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## Patterns of seed persistence in South African fynbos

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**Key words:** Dormancy, Fire, Germination, Life history, Seed bank, Seed characteristics

### Abstract

In fire-prone communities such as fynbos, many species rely on regeneration from seed banks in the soil. Persistent seed banks are particularly important for species with life spans shorter than the average fire cycle, in order to counter local extinction. Persistent seed banks also give potential for restoring ecosystems following disturbances such as alien plant invasion. This study investigated the seed persistence patterns of 25 perennial species, representing several growth forms and life histories, during a three-year burial. Long-term persistence (i.e., seed bank half-life exceeding two years) was found in the hard-seeded Fabaceae and *Pelargonium*, and the nut-fruited Proteaceae. In this group, germinability was low and dormancy increased further following burial, resulting in a highly viable, dormant seed bank after three-year's burial. A second group with potentially long-term persistent seeds includes four taxa (*Pseudopentameris*, *Passerina*, *Elegia* and *Restio*) that either have low germinability or develop secondary dormancy following burial. Dormancy in the latter group was partially countered by exposure to smoke-seed primer. Of the small-seeded species, only two *Erica* species with high initial dormancy had long-term persistent seed banks. The other species mostly displayed high initial germinability and short-term persistent seed banks (i.e., seed bank half-life less than two years). This group included taxa with short to medium life-spans (*Syncarpha*, *Roella*) that were expected to have long-term persistent seeds in order to buffer against local extinction following average to long fire-return intervals. We hypothesize that light may play a role in overcoming secondary dormancy in those species, and could have resulted in an underestimate for seed persistence in this study. Alternatively, those short to medium life-span species persist via inter-fire recruitment in gaps or long-distance dispersal (of the smallest seed). No correlations were found between seed persistence and seed mass or variance in seed dimensions. Nor was a correlation found between seed persistence and phenol concentration. In fynbos, seed burial of larger seeds by ants and rodents are major processes that operate in conjunction with passive burial of small seeds. Selection for persistence can be expected to operate across all seed sizes and shapes in fire-prone communities.

### Introduction

In fire-prone plant communities, recruitment generally is coupled to fires, both as a result of direct fire effects, such as the stimulation of germination, and indirect fire effects, such as a reduction in competition and herbivory (Tyler 1996). In the Mediterranean-climate shrubland types of Californian chaparral, Australian kwongan and South African fynbos, a large proportion of species are killed by fire (obligate

seeders) and rely on seed banks for regeneration (Le Maitre and Midgley 1992). Although serotiny (canopy seed storage) is an important means of seed storage for community dominants in some kwongan and fynbos communities, the majority of species rely on recruitment from seed banks in the soil.

Of the two main functional types of seed bank (transient and persistent) proposed by Thompson and Grime (1979), persistent seed banks are important for species with life-spans shorter than the average dis-

turbance (e.g., fire) cycle. For all species, either persistent seed banks, or large annual seed production in the pre-fire year, is required to enable population expansion post-fire. Many of the species studied in Mediterranean-climate shrublands have persistent soil seed banks, but some show little seed bank accumulation over time, as a result of large annual losses following seed shed and deterioration of soil-stored seeds (Zammit and Zedler 1988; Musil 1991; Pierce and Cowling 1991; Meney et al. 1994).

Persistent soil seed banks are important for regeneration in obligate seeders and to compensate mortality in resprouters, especially those resprouters that are sensitive to fires of high intensity (Bond et al. 1990). Auld et al. (2000) also suggest that seed banks may be important for resprouters that are subject to competitive exclusion by site dominants, and in species for which seed production is suppressed by increasing seed predation with time since fire. Knowledge of seed bank dynamics, including persistence, is important for management and for planning restoration programmes in degraded ecosystems (Holmes 2001).

Viable soil seed banks of a range of mountain fynbos species and growth forms were found beneath monocultures of the invasive alien shrub *Acacia saligna* (Labill.) H.L.Wendl. on the Cape Peninsula (Holmes and Cowling 1997). The most likely explanation for this observation is long-term persistence in the seed banks of those species, indicating good potential to restore mountain fynbos following alien plant clearance. Van Wilgen and Forsyth (1992) inferred long-term persistent seed banks for short to medium life-span species in mountain fynbos. However, studies of seed bank dynamics in several long life-span fynbos species suggest that seed banks may not be long-term persistent owing to high seed predation levels, seed decay or a combination of both (Musil 1991; Pierce and Cowling 1991). Further research is needed to investigate patterns of persistence in fynbos seed banks.

In order to investigate patterns of seed persistence and factors promoting it, a three-year experimental burial was conducted on 24 perennial indigenous species from the Cape Peninsula, representing prominent fynbos plant families, different growth forms and seed-types, and one prominent invasive alien species (*Acacia saligna*) from Australia (Table 1). At various intervals throughout the trial, seeds were tested for persistence, germinability and viability. We investigated whether fynbos seed persistence in the soil is correlated to seed size, shape and phenol concentra-

tion, as has been shown in some other floras (Thompson et al. 1993; Hendry et al. 1994; Funes et al. 1999; Thompson et al. 2001).

## Methods

### *Study area*

The study was conducted on the Cape Peninsula, which is located at the southwest corner of the Cape Floristic Region in South Africa. The Cape Peninsula is renowned for its exceptionally high plant species richness and diversity: 2285 species within 471 km<sup>2</sup> (Trinder-Smith et al. 1996). This has been attributed to the extraordinarily steep and long habitat gradients along which species are packed and the high degree of rarity (Simmons and Cowling 1996). The Cape Peninsula has a Mediterranean-type climate with most rain falling in the winter months. The dominant vegetation type is fire-prone fynbos, occurring on oligotrophic soils. Fynbos is characterized structurally by a prominence of fine-leaved shrubs and aphyllous graminoids, and frequently an overstorey of proteoid shrubs (Cowling et al. 1997). Fires return at intervals averaging 15 years (range 4–45, van Wilgen et al. 1992) and species persist by resprouting from fire-protected buds and underground storage organs, or by germinating either from seed released from fire-protected cones or soil-stored seed banks.

### *Seed collection*

Seeds of the 25 species were collected by hand, directly from plants, from mesh bags placed around maturing fruits, or from the soil surface below parent plants during 1995 and 1996 at various localities south of Cape Town on the Cape Peninsula. For each species, several parent plants were sampled and the seeds stored in paper bags at room temperature until required for the burial trial.

### *Seed burial*

In May 1996, prior to the onset of heavy winter rains, five replicates each of 100 plump seeds per species were placed in porous nylon bags (sufficient seeds for only four replicates were available for *Edmondia sesamoides*). Five burial microsites within a 50 metre radius were located in a stand of five-year old fynbos vegetation (that had a low probability of burning dur-

Table 1. Characteristics of the perennial fynbos species used in the seed burial experiment: plant longevity was categorized as short-lived (S:  $\leq 4$  years), medium-lived (M: 5–15 yr) and long-lived (L:  $> 15$  yr); regeneration modes are: S = obligate seeder, E = proportion escape fire and R = ability to resprout after fire; germination cues are: A = alternating temperature, C = low temperature, H = heat, L = light, S = smoke, U = unknown; variance of seed dimensions calculated after transforming the longest dimension to unity. Data for estimated half-life are means (range of one standard error above and below mean decay rate) calculated from year three persistence, except for italicized values that were calculated from year one persistence. Species of Poaceae and Restionaceae are herbaceous graminoids; the others are shrublets or shrubs. Nomenclature follows Goldblatt and Manning (2000); "seed" refers to true seeds and diaspores without easily detachable structures.

Family	Species	Plant longevity	Regeneration mode	Dispersal mode	Germination cues	Seed mass (mg)	Variance in seed dimensions <sup>1</sup> (mm)	Seed coat thickness (mm)	Seed phenols (mg)	Phenol conc. (mg/g)	Seed bank half-life (years)
Asteraceae	<i>Edmondia sesamoides</i> (L.) Hilliard	M	S	wind	U	0.174	0.124	0.066	nd	nd	0.8 (0.7–0.8)
Asteraceae	<i>Metastasia muricata</i> (L.) D.Don	L	S	Wind	ALHS <sup>3,4,5</sup>	0.284	0.129	0.080	0.139	24.506	0.7 (0.6–0.7)
Asteraceae	<i>Syncarpha speciosissima</i> (L.) B.Nord.	M	S	wind	SL <sup>2</sup>	8.456	0.058	0.444	0.216	1.276	0.6 (0.5–0.6)
Asteraceae	<i>Syncarpha vestita</i> (L.) B.Nord.	M	S	wind	S <sup>5</sup>	0.536	0.066	0.072	0.041	3.842	1.3 (1.2–1.3)
Campanulaceae	<i>Roellia ciliata</i> L.	S	S	passive	U	0.113	0.105	0.072	0.010	4.336	0.8 (0.7–0.8)
Campanulaceae	<i>Roellia triflora</i> (R.D.Good) Adamson	S	S	passive	U	0.116	0.100	0.058	0.032	13.887	1.2 (1.2–1.3)
Ericaceae	<i>Erica abietina</i> L.	L	S	passive	U	0.104	0.041	0.036	0.029	13.961	3.4 (3.1–3.8)
Ericaceae	<i>Erica baccans</i> L.	L	S	passive	U	0.067	0.066	0.036	0.023	19.829	1.6 (1.6–1.7)
Ericaceae	<i>Erica ericoides</i> (L.) E.G.H. Oliver	L	S	wind	S <sup>1</sup>	0.045	0.093	0.024	0.014	15.657	1.5 (1.4–1.6)
Ericaceae	<i>Erica plukenetii</i> L.	L	S	passive	S <sup>1</sup>	0.074	0.102	0.034	0.019	13.057	2.0 (1.9–2.1)
Fabaceae	<i>Acacia saligna</i> (Labill.) H.L. Wendl.*	L	R	ant	H <sup>9</sup>	18.66	0.120	0.168	0.338	2.641	18.5 (17.3–20.0)
Fabaceae	<i>Aspalathus camosa</i> P.J. Bergius	M	S	ballistic	U	5.088	0.021	0.056	0.087	0.087	5.6 (5.4–5.8)
Fabaceae	<i>Indigofera filifolia</i> Thunb.	L	S	ballistic	U	11.23	0.021	0.168	0.037	0.333	13.6 (12.5–14.9)
Fabaceae	<i>Otholobium fruticans</i> (L.) C.H. Stirt.	L	S	ballistic	U	3.608	0.052	0.086	0.116	1.612	3.3 (3.2–3.5)
Geraniaceae	<i>Pelargonium capitatum</i> (L.) L'Hér.	S	S	wind	U	3.317	0.189	0.090	0.141	2.132	7.2 (6.8–7.6)
Poaceae	<i>Pseudopentameris macrantha</i> (Schrad.) Conert	L	R	passive	U	4.328	0.245	0.096	0.084	0.976	5.3 (4.9–5.8)
Proteaceae	<i>Leucadendron xanthoconus</i> (Kuntze) K. Schum. <sup>5</sup>	L	S	Wind	C <sup>7</sup>	5.924	0.110	0.106	1.809	27.003	0.8 (0.8–0.9)
Proteaceae	<i>Leucospermum conocarpodendron</i> (L.) H. Buek	L	E	ant	H <sup>11</sup>	108.9	0.045	0.448	34.510	26.144	9.5 (8.4–10.8)
Proteaceae	<i>Protea repens</i> (L.) L. <sup>5</sup>	L	S	wind	C <sup>7</sup>	58.31	0.126	0.455	nd	nd	0
Proteaceae	<i>Serruria villosa</i> (Lam.) R.Br.	L	S	ant	U	9.073	0.113	0.184	2.732	17.975	5.9 (5.4–6.4)
Restionaceae	<i>Cammonia virgata</i> (Rottb.) Steud	L	S	ant	S <sup>8,10</sup>	57.39	0.131	0.164	1.061	2.559	18.2*(15.4–22.4)
Restionaceae	<i>Elegia cuspidata</i> Mast.	L	S	passive	S <sup>8</sup>	1.228	0.056	0.092	0.085	3.473	5.8 (3.6–11.8)
Restionaceae	<i>Restio bifurcus</i> Nees ex Mast.	L	S	passive	U	1.226	0.046	0.056	0.056	2.270	1.2 (1.2–1.3)
Restionaceae	<i>Staberoha distachyos</i> (Rottb.) Kunth.	L	R	passive	HS <sup>56</sup>	1.097	0.071	0.156	0.062	2.805	0.8 (0.8–0.9)
Restionaceae	<i>Willdenowia incurvata</i>	L	S	ant	U	147.4	0.045	0.910	24.175	11.360	8.2*(7.4–9.1)
Rutaceae	<i>Diosma hirsuta</i> L.	L	S	ballistic, ant	U	9.366	0.115	0.132	0.301	1.607	0.6 (0.5–0.6)
Thymeliaceae	<i>Passerina vulgaris</i> Thoday	L	S	passive	A <sup>3</sup>	0.976	0.096	0.068	0.131	6.699	1.0 (0.9–1.0)

\* invasive alien species; <sup>5</sup> serotinous species; # data from Newton (2000); nd = not done; <sup>1</sup> Brown (1993), <sup>2</sup> Keeley and Bond (1997), <sup>3</sup> Pierce and Moll (1994), <sup>4</sup> Musil (1991), <sup>5</sup> Brown (1993), <sup>6</sup> Musil and de Witt (1991), <sup>7</sup> Brown et al. (1996), <sup>8</sup> Brown et al. (1988), <sup>9</sup> Jeffery et al. (1995), <sup>10</sup> Newton (2000), <sup>11</sup> Brits et al. (1993).

ing the three-year study period) at the Cape of Good Hope Nature Reserve (34°19'30" S, 18°26'24" E) in the southern Cape Peninsula. Soil was excavated to 50 mm depth at each microsite and a steel enclosure made of 2 mm-sized mesh (to exclude burrowing rodents) was placed in each hole. The 25 nylon mesh bags were placed inside the steel enclosure and the soil replaced so that each bag was in close contact with soil. Fungal hyphae and fine roots penetrated the bags by six months burial. At five intervals over three years (6, 12, 18, 24 and 36 months) the samples were exhumed and removed to the laboratory to search for the presence of seeds or seed remains. Samples were kept out of direct sunlight. At the first sampling time (6 months) 80 intact seeds (or all intact seeds if the number persisting was lower than this) were returned to the mesh bags following examination, and reburied as described above until the next sampling time. Any intact seeds in excess of the 80 reburied (i.e., 1–20 seeds) were tested for germinability and viability. At each sampling time, the samples were examined as described above, and 20 fewer seeds reburied per sample. Any intact seeds in excess of this were tested for germinability and viability. At the final census all remaining intact seeds were tested for germinability and viability.

#### *Seed germinability and viability*

Pre-burial samples of plump seeds were tested for germinability and viability. Four replicates of 25 seeds per species were placed in petri dishes containing a disk of Whatman no. 1 filter paper soaked in 3 ml 0.1% benlate solution to prevent fungal growth. Dishes were sealed in plastic ziplock bags and placed in a growth chamber set to a 12-hour photoperiod using light from fluorescent tubes. For the first week an autumnal diurnal temperature regime of high alternating temperature (10 °C and 28 °C) was given, followed by a winter temperature regime alternating between 10 °C and 20 °C. Germination was monitored every two weeks and germinants (with > 1 mm radical protruding) recorded and removed. Moisture levels were maintained where necessary by adding distilled water. After two months, distilled water was replaced with a solution of smoke seed primer (Kirstenbosch Instant Smoke Plus) and non-germinated seeds were returned to the growth chamber for another two months. Smoke and smoke extracts have been shown to stimulate germination in a wide variety of fynbos taxa, including some of the species in

this study (Table 1; Brown 1993, Brown et al. 1993, Brown et al. 1994, Brown et al. 1996, Keeley and Bond 1997). The seed primer contains aqueous smoke extract derived from burning wet and dry material of the fynbos plant *Passerina vulgaris*, prepared as described in Brown (1993), and a selection of natural growth stimulants including gibberellin. The dilution of the smoke extract (1:50) is in the optimal range for stimulating germination in fynbos species (N. A. C. Brown personal communication).

Non-germinated seeds were tested for viability, using the tetrazolium salt test (ISTA (International Seed Testing Association) 1999) for larger seeds, and for small seeds by slicing open the seeds using a freezing microtome and examining under a binocular microscope. In the latter method, it was assumed that plump seeds containing embryos were viable.

Samples of seeds surviving burial were tested for germinability and viability at each sampling time using the same methods described above.

#### *Seed measurements*

In this study, the term "seed" refers both to true seeds and diaspores without easily detachable structures. Seed size (i.e., mass) was determined by weighing batches of fifty (large) or 100 (small) air-dried seeds. The length, breadth and width of five seeds were measured under stereo and compound microscopes using a graduated eyepiece. As an index of the deviance of seed shape from spherical, the variance in seed dimensions was obtained by transforming length, breadth and width so that length was unity and calculating the variance of the transformed values (Thompson et al. 1993). Mean seed (or diaspore) coat thickness was calculated from sections of five seeds from which perpendicular measurements were taken with a graduated eyepiece while viewing under a compound microscope. Two nut-fruited Restionaceae species, for which seed persistence data were available from a condensed-seasons experiment (Newton 2000) were included in these measurements (Table 1).

#### *Analysis of phenol content*

Alkali soluble phenols were determined for the seed coat of larger seeds, and for the whole seed where separation of the coat from the seed was not possible. Seed or seed coats ( $n \geq 5$ ) were ground in 10 ml methanol, filtered, rinsed and dried at 60 °C. Each dried sample of 50 mg was boiled for 4 h in 5 ml 2

M HCl containing 0.5 M thioglycolic acid (Schneiderbauer et al. 1991). Phenols were extracted by centrifuging the thioglycolic extracts at 30 000 g for 10 min, after which the supernatant was discarded. The pellet was washed with 5 ml water, resuspended in 5 ml of 0.5 M NaOH, and then gently agitated at 25 °C for 18 h before recentrifuging at 30 000 g for 10 min. The supernatant was allowed to precipitate at 4 °C for 4 h following the addition of 1 ml of concentrated HCl to the supernatant. The resulting pellet was dissolved in 1 ml 0.5 M NaOH and the amount of alkali-soluble polyphenolics determined spectrophotometrically at 280 nm (Bruce and West 1989). A commercial polyphenolic extract from green tea (Sigma) was used to quantify the amount of polyphenolics in the seeds.

#### Data analysis

Seed decay rate was calculated using the exponential equation:

$$N_2 = N_1 \times e^{-\lambda \Delta t}$$

where  $N_1$  and  $N_2$  are the numbers of viable seeds remaining at  $t_1$  and  $t_2$  respectively,  $\lambda$  is the decay rate and  $\Delta t$  is the time interval between  $t_1$  and  $t_2$  (Roberts 1972). Seed half-life (i.e. the time for half the seeds to decay in the soil) was calculated by substituting the decay rate into the exponential equation and solving for  $N_2 = 0.5 N_1$ . The exponential decay curve is frequently used to model seed bank decay (Roberts 1972) and was found to be consistently the best fit of several models tested for species from fire-prone Australian vegetation (Auld et al. 2000). We used the numbers of viable seeds at the start of the burial trial ( $t_1$ ) and after three years burial ( $t_2$ ), except in the case of species in which no seeds remained viable after three years, when one-year results were used. We also used one-year results for some of the small-seeded species that appeared to lose dormancy as a result of being exhumed.

Correlations between seed persistence (expressed as seed half-life) and various seed characteristics were tested using the Spearman rank correlation coefficient. Comparisons in seed germinability between sampling times and before and after seed primer application were tested using unpaired and paired Student's *t*-tests, respectively, on arc-sine transformed data for each species separately.

## Results

### Seed persistence

Buried seeds that did not persist either germinated or rotted (it generally was not possible to distinguish the two). Seed bank decay was most pronounced during the wet winter months (0–6, 12–18 months; Figure 1).

Highest persistence was found in the hard-seeded Fabaceae (Figure 1). This group recorded high estimated seed bank half-lives, with the invasive alien species, *Acacia saligna*, scoring the highest value (18.5 years; Table 1). Following some slight decay during the first winter, seed cohorts largely remained intact. Other species that followed a similar pattern of persistence to the hard-seeded legumes included the shrublet *Pelargonium*, the grass *Pseudopentameris*, and the nut-fruited, myrmecochorous Proteaceae shrubs *Leucospermum* and *Serruria*.

Of the remaining species buried, those that showed potential for long-term seed bank persistence (i.e., half-life exceeding two years) included two heath species (*E. abietina* and *E. plukenetii*) and the restios *Elegia* and *Restio* (Table 1). Two Asteraceae (*Syncarpha vestita* and *Metalsia*) and *Passerina* recorded relatively high persistence after three years' burial, but viability of seeds was low and calculated half-lives were below two years. Remaining non-serotinous species had short-term persistent seed banks (half-life 0.5–2 years) and generally followed a steeper exponential decay curve than the long-term persistent species.

Of the two serotinous Proteaceae species buried, *Protea* maintained no soil seed bank, but a few *Leucadendron* seeds survived three years' burial intact and viable.

### Seed viability and germinability

With the exception of a few species, initial pre-burial seed viability was relatively high (Table 2). Only 24% of plump woody *Protea* achenes contained seeds; likewise 94% of *Elegia* nutlets were empty, and 68% of *Diosma* seeds were non-viable (Table 2). Despite the use of benlate solution, the 12-month cohort of *Leucospermum* seeds suffered some fungal growth that may have contributed to that lower viability result.

Species with consistently high viability in persisting seeds throughout the trial included all hard-seeded legume species tested, *Pelargonium* and *Pseudopen-*

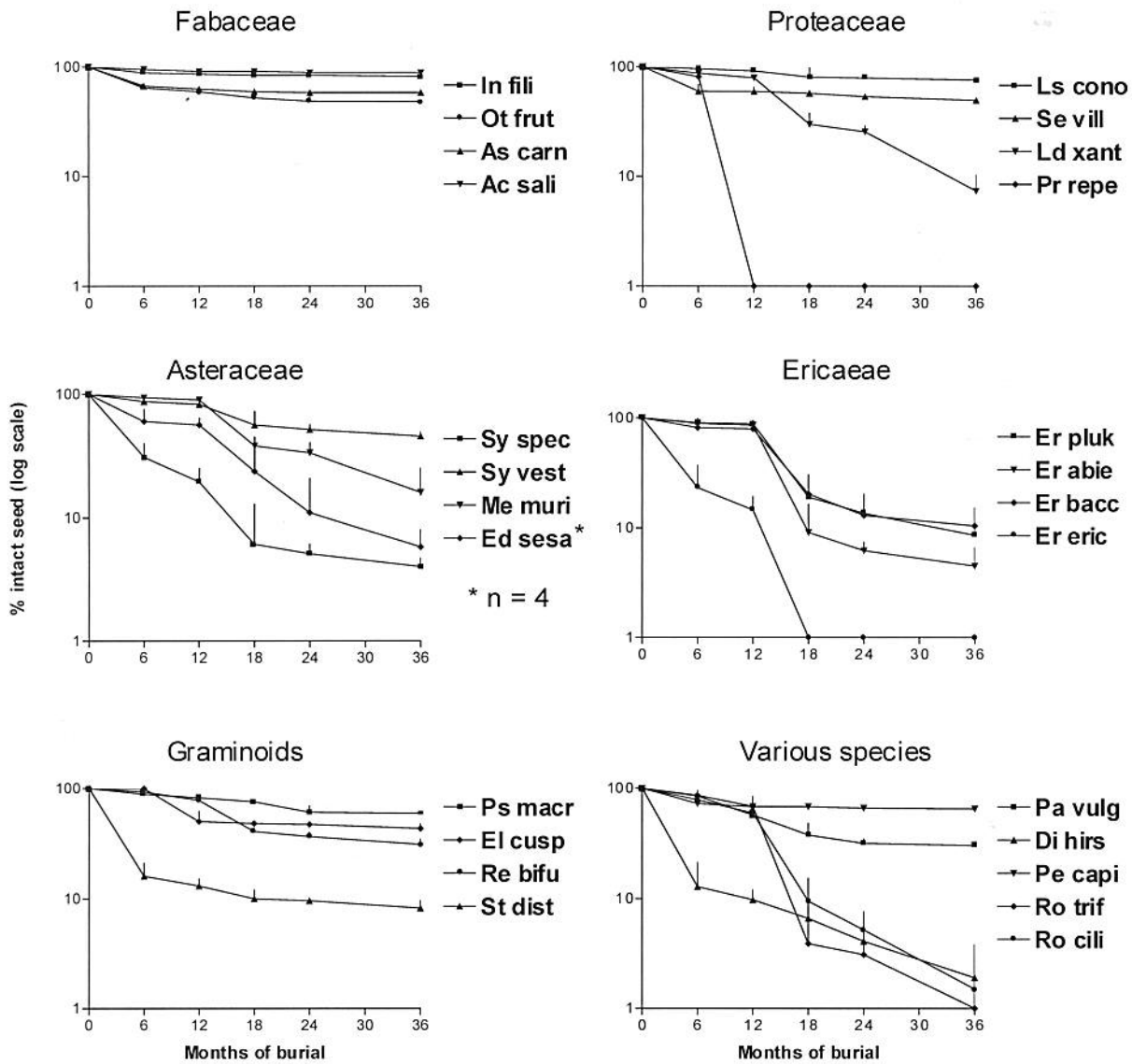


Figure 1. Seed bank decay curves: mean percentage (+ 1 SD; n = 5) of intact seeds remaining in the soil (see Table 1 for full species names).

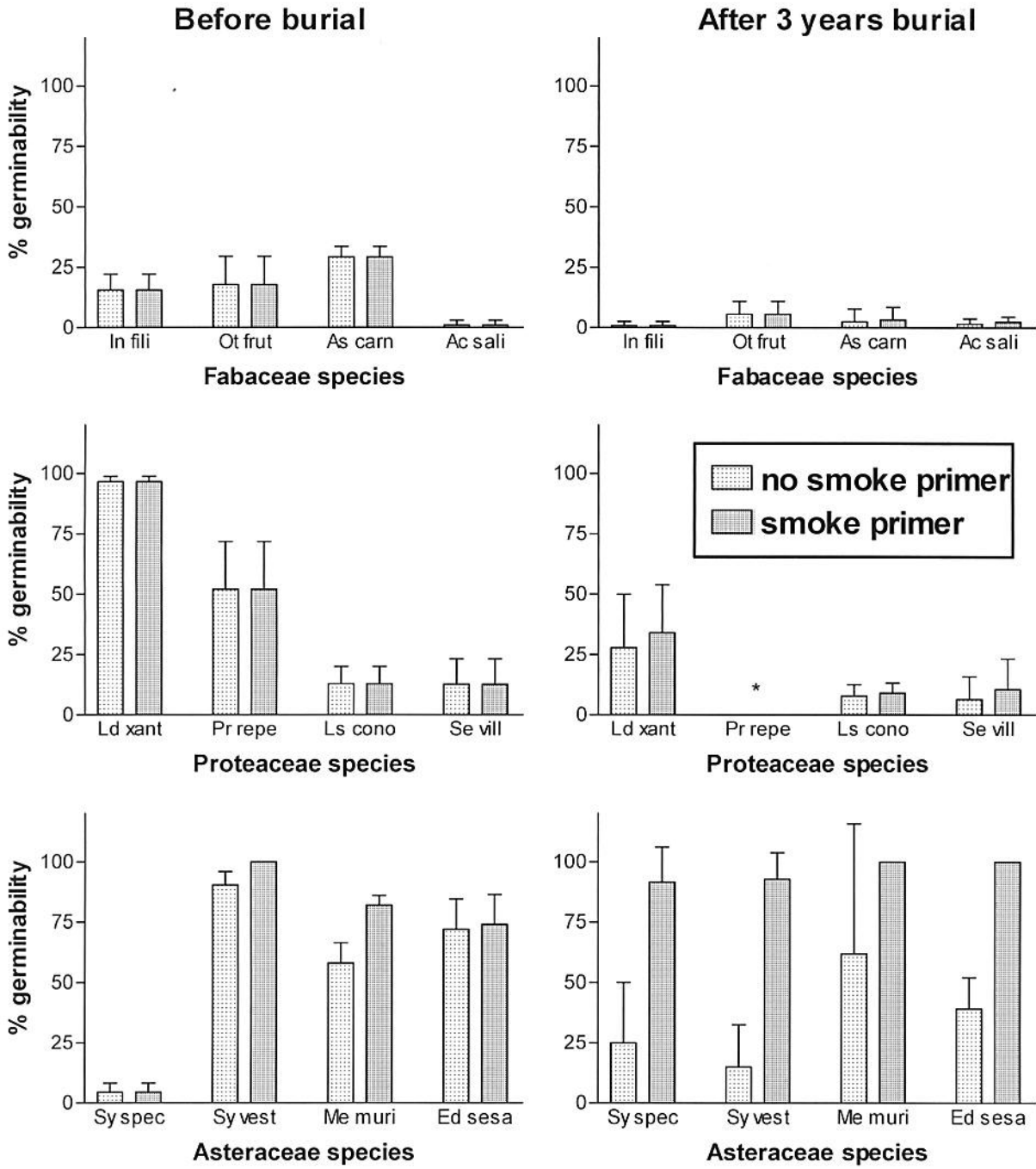
*tameris* (Table 2). Although viability dipped during the trial for persisting *Leucospermum* and *Serruria* seeds, after three years' burial it was high. The small proportion of *Leucadendron* and *Staberoha* seeds that persisted three years' burial also had high viability. Viability of persisting *Elegia* seed was relatively constant throughout the burial trial. All remaining species showed some decline in viability of persisting seeds over time, with *Edmondia* retaining the highest viability (80%) among this group after three year's burial.

Before burial, seed germinability was lowest in the Fabaceae, Restionaceae, *Leucospermum*, *Serruria*,

*Pelargonium*, *Syncarpha speciosissima* and two Ericaceae (*E. plukenetii* and *E. abietina*; Figure 2). Germinability in *Erica ericoides* initially was very low, but increased significantly following the application of smoke seed primer ( $t = 7.517, P = 0.0049$ ). After three years' burial, germinability declined further in the indigenous Fabaceae (significant for *Indigofera*:  $t = 4.798, P = 0.002$ ; *Aspalathus*:  $t = 8.037, P < 0.0001$ ), *Pseudopentameris* ( $t = 2.594, P = 0.0357$ ) and *Pelargonium* ( $t = 11.603, P < 0.0001$ ). Smoke seed primer increased germinability following burial in *Pseudopentameris* ( $t = 2.800, P = 0.0488$ ).





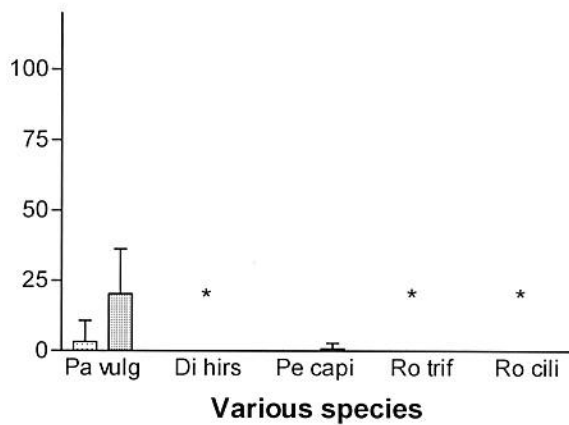
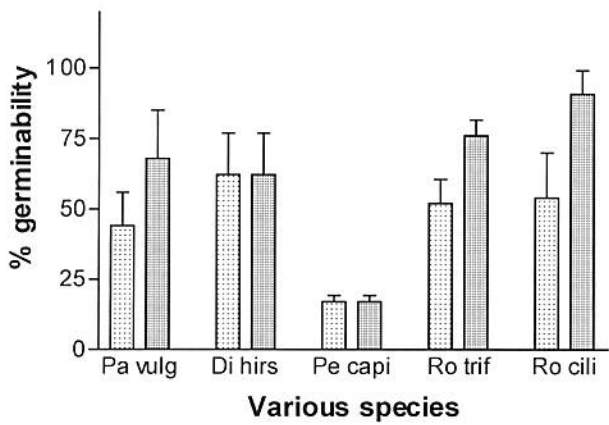
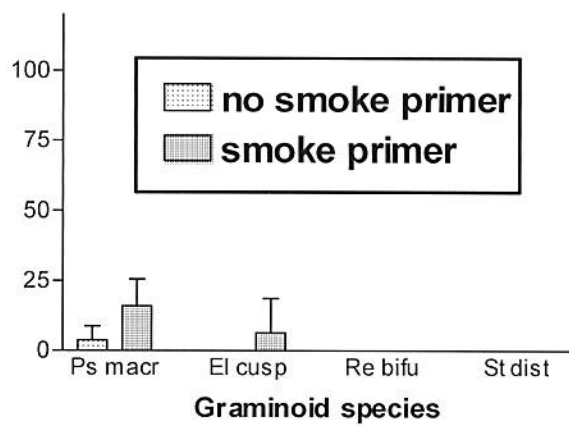
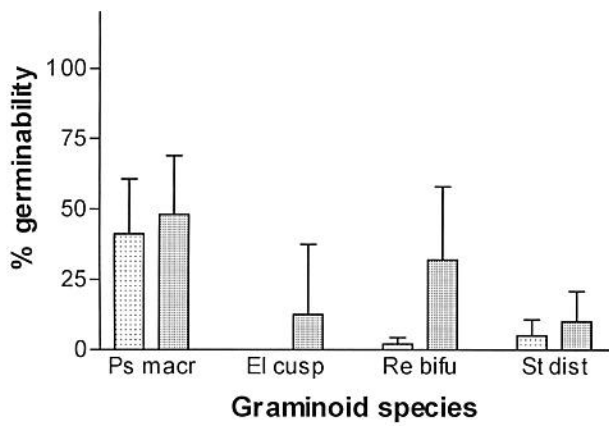
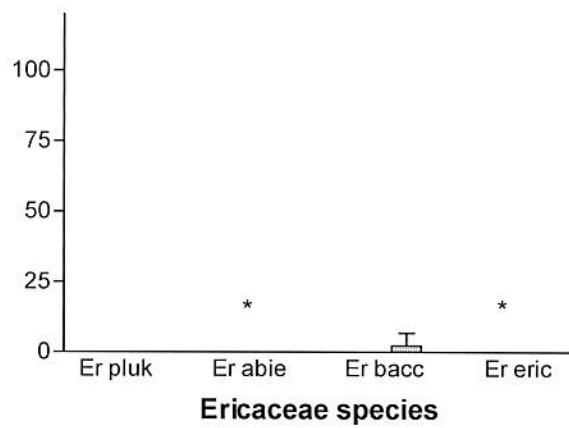
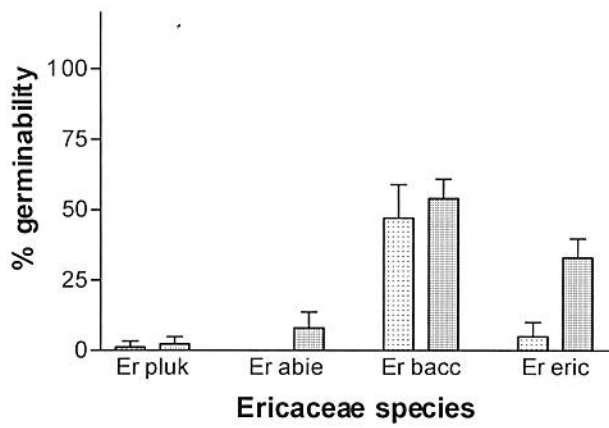


\* No viable seeds remain

Figure 2. Seed germinability expressed as a percentage of viable seeds (mean + SD, n = 3–5). Seeds were germinated under a 12 h photo-period for one week with autumn temperatures followed by seven weeks with winter temperatures (= no smoke primer) then for a further eight weeks placed in smoke seed primer (= smoke primer). See Table 1. for full species names.

**Before burial**

**After 3 years burial**



\* No viable seeds remain

Figure 2. Continued.

Seed germinability in the small-seeded Asteraceae was high before burial and only in *Metalasia* did the application of smoke seed primer increase it further ( $t = 10.43$ ,  $P = 0.0019$ ; Figure 2). After three years' burial, initial germinability in *Syncarpha vestita* and *Edmondia* was lower than preburial germinability, but was enhanced by smoke seed primer ( $t = 9.16$ ,  $P = 0.0008$ ;  $t = 14.5$ ,  $P = 0.0047$ , respectively). Of the remaining small-seeded species, *Erica baccans* and *Roella* germinated readily before burial, and in *Roella* germinability increased further following the application of smoke seed primer (*R. triflora*:  $t = 3.477$ ,  $P = 0.0401$ ; *R. ciliata*:  $t = 9.528$ ,  $P = 0.0025$ ). The *Roella* seeds did not persist for three years, but in *Erica baccans*, germinability was much lower following burial ( $t = 13.106$ ,  $P < 0.0001$ ).

Pre-burial germinability in the large-seeded *Diosma* was high and too few seeds persisted to test this species again following burial.

#### Correlates of seed persistence

No significant correlations were found between seed persistence (expressed as seed half-life) and total seed phenol content ( $r = 0.274$ ,  $P = 0.185$ ,  $n = 25$ ), phenol concentration ( $r = -0.134$ ,  $P = 0.524$ ,  $n = 25$ ) and seed coat thickness ( $r = 0.181$ ,  $P = 0.366$ ,  $n = 27$ ). There were strong positive correlations between total seed phenols and seed mass and coat thickness ( $r = 0.721$  and  $r = 0.624$  respectively,  $P < 0.001$ ,  $n = 25$ ), as well as between seed mass and coat thickness ( $r = 0.843$ ,  $P < 0.0001$ ,  $n = 27$ ).

There was a trend for a positive correlation between seed mass and persistence ( $r = 0.347$ ,  $n = 27$ ,  $P = 0.076$ ). However, there was no relationship between the variance in seed dimensions and persistence ( $r = -0.220$ ,  $P = 0.270$ ,  $n = 27$ ; Figure 3). Analyses of genera only (using one species from each genus) yielded very similar results.

## Discussion

#### Patterns of seed persistence

Several patterns of seed persistence in the soil are apparent from the range of fynbos species tested. The Fabaceae, *Pelargonium*, and the nut-fruited Proteaceae have long-term persistent seed banks. These species maintain high seed viability and dormancy levels and do not respond to smoke seed primer. Fol-

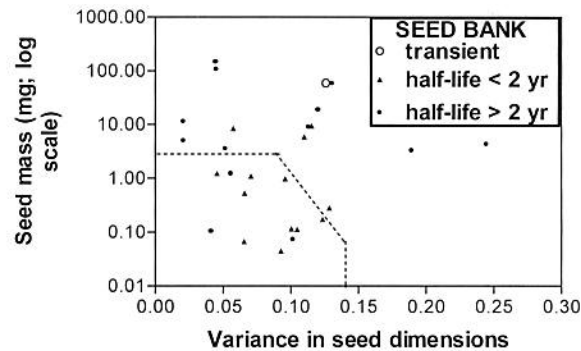


Figure 3. Seed mass and variance of seed dimensions for 26 species from the Cape Fynbos flora and one invasive alien *Acacia* species from Australia. The dashed line shows the threshold below which all species in the British flora had seeds that could persist in the soil for at least 5 years (Thompson et al. 1993).

lowing three years' burial, germinability decreases and viability increases. The permeable, non-dormant fraction of the seed cohort either germinates or rots soon after burial, resulting in the persisting portion being more hard-seeded or dormant. This pattern of seed bank decay, in which persisting seeds become more resistant to decay over time, is known for legume seeds (Ralphs and Cronin 1987; Holmes 1989).

Dormancy is likely maintained either by a water-impermeable layer in the seed coat or alternative physical barrier to water or oxygen uptake by the seed. Such traits permit the distribution of seeds in time as well as space since impermeable seeds potentially may remain viable for a long time. The Fabaceae and Geraniaceae are known to comprise many hard-seeded species (Rolston 1978). Seeds of *Pelargonium capitatum* are 98% impermeable (Meisert 2002). Water-impermeable dormancy usually is broken when a specialized area of the seed coat, such as the strophiole, hilum or lens, becomes permeable (Tran and Cavanagh 1984). This may occur following gradual scarification under natural conditions in the soil, ingestion by animals or in the case of fire-prone ecosystems, following exposure to the heat of a fire (Rolston 1978; Jeffery et al. 1988). It is probable that heat stimulation, in the form of a heat pulse, plays a prominent role in breaking water-impermeable dormancy in all the legume species tested (Jeffery et al. 1988; Cocks and Stock 1997). To what extent *Pelargonium* responds to heat shock is not known, but it is likely that either direct heat shock during fire, or high alternating diurnal temperatures post-fire, plays a role in breaking dormancy.

In the nut-fruited Proteaceae, the intact testa imposes dormancy on the embryo via oxygen exclusion (Brits et al. 1993). Desiccation-mediated scarification of the testal layers, which may occur during heat shock or through repeated exposure to high soil temperatures, ruptures the barrier and promotes germination (Brits et al. 1999). In the field *Leucospermum* shows greater seedling recruitment following fires of high intensity compared to those of low intensity (Bond et al. 1990).

The nut-fruited restios (*Cannomois* and *Willdenowia*) that were given a condensed seasons burial treatment by Newton (2000) also exhibited long-term persistence. Low germinability in these species appears to be a result of both morphological and chemical dormancy mechanisms. Seeds exhibited embryo maturation during a period of soil storage and the concomitant wetting/drying and high/low temperature cycles. Following this, exposure to smoke treatment promoted germination in *Cannomois* (but not in *Willdenowia*).

A second group with potentially long-term persistent seed banks includes four species: *Pseudopentameris*, *Passerina*, *Elegia* and *Restio*. Germinability either is low initially (*Restio*, *Elegia*) or secondary dormancy develops following burial (*Passerina*, *Pseudopentameris*). Germinability increases following exposure of seeds to smoke seed primer. Viable *Passerina* seeds were present under a monoculture of alien *Acacia* and inferred from post-fire vegetation age to be a minimum of 16 years old (Holmes 2002), and 97% of *Passerina* seeds survived 14 months' burial intact (Pierce and Cowling 1991).

A third pattern, of predominantly short-term persistence, was displayed by most of the very small-seeded (0.05–0.5 mg) species and *Syncarpha speciosissima*. Only two small-seeded species with low pre-burial germinability (*Erica plukenetii* and *E. abietina*) recorded a half-life exceeding two years. This group includes species with life-spans shorter than the average fire cycle (*Syncarpha*, *Roella*) that are predicted to have long-term persistent seed banks in order to recruit post-fire (Van Wilgen and Forsyth 1992). Seed bank decay was most pronounced during the wet winter months and losses were particularly high during the second winter following the twelve-month exhumation. It is suspected that the action of removing seeds from the soil to score persistence levels may have stimulated germination in some species via exposure to indirect light.

Most studies to date suggest that light is not a major germination cue in fynbos (Keeley and Bond 1997) or in Australian mediterranean-climate vegetation (Bell et al. 1995). However light is an important germination cue in other floras (Pons 1991), and small-seeded species have a greater dependence on light than larger-seeded species, suggesting the ecological role of gauging depth of burial that is critical for successful emergence from small seeds (Milberg et al. 2000). Light and light quality should be investigated as potential germination cues in small-seeded fynbos species, especially those of the Ericaceae, Campanulaceae and Asteraceae. Pierce and Moll (1994) found that alternating diurnal temperature and light both enhanced germination in *Metalasia*, but found no effect of light on five other species tested. Light was one of the multiple cues identified in stimulating germination in *Erica hebecalyx* (Van de Venter and Esterhuizen 1988). It is possible that some fynbos species shown not to respond to light in earlier studies may develop a light response following burial, as has been shown for weed seeds (Wesson and Wareing 1969). Should the fynbos species investigated here respond to light following burial, then their seed bank persistence is underestimated. For example, *Erica baccans*, *Metalasia muricata* and *Roella ciliata* seeds were present under monocultures of *Acacia* and inferred to be a minimum of six, 16 and 11 years old respectively (Holmes and Cowling 1997; Holmes 2002) and 63% of *Metalasia* seeds survived 14 months' burial intact (Pierce and Cowling 1991). It is recommended that in future seed burial trials, sufficient quantities of seed are collected to obviate the need for reburial after exhumation.

Initial germinability in *Edmondia* and *Syncarpha vestita* was lower following three-years' burial, but increased to pre-burial levels following exposure to smoke seed primer. This suggests that burial imposed secondary, physiological dormancy in these species. *Syncarpha vestita* and *S. speciosissima* are both known to respond to smoke (Brown 1993; Keeley and Bond 1997), but in this study the smoke seed primer increased germinability only following burial, as found for *Cannomois* (Newton 2000).

The resprouter graminoid, *Staberoha*, produces seeds that may form a short-term persistent seed bank, unlike the other resprouter graminoid, *Pseudopentameris*, which forms a long-term persistent seed bank. *Staberoha* is stimulated to germinate both by heat pulse and smoke (Musil and de Witt 1991; Brown 1993), but in this study had low germinability

following the application of smoke seed primer, suggesting that it requires a combination of germination cues. The long-lived obligate seeder species, *Diosma*, also forms a short-term persistent seed bank. The low dormancy level is the likely cause of rapid seed bank attrition in this species.

Of the two serotinous species tested, *Protea* has a transient seed bank with the majority of seeds losing viability within six months. By contrast, the weakly serotinous *Leucadendron* has a short-term persistent seed bank, with high viability in the small proportion of seeds that survived three years' burial. Davis (1992) earlier noted that seeds of *Leucadendron xanthoconus* could remain viable in the soil over two dry summer seasons. Whether this persistence ability confers any functional value for the long-term survival of *Leucadendron* populations would depend on whether seeds become incorporated into the soil following release from cones during the inter-fire period. Without burial, seeds are likely to succumb to post-dispersal predation (Pierce and Cowling 1991) and would be killed by fire if they remained on the soil surface.

#### *Correlates of seed persistence*

Although the number of South African Cape fynbos species tested was small, seed persistence is not correlated negatively to seed mass and the variance in seed dimensions, as was found for the British flora (Figure 3; Thompson et al. 1993, Bekker et al. 1998) and the temperate grasslands of Argentina (Funes et al. 1999). Species with an estimated seed half-life exceeding two years were considered equivalent to those with long-term persistence (surviving five years or more) in Thompson et al. (1993). Persistent soil seed banks are important in maintaining populations of many species in fire-prone communities, particularly the obligate seeders, and germination is cued either directly or indirectly by fire (Keeley and Bond 1997; Bell et al. 1993; Meney et al. 1994; Auld et al. 2000). In fire-prone communities selection for seed persistence, and germination cued by fire, can be expected to operate across all seed sizes and shapes.

Seed predation undoubtedly is a strong selective force preventing persistence of large seeds in South African fynbos (Pierce and Cowling 1991), as in most floras (Hulme 1994; Thompson et al. 2001). Burial confers some protection from seed predators (Hulme 1998), hence seeds that are more easily buried (small, compact seeds) tend to have higher persistence (Th-

ompson et al. 1993). However, in fynbos, processes other than passive burial operate to bury seeds, namely myrmecochory (Bond and Slingsby 1983; Christian 2001) and scatter-hoarding by rodents (Midgley 2002). At least 29 families and 78 genera in the Cape Floristic Region, including many of the larger-seeded species, are myrmecochorous (Bond and Slingsby 1983), conferring the potential for seed persistence. In Australia, where ants also are one of the major seed dispersal vectors (Berg 1975; Rice and Westoby 1981), a similar lack of correlation between seed size and shape and persistence in the soil was found (Leishman and Westoby 1998).

Moles et al. (2000) suggested that dormancy is important in determining whether seed persistence in a flora relates to seed size and shape. Thus species with small rounded seeds would have a high probability of forming persistent seed banks provided that the seeds did not germinate immediately, as such seeds are readily buried. However, in the fynbos flora some small-seeded species readily germinate prior to burial, as was found in the Australian study (Leishman and Westoby 1998), and unless secondary dormancy is imposed after burial, such seeds would not survive to form persistent seed banks. The germinability results indicate that in some (e.g., Asteraceae), but not all species, burial imposes secondary dormancy.

No positive correlation was found between seed phenol concentration and persistence as was found for the British flora. Hendry et al. (1994) found that *ortho*-dihydroxyphenol concentration was highly significantly correlated to seed persistence in the soil and concluded that phenolic chemicals operate by decreasing the rate of decomposition by microbes and defending against herbivory. Our results suggest that there is a taxonomic overlay to the distribution of phenolic compounds in fynbos seeds, as certain families (e.g., Ericaceae and Proteaceae) had consistently high phenol concentrations. Species with hard, water-impermeable seed coats that provide an effective barrier to decay recorded low phenol concentrations.

#### *Implications for persistence in plant populations*

Fire return intervals average about 15 years in mesic fynbos, but vegetation may burn from as early as four years' post-fire age (Van Wilgen et al. 1992). At the other extreme, it is rare to find stands of mesic fynbos exceeding 45 years' post-fire age (Van Wilgen et al. 1992). Species with long-term persistent seed

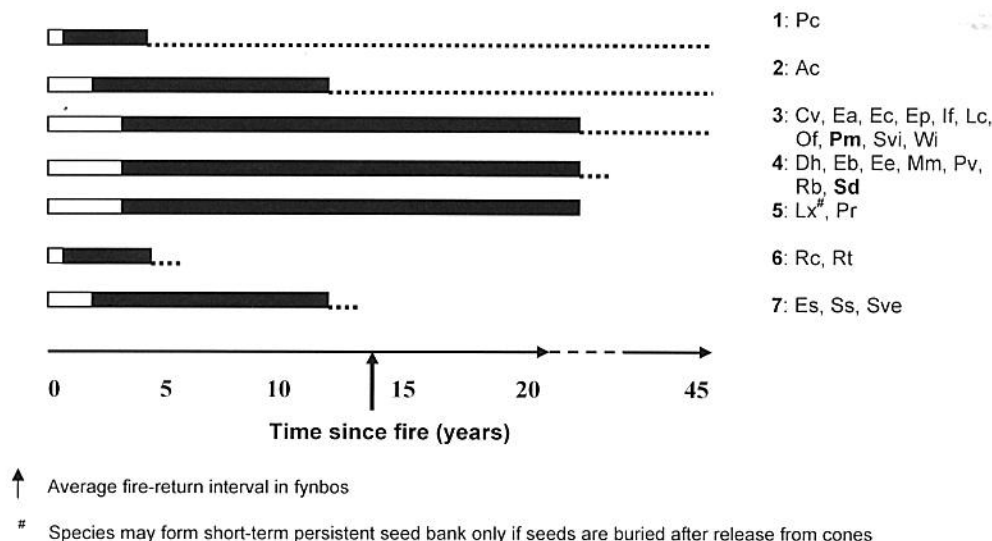


Figure 4. Seven patterns of persistence for indigenous fynbos species based on life-history attributes. Species are listed by genus and species initials (see Table 1 for full species names). Bars indicate presence of individuals, with filled bars indicating periods of seed production. Persistent soil seed banks are indicated by the dotted lines. Species in bold resprout after fire.

banks are unlikely to become locally extinct even following a relatively long fire-free interval. This includes species of all life spans (persistence patterns 1–3 illustrated in Figure 4).

Species with life spans exceeding the average fire-return interval and transient or short-term persistent seed banks would be at risk from local extinction only when the fire-free interval exceeds the life span. Should this occur, species with short-term persistent seed banks (pattern 4 in Figure 4) would have a better chance of persisting in the vegetation than those with transient seed banks (pattern 5). However, the observed patterns of short to medium life spans coupled with short-term persistent seed banks (patterns 6 and 7 in Figure 4) seem untenable in fynbos, as local extinction would arise following all but the shortest of fire-return intervals. Such a strategy would need to be combined either with long-distance dispersal, or inter-fire recruitment in gaps, for species to persist in the long-term. Most wind-dispersed seeds travel tens of metres rather than several kilometres and would not quickly recolonize after extensive fires. None of the study species have large wings or pappus to aid wind-dispersal, and only very tiny seeds (< 0.10 mg) have the potential for long-distance, unassisted dispersal as buoyant particles in the air (McCartney 1990). Three of the *Erica* study species have sufficiently small seeds for potential long-distance dispersal.

Some of the longer-lived obligate seeder species in this study had short-term persistent seed banks, and may rely on annual seed inputs to maintain their soil seed banks, as has been suggested by Musil (1991) and Pierce and Cowling (1991) for sand plain and dune fynbos species, respectively. Recruitment capability largely will depend upon seed production in the year before fire (Pierce and Cowling 1991). Such species are at a high risk of local extinction following a fire event when soil-stored seed reserves are low (Auld et al. 2000). It is possible that for some species, the constant decay rate model used to calculate seed half-life actually underestimates longevity (Auld et al. 2000), as a small proportion of the seed cohort remains dormant and viable for a longer time than predicted. A small proportion of long-lived seeds would buffer populations against local extinction.

While one of the resprouter species (*Staberoha*) had a seed half-life below two years, the others (*Acacia*, *Pseudopentameris*) had seed half-lives exceeding five years. In fynbos, resprouter species normally survive fires by resprouting and seedlings are relatively rare. Nevertheless, the production of persistent seeds gives the potential for population expansion and replacement of individuals following an unfavourable fire event. *Leucospermum conocarpodendron* resprouts only from undamaged epicormic buds, but is killed by high intensity fires (Bond et al. 1990). In this species, seed banks are critically important for

the maintenance of populations, and germination response is correlated to fire intensity (Bond et al. 1990). Although the alien *Acacia* is capable of re-sprouting after fire, where the fire cycle is longer than the plant's life-span, as in its native habitat (Christensen et al. 1981), recruitment is from seed.

Further studies are required to clarify the role of light in overcoming seed dormancy in small-seeded fynbos species, and the roles of long-distance dispersal and inter-fire recruitment in maintaining populations of shorter lived obligate seeder species with short-term persistent seed banks.

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