

Seed size and survival in the soil in arid Australia

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Abstract We investigated the relationship between seed size and seed survival in the soil in 67 species from arid Australia. There was a very weak, marginally significant positive relationship between the viability of fresh seeds and diaspore mass. However, by the time seeds had been buried in the soil for 1 year in nylon mesh bags, there was a highly significant positive relationship between diaspore mass and diaspore viability. Over the range of seed masses observed, a tenfold increase in diaspore mass was associated with a threefold increase in the odds of surviving 1 year of burial in the soil. Thus, large-seeded species were favoured over small-seeded species during this important selective process. However, the magnitude of this advantage was small compared with the advantage experienced by small-seeded species during seed production. We also investigated aspects of diaspore morphology in relation to viability retention during burial. We found no relationship between seed survival and the amount of protective tissue per unit diaspore surface area. Diaspore mass was a better predictor of survival than was diaspore surface area.

Key words: comparative ecology, seed defence, seed mass, Sturt National Park, viability.

INTRODUCTION

There are generally five to six orders of magnitude of variation in seed mass across the species found within a given flora (Leishman *et al.* 2000). This variation is important, because seed mass can affect the probability that an individual seed or seedling will survive many of the selective processes that occur during seed production and seedling establishment. Small-seeded species are at an advantage during seed production, as they can produce a far greater number of seeds for a given amount of energy than can large-seeded species (Jakobsson & Eriksson 2000; Henery & Westoby 2001). The smaller number of seeds produced by large-seeded species is thought to be compensated for mainly during seedling establishment. Seedlings from large-seeded species have been shown to be stronger competitors than seedlings from small-seeded species (Leishman 2001). Seedlings from large-seeded species have also been shown to be better at tolerating a wide range of environmental stresses, such as herbivory, nutrient deprivation, or prolonged periods in deep shade (reviewed in Leishman *et al.* 2000). Another selective process that might act differentially on seeds of different sizes is mortality during the time seeds spend buried in the soil.

Regeneration from seed stored in the soil seed bank is an important component of ecosystem dynamics, particularly in habitats subject to broad-scale disturbances, or habitats where long periods of time may elapse during which environmental conditions are

unfavourable for plant growth or survival. But not all plant species maintain a soil seed bank. Although the seeds of some species can persist for tens to hundreds or even thousands of years in the soil (Bakker *et al.* 1996; Murdoch & Ellis 2000), the seeds of other species are unable to persist for even moderate periods in the soil and must either germinate at the first available opportunity, or perish.

Theory suggests that seed size should be negatively related to persistence in the soil. Venable and Brown's (1988) model treats increasing seed size, ability to persist over long periods in the soil and seed dispersal ability as alternative ways to ameliorate the effects of environmental heterogeneity. Thus, plants can hedge their bets by dispersing numerous propagules in time, or in space, or can produce larger propagules that are able to establish under a wider range of environmental conditions. As these alternative strategies each have fitness costs to the plant (Venable & Brown 1988), the optimal level of any one of these traits is predicted to decrease with increases in any other.

Small seeds have been shown to have greater persistence in the soil than large seeds in several multi-species studies of the European flora (Thompson & Grime 1979; Thompson 1987; Thompson *et al.* 1993; Bekker *et al.* 1998; Hodkinson *et al.* 1998), across 71 species from a montane grassland in Argentina (Funes *et al.* 1999), across 311 species from north-west Iran (Thompson *et al.* 2001), across 24 wetland species (Leck 1989) and across 47 species from New Zealand forests (Moles *et al.* 2000). Large seeds were also under-represented in the seed bank relative to their density in the seed rain in the Mojave desert, California (Price & Joyner 1997). These studies

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have led to an international perception that small seeds persist for longer in the soil than large seeds (Thompson 2000). However, the few Australian studies performed so far have shown no relationship, or even a positive relationship between seed size and seed survival in the soil. For example, Lunt (1995) found no relationship between seed size and persistence in the soil for six species of forbs from grasslands in Victoria. An analysis of data for 101 species from a range of Australian habitats (from Leishman & Westoby 1998) showed that species with long-term (>5 year) persistence in the soil had significantly larger seeds than those species with transient seed banks ($P = 0.003$). Finally, Leishman and Westoby (1994) found no significant difference in the mean seed size of species with seed dormancy (not persistence *per se*) and those without dormancy across 83 species from semiarid woodlands in Australia.

In this study, we aimed to gather quantitative data regarding the relative vulnerability of seeds of different sizes to losses during storage in the soil. Quantifying this relationship will allow us to assess the importance of seed loss during seed storage in the soil as a selective filter in the establishment of plants. These data will also give us further information about the relative advantages of making large versus small seeds.

Another purpose of this study was to determine whether there is a relationship between seed size and the proportion of viable seeds produced by plant species. We had no particular reason to expect a relationship between these variables, but any deviation from a zero slope could make a potentially important modification to the relationship between the size of seeds made by a plant and the number of viable offspring produced.

We were also interested in investigating possible relationships between seed morphology and susceptibility to death during a period of burial in the soil. Once seeds are beneath the surface and have been incorporated into the soil profile, losses to vertebrate and invertebrate seed predators are likely to decrease (Hulme 1994, 1998; Maron & Simms 1997; Hulme & Borelli 1999), and the major sources of mortality are likely to be internal breakdown, fatal germination and fungal attack (Thompson 2000). Fungal attack has been shown to be a significant source of mortality for seeds. For instance, Zhong and Van der Kamp (1999) showed that there was a negative relationship between the abundance of fungal pathogens in the soil and seed viability in two species of conifer from British Columbia, and Blaney and Kotanen (2001) found that fungicide application significantly increased seed survival in wetland soil. There is also some evidence of a relationship between seed size and susceptibility to fungal attack. Crist and Friese (1993) showed that smaller-seeded species were more likely to succumb to microbial attack than were larger-seeded species in five

species from a shrub-steppe ecosystem in Wyoming. Two critical features of seed morphology with respect to fungal attack are: (i) the amount of protective tissue per unit surface area, which might influence the chances of fungal hyphae penetrating the defences of the diaspore and killing the embryo; and (ii) the diaspore surface area, which might influence the probability of encounter. This leads to two questions: (i) do seeds that are protected by relatively high amounts of protective tissue (such as seed coats and woody pericarps) experience less viability decline during a year of burial in the soil; and (ii) is diaspore surface area a better predictor of viability loss than diaspore mass?

In summary, the questions addressed in this paper are:

1. Is there a relationship between initial seed viability and diaspore mass?
2. Is there a relationship between diaspore mass and the proportion of seeds that are viable after 1 year of burial in the field?
3. Is there a relationship between diaspore mass and survival through a year of burial in the soil?
4. Is there a relationship between defensive tissue mass per area and seed survival?
5. Is diaspore surface area a better predictor of seed survival than diaspore mass?

METHODS

Study sites

This study was performed in Sturt National Park, north-west New South Wales, Australia. Sturt National Park receives an average of 230 mm rain per year (Australian Bureau of Meteorology station in Tiboo-burra) and is dominated by chenopod shrublands and grasslands. Seven sites were located within Sturt National Park, in order to maximize the number of species included in this study. The sites included a granite outcrop (Dead Horse Gully; 29°25'38''S, 141°59'36''E); granite covered plains (8-mile Creek; 29°20'08''S, 142°01'49''E and Gum Vale; 29°12'52''S, 141°53'49''E); the shores of Lake Pinaroo (29°05'21''S, 141°13'03''E); sand dunes near Fort Grey (a dune crest; 29°02'50''S, 141°11'38''E and a dune swale; 29°01'50''S; 141°11'27''E), and the Olive Downs plateau (29°03'40''S; 141°51'45''E).

Species selection

All species that were represented by at least five fruiting individuals, carrying a combined total of at least 150 ripe seeds at the time of fieldwork, were included in this

study. This resulted in initial viability data for 68 species, and survival data for 67 species from 14 families (Table 1). Diaspores rather than seeds were used as the unit of study, as it is the diaspore rather than the seed that is dispersed and incorporated into the soil.

Seed collection and burial

A minimum of 110 apparently viable (filled and undamaged) diaspores of each species was collected between 29 July and 4 August 2000. Forty-five of these diaspores were prepared for burial, and the remainder were taken back to the laboratory for weighing and viability testing.

Diaspores were buried at the site from which they were harvested, in groups of 15 in fine nylon mesh bags. The weave of the nylon fabric used (openings <0.3 mm square) was fine enough to prevent the escape of any of the enclosed diaspores, but still open enough to provide access to water and soil microbes. Three burial locations were haphazardly located within each field site. For each species, one bag containing 15 diaspores was buried at each of the three locations. At each of these locations, bags of diaspores were buried at 1–2-cm intervals along a 6–10-cm deep trench, within 2 days of collection.

Seeds were exhumed and their viability was assessed between 20 and 24 July 2001.

Diaspore mass and shape

Twenty diaspores of each species were oven-dried at 60°C for at least 3 days, allowed to cool in a desiccator and then weighed on a Cahn microbalance. Length, breadth and width were measured with Vernier callipers on 10 fresh diaspores of each species. We modelled the surface area of the diaspores using the formula for an elliptical prism (a pillbox shape). This information was combined with the mass of protective structures from Moles *et al.* (in press) to approximate defence per unit diaspore surface area for each species.

Viability testing

Viability was assessed using standard tetrazolium chloride staining techniques (Moore 1985). Where necessary, diaspores were dissected before staining such that the embryos were exposed to the tetrazolium solution. Diaspores were soaked in a 0.5% solution of tetrazolium chloride at room temperature for approximately 24 h before assessment. Seeds were considered to be viable if the entire embryo stained red (for more detail on assessment criteria see Moore 1985). A minimum of 45 seeds of each species were tested in

each year, and viability was assessed within 10 days of collection in 2000, and within 5 days of exhumation in 2001. When seeds were exhumed, we recorded the number of seeds that had decomposed entirely, the number that had germinated (radicle protruding), the number that appeared sound but did not stain with tetrazolium, and the number of viable seeds. As the first two categories cannot be separated (a seed can germinate and then decompose entirely), we have only performed analyses on viable versus non-viable seeds.

Statistics

We began by analysing the relationship between seed mass and the initial viability of seeds, and the relationship between seed mass and the viability of seeds that had been buried in the soil for 1 year. Because the viability data were binary (a given seed was either viable or not), we analysed these data with logistic regression, which appropriately uses a binomial data structure within each species. Because not all between-species variation in viability was expected to be due to seed mass or surface area, a term was needed in the model for viability to account for species-to-species variation. Therefore, we used a random effects logistic regression to estimate the relationship between viability and each of seed mass and surface area (McCulloch & Searle 2001). A separate model was fitted for each year, using winBUGS version 1.3 (MRC Biostatistics Unit, Cambridge University, 2002). This program uses the Monte Carlo Markov chain method (Gilks *et al.* 1996) for estimation. In fitting models, we used a burn-in of 1000 updates, followed by 50 000 updates.

Seed survival was not a binary variable (measurements were not made on the same seeds in consecutive years because tetrazolium testing is fatal). Therefore survival could not be analysed using logistic regression. Instead, we calculated survival for each species (proportion of seeds that were viable in 2001, divided by the proportion that were viable in 2000), then analysed the relationship between $\log_{10}(\text{seed mass})$ or $\log_{10}(\text{surface area})$ and survival using linear regression with survival plotted on a logit scale (a logit scale has increments of $\ln(p/1-p)$). In order to avoid computational problems with zero values, 0.5 was added to the number of viable and inviable seeds recorded for each species in each year. The resulting adjusted viability values were used in all statistical tests and figures in this paper, except the logistic regressions. We used ANOVA (Sokal & Rohlf 1995) to test for differences in logit-transformed seed survival between species of different growth forms and life history strategies. Neither strong skewedness nor outliers were observed in any of the above analyses, when viability was plotted on a logit scale and measures of seed size on the logarithmic scale.

Table 1. Table of raw data

Species	Diaspore mass (mg)	Viability 2000 (%)	Viability 2001 (%)	Life history	Growth form
<i>Abutilon otocarpum</i>	2.575	52	60	Perennial	Subshrub
<i>Astrebla pectinata</i>	12.67	72	62	Perennial	Grass
<i>Atriplex angulata</i>	0.607	86	5	Perennial	Subshrub
<i>Atriplex holocarpa</i>	1.305	100	3	Annual	Forb
<i>Atriplex lindleyi</i>	0.953	100	0	Annual	Subshrub
<i>Atriplex spongiosa</i>	0.55	79	8	Annual	Forb
<i>Atriplex vesicaria</i>	0.736	35	3	Perennial	Shrub
<i>Brachycome ciliaris</i>	0.14	72	0	Perennial	Forb
<i>Calotis erinacea</i>	1.63	50	41	Perennial	Forb
<i>Calotis hispida</i>	0.59	65	36	Annual	Forb
<i>Chenopodium desertorum</i> ssp. <i>anidiophyllum</i>	0.48	55	8	Perennial	Subshrub
<i>Chenopodium truncatum</i>	0.159	31	0	Annual	Forb
<i>Chrysocephalum apiculatum</i>	0.15	5	0	Perennial	Forb
<i>Cymbopogon obiectus</i>	4.475	67	70	Perennial	Grass
<i>Dactyloctenium radulans</i>	0.292	6	3	Annual	Grass
<i>Digitaria coenocola</i>	1.01	54	22	Perennial	Grass
<i>Dissocarpus biflorus</i> var. <i>cephalocarpus</i>	20.29	84	44	Perennial	Subshrub
<i>Dissocarpus paradoxus</i>	318.86	88	55	Short-lived perennial	Subshrub
<i>Einadia nutans</i>	0.665	94	58	Perennial	Subshrub
<i>Enchylaena tomentosa</i>	4.18	82	4	Perennial	Shrub
<i>Enneapogon avenaceus</i>	0.9	70	9	Annual occasionally perennial	Grass
<i>Enneapogon polyphyllus</i>	2.34	70	0	Annual or short-lived perennial	Grass
<i>Enteropogon</i> sp.	0.58	92	9	Grass	Grass
<i>Eragrostis eriopoda</i>	0.1	7	0	Perennial	Grass
<i>Eriachne aristidea</i>	1.4	86	0	Annual or short-lived perennial	Grass
<i>Glossogyne tannensis</i>	1.03	24	14	Perennial	Forb
<i>Glycine</i> sp.	8.62	45	0	Perennial	Twining forb
<i>Harmsiodoxa blennodioides</i>	0.74	71	0	Annual	Forb
<i>Harmsiodoxa brevipes</i> var. <i>brevipes</i>	0.046	27	0	Annual	Forb
<i>Lavatera plebeia</i>	5.01	91	25	Annual or perennial	Forb
<i>Leptorhynchos panaetiooides</i>	0.201	93	0	Perennial	Subshrub
<i>Lotus cruentus</i>	1.77	68	22	Annual or perennial	Forb
<i>Maireana pyramidata</i>	12.78	92	0	Perennial	Shrub
<i>Maireana triptera</i>	15.76	88	42	Perennial	Subshrub
<i>Matrastrum americanum</i>	1.58	29	36	Perennial	Forb
<i>Monachather paradoxo</i>	2.875	76	46	Perennial	Grass
<i>Myoporum montanum</i>	0.96	21	17	Perennial	Shrub
<i>Nicotiana velutina</i>	0.095	62	0	Annual	Forb
<i>Osteocarpum acropterum</i>	1.66	100	82	Perennial	Forb
<i>Panicum decompositum</i>	0.45	16	0	Perennial	Grass
<i>Paspalidium jubiflorum</i>	0.98	10	0	Perennial	Grass
<i>Portulaca oleracea</i>	0.43	88	46	Annual	Forb
<i>Ptilotus polystachus</i>	1.085	71	0	Perennial	Forb

Table 1. continued

Species	Diaspore mass (mg)	Viability 2000 (%)	Viability 2001 (%)	Life history	Growth form
<i>Salsola kali</i>	2.925	83	0	Annual or biennial	Subshrub
<i>Santalum lanceolatum</i>	46.53	73	44	Perennial	Shrub
<i>Scaevola spinescens</i>	6.12	58	20	Perennial	Shrub
<i>Sclerolaena bicornis</i> var. <i>bicornis</i>	0.519	72	57	Short-lived perennial	Shrub
<i>Sclerolaena bicornis</i> var. <i>horrida</i>	2.83	100	0	Short-lived perennial	Shrub
<i>Sclerolaena brachyptera</i>	1.25	67	37	Perennial	Forb
<i>Sclerolaena contexula</i>	4.7	44	19	Perennial	Subshrub
<i>Sclerolaena diacantha</i>	3.15	33	22	Perennial	Subshrub
<i>Sclerolaena glabra</i>	3.78	55	51	Perennial	Shrub
<i>Senecio gregorii</i>	4.185	75	5	Annual	Forb
<i>Senna artemisioides</i> nothosp. <i>coriacea</i>	20.66	40	0	Perennial	Shrub
<i>Senna artemisioides</i> ssp. <i>alicia</i>	14.92	20	0	Perennial	Shrub
<i>Sida amnophila</i>	1.96	35	24	Perennial	Forb
<i>Sida fibulifera</i>	1.1	13	10	Perennial	Forb
<i>Sida petrophila</i>	3.52	16	0	Perennial	Forb
<i>Solanum esuriale</i>	2.28	93	34	Perennial	Forb
<i>Solanum oligacanthum</i>	10.17	96	63	Perennial	Shrub
<i>Thyridolepis mitchelliana</i>	2.69	91	55	Perennial	Grass
<i>Trinaphus mollis</i>	0.252	77	0	Perennial	Grass
<i>Tetragonia tetragonoides</i>	118.88	76	86	Annual or biennial	Forb
<i>Vitadimia cuneata</i> var. <i>hirsuta</i>	1.54	70	5	Short-lived perennial	Forb
<i>Vitadimia eremaea</i>	1.44	96	0	Short-lived perennial	Forb
<i>Zygophyllum iodocarpum</i>	3.12	98	15	Annual	Forb
<i>Zygophyllum prismatoliteum</i>	1.13	70	9	Annual	Forb

Life history and growth form data taken from Cunningham *et al.* (1992) Species names follow Harden (1993)

A phylogenetic regression (Grafen 1989; Westoby 1999) was performed on the relationship between \log_{10} seed mass and logit-transformed seed survival, using a generalized linear interactive modelling program (Phylo.glm version 1.03; Grafen 1989). The phylogenetic tree used was the same as that used by Moles *et al.* (in press). Path segment lengths for the phylogenetic trees were calculated by assigning a height to each node that was one less than the number of species

below or at that node in the tree (Grafen 1989). Note that the model used for the phylogenetic regression did not include a term for species effect.

RESULTS

Diaspores of the species studied ranged from 0.05 mg (*Harmsiodoxa brevipes* var. *brevipes*; Brassicaceae) to 319 mg (*Dissocarpus paradoxus*; Chenopodiaceae; Table 1). Initial viability ranged from 5% (*Chrysocephalum apiculatum*; Asteraceae) to 100% (four species in Chenopodiaceae). The mean percentage viability of fresh seeds across all species was 63% (standard error = 3.5%). After the seeds had been buried for a year in the soil, mean viability had dropped to 20.7% (standard error = 3.0%), and maximum to 86% (*Tetragonia tetragonioides*; Chenopodiaceae).

One-third of the study species appeared to have lost all viability by the end of 1 year of burial, including four species recorded in Cunningham *et al.* (1992) as annuals, and three that are listed as annual or short-lived perennial. However, finding no viable seeds of a species after 1 year of burial does not necessarily mean that survival for this species is zero, rather that the proportion of viable seeds of these species remaining after 1 year was too low to be detected. In this study, the sample size for each species for each year was approximately 45. Thus, most species with levels of survival below about 2% will appear to have zero survival. In addition, the viability of the fresh seeds varied from 5 to 100% (Table 1), meaning that the expected number of viable diasporos buried was substantially lower than 45 in some cases. Thus, zero survival for a species is almost certainly an artefact resulting from low sample sizes. The sampling scheme was designed to give a broad sweep of species, rather than to give narrow confidence intervals on results from any one species. Note that the logistic regression

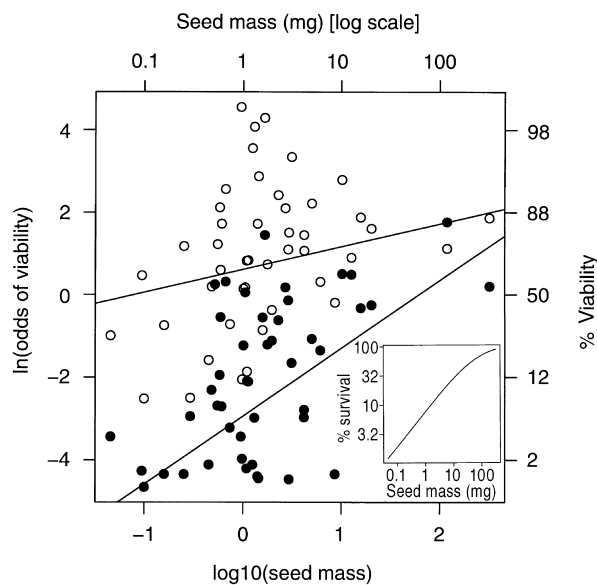


Fig. 1. Relationship between diaspore mass and viability for a wide range of species from Sturt National Park, New South Wales, Australia. (○), Mean mass and viability of freshly harvested diasporos for each of 68 species; (●), mean mass and viability of diasporos for each of 67 species after the seeds had spent 1 year buried in the soil in the national park. The regression lines were fitted using random effects logistic regressions (see Methods for details). The inset shows the relationship between seed mass and survival of one year of burial, plotted on a logarithmic scale.

Table 2. Viability retention rates in this study compared to previous studies

Ecosystem	No. species	Survival (%)	Duration of burial	Source
Arid Australia	67	31.7	1 year	The present study
Semiarid shrub-steppe, Wyoming	5	5.2	10 months	Crist and Friese (1993)
Neotropical secondary forest, Costa Rica	9	6	1 year	Guariguata (2000)
Rainforest, north-eastern Australia	16 (primary species)	2.1	1 year	Hopkins and Graham (1987)
Agricultural land, Virginia, USA	31 (pioneer or 2° species)	63.2		
Agricultural land, Virginia, USA	107	13	1 year	Duvel buried seed experiment: Toole (1946)
Agricultural land, Alaska	17 (weeds)	41.9	2.7 years	Conn and Deck (1995)
Afromontane forest, Ethiopia	8	66	1 year	Teketay and Granstrom (1997)

Viability retention is the percentage of seeds that were viable after burial divided by the percentage of seeds initially recorded as viable. All studies except the Duvel buried seed experiment buried seeds in nylon (or similar) mesh bags in natural ecosystems. In the Duvel study, seeds were buried in garden plots in porous flower pots.

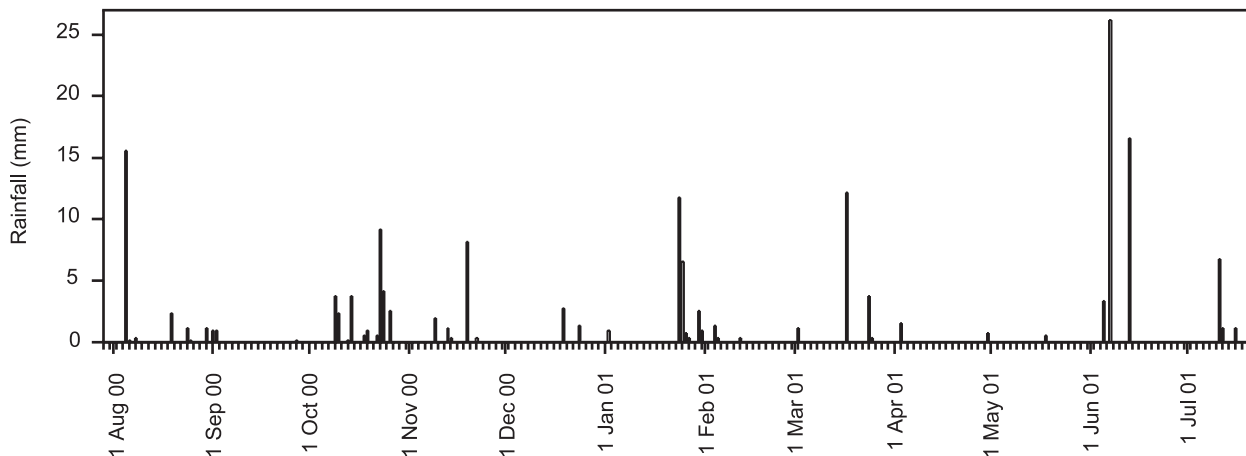


Fig. 2. Rainfall data from the Bureau of Meteorology rain station at Tibooburra during the time seeds were buried. These data are presented as an indication only, as rainfall in Tibooburra does not imply rainfall at all study sites, and microtopography can greatly affect the amount of water a given patch of ground receives.

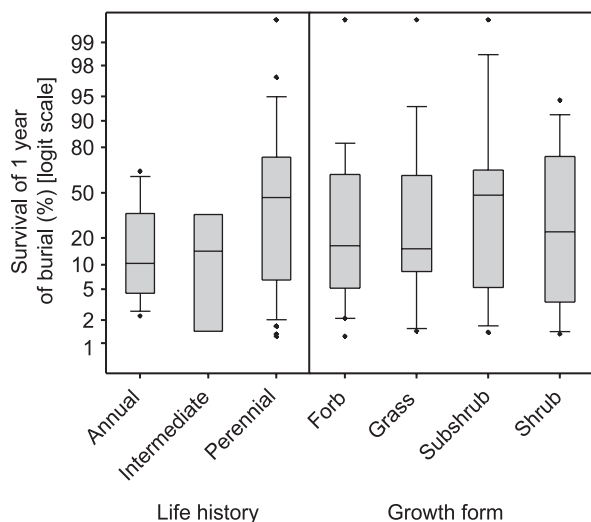


Fig. 3. Seed survival after 1 year of burial in the soil for species of different life history strategies and growth forms. Numbers in parentheses represent the number of species in each category. The boxes span from the 25th percentile to the 75th percentile. The line inside the box represents the sample median. Whiskers indicate the 10th and 90th percentiles. Outliers are shown as dots. Growth form for each species after Cunningham *et al.* (1992).

method used takes the sample size (and therefore variance) into account.

Four of the 67 species studied showed an apparent increase in viability during the year of burial. None of these increases was significant (at $P < 0.05$), and it seems most likely that they are attributable to our relatively low sample size. As values greater than or equal to 100% survival cannot be plotted on a logit scale, survival for these four species was set to 0.97 (halfway between 100% survival and the next highest seed survival of the remaining species).

There was a marginally significant positive relationship between diaspore mass and initial viability ($P = 0.048$, $n = 68$, slope = 0.55, 95% confidence interval (95% CI): 0.08–1.01; Fig. 1). However, after 1 year of burial there was a highly significant positive relationship between diaspore mass and viability ($P < 0.001$, $n = 67$, slope = 1.64, 95% CI: 1.00–2.32; Fig. 1). Thus after 1 year of burial in the soil, a tenfold increase in diaspore mass corresponded to a fivefold increase in the odds (proportion viable/proportion inviable) that a seed would be viable. The estimated standard error of the species random effect was 2.1 (95% CI: 1.7–2.6), which was substantial compared with the full range of expected values of $\log_e(\text{odds of viability after 1 year})$, which varied from -4.8 – 1.3 in Fig. 1. Thus much of the variation in viability across species was not explained by seed mass, as indicated by the scatter around each line in Fig. 1.

Seed survival through the year of burial was calculated using the logistic regression results (Fig. 1), dividing the fitted value for viability in 2001 for each seed mass by the fitted value for viability in 2000. The relationship between seed survival and seed mass found in this way is given as an inset to Fig. 1 (plotted on a logarithmic scale, since proportional differences are of biological importance). Over the range of seed masses observed, a tenfold increase in diaspore mass was associated with a threefold increase in the odds of survival. At the lower end of the range, a tenfold increase in diaspore mass was associated with an approximately 3.8-fold increase in survival rate. The magnitude of this change decreased with increasing seed mass (as seed survival approached 100%), to an approximately 1.2-fold increase in survival rate for a tenfold increase in diaspore mass at the upper end of the range of diaspore masses included in this study (Fig. 1, inset).

The relationship between diaspore mass and seed survival was significant (linear regression $P = 0.02$, $R^2 = 0.08$). The predicted survival for a species with seeds weighing 0.046 mg (the smallest observed in this study) was only 1.25% over a year, compared with approximately 87% for seeds weighing 319 mg (the largest observed in this study). Thus, the seeds of the largest-seeded species were almost 70 times more likely to retain viability than the seeds of the smallest-seeded species. However, this advantage was small relative to the almost 10 000-fold (over this range of seed mass) advantage of the small-seeded species at seed production, which would result from the inversely proportional relationship between seed mass and the number of seeds made per unit effort allocated to reproduction (Henery & Westoby 2001).

The phylogenetic regression also showed a significant positive relationship between logit-transformed probability of surviving a year of burial and diaspore mass ($P = 0.014$, d.f. = 1,37, $R^2 = 0.15$). The fact that the results of the phylogenetic regression were similar to the results of the cross-species regression suggests that this relationship exists at many taxonomic levels, and eliminates the possibility that the cross-species relationship was underlain by just one or two deep divergences.

Seed morphology and seed survival

There was no relationship between the amount of protective tissue per unit diaspore surface area (mg mm^{-2}) and survival through 1 year of burial in the soil ($P = 0.17$, $n = 37$). There was also no relationship between the amount of protective tissue per unit diaspore surface area and diaspore mass ($P = 0.417$, $n = 38$).

As expected, there was a strong relationship between diaspore surface area and diaspore mass ($n = 46$, $P < 0.001$, slope = 0.68). However, diaspore surface area was not correlated with seed survival ($n = 45$, $R^2 = 0.02$, $P = 0.35$), and diaspore mass remained significantly correlated with seed survival when diaspore area was controlled for ($n = 45$, $P = 0.012$), whereas the reverse was not true ($P = 0.65$). Thus, diaspore mass was a far better predictor of seed survival than was diaspore surface area, and knowing the surface area of diaspores did not significantly increase our ability to predict seed survival.

DISCUSSION

Magnitude of seed losses during burial

In this study we found that less than one-third of the initially viable seed crop was still viable after 1 year in

the soil. We were somewhat surprised by the magnitude of this decline, as rainfall in arid Australia is notoriously unpredictable (Stafford-Smith & Morton 1990), and periods of over a year without sufficient rain for germination are likely to occur relatively frequently in this area. A compilation of data from similar studies in other ecosystems (Table 2) showed that the rate of seed survival observed in the Sturt National Park was well within the range of previously observed values. However, higher rates of seed survival might be expected in arid zones than in many other vegetation types, as species must be able to survive the long periods during which conditions are unsuitable for germination.

It is possible that large rainfalls throughout the study year might have triggered unusually large numbers of seeds to germinate, thus reducing the proportion of viable seeds remaining in the soil. Two lines of evidence suggest that this is not the case. First, only 170.6 mm of rain fell during the year the seeds were buried compared with an average annual rainfall of 229.3 mm (Fig. 2), although some batches of seeds might have received considerably more water than others because of patchiness in rainfall and local water redistribution. Second, the highest rate of germination observed was 56% (*Atriplex vesicaria*, Chenopodiaceae), and across all species only 3.4% of the seeds showed signs of having attempted germination. However, the proportion of seeds that were observed to germinate must be interpreted as a minimum value, as some germinated seeds might have rotted away entirely during the burial period, and have become indistinguishable from ungerminated rotten seeds. Thus, it is still possible that some seeds died because they attempted to germinate in response to rainfall events during the year rather than because they lacked the ability to persist for a year in the soil.

Relationship between seed size and seed survival in the soil

A tenfold increase in seed size was associated with an approximately threefold increase in the odds of viability (a maximum of a 3.8-fold increase in survival rate per tenfold increase in diaspore mass over the range of diaspores included in this study). By comparison, the slope of the relationship between seed mass and the number of seeds produced per unit canopy area is approximately -1 (Henery & Westoby 2001). Thus, while mortality during the time seeds spend buried in soil is higher for smaller-seeded species, the magnitude of the advantage of the large-seeded species during this selective phase is small compared with the advantage of the small-seeded species during seed production. In the long term, both large- and small-seeded strategies must be successful, or a range of seed sizes could not exist in nature. Thus, although the advantage of the small-seeded species is somewhat reduced by selection during

seed storage in the soil, further processes in which large-seeded species are favoured are necessary to make up the remainder of the variation in reproductive success among seeds of different sizes. It is generally thought that this difference is made up during the seedling establishment phase (Leishman *et al.* 2000), but the magnitude of the selective advantage of large-seeded species during seedling establishment in natural conditions has not yet been quantified.

Why is there a relationship between seed size and seed survival in the soil?

Venable and Brown (1988) predicted a negative relationship between seed size and seed survival in the soil, on the basis that large seed size and persistence in the soil act as alternative strategies in unpredictable environments. Under this hypothesis, the ability of large seeds to establish in a wider range of environmental conditions than small seeds (as yet unproven) decreases spatial and temporal variation in reproductive success. However, we suggest that the hypothesized advantages of large seeds at establishment phase are likely to be balanced by the reduced number and variety of patches encountered by large-seeded species as a result of the smaller number of propagules produced for a given amount of reproductive effort (Smith & Fretwell 1974; Henery & Westoby 2001). Thus, seed mass might trade-off mainly with dispersal through space, and not detectably with dispersal through time.

It is possible that the positive relationship between seed size and survival in the soil observed in the present study might be a secondary correlation caused by an association between survival capacity and other traits. Growth form and life history are known to vary with seed mass, and might co-vary with seed persistence (reviewed in Leishman *et al.* 2000). However, we found no significant difference in decline in seed viability over 1 year of burial between species with different life histories (one-way ANOVA, d.f. = 2, 69, $F = 1.91$, $P = 0.16$), or species of different growth forms (one-way ANOVA, d.f. = 3, 64, $F = 0.20$, $P = 0.89$; Fig. 3). Of course, it is still possible that correlations between seed mass and seed survival in soil result from a secondary correlation between seed mass and some other trait not measured in this study.

It has been suggested that size-selective seed predation on buried seeds might be a major force in preventing large seeds from persisting in the soil in Europe (Thompson *et al.* 1993, 2001).

Could an unusual predation regime underlie this unusual result?

The positive relationship between seed size and seed survival in the soil in this study was opposite to that

previously found elsewhere in the world (see Introduction). However, the few studies performed to date in semiarid Australia have shown no relationship, or similar positive relationships between seed size and seed survival in the soil (reviewed in the Introduction). One possibility is that differences in seed survival among habitats might be underlain by differences in size-selective predation on buried seeds. Australian desert mammals differ from mammals in many other ecosystems in that they tend not to dig for buried seeds of any size, even when the depth of burial is relatively trivial (Murray & Dickman 1994; C. Dickman, pers. comm.). In addition, there is some evidence that large seeds in Europe have higher seed predation rates after burial than small seeds (Hulme & Borelli 1999). Thus, this potentially important size-selective force acting on buried seeds in Europe does not act in arid Australia. However, there are few data available regarding the strength of differential seed predation on buried seeds in Europe, and no data available for Australia. Further work will be required to determine the importance of differential seed predation on buried seeds as a selective pressure in seed ecology.

It is possible that Australian desert mammals are unable to detect the presence of buried seeds dry soils, and thus do not dig them up (Thompson *et al.* 2001). Rodents are many times more effective at locating buried seeds if the seeds are hydrated than if the seeds are dry (Simon & Raja Harun 1972; Johnson & Jorgensen 1981; Duke *et al.* 1983; Vander Wall 1993, 1995, 1998, 2000). However, rodents have often been reported to exhume buried seeds in arid ecosystems (Reichman & Oberstein 1977; Brown *et al.* 1979; Reichman 1979; Abramsky 1983). Thus, further work on the foraging efficiency of Australian desert mammals on imbibed versus dry seeds would be necessary to determine whether low levels of predation on buried seeds, resulting from aridity, might underlie the seed survival pattern observed in the present study.

Seed defences and viability decline

Previous work with the species from Sturt National Park has shown that plant species, on average, allocate approximately equal amounts of dry mass to physical seed defences (protective tissues such as seed coats and woody exocarps) and seed reserves (endosperm and embryo; Moles *et al.* in press). That is, plants could make, on average, twice as many seeds as they do at present if they did not allocate dry mass to defensive structures. This investment in protective tissue mass might advantage the plant species by reducing losses to postdispersal seed predators and losses to seed pathogens during seed storage in the soil. However, we do not necessarily expect a correlation between seed defensive tissue mass and losses to seed predators or pathogens. This is because species whose ancestors

experienced high levels of predation would have been selected to increase their allocation to protection, resulting in a positive correlation between protection and predation. Thus, there is a negative feedback loop: protection decreases predation in ecological time, but predation increases protection in evolutionary time, and the net consequence is that no particular correlation between the two is expected. This is what we have observed for postdispersal seed removal (Moles *et al.* in press), and for seed survival in the soil (the present study). Note that chemical defences might also affect seed survival in soil.

Summary

We found only a very weak, marginally significant positive relationship between seed size and initial viability. However, there was a highly significant positive relationship between diaspore mass and the proportion of seeds that were viable after 1 year of burial in the soil. Thus, differential survival during the time seeds spend buried in the soil in this study favoured large-seeded species over small-seeded species. However, the amount of variation explained by this relationship was low, and the magnitude of the advantage of large-seeded species during this selective process contributes only a small amount to negating the initial advantage of the smaller-seeded species resulting from their higher levels of fecundity.

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