way of using easily measurable seed and germination characteristics to classify and predict seed bank strategies of species in the Strandveld Succulent Karoo, South Africa. Such a classification can be used to understand how to best manage the seeds of Karoo plants to revegetate damaged lands.

Materials and methods

Numerous laboratory characteristics of diaspores (henceforth referred to as seeds) of Strandveld Succulent Karoo species were determined. The key of Grime and Hillier (1981) was used as a template to incorporate these data into a key to distinguish seed bank types.

Mature seeds of 37 local plant species (41 seed types) were collected during spring from natural populations in the vicinity of the area to be mined at Brand-se-Baai (31°18′S, 17°54′E), South Africa (De Villiers *et al.*, 1999). This area is within the Namaqualand coastal belt and has an average winter rainfall of 160 mm per annum. Average annual temperature at the study site is 15.8°C, with a relatively small annual fluctuation due to the marine influence (De Villiers *et al.*, 1999). Vegetation of the area is classified as Strandveld Succulent Karoo (Low and Rebelo, 1998) and contains many drought-resistant and succulent species associated with areas of calcareous sand. Vegetation varies in height depending on depth of the sand – with the shortest vegetation growing on exposed calcrete and coastal rocks and the tallest in deep calcareous sand (Boucher and Le Roux, 1990).

Both fresh seeds (air-dried for 2 weeks) and those stored dry at 20°C for 1 month after the initial air-drying period of 2 weeks were used in the germination trials. Seeds were incubated in Petri dishes on two layers of moist filter paper (Schleicher and Schüll, no. 595, Dassel, Germany). Germination tests were carried out in germination cabinets at a constant temperature of 17°C in light and in darkness. This temperature was found to be favourable for the germination of many Namaqualand species (Beneke *et al.*, 1993; Visser, 1993; De Villiers *et al.*, 1994). Seeds of the light treatments were exposed to constant fluorescent light with a photon flux density of 9.3 μmol m^{-2} s^{-1} (400–710 nm). Petri dishes in the dark treatments were sealed in cardboard boxes and covered with aluminium foil. Five replicates of 50 seeds were used for each species.

Germination trials were continued for a period of 30 days, during which time seeds were examined every second day and germinated seeds counted and removed. Germination counts for the dark treatments were carried out under a green safe light (Baskin and Baskin, 1998). Emergence of the radicle was used as the germination criterion.

Mean seed length was determined by measuring the length of 100 seeds for each species. Small seeds were measured under a stereomicroscope. Mean seed mass was determined by weighing 100 seeds collectively on a Mettler AT100 balance. Four replicates of 100 seeds were weighed. Abscission of seeds from the mother plant and presence of a woody structure, as well as dispersal types, were inferred from seed morphological characteristics. The lowest temperature for 50% germination of the total number of seeds (T_L) was determined from data on stored seeds of these species, germinated at various temperatures (De Villiers *et al.*, 2002).

Results and discussion

The original key of Grime and Hillier (1981) distinguished four main seed bank types: (I) annual and perennial grasses of dry or disturbed habitats capable of immediate germination; (II) annual and perennial herbs colonizing vegetation gaps in early spring; (III) annual and perennial herbs mainly germinating in the autumn but maintaining a small seed bank; and (IV) annual and perennial herbs and shrubs with large, persistent seed banks. The type III seed bank strategy was subdivided into types: (IIIa) perennial herb species germinating mainly in autumn and (IIIb) annual species that germinate during autumn (Grime, 1981). Seeds of species with type IIIa or IIIb seed bank strategies usually have a light requirement for germination. Consequently, seeds that become buried before the first rainfall promoting germination become incorporated into a persistent seed bank.

The modified key used to predict seed bank types of species from the Strandveld Succulent Karoo is shown in Fig. 1. Since the Strandveld Succulent Karoo is in a winter rainfall region and rain during summer months is extremely uncommon, most local species germinate in autumn and there are probably no winter-transient species. For this reason, the seed bank type characterized by spring-germinating species (Grime and Hillier, 1981, type II) was omitted. Since germination occurs mainly in autumn, a dry heat pre-treatment (Baskin and Baskin, 1998) is more representative of the hot summer months preceding germination than is cold stratification for after-ripening seeds.

The key of Grime and Hillier (1981) does not make provision for small non-photoblastic seeds with high initial germination percentages. Germination percentages of both fresh and stored (20°C for 1

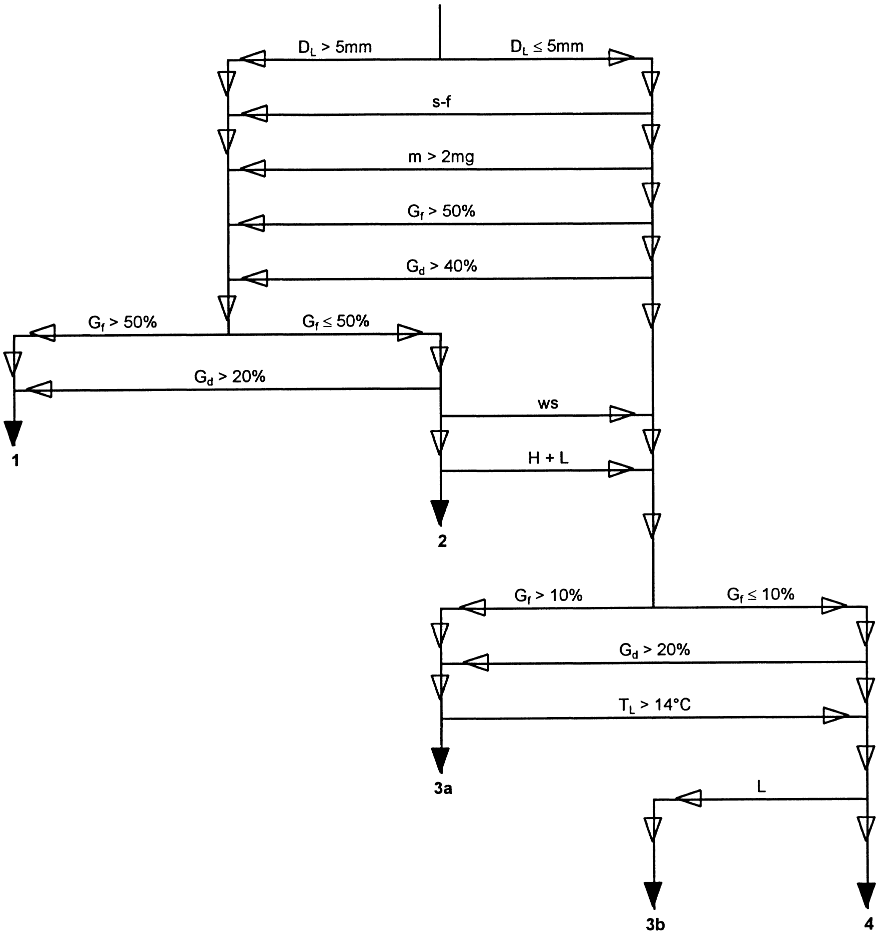

Figure 1. A key with laboratory characteristics of seeds developed to predict five seed bank types in the Strandveld Succulent Karoo (after Grime and Hillier, 1981). 1, Perennial herbs and shrubs capable of immediate germination; 2, annual and perennial grasses, and perennial herbs germinating in early autumn; 3a, perennial herbs and shrubs mainly germinating in autumn and winter but maintaining a small seed bank; 3b, annuals germinating in autumn but maintaining a small persistent seed bank; 4, annuals and perennial herbs and shrubs germinating in autumn with a large persistent seed bank. D_L (mm), Length of diaspore; m (mg), mass of seed; s-f, seed not readily abscised from mother plant; ws, >1 seed embedded in a woody structure; L, seed requires light to break dormancy; G_f (%), maximum percentage germination achieved by fresh seed; G_d (%), maximum percentage germination achieved by seed stored at 20°C for 1 month; H + L, seed requires heat and light to break dormancy; T_L, lowest temperature at which 50% germination is achieved.

Table 1. Seed characteristics of 37 Strandveld Succulent Karoo plant species (41 seed types) used in predicting seed bank types

Seed bank		Growth	Seed characteristic								
type	Species (seed type)	form	D_L (mm)	S-F	m (mg)	G_f (%)	G_d (%)	ws	H	L	$T_L > 14°C$
1	*Albuca exuviata* Bak.	PH	4.2	Y	0.8	38.0	96.0				
	Amellus tenuifolius Burm.	PS	3.1	Y	0.4	51.0	36.0				
	Chrysocoma longifolia DC.	PS	1.2	Y	0.2	72.0	53.0				
	Dimorphotheca tragus (Ait.) T.Norl.	PH	10.1	Y	4.3	44.0	54.0				
	Hypertelis salsoloides (Burch.) Adamson	PH	0.8	Y	0.1	94.0	90.0				
	Pteronia divaricata (Berg.) Less.	PS	3.7	Y	2.2	23.0	47.0				
	Tripteris oppositifolia (Ait.) T.Norl.	PS	11.6	Y	13.6	37.0	52.0				
	Zygophyllum morgsana L.	PS	33.3	N	8.8	88.0	72.0				
2	*Arctotis acaulis* L.	PH	3.0	Y	4.5	0.0	0.0	N	Y	N	
	Arctotis stoechadifolia Berg.	PH	2.9	Y	4.0	0.0	0.0	N	Y	N	
	Ehrharta calycina J.E. Sm.	PG	5.3	N	1.0	0.0	0.0	N	Y	N	
	Gazania leiopoda (DC.) Rössl.	PH	3.5	Y	2.4	2.0	8.4	N	Y	N	
3a	*Cephalophyllum spongiosum* (L.Bol.) L.Bol.	PH	0.6	Y	0.1	2.0	32.0	N	Y	Y	N
	Stoeberia sp.	PS	0.7	Y	0.0	24.0	10.0	N	Y	Y	N
3b	*Arctotheca calendula* (L.) Levyns	A	2.9	Y	0.7	0.0	0.0	N	Y	Y	Y
	Cotula thunbergii Harv.	A	1.5	Y	0.3	1.2	5.6	N	Y	Y	Y
	Dimorphotheca pluvialis (L.) Moench. (disc)	A	8.8	Y	3.3	0.0	0.4	N	Y	Y	Y
	Dimorphotheca pluvialis (L.) Moench. (ray)	A	7.1	Y	5.2	0.0	0.0	N	Y	Y	
	Nemesia bicornis (L.) Pers.	A	2.1	Y	0.3	0.0	0.0	N	Y	Y	Y
	Senecio arenarius Thunb.	A	2.9	Y	0.3	0.0	0.0	N	Y	Y	N
	Silene clandestina Jacq.	A	1.2	Y	0.3	0.0	0.0	N	Y	Y	
	Ursinia anthemoides (L.) Poir. (black)	A	5.7	Y	2.1	0.0	0.0	N	Y	Y	
	Ursinia anthemoides (L.) Poir. (grey)	A	5.5	Y	2.1	0.0	0.0	N	Y	Y	Y
	Ursinia anthemoides (L.) Poir. (white)	A	5.5	Y	2.2	0.0	0.0	N	Y	Y	
	Ursinia speciosa DC. (white)	A	2.9	Y	1.2	0.4	0.4	N	Y	Y	Y
	Wahlenbergia paniculata (Thunb.) A.DC.	A	0.4	Y	0.0	0.0	0.0	N	Y	Y	Y
4	*Ballota africana* (L.) Benth.	PS	2.0	Y	0.8	10.0	10.0	N	Y	N	
	Conicosia pugioniformis (L.) N.E.Br.	PH	1.1	Y	0.7	0.0	0.0	N	Y	N	
	Cysticapnos cracca (Cham. & Schlechtd.) Liden	A	1.3	Y	0.5	0.0	0.0	N	Y	N	
	Didelta carnosa (L.f.) Ait.	A	8.8	N	73.5	6.0	8.0	Y	Y	N	
	Grielum grandiflorum (L.) Druce	PH	19.1	N	791.0	0.0	0.0	Y	N	N	
	Hebenstretia dentata L.	A	3.8	Y	1.0	0.0	0.0	N	Y	N	
	Hebenstretia repens Jarosz	A	1.9	Y	0.5	0.0	0.0	N	Y	N	
	Heliophila coronopifolia L.	A	0.8	Y	0.1	6.0	2.0	N	Y	N	
	Pharnaceum aurantium (DC.) Druce	PH	0.5	Y	0.1	0.0	2.0	N	Y	N	
	Pharnaceum exiguum Adamson	A	0.5	Y	0.1	0.0	0.0	N	Y	N	
	Pharnaceum lanatum Bartl.	PH	0.8	Y	0.1	0.0	6.0	N	Y	N	
	Polycarena pumila (Benth.) Levyns	A	0.3	Y	0.0	4.0	4.0	N	Y	N	

Table 1. *continued.*

Seed bank		Growth	Seed characteristic								
type	Species (seed type)	form	D_L (mm)	S-F	m (mg)	G_f (%)	G_d (%)	ws	H	L	$T_L > 14$°C
	Ruschia bolusiae Schwant.	PS	1.0	Y	0.3	0.0	2.0	N	Y	N	
	Tetragonia virgata Schltr.	PS	6.9	N	40.4	0.0	0.0	Y	Y	N	
	Ursinia speciosa DC. (black)	A	2.9	Y	1.3	0.0	0.0	N	Y	N	

D_L (mm), length of diaspore; m (mg), mass of seed; G_f (%), maximum percentage germination achieved by fresh seed; G_d (%), maximum percentage germination achieved by seed stored dry at 20°C for 1 month; S-F, seed readily abscised from mother plant; H, seed requires heat to break dormancy (after-ripen); T_L, lowest temperature at which 50% germination is achieved; L, seed requires light to break dormancy; ws, more than one seed embedded in a woody structure; A, annual; PS, perennial shrub; PH, perennial herb; PG, perennial grass; Y, yes; N, no.

1, Perennial herbs and shrubs capable of immediate germination; **2**, annual and perennial grasses, and perennial herbs germinating in early autumn; **3a**, perennial herbs and shrubs mainly germinating in autumn and winter but maintaining a small seed bank; **3b**, annuals germinating in autumn but maintaining a small persistent seed bank; **4**, annuals and perennial herbs and shrubs germinating in autumn with a large persistent seed bank.

month) seeds were considered to categorize small seeds. Furthermore, Grime and Hillier (1981) used the time taken by seeds, stored dry at 20°C for 1 month, to reach 50% germination (t50) to distinguish between seed bank types IIIa and IIIb or IV. Since all of the investigated Strandveld Succulent Karoo species in these categories had low germination percentages (<10%, most of which were 0%; Fig. 1, Table 1) this parameter was not included.

Type 3 seed bank strategy was subdivided into types 3a and 3b (Fig. 1) according to the type IIIa and IIIb strategies described by Grime (1981). Type 3a corresponds to the original type III (Grime and Hillier, 1981), but type 3b was derived from seed bank type IV (Grime and Hillier, 1981), i.e. species requiring light for optimum germination.

Seed characteristics such as mass, size and shape may be linked to both seed longevity and dispersal distance. On species, genus or family level, small, light and round seeds with smooth coats are more likely to form persistent seed banks than large, heavy, flattened or elongated seeds with hooks, awns, spines or other kinds of projections on the seed coat (Thompson *et al.*, 1993, 1998; Bakker *et al.*, 1996; Baskin and Baskin, 1998). The underlying cause of this relationship is assumed to be relative ease of burial. Large seeds are not readily buried by rain, animals or gravity, and they experience high levels of predation on the soil surface (Thompson *et al.*, 1993).

Seed bank type 1

Of the 37 species investigated, eight species exhibited type 1 seed bank strategy (Table 1; Fig. 2), all of which were perennial with wind-dispersed seeds. Plant species of Namaqualand are predominantly

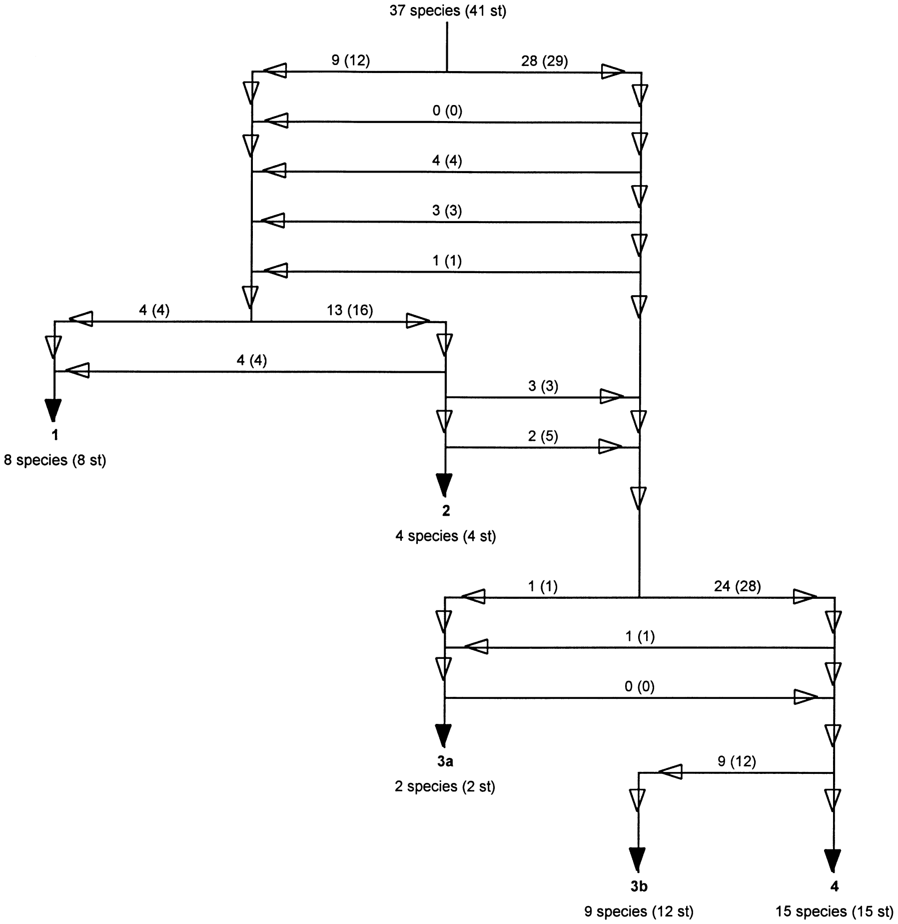

Figure 2. Distribution of 37 Strandveld Succulent Karoo species (41 seed types) between seed bank strategies predicted by using a modified key with laboratory characteristics of seeds. 1, Perennial herbs and shrubs capable of immediate germination; 2, annual and perennial grasses, and perennial herbs germinating in early autumn; 3a, perennial herbs and shrubs mainly germinating in autumn and winter but maintaining a small seed bank; 3b, annuals germinating in autumn but maintaining a small persistent seed bank; 4, annuals and perennial herbs and shrubs germinating in autumn with a large persistent seed bank. st, Seed type.

anemochorous (66.3% of all species) (Van Rooyen *et al.*, 1990). In contrast to the type I strategy of Grime and Hillier (1981), which included annual and perennial grasses, no grass species of the Strandveld Succulent Karoo belonged to this group. Type 1 consisted of perennial herbs and shrubs capable of immediate germination. Both large- and small-seeded species have this strategy (Table 1).

Seed bank type 1 species can germinate over a wide range of temperatures and under different light conditions (De Villiers *et al.*, 2002). Rainfall plays a crucial role in timing germination to ensure successful seedling establishment and survival in these species. Occasional out-of-season rainfall may result in germination; however, many seedlings will not survive the dry summer months. To some extent, the loss of offspring will be buffered by the perennial nature of these species.

Seeds of these anemochorous species (type 1) have the potential to be dispersed by wind over long distances (Sheldon and Burrows, 1973; Bakker *et al.*, 1996). However, antitelechorous mechanisms, such as myxospermy and synaptospermy (Van Rheede van Oudtshoorn and Van Rooyen, 1999), are also present in some of them. Although these mechanisms do not prevent dispersal, they often restrict dispersal in space on a small scale. *Amellus tenuifolius* is a short-term bradysporic species, and mature seeds are retained on the mother plant for a relatively short period.

Several authors have speculated on a trade-off between dispersal and persistence, hypothesizing that species are specialized either for good dispersal or for forming a persistent seed bank (Klinkhamer *et al.*, 1987; Poschlod and Jackel, 1993; Bakker *et al.*, 1996). Although Strandveld Succulent Karoo species with a type 1 seed bank strategy do not produce a persistent seed bank that will aid rehabilitation by topsoil replacement, they may be dispersed to newly revegetated areas from surrounding vegetation. Natural dispersal is, however, often slow and unreliable (Bauer, 1973; Van der Valk and Pederson, 1989). Transplanting adult plants is labour intensive, but it is recommended for initial re-establishment of seed bank type 1 shrub species. Transplanting shrubs has the added advantage that they may reduce wind speed at ground level and thereby combat wind erosion at reclamation sites. Herbaceous perennials with type 1 seed banks should be reintroduced by sowing.

Seed bank type 2

Species characteristic of seed bank type 2 typically have seeds that are >5 mm long, and/or seeds with a mass >2 mg, and/or not readily abscised from the mother plant (Fig. 1). Seeds of these species have low germination percentages when fresh or after dry storage at 20°C for 1 month. They do not require light to germinate, but they do require high temperatures to after-ripen (Table 1).

This strategy occurred in four of the species examined, all of which were perennials with anemochorous seeds (Fig. 2). A few other local perennial and annual grass species are expected to have this type of seed bank strategy, since their germination requirements are similar to that of *Ehrharta calycina* (De Villiers *et al.*, 2002).

Seeds with this strategy require an after-ripening period (Table 1), after which most of them germinate at the first fall of sufficient rains, usually in autumn. Seeds can germinate over a wide range of temperatures in both light and darkness (De Villiers *et al.,* 2002). These species have a summer-transient seed bank, although some may be short-term persistent. The type 2 seed bank strategy was exhibited by perennial herb and grass species (Table 1). Anemochory is common among these species, but antitelechorous mechanisms, such as myxospermy, are also evident. Species in this category often occur in environments that produce predictable circumstances for establishment in space as well as in time, often relying on clonal colonization (Bakker *et al.*, 1996). These species are likely to re-establish easily during natural regeneration, although during revegetation they may need deliberate re-introduction.

Seed bank type 3a

Seed bank type 3a strategy is characterized by species with small photoblastic seeds (<5 mm) that require a short after-ripening period. These seeds germinate to more than 50% at temperatures lower than 14°C (Table 1, Figs 1 and 2), indicating that germination could also occur in winter. This category includes perennial herbs and shrubs, mainly germinating during autumn and winter but maintaining a small, short-term persistent seed bank.

Both species with type 3a seed bank strategy belong to the *Mesembryanthemaceae* and have a rain ballistic seed dispersal mechanism. Not all the seeds in a capsule are dispersed at the same time. Therefore, dispersal is restricted in time and a canopy seed bank is present in these species (Van Rheede van Oudtshoorn and Van Rooyen, 1999).

Mass germination and loss of seedlings during unfavourable conditions will be buffered by the perennial nature of species with this type of seed bank (Table 1). Since the probability of seedling establishment under severe competition from other plants is lower in species with small seeds than in those with large seeds (Hodgson and Thompson, 1993), establishment of these small-seeded species (type 3a) may depend on availability of sites where the canopy cover is low. Because light is required for germination, burial inhibits germination, which results in the formation of a small seed bank. Topsoil replacement should be sufficient for revegetation of mined areas with these species, provided topsoil is not stored too long prior to replacement. Due to the limited distribution of these species (De Villiers *et al.*, 1999), post-mining re-introduction by sowing should be considered in coastal communities where these species were previously abundant.

Seed bank type 3b

Nine annual species (12 seed types) were classified into this category (Fig. 2). Seeds of type 3b species are usually small, require a high temperature after-ripening period and light to germinate, and they have a narrow temperature range for germination (Fig. 1, Table 1). Some seeds become buried during the summer after-ripening period, and a light requirement for germination prevents germination of buried seeds (Baskin and Baskin, 1998). At the start of the rainy season (autumn), a large portion of type 3b species germinate, but many seeds may persist in the soil for more than 1 year in a short-term persistent seed bank.

Seed dispersal of these winter annual species is mainly by wind, although antitelechorous mechanisms such as myxospermy and heterodiaspory are abundant. Heterodiaspory occurred in three species: *Dimorphotheca pluvialis*, *Ursinia anthemoides* and *Ursinia speciosa*. In some cases, one seed type of these species was classified as type 3b, whereas the other seed type belonged to type 4. Heterodiaspory provides two germination strategies and greatly enhances the ability of a species to live in highly variable environments. In heterodiasporic species, one seed type often germinates to a high percentage under favourable conditions and is responsible for the relative abundance and range extension of the species. The other seed type often has delayed germination (De Villiers, 2000), which reduces the chances of extinction of a complete generation (Berger, 1985).

Seed bank type 3b species should make a major contribution towards revegetation by means of topsoil replacement, since a short-term persistent seed bank is formed (Table 1). For these species, seed input by humans (sowing) should not be necessary after topsoil has been replaced. Furthermore, most of these species are anemochorous and may be re-introduced by dispersal from surrounding vegetation. However, stockpiling soils before they are used for revegetation can hinder recruitment in two ways. Short-lived viable seeds may be lost if the soil is stored too long, and environmental conditions, particularly unfavourable temperatures, in the stockpiled soil may kill them (Van der Valk *et al.*, 1992).

Seed bank type 4

A type 4 seed bank strategy is found in species where the seed bank is large relative to annual input. These species commonly have small seeds or seeds with hard pericarps or seed coats, and usually require a summer after-ripening period (Fig. 1, Table 1). Type 4 species are annuals (8 species) and perennial herbs and shrubs (7 species) with seeds that germinate in autumn and form a long-term persistent seed bank (Figs 1 and 2, Table 1). If the environment is moderately predictable over time and is confined spatially, building a persistent seed bank is apparently a common strategy (Bakker *et al.*, 1996).

Seeds of species with this seed bank type are mainly anemochorous, but several species were found to be epizoochorous and rain ballistic. Antitelechorous mechanisms found among these species include synaptospermy, heterodiaspory, hygrochasy and myxospermy.

The importance of seed bank type 4 in revegetation efforts relates to its long-term persistence. Topsoil replacement should be sufficient for the re-introduction of this group of species during post-mining revegetation processes. If seeds of these species have to be sown, sowing should probably be preceded by scarification and/or a heat pre-treatment because of a hard pericarp or testa, or woody structure in some of these species.

Seed bank type and revegetation

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

Restoration management has only recently taken into account the importance of dispersal in establishment of 'target' communities or species (Bakker *et al.*, 1996). Dispersal was the most important factor in a second phase of restoration, after activating the seed bank (Salonen, 1987; Poschlod, 1995). However, it was also shown that even species occurring close to restoration sites were absent from the seed rain (Poschlod, 1995).

Species of all five seed bank types will be important in revegetating mined areas in the Strandveld Succulent Karoo, since each type contains species dominant in specific communities (De Villiers *et al.*, 1999). The revegetation process will, however, differ for species with different seed bank types. The seed bank alone will not be sufficient to revegetate this area, because many of the species that dominate in the aboveground vegetation do not produce persistent seed banks (types 1 and 2). Topsoil replacement as the first step is essential because of difficulties involved in collection, treatment and sowing of small seeds in the persistent seed bank (types 3a, 3b and 4).

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

Conclusions

The proposed key, using easily measurable seed and germination characteristics, developed to predict seed bank types, seems to be well-suited to classify seed banks of the Strandveld Succulent Karoo. A few adaptations had to be made to the Grime and Hillier (1981) key to make it work for Strandveld Succulent Karoo species. First, the requirement of a dry heat pre-treatment during the summer after-ripening period, rather than cold stratification, had to be incorporated. Secondly, mean germination percentages of fresh and stored seeds (20°C for 1 month) were considered for both large and small seeds. Consequently, seed size and abscised status were not the only criteria for classification into transient or persistent seed bank types. Thirdly, a subdivision of the persistent seed bank category according to the categories described by Grime (1981) was desirable. Finally, the time taken by seeds stored dry at 20°C for 1 month to reach 50% germination was not used to distinguish between seed bank types 3a and 3b or 4, since these species did not attain 50% germination when stored for such a short period. In contrast to the four main seed bank types distinguished by the original key of Grime and Hillier (1981), this modified key recognizes five seed bank types, two of which are classified as transient seed bank strategies (types 1 and 2) and three as persistent seed bank strategies (types 3a, 3b and 4).

Of the 37 species investigated, 32% have a transient seed bank strategy and 68% persistent seed bank strategies. Five per cent of the species produced small, persistent seed banks, while 24% and 41% of the species have seed types that accumulate short-term persistent seed banks and long-term persistent seed banks, respectively. In general, these seed bank strategies have been confirmed by seed bank studies in the Strandveld Succulent Karoo (De Villiers, 2000). However, predicted seed bank strategies should be examined and checked in the field for each species individually.

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

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