Evolutionary Ecology Research, 2007, **9**: 325–340

Seed mass, shape, and persistence in the soil seed bank of Israeli coastal sand dune flora

Shunli Yu,[1,2]* Marcelo Sternberg,[3] Pua Kutiel[4] and Hongwei Chen[5]

[1]*Laboratory of Quantitative Vegetation Ecology, Institute of Botany, The Chinese Academy of Sciences, Beijing, People's Republic of China,* [2]*Department of Geography, Bar-Ilan University, Ramat Gan, Israel,* [3]*Department of Plant Sciences, Wise Faculty of Life Sciences, Tel Aviv University, Tel Aviv, Israel,* [4]*Department of Geography and Environmental Development, Ben-Gurion University of the Negev, Be'er Sheva, Israel and* [5]*The Forsetry Academy of Yunnan Province, Kunming, People's Republic of China*

ABSTRACT

Question: Are seed mass and shape related to persistence in the soil seed bank among 54 species of the Israeli flora?

Search method: Persistence was determined by soil seed bank investigations in which the fraction of non-germinated viable seeds was regarded as the persistent soil seed bank. When seedling emergence had ceased but before new seeds were shed, all soil from the upper 5 cm of 120 quadrats was removed to the laboratory. At that time, the seeds sampled were those from previous seed rains.

Data description: Plant species with persistent and transient seeds were widely scattered across the range of seed mass or dimension and variances. A significant relationship was found between seed mass (or dimension) and seed persistence with persistent seeds tending to have larger mass. However, no significant relationship was found between seed shape and seed persistence. Species with persistent seeds had significantly higher seed mass than those with transient seeds (one-tailed t-test = 1.68, $n = 48$, $P = 0.007$), but there was no significant difference in shape between them (one-tailed t-test = 1.68, $n = 48$, $P = 0.076$; t-test = 1.68, $n = 45$, $P = 0.124$). Species with persistent seeds yielded significantly higher seed dimensions than those with transient seeds (one-tailed t-test = 1.95, $n = 48$, $P = 0.029$). In this study, there was no threshold in seed mass (or dimension) and shape that distinguished transient from persistent seeds.

Conclusions: Species with persistent seeds have significantly larger seeds than species with transient seeds. However, species with small and/or round persistent seeds were relatively common. The underlying mechanism proposed for the observed pattern is a high proportion of large-seeded, persistent species with hard seed coat dormancy and abundant litter on the surface of the soil. Data from all eight floras studied to date suggest that significant differences in climate may determine diverse patterns in the relationships between seed mass and shape and persistence. Small and compact seeds are likely to occur in soil seed banks in humid climates,

* Author to whom all correspondence should be addressed. e-mail: shunliyu@ibcas.ac.cn

whereas large-seeded species with persistent seed banks are more likely to be abundant in arid climates. In addition, the importance of the spatial scale of investigations (or the range of habitats) is emphasized for studying the relationships between seed mass and shape and persistence.

Keywords: Israeli coastal sand dune flora, persistence, seed mass, seed shape.

INTRODUCTION

Seeds that persist in the soil seed bank for more than one year are considered to exhibit a bet-hedging adaptation to environmental uncertainty (Venable and Brown, 1988; Philippi, 1993; Pake and Venables, 1996). Based on seed longevity in soil and litter, soil seed banks are divided into transient and persistent types (Thompson and Grime, 1979). A soil seed bank is considered to be persistent when the dispersed seeds remain viable for more than one year.

As a property of a species, persistence refers to the ability of that species to survive in the soil seed bank. Seed persistence has been demonstrated in many floras/ecosystems around the world, including the desert in Arizona, USA (Philippi, 1993), the northwest European flora (Thompson *et al.*, 1993), Mediterranean old-fields in France (Lavorel *et al.*, 1993), and Argentina montane grasslands (Funes *et al.*, 1999). Persistence has received much attention in the literature. The relationships between seed mass, shape, and persistence have become a favourite topic and the source of much controversy recently. Previous studies have reported three different patterns to these relationships.

1. For seed mass and shape to predict persistence, it was proposed that small and compact seeds are related to ease of burial (Thompson *et al.*, 1993; Bakker *et al.*, 1996; Bekker *et al.*, 1998), since small and compact seeds can easily penetrate cracks in the soil or are washed in by rainwater and thus escape post-dispersal predation. Thompson *et al.* (1999) also considered persistence to be affected by other ecological factors, including germination requirements, dormancy mechanisms, and resistance to pathogens. This pattern is strengthened by results for other floras, including those of the Argentine grasslands (Funes *et al.*, 1999) and the Italian flora (Cerabolini *et al.*, 2003).
2. A study of the Iranian flora found that seed mass was related to persistence in the soil, but seed shape was not (Thompson *et al.*, 2001). Similar results were demonstrated for other ecosystems, including the Mediterranean grasslands in central Spain (Peco *et al.*, 2003) and lowland forest in New Zealand (Moles *et al.*, 2000). The reason why seed shape was not related to persistence in the Iranian flora was that predation prevents persistence of large seeds. However, the reason why the same pattern occurs in Spain is probably that small seeds are buried more easily and are therefore much less subject to predation. Absolute seed dimension is important in avoiding burial, but an elongated or flat shape may be less of an impediment to burial in small seeds than in large seeds (Peco *et al.*, 2003). In New Zealand, burial mechanisms and low rates of seed predation could explain the relationships between seed mass, shape, and persistence.
3. In Australia, Leishman and Westoby (1998) found no apparent relationships between seed mass, shape, and persistence. Because fire is the major form of disturbance in Australian habitats, hard-seeded species tend to form a persistent soil seed bank. The Australian

flora includes a high proportion of large-seeded, persistent species with hard seed coat dormancy. The lack of signicant relationships between seed attributes and persistence may be due to Australian plant species' attributes and the structure of plant flora and fauna communities (Moles *et al.*, 2000).

The above studies indicate that different communities or habitats in different regions may contain species with different life histories and different seed attributes, and thus a rule for relationships between seed mass, shape, and persistence may not be univerally applicable. Mechanisms to explain the various patterns are themselves diverse and complex in different ecosystems around the world. Therefore, the relationships between seed mass, shape, and persistence should be examined in many more floras and the mechanisms behind the patterns should be explored further.

Studies of the Italian flora, from an ecosystem situated in the northern Mediterranean area, suggested that not only seed mass, but also seed shape, was key in determining seed fate and seed persistence in soil (Cerabolini *et al.*, 2003). However, seed shape was not related to persistence in the flora of Spain, which belongs to the same area (in the western Mediterranean area) (Peco *et al.*, 2003). These puzzling differences in the two ecosystems, which are not far from each other in the same region, indicate that investigation of further Mediterranean ecosystems or communities is required to test relationships between seed mass, shape, and persistence in the soil.

Plant species in Israel, situated in the eastern Mediterranean area, could provide another useful case study for examining these relationships. At present, for example, it is unclear which relationship rule applies to the eastern Mediterranean coastal sand dune communities in Israel, which are dominated by shrubs such as *Retama raetam* and annuals. In this study, we assess whether seed mass and shape are related to persistence in the soil seed bank among 54 species of the Israeli flora. The mechanisms affecting its seed bank patterns are also discussed.

MATERIALS AND METHODS

Study site

The study was conducted between October 2000 and June 2001 at the Poleg Nature Reserve, located in the middle of Israel (34°45′N, 30°32′E, altitude 5–15 m), 10 km from Tel Aviv. The study area has a typical Mediterranean climate with a long and significant drought from April to August. Estimated mean rainfall is 500 mm with high inter-annual fluctuations. Precipitation occurs mainly from late autumn throughout the winter, with the timing and amount of rain in rainfall events being highly unpredictable. Mean maximum temperatures can reach 37°C in July, while mean minimum temperatures can reach 5°C in January. Wind has an important impact on the dynamics of vegetation in this sandy area. The soil is sandy regosol with an A–C soil profile (Dan *et al.*, 1970). For the duration of our study at the Poleg Nature Reserve, total rainfall was about 380 mm.

The vegetation at the coastal sand dunes is dominanted by shrubs (such as *Retama raetam*), annual herbaceous plants, and perennial herbs. A semi-stabilized sand dune, on which the vegetation is characterized by a heterogeneous matrix of shrubs and open patches dominated by herbs, was used for field sampling. The nature reserve had been open to the public for a long period, and a vast number of trails had been formed by pedestrians and vehicles, where the sand surface had become semi-mobile or mobile. For the purposes of restoration, the reserve had been closed to the public a year before the experiment was conducted.

Estimation of transient soil seed banks

Because microhabitats affect the distribution of the soil seed bank, seedling emergence was monitored within each microhabitat type using forty 25×25 cm^2 quadrats, randomly distributed and secured in place with a steel peg in each corner of the quadrat. Seedling emergence was monitored on the 10th day after important rainfall events from early November 2000 until late April 2001. Emerging seedlings in each quadrat were identified, counted, and removed at each sampling event. The number of seedlings emerging from seeds in the field was used as an estimate of the transient soil seed bank. Seedling emergence varies between these microhabitats, which is the topic of another forthcoming article.

Acquirement of persistent soil seed banks and the determination of persistence

The fraction of non-germinated viable seeds was regarded as the persistent soil seed bank and persistence was determined by the soil seed bank investigations. When seedling emergence had ceased but before new seeds were shed, and in the same locations used for seedling emergence, all litter and soil from the upper 5 cm of 120 quadrats was removed to the laboratory. Thus, seeds from previous vegetation periods were sampled. According to Simpson's (1989) concept for soil seed banks, all viable seeds present on or in the soil or associated litter constitute the soil seed bank. Therefore, plant litter samples were also included in the samples. All soil samples were sieved through 5-mm, 1-mm, 0.5-mm, and 0.3-mm sieves and visible seeds removed. All litter was sieved and seeds were extracted from the retained organic material, sand, and small stones. To ensure that all (most) seeds were recovered, the soil (sand) samples were floated in water. Visible seeds were dissected under a binocular microscope and those with juicy, oily or fleshy embryos were regarded as viable. This technique was deemed better than tetrazolium chloride testing for viability because of the difficulty manipulating the smallest seeds (Pake and Venables, 1996). Broken seeds, decayed seeds, and seeds with damaged embryos were considered to be non-viable and discarded. The viable seeds detected in the soil and litter were considered to belong to the persistent soil seed bank. In this study, species with a persistent soil seed bank were found to have at least three viable seeds in the soil. In addition, the persistent seed bank varied between microhabitats (again this is the topic of another forthcoming article).

Seed mass, dimensions, and shape

For identifying seeds and for measuring seed dimensions and mass, seeds of each species were collected from plants in the field. Data on seed mass and seed dimensions were collected for 54 species of the Israel flora, from 50 genera and 20 families, which occur within the range of the three microhabitats.

For each plant species, seed mass was the average of 10 seeds. More seeds were used for species with lower seed mass (e.g. for some species, in lots of 100 seeds). Seed mass was measured to microgram precison on a PB303 balance (Mettler Toledo). Seed length, width, and height were measured (to microgram precison using Vernier calipers) on 10 seeds per species. The sum of seed length, width, and height was used to denote seed dimension. Seed dimension variance was then calculated following the methods of Thompson *et al.* (1993) to give a measure of seed shape from a sample of 10 seeds. The longest seed dimension (length) was transformed to 1 and the other two dimensions were expressed as proportions of that dimension. The variance, named variance_1, was calculated as follows:

$$\text{variance}_1 = \{[(1 - \text{width/length})^2 + (1 - \text{height/length})^2 + (1 - \text{height/width})^2]/3\}^{1/2}$$

The values of variance_1 are shown in Table 1. Another value, variance_2 (see Table 1), was calculated as follows:

$$\text{variance}_2 = [\text{relative length} - \text{minimum(relative width or relative height)}]/3$$

Variance_2 was thought to characterize seed shape better than variance_1. This ensured that the variance of the three dimensions depended only on their relative sizes and not on their absolute sizes. This gave a value for seed shape such that spherical seeds had a variance of 0 and elongated or flattened seeds had variances of up to 0.33. In this article, 'seeds' refers both to seeds and to fruits with not easily detached structures. For example, grass caryopses and the achenes of Asteraceae without the pappus were measured as seeds.

The litter in the community

Plant litter samples were collected from the soil surface, in areas adjacent to the seedling monitoring plots. The litter in four quadrats (25 × 25 cm per quadrat) was collected in each microhabitat type in four patches, giving a total of 16 samples per microhabitat. Plant litter was dried in the open air and weighed to the nearest 0.01 g.

Statistical analyses

Differences in seed mass and shape between transient and persistent species were evaluated using a *t*-test after seed mass was log transformed to achieve the normality assumption. We also used *t*-tests to analyse the differences in seed dimension between transient and persistent species. The relationship between seed mass and seed dimension was analysed using relative analysis. The SPSS software package (Version 10.0, SPSS Inc., Chicago, IL, USA) was used for all statistical analyses.

RESULTS

Seed mass, seed dimensions, seed dimensions variance, and persistence

In this data set, 23 species (including 11 species of legumes) were classified as having strictly transient seeds, and 2 were classified as having strictly persistent seeds (Table 1). The seeds of 25 species displayed features of both transient and persistent seeds. The seed banks of the other 8 species could not be determined owing to insufficient information. The percentage of persistent seeds of annual plants (74.9%) in soil seed banks was much greater than that of herbs (25.1%). The percentage of species with persistent banks was relatively low (54%) compared with other studies on dry Mediterrannean grasslands and scrublands (Peco *et al.*, 2003).

Table 1. Seed dimension, mass, and variance of disapore dimensions for all species used in this study

Species	Family	Life form	$Variance_1$	$Variance_2$	Seed mass (mg)	Seed dimension (mm)	Seed found in litter (+)
Species with persistent and transient seeds							
Anagallis arvensis	Primulaceae	Annual	0.016	0.084	0.51	0.99	–
Anthemis leucanthemifolia var. *leucanthemifolia*	Asteraceae	Annual	0.152	0.259	0.235	1.04	–
Asparagus stipularis	Liliaceae	Perennial herb	0.019	0.089	18.98	3.05	+
Centaurea speciosa	Asteraceae	Sub-shrub	0.161	0.242	3.21	1.90	–
Crepis aculeata	Asteraceae	Annual	0.182	0.316	0.39	2.28	–
Hippocrepis unisiliquosa	Fabaceae	Annual	0.184	0.258	2.54	2.10	+
Hymenocarpos circinnatus	Fabaceae	Annual	0.114	0.224	3.68	1.97	–
Lappula spinocarpos	Boraginaceae	Annual	0.062	0.154	0.85	2.83	–
Lathyrus marmoratus	Fabaceae	Annual	0.057	0.054	55.4	4.29	–
Lotus halophilus var. *halophilus*	Fabaceae	Annual	0.002	0.030	0.33	0.86	–
Medicago constricta	Fabaceae	Annual	0.133	0.241	2.2	1.78	+
Ononis viscosa	Fabaceae	Annual	0.017	0.087	3.54	1.87	–
Paronychia argentea	Caryophyllaceae	Sub-shrub	0.038	0.123	0.84	1.23	–
Plantago albicans	Plantaginaceae	Perennial herb	0.133	0.279	0.65	1.36	–
Polycarpon succulentum	Caryophyllaceae	Annual	0.014	0.078	0.35	1.02	–
Pseudorlay pumila	Umbelliferae	Annual	0.216	0.112	4.39	2.97	–
Retama raetam	Fabaceae	Shrub	0.031	0.109	94.56	4.75	+
Rumex bucephalophorus	Polygonaceae	Annual	0.101	0.189	0.34	1.37	–
Senecio vernalis	Asteraceae	Annual	0.244	0.292	0.175	2.01	–
Silene colorata	Caryophyllaceae	Annual	0.024	0.102	0.15	0.68	–
Trifolium campestre	Fabaceae	Annual	0.065	0.165	0.28	0.85	–
Trifolium palaestinum	Fabaceae	Annual	0.029	0.111	2.56	1.70	+
Trigonella cylindracea	Fabaceae	Annual	0.143	0.219	1.77	1.65	+
Tulipa agenensis	Liliaceae	Perennial herb	0.258	0.318	1.55	3.34	–
Vicia tetrasperma	Fabaceae	Annual	0.002	0.030	18.55	3.03	–

Species with persistent seeds only							
Chrysanthemum coronarium	Asteraceae	Annual	0.188	0.267	2.088	2.40	+
Osyris alba	Santalaceae	Sub-shrub	0.000	0.006	147.37	7.40	–
Species with transient seeds only							
Ainsworthia trachycarpa	Umbelliferae	Annual	0.172	0.277	0.892	1.46	–
Allium curtum subsp. *curtum*	Liliaceae	Perennial herb	0.058	0.158	0.58	1.22	–
Ammochloa palaestina	Gramineae	Annual	0.098	0.209	0.80	1.26	–
Avena barbata	Gramineae	Annual	0.017	0.291	9.12	2.20	–
Arenaria leptocladus	Caryophyllaceae	Annual	0.005	0.044	0.04	0.43	–
Bromus rigidus	Gramineae	Annual	0.283	0.308	7.29	5.19	–
Coronilla scorpioides	Fabaceae	Annual	0.200	0.279	0.76	1.27	–
Cutandia philistaea	Gramineae	Annual	0.217	0.282	0.25	1.32	–
Cyperus conglomeratus	Cyperaceae	Perennial herb	0.115	0.220	1.98	1.94	–
Erodium alnifolium	Geraniaceae	Annual	0.173	0.261	2.44	2.45	–
Euphorbia peplus	Euphorbiaceae	Annual	0.064	0.147	0.18	0.96	–
Fumaria judaica	Fumariaceae	Annual	0.004	0.042	7.13	3.75	–
Galium philistaeum	Rubiaceae	Annual	0.015	0.025	0.31	0.81	–
Ifloga spicata	Asteraceae	Annual	0.203	0.261	0.038	0.51	–
Lagurus ovatus	Gramineae	Annual	0.239	0.292	0.63	1.38	–
Maresia pulchella	Cruciferae	Annual	0.116	0.223	0.045	0.08	–
Mercurialis annua	Euphorbiaceae	Annual	0.022	0.091	0.75	1.65	–
Nigella arvensis var. *palaestina*	Ranunculaceae	Annual	0.182	0.284	0.39	1.30	–
Papaver humile	Papaveraceae	Annual	0.149	0.227	0.07	0.86	–
Phagnalon rupestre	Asteraceae	Sub-shrub	0.215	0.270	0.057	0.64	–
Plantago sacrophylla	Plantaginaceae	Annual	0.088	0.197	0.605	1.21	–
Prasium majus	Labiatae	Perennial herb	0.002	0.112	4.56	2.30	–
Sonchus oleraceus	Asteraceae	Annual	0.216	0.286	0.26	1.24	–

Note: Persistent = seeds persist in the soil for at least 1 year; transient = seeds persist for less than 1 year. As a property of a species, persistence refers to the ability of the seeds of a species to survive in the soil seed banks; seed mass is the average air dry mass from 10 seeds (for small seeds, 100 seeds).

In this Mediterranean sand dune community, mean seed mass ranged from 0.038 to 147.37 mg, mean seed dimensions ranged from 0.08 to 4.75 mm, and seed dimension $variance_1$ ranged from 0.000 to 0.283 (Table 1). Seed mass was positively related to seed dimensions ($P < 0.01$). For persistent species as well as for transient species, seed dimension variance differed across the entire range. The seed dimensions $variance_1$ of persistent seeds ranged from 0.000 to 0.258, while that of transient seeds ranged from 0.000 to 0.283 (Table 1). Another parameter of seed dimension, $variance_2$, ranged from 0.006 to 0.318. Within the sand dune community, there were six orders of magnitude of variation in seed mass across the species. The mean mass of persistent seeds was 13.6 ± 33.7 mg and that of transient seeds 1.70 ± 1.94 mg. The mean dimension of persistent seeds was 2.25 ± 1.46 mm and that of transient seeds 1.54 ± 1.12 mm.

Plant species with persistent and transient seeds were widely scattered across the range of seed mass or dimension and variances (Fig. 1). Species with persistent seeds had significantly higher seed mass than those with transient seeds (one-tailed t-test = 1.68, $n = 48$, $P = 0.007$), but there was no significant difference in shape between them (one-tailed t-test = 1.68, $n = 48$, $P = 0.076$; t-test = 1.68, $n = 45$, $P = 0.124$) (Fig. 2). Species with persistent seeds yielded significantly higher seed dimensions than those with transient seeds (one-tailed t-test = 1.95, $n = 48$, $P = 0.029$). In this study, there was no threshold in seed mass (or dimension) and shape that distinguished transient from persistent seeds.

Comparison of litter mass among three microhabitats

Significant differences in litter mass was observed among the three microhabitats ($P < 0.0001$). Greater litter mass ($1693.7 \pm 86.8\ g \cdot m^{-2}$) was observed in the understory than in the open ($356.2 \pm 33.31\ g \cdot m^{-2}$) or on the trail ($51.52 \pm 20.17\ g \cdot m^{-2}$). Shrub understory had higher litter coverage (90–100%) than in the open (45–55%) or on the trail (2–5%).

DISCUSSION

This study provides an example of a flora in which a large proportion of species with bigger seeds tend to have persistent soil seed banks relative to those species with smaller seeds. This result is different from that of many floras around the world, including the flora of England (Thompson *et al.*, 1993), Italy (Cerabolini *et al.*, 2003), Iran (Thompson *et al.*, 2001), Argentina (Funes *et al.*, 1999), and to a lesser extent New Zealand (Moles *et al.*, 2000). In this study, the species with higher seed mass tend to form persistent seed banks in the soil, but there are also many species with persistent seeds that have small and/or compact seeds, and there is no significant difference in diaspore shape between species with persistent and transient seeds. Persistent seeds may be round/compact, elongated or flattened in shape. No thresholds or a line can be used (Moles *et al.*, 2000) to distinguish persistent seeds from transient seeds in seed mass and shape. Overall, seed mass and shape do not appear to be related to persistence in Israel. These results are similar to those for Australia (Leishman and Westoby, 1998). The method used to predict seed persistence in the soil based on British species, Argentina flora, and Italian flora cannot be extended to the flora of this sand dune community in Israel.

These unexpected results imply that the underlying mechanism of the patterns observed is unlikely to be ease of seed burial. We propose five factors that might explain these particular patterns: a distinctive vegetation composition; a barrier to burial of larger seeds due to litter and siliceous soil; persistence of the fruit coat; ease of transport for smaller

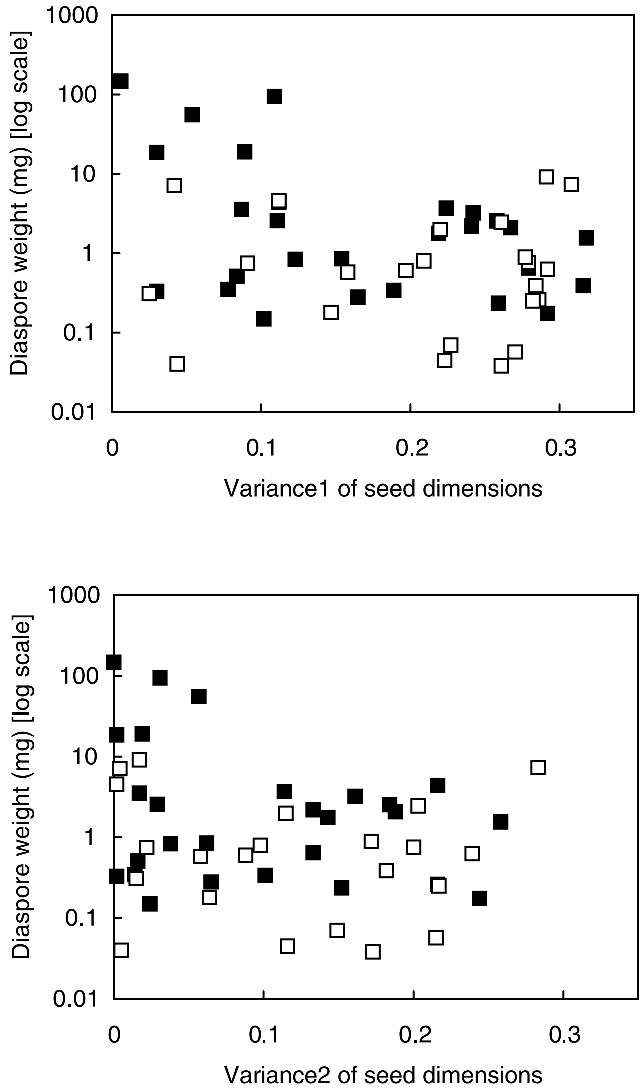

Fig. 1. Seed mass and variance of seed dimensions for 50 species from the Israel flora. Solid squares represent species whose seeds can persist for at least 1 year in the soil, whereas open squares represent species whose seeds persist for less than one year.

seeds by rain and wind; and differences in predator groups. First, the composition and structure of vegetation may be the prime factor determining the relationships between seed mass, shape, and persistence in soil seed banks. The underlying cause determining the pattern observed in this study is also very similar to that in Australia (Leishman and Westoby, 1998). In the flora of a Mediterannean coastal sand dune ecosystem, we found that many more legume seeds tended to persist in soil than those of plant functional groups (these have hard seeds that need more time to break the testa). In this ecosystem, legume seeds accounted for 76.0% of the total persistent soil seed banks (Yu *et al.*, 2003). These hard-seeded species

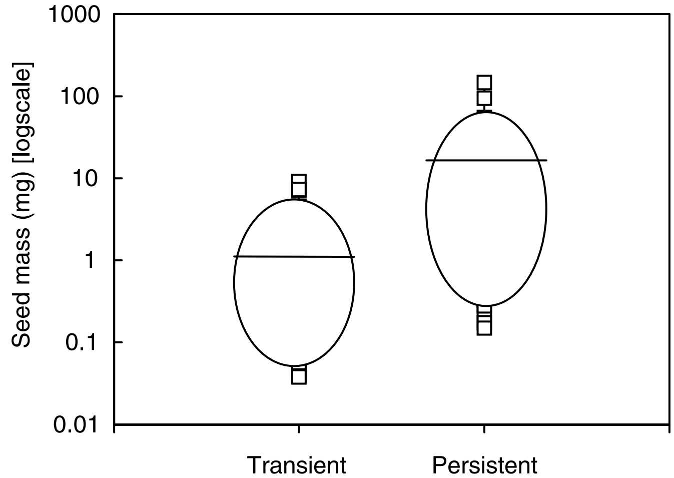

Fig. 2. Seed mass and persistence in the soil. Seed mass is the mean air-dried mass from at least 10 seeds. Log seed mass of species with persistent seeds is significantly higher than that of species with transient seeds (one-tailed *t*-test: $P = 0.007$). The bar across the box shows the median seed mass. The ellipse shows the number of species with mainly medium-sized seeds.

typically have a greater seed mass (mean mass 15.5 mg) than non-hard-seeded species (mean mass 5.8 mg). Legumes are known to form persistent seed banks because of their seed coat impermeability (Baskin and Baskin, 1989) and seed longevity (Hull, 1973). In other ecosystems of the Mediterranean region close to Israel, such as in Syria and Spain, many legumes have also been shown to form persistent seed banks (Russi *et al.*, 1992; Peco *et al.*, 1998). In the Poleg Nature Reserve, an abundance of legume species leads to a greater ouput of large seeds. The reason why legumes are abundant is not discussed here but may be due to some aspect of the Poleg Nature Reserve's vegetation successional history. Of the species with persistent seeds, five species are of the family Asteracae, none are grasses, and eleven are legumes. Of the species with non-persistent seeds, five species are of the family Asteaceae, five are grasses, and only one is a legume. This result may have a phylogenetic bias because of the preponderance of legume seeds.

Second, difficulty of burial because of soil texture (sand) and because of the presence of abundant litter in the shrub understory and in the open area could lead to greater numbers of persistent seeds of *Retama raetam*. Some persistent seeds might not germinate simply because of unsuitable conditions (e.g. they may require burial, or at least moisture, for germination). Therefore, some seeds are in a state of quiescence awaiting appropriate conditions for germination. Large seeds are less likely to be easily buried due to the scarcity of gaps and cracks in sandy soil and to the presence of litter on the surface of the soil in this Mediterranean coastal sand dune ecosystem. Moreover, abundant litter can protect seeds from predation. Thompson *et al.* (1993) emphasized the importance of seed burial to seed persistence in the British flora. However, whether seed burial is the underlying factor for seed persistence in the flora of Israel requires direct evidence and further experimental work.

Third, in this Mediterranean coastal sand dune community, in a few species that can form persistent soil seed banks (e.g. *Hippocrepis unisiliquosa* and *Medicago constricta*), detachment of the seeds from dry fruit coat does not occur in litter. This persistent fruit coat can protect its seeds from predation, pathogen invasion, and other environmental mechanisms that could affect seed longevity. Dry fruit coat persistence, however, is disadvantageous for seed burial and limits germination in *Hippocrepis unisiliquosa*. This special case has not been reported before.

Fourth, removal of seeds by rainwater and wind could be important for persistence in Mediterannean coastal sand dune ecosysytems. Previous studies found that small seeds were easily blown away or removed by water flow along the soil surface, and therefore seed mass had a negative relationship with its dispersion distance (Werner and Platt, 1976; Garcia-Fayos and Cerda, 1997). In Mediterranean coastal sand dune ecosystems, strong winds occur often and smaller seeds are easily blown away. Rainwater is the major agent of burial in the loam soil in New Zealand as in Britain (Moles *et al.*, 2000); however, in Mediterranean coastal sand dune ecosystems, surface water flow caused by heavy rainfall in siliceous soil could carry away rather than bury small seeds.

Lastly, larger seeds are likely to persist owing to the limited predation of such seeds in Mediterranean coastal sand dune ecosystems. Post-dispersal seed predation is very important for seed persistence (Hulme, 1994). For some considerable time, the ecosystem in Poleg Nature Reserve has been subject to human disturbance (visitor trampling), which has led to a significant decrease in predators such as gerbils and other rodents, which mainly consume bigger seeds. In Poleg Nature Reserve, the main granivores are ants, which mostly consume smaller seeds. In this community, we also observed that many small seeds, such as those of *Anagallis arvensis*, had lost viability owing to pathogon infestations or ageing.

In Mediterranean grasslands in central Spain, small-seeded species tend to form persistent seed banks, probably because they are buried more easily and they are less subject to predation (Peco *et al.*, 2003). In the Italian flora from the Alps to the Mediterranean coasts, not only seed mass, but also seed shape, is a key factor in determining seed fate and seed persistence in soil. In this study of the floras of the eastern Mediterranean coast, large seeds tend to form persistent seed banks due to the combination of vegetation composition and poor germination conditions because of much litter and sandy soil. Persistence is partly due to some inherent capacity of seeds to survive for a long period whether buried or not. In fact, many seeds are less likely to persist on the surface of the soil due to exposure (and hence being preyed upon), while other seeds are likely to persist on the surface of the soil simply due to exposure (poor conditions for germination).

In summary, the following ecological factors are suggested to affect the relationships between seed mass, shape, and persistence in soil seed banks (summarized in Table 2) (Thompson *et al.*, 1993, 1998, 2001; Hulme, 1998; Leishman and Westoby, 1998; Moles *et al.*, 2000, 2003; Cerabolini *et al.*, 2003; Peco *et al.*, 2003): (1) seed dispersal; (2) predation; (3) species composition of vegetation; (4) wind speed; (5) rainfall characteristics; (6) soil characteristics, including gaps and soil substrate [e.g. siliceous soils reduce the number of gaps and thus seeds have more time to become buried (Thompson *et al.*, 1993; Peco *et al.*, 2003)]; (7) fire; and (8) disturbance. Because of differences in the relative importance of these factors to different ecosystems, various patterns are observed in the relationships between seed mass, shape, and persistence. Therefore, environmental factors are as important as innate seed traits in determining the relationships between seed mass, shape, and persistence. (In addition, some factors have dual functions in these relationships.)

In this study, persistent soil seed banks were estimated by sampling soil at a particular time. Previously, persistence data were sourced from the published literature (Thompson *et al.*,

Table 2. Significant relations detected in several papers that link persistence to seed mass and shape and their possible causes

Region	Species type	Significant relationship with mass	Significant relationship with shape	Predation	Mean annual rainfall amount	High proportion of large and persistent–seeded species in vegetation	Soil texture	Fire	Authors
North-west Europe	Herbaceous	Yes	Yes	Low rate because of burial for small seeds	>1000 mm	Not	Not siliceous	No	Thompson *et al.* (1993)
Sweden	Trees, shrubs, herbaceous	Yes	Yes	Low rate because of burial for small seeds	600–800 mm	Not	Not siliceous	No	Bakker *et al.* (1996)
Southern England	Herbaceous	Yes	Yes	Low rate because of burial for small seeds	>1000 mm	Not	Not siliceous	No	McDonald *et al.* (1996)

Central Argentina	Herbaceous	Yes	Yes	Low rate because of burial for small seeds	800–911 mm	Not	Not siliceous	No	Funes *et al.* (1999)
Italy	Shrubs, herbaceous	Yes	Yes	Low rate because of burial for small seeds	>1000 mm	Not	Coarse soil	No	Cerabolini *et al.* (2003)
Australia	Trees, shrubs, herbaceous	No	No	High rate by birds	250–2000 mm	Yes	Siliceous or not	Yes	Leishman and Westoby (1998)
New Zealand	Trees, shrubs, herbaceous	Yes, negative	No	Low rate	1000–3000 mm	Not	Not siliceous	No	Moles *et al.* (2000)
Iran	Trees, shrubs	Yes	No	High rates for small seeds	316–686 mm	Not	Sandy loam	No	Thompson *et al.* (2001)
Central Spain	Herbaceous	Yes	No	Low rates for small seeds	450–500 mm	Not	Siliceous substrata	No	Peco *et al.* (2003)
This study	Shrubs, herbaceous	Yes, positive	No	Lack of large seeds	350–600 mm	Yes	Siliceous substrata	No	This study

1993, Leishman and Westoby, 1998, Peco *et al.*, 2003). The method of seed extraction by using a microscope would likely bias the sample towards larger seeds. However, many smaller seeds were still observed under the microscope.

The relationships between seed mass, shape, and persistence could be habitat-specific, and affected by the spatial scale of flora investigation. Scale is very important in some ecological relationships (Auerbach and Shmida, 1987; Palmer and White, 1994). The patterns seen in a narrow range of habitats may be different from those in wide habitats. For example, seed mass and shape are not related to persistence in Australia, since the species investigated in the Australian study belong to a wide range of habitats, from heaths and woodland in western Australia to tall forests in Victoria (Leishman and Westoby, 1998). We suggest that the patterns observed in the present study (in a Mediterannean coastal sand dune ecosysytem in the middle of Israel) could occur in woodland in the winter wet/summer dry climate of Western Australia.

The exclusion/inclusion of litter is also very important when analysing the relationships between seed mass, shape, and persistence, since many persistent seeds may occur in litter. Our results show that many persistent seeds can be found in litter. However, others (e.g. Thompson *et al.*, 2001) discussed the persistence of seeds in soil, not in the total soil seed bank. Persistence may be underestimated if litter is not included.

In addition, the confusion between dormancy and persistence could lead to the partial lack of a relationship between seed mass, shape, and persistence. There is no close relationship between seed dormancy and persistence. Dormancy is neither a necessary nor a sufficient condition for the accumulation of a persistent seed bank (Thompson *et al.*, 2003). Persistence may be underestimated when using the germination method to study the soil seed bank because of dormancy. Moreover, all viable seeds in the soil and associated litter constitute soil seed bank (Simpson, 1989), and therefore the exclusion of litter, which might include viable seeds, could underestimate the persistent seed bank.

In Mediterranean coastal sand dune communities, there are many species with persistent and large seeds that have different shapes (elongated or flattened seeds). These data illustrate that the likelihood of a diaspore persisting in the soil is determined to a large extent not by its mass and shape, but by the internal characteristics of seeds, such as a hard seed coat, and other biological factors (e.g. its survival mechanism mode, such as persistent protective fruit coat, in the soil seed bank).

In this study, persistent species were defined as those whose seeds persist in the soil for more than one year, and transient species as those whose seeds persist for less than one year. In the New Zealand study (Moles *et al.*, 2000), species were defined as being persistent if their seeds persisted in soil for more than two years, while in the Australian (Leishman and Westoby, 1998) and British (Thompson *et al.*, 1993) studies, seeds should persist in soil for more than 5 years to be persistent. According to Moles *et al.* (2000), this difference in classification should not affect the overall pattern observed. The link between persistence classifications and explanatory mechanisms also requires further work. Another unanswered question is whether the relationship is the result of scale-specific mechanisms.

Our belief, which is supported by similar results from Australia and New Zealand, is that using seed mass and morphology to predict the ability of a species' seeds to persist in the soil is not appropriate for the floras of the Mediterranean coastal sand dune ecosystem in Israel. Further work needs to be done to investigate other floras at a range of scales in many more regions. We suggest that further research develop and test these important hypotheses on the underlying mechanisms of seed persistence rather than pursue a 'stamp-collecting' approach from individual floras.

ACKNOWLEDGEMENTS

The study was carried out as part of postdoctoral studies by the first author at the Faculty of Life Sciences at Bar Ilan University. Thanks are extended to the National Natural Science Foundation of China (No. 40641004), the Kort Foundation, and the Key Project of Natural Foundation of Yunan Province in China (No. 2002C0100Z and No. 2004NG05-01) for supporting the study. We would like to thank Dorothy Bell for her valuable suggestions on an earlier version of the manuscript.

REFERENCES

Auerbach, A. and Shmida, A. 1987. Spatial scale and determinants of plant species richness. *Trend Ecol. Evol.*, **2**: 238–242.

Bakker, J.P., Bakker, E.S., Rosén, E., Verweij, G.L. and Bekker, R.M. 1996. Soil seed bank composition along a gradient from dry *alvar* to *Juniperus* shrubland. *J. Veg. Sci.*, **7**: 165–176.

Baskin, J.M. and Baskin, C.C. 1989. Physiology of dormancy and germination in relation to seed bank ecology. In *Ecology of Soil Seed Banks* (M.A. Leck, V.T. Parker and R.L. Simpson, eds.), pp. 53–66. New York: Academic Press.

Bekker, R.M., Bakker, J.P., Grandin, U., Kalamees, R., Milberg, P., Poschlod, P. *et al.* 1998. Seed size, shape and vertical distribution in the soil: indicators of seed longevity. *Funct. Ecol.*, **12**: 834–842.

Cerabolini, B., Ceruani, R.M., Caccianiga, M., Andreis, R.D. and Raimondi, B. 2003. Seed size, shape and persistence in soil: a test on Italian flora from Alps to Mediterranean coasts. *Seed Sci. Res.*, **13**: 75–85.

Dan, J., Yaalon, D.H., Koyumdjisky, H. and Raz, Z. 1970. The soil association map of Israel (1:1000,000). *Isr. J. Earth Sci.*, **21**: 29–49.

Funes, G., Basconcelo, S., Diaz, S. and Cabido, M. 1999. Seed size and shape are good predictors of seed persistence in soil in temperate mountain grasslands of Argentina. *Seed Sci. Res.*, **9**: 341–345.

Garcia-Fayos, P. and Cerda, A. 1997. Seed losses by surface wash in degraded Mediterranean environments. *Catena*, **29**: 73–83.

Hull, A.C. 1973. Germination of range plant seeds after long periods of uncontrolled storage. *J. Range Manage.*, **26**: 198–200.

Hulme, P.E. 1994. Post-dispersal seed predation in grassland – Its magnitude and sources of variation. *J. Ecol.*, **82**: 645–652.

Hulme, P.E. 1998. Post-dispersal seed predation and seed bank persistence. *Seed Sci. Res.*, **8**: 513–519.

Lavorel, S., Debussche, M., Lebreton, J.D. and Lepart, J. 1993. Seasonal patterns in the seed bank of Mediterranean old fields. *Oikos*, **67**: 114–128.

Leishman, M.R. and Westoby, M. 1998. Seed size and shape are not related to persistence in soil in Australia in the same way as in Britain. *Funct. Ecol.*, **12**: 480–485.

McDonald, A.W., Bakker, J.P. and Vegelin, K. 1996. Seed bank classification and its importance for the restoration of species-rich flood-meadows. *J. Veg. Sci.*, **7**: 157–164.

Moles, A.T., Hodson, D.W. and Webb, C.J. 2000. Seed size and shape and persistence in the soil in the New Zealand flora. *Oikos*, **89**: 541–545.

Moles, A.T., Warton, D.I. and Westoby, M. 2003. Do small-seeded species have higher survival through seed predation than large-seeded species? *Ecology*, **84**: 3148–3161.

Pake, C.E. and Venables, D.L. 1996. Seed banks in desert annuals: implications for persistence and coexistence in variable environments. *Ecology*, **77**: 1427–1435.

Palmer, M.W. and White, P.S. 1994. Scale dependence and species–area relationship. *Am. Nat.*, **144**: 717–740.

Peco, B., Ortego, M. and Levassor, C. 1998. Similarity between seed bank and vegetation in Mediterranean grassland: a predictive model. *J. Veg. Sci.*, **9**: 815–828.

Peco, B., Traba, J., Levasor, C., Sánchez, A.M. and Azcánteran, F.M. 2003. Seed size, shape and persistence in dry Mediterrannean grass and scrublands. *Seed Sci. Res.*, **13**: 87–95.

Philippi, T. 1993. Bet-hedging germination of desert annuals: beyond the first year. *Am. Nat.*, **142**: 474–487.

Russi, L., Cocks, P.S. and Roberts, E.H. 1992. Seed bank dynamics in a Mediterranean grassland. *J. Appl. Ecol.*, **29**: 763–771.

Simpson, R.L. 1989. *Ecology of Soil Seed Bank*, pp. 149–209. San Diego, CA: Academic Press.

Thompson, K. and Grime, J.P. 1979. Seasonal variation in the seed banks of herbaceous species in ten contrasting habitats. *J. Ecol.*, **67**: 893–921.

Thompson, K., Band, S.R. and Hodgson J.G. 1993. Seed size and shape predict persistence in soil. *Funct. Ecol.*, **7**: 236–241.

Thompson, K., Bakker, J.P., Bekker, R.M. and Hodgson, J.G. 1998. Ecological correlates of seed persistence in soil in the north-west European flora. *J. Ecol.*, **86**: 163–169.

Thompson, K., Jalili, A., Hodgson, J., Hamzeh'ee, B., Asri, Y., Shaw, S. *et al.* 2001. Seed size, shape, and persistence in the soil in an Iranian flora. *Seed Sci. Res.*, **11**: 345–355.

Thompson, K., Ceriani, R.M., Bakker, J.P. and Bekker, R.M. 2003. Are seed dormancy and persistence in soil related? *Seed Sci. Res.* **13**: 97–100.

Venable, D.L. and Brown, J.S. 1988. The selective interactions of dispersal, dormancy, and seed size as adaptations for reducing risk in variable environments. *Am. Nat.*, **131**: 360–384.

Werner, P.A. and Platt, W.J. 1976. Ecological relationships of co-occurring goldenrods (*Solidago*: Asteraceac). *Am. Nat.*, **10**: 959–971.

Yu, S.L., Sternberg, M., Jiang, G.M. and Kutiel, P. 2003. Heterogeneity in soil seed banks in a Mediterranean coastal sand dune. *Acta Bot. Sin.*, **45**: 536–543.