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Seed size and shape and persistence in the soil in the New Zealand flora

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Seed size and shape predict seed persistence in the soil for British and Argentinian herbaceous plant species. Those species with small, rounded seeds tend to have persistent seeds while those with larger, more elongate or flattened seeds usually lack persistence. It has been suggested that the mechanism underlying this pattern may be ease of burial, as small, rounded seeds are incorporated into the soil more easily than large, elongate or flattened seeds and are therefore less likely to be eaten by seed predators. We tested whether seed size and shape were related to persistence in the soil for 47 species native to New Zealand forests. There was a tendency for species with persistent seeds to have smaller seeds than species with transient seeds. However, species with large and/or elongate or flattened persistent seeds were relatively common. This indicates that seed size and shape are not related to persistence in New Zealand in the same way as in Britain and Argentina. A similar negative result has been found in Australia. The underlying cause of the patterns observed is unlikely to be ease of burial, since incorporation of seeds into the soil is likely to operate in all countries in a similar manner on seeds without specialised seed burial mechanisms. Data from all four floras studied to date also suggest that species with small, rounded seeds that do not germinate immediately must have the ability to survive periods of burial.

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British herbaceous plant species are more likely to have seeds that persist for long periods in the soil if their seeds are small and/or rounded than if they are larger, elongate or flattened (Thompson and Grime 1979, Thompson 1987, Thompson et al. 1993, Bekker et al. 1998). Thompson et al. (1993) proposed that the mechanism underlying the relationship between seed size and shape and persistence in the soil could be ease of burial, since buried seeds have lower rates of seed predation than those that remain on the soil surface (Hulme 1994), and seed predation is one of the major determinants of seed longevity (Hulme 1998). There is some evidence that small and/or round seeds are incorporated into the soil profile more easily than large and/or irregularly shaped seeds in Europe (Thompson et al. 1994, Bekker et al. 1998), where seeds are most likely to be buried by penetrating cracks in the soil, percolating through the soil with rainwater, or through the action of invertebrates (Thompson et al. 1993, 1994).

Burial of seeds by mechanisms such as those listed above is likely to occur in most ecosystems. Therefore, if ease of burial is the strongest determinant of seed longevity, one would expect a relationship between seed morphology and persistence in the soil in floras outside northwest Europe (Thompson et al. 1993). This theory is supported by a study by Funes et al. (1999), which demonstrated that seed size and shape are important determinants of persistence in the soil for 71 herbaceous

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species from a montane grassland in Argentina. However, Leishman and Westoby (1998) analysed the relationship between seed size and shape and persistence in the soil for 101 Australian species from a range of habitats, and found that seed size and shape were not related to persistence in the soil in Australia in the same way as in Britain.

The lack of a correlation between seed size and shape and persistence in the soil in Australia casts some doubt on the generality of the mechanism proposed by Thompson et al. (1993). At first glance it would seem that the differences between the British and Australian floras could result from differences in burial mechanisms. In Australia, ants are one of the major seed dispersal vectors (Berg 1975, Rice and Westoby 1981, Hughes and Westoby 1990), and are known to bury seeds at depths of at least 12 cm (Hughes and Westoby 1992). However, the lack of a clear trend in the Australian data remains when species that are adapted for burial by ants (elaiosome-bearing seeds) or self-burial (seeds with hygroscopic awns) are removed from the data (Leishman and Westoby 1998). Nevertheless, even seeds which lack elaiosomes may be buried by ants in Australia, although these seeds are likely to be subject to high levels of seed predation (Andersen 1991). It is therefore unclear whether there is some fundamental difference between Australia and Britain that is yet to be accounted for, or whether the burial mechanism is less ubiquitous than previously supposed.

To more thoroughly test the burial hypothesis put forward by Thompson et al. (1993), another multispecies study needed to be carried out in another flora with a different evolutionary history than the European flora, and which has comparable processes for the incorporation of seeds into the soil profile. New Zealand offers such a system, with a unique flora thought to be derived largely from Gondwanan origins, and a relatively depauperate ant fauna (Howarth and Ramsay 1990). To our knowledge, no studies have been formally conducted in New Zealand to investigate the processes by which seeds are incorporated in to the soil. However, it seems likely that invertebrates and rainwater are the major agents of burial in New Zealand as in Britain.

In this study we tested whether seed size and shape were related to persistence in the soil in the New Zealand lowland forest flora.

Materials and methods

Data were gathered for 47 species (from 41 genera in 31 families) native to New Zealand lowland forests (Table 1). The study species included plants with a range of growth forms including trees, shrubs and herbs. Seeds were obtained from the H. D. Gordon Herbarium at Victoria Univ. of Wellington (WELTU) and the Landcare Research Herbarium at Lincoln (CHR).

In this study, persistent species were defined as those whose seeds persist in the soil for more than 2 yr, and transient species were defined as those whose seeds persist for less than 2 yr. In the Australian (Leishman and Westoby 1998) and British (Thompson et al. 1993) studies seeds had to persist for at least 5 yr to be defined as persistent. This difference is unlikely to influence the overall pattern of our results as: 1) a large enough proportion of the New Zealand species with persistent seeds were large, elongate or flattened that the reclassification of a few species would not significantly alter the overall pattern; 2) the result of the Australian study remains unchanged if species whose seeds persist for 1 to 5 yr are reclassified as persistent; 3) the Argentinian study showed a similar result to the British study with a definition of persistent seeds as those that are able to germinate after just one year in the soil.

Species were considered to have seeds which persisted for more than 2 yr if their seeds germinated from soil samples which had been protected from seed inputs for 2 yr (by the placement of trays of soil above the sample area (see Enright and Cameron (1988)), or if the overall density of seeds in the seed bank at a site was more than twice the density of the seeds in the annual seed rain at the same site and at least 5 seeds were present in the seed bank (a simple threshold established to prevent misclassifications caused by low sample size). Species were considered to have transient seeds if they were represented by more than 5 seeds in the seed rain, and present in the seed rain at more than twice the density they were found at in the seed bank, or if they were absent from 2 to 3 soil samples giving a total sample area of at least 20×20 cm wide and 7 cm deep from beneath 1 to 3 plants that were known to have fruited heavily 6 months to one year before sampling. Data from four studies of the seed rain and seed bank were used to classify seeds as persistent or transient (Table 1). The level of consistency in classification of species using these methods on data from different studies was high, with only two species being classified differently according to data from separate studies (Table 1).

Ten seeds of each species were air-dried and weighed to 10 μg accuracy. Measurements were made on the persistent part of the diaspore for each species, since this is the unit that must be incorporated into the soil and persist until germination. Variance in diaspore dimensions was obtained by transforming the average length, breadth and width for 10 seeds of each species so that length was unity, and calculating the variance of the transformed values (as in Thompson et al. (1993)). This gives a value for seed shape such that spherical seeds have a variance of 0 and elongated or flattened seeds have variances of up to 0.33.

Results

Seed mass ranged from 0.01 mg to 1080 mg (Table 1). This is a wider range of seed mass than that recorded in the Australian (Leishman and Westoby 1998), Argentinian (Funes et al. 1999) or British (Thompson et al. 1993) studies. Variance in diaspore dimensions ranged from 0.01 to 0.25, indicating that a wide range of seed shapes were present in the sample. None of the species studied had seeds with specialised burial mechanisms such as elaiosomes or hygroscopic awns. Thirty species were classified as having persistent seeds, and 17 were classified as having transient seeds.

Species with persistent and transient seeds were widely scattered across the range of seed sizes and variances (Fig. 1), including many large and/or elongate or flattened seeds that were persistent. In other words, seed size and shape are not related to persistence in the

Table 1. Seed mass and variance of diaspore dimensions (transformed so that length is unity) for all species used in this study, showing persistence category (persistent = seeds persist in the soil for at least 2 yr; transient = seeds persist less than 2 yr in the soil). Letters in the source column represent the reference/method used to designate a species to a persistence category (C = Court and Mitchell (1988); E = Enright and Cameron (1988); S = Sem and Enright (1996); M = Moles and Drake (1999); A = assessed by soil sieving from under adult trees of that species known to have fruited the previous year). Letters in brackets in the source column represent instances where persistence was different in different studies. In these cases the result from the study in brackets was overruled. Seed mass is the average air dry weight from 10 seeds.

	Family	Data source	Variance in seed dimensions	Seed mass (mg)
Species with persistent seeds ($n = 30$)				
Aristotelia serrata	Elaeocarpaceae	M, S	0.035	3.74
Baumea articulata	Cyperaceae	S	0.084	1.32
Coprosma robusta	Rubiaceae	M	0.156	7.94
Cordyline australis	Asphodelaceae	E, S	0.057	2.30
Coriaria arborea	Coriariaceae	M	0.058	0.17
Dacrycarpus dacrydioides	Podocarpaceae	E	0.024	29.91
Epilobium nummulariifolium	Onagraceae	M	0.131	0.01
Euchiton gymnocephalus	Asteraceae	E	0.176	0.03
Fuchsia excorticata	Onagraceae	M, E	0.076	0.06
Gahnia pauciflora	Cyperaceae	E	0.104	15.00
Gahnia xanthocarpa	Cyperaceae	S	0.087	13.00
Geniostoma rupestre	Geniostomaceae	M, E, S	0.041	0.34
Hebe stricta	Scrophulariaceae	S	0.185	0.06
Hydrocotyle moschata	Apiaceae	S	0.103	0.07
Isolepis inundatus	Cyperaceae	S	0.091	0.07
Isolepis prolifer	Cyperaceae	M	0.098	0.04
Juncus planifolius	Juncaceae	E, S	0.056	0.01
Kunzea ericoides	Myrtaceae	E, S	0.250	0.01
Lobelia anceps	Lobeliaceae	S	0.070	0.01
Myoporum laetum	Myoporaceae	M	0.084	101.26
Myrsine australis	Myrsinaceae	E (M)	0.037	17.41
Nertera dichondrifolia	Rubiaceae	S	0.141	1.70
Olearia rani	Asteraceae	E	0.190	0.12
Pittosporum tenuifolium	Pittosporaceae	E	0.045	1.30
Rhopalostylis sapida	Arecaceae	S	0.086	228.38
Schefflera digitata	Araliaceae	E (M)	0.093	1.80
Solanum americanum	Solanaceae	E	0.103	0.73
Solanum laciniatum	Solanaceae	M	0.024	2.20
Vitex lucens	Verbenaceae	E	0.032	676.31
Wahlenbergia gracilis	Campanulaceae	M, S	0.109	0.03
Species with transient seeds ($n = 17$)				
Beilschmiedia tawa	Lauraceae	A	0.110	1081.33
Brachyglottis repanda	Asteraceae	M	0.226	0.19
Carpodetus serratus	Carpodetaceae	E, S	0.057	0.48
Coprosma grandifolia	Rubiaceae	M, E	0.112	27.38
Dacrydium cupressinum	Podocarpaceae	A	0.047	4.78
Dysoxylum spectabile	Meliaceae	C	0.076	107.13
Freycinetia baueriana	Pandanaceae	S	0.120	0.08
Knightia excelsa	Proteaceae	A	0.204	30.29
Macropiper excelsum	Piperaceae	M	0.038	1.90
Melicytus ramiflorus	Violaceae	M, S	0.026	0.76
Metrosideros perforata	Myrtaceae	S	0.231	0.04
Prumnopitys ferruginea	Podocarpaceae	A	0.074	665.58
Prumnopitys taxifolia	Podocarpaceae	A	0.019	101.66
Pseudopanax arboreus	Araliaceae	M	0.088	6.30
Pseudopanax crassifolius	Araliaceae	E	0.065	18.46
Ripogonium scandens	Ripogoniaceae	M	0.010	249.61
Uncinia uncinata	Cyperaceae	E	0.125	0.42

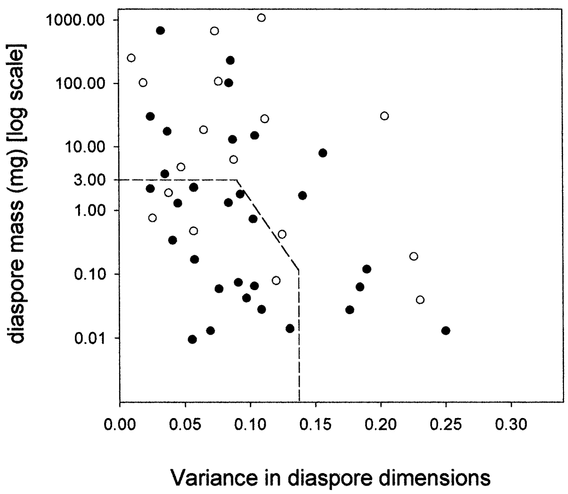

Fig. 1. Seed mass and variance of seed dimensions for 47 species from the New Zealand flora. Filled dots represent species whose seeds persist for at least 2 yr in the soil, hollow dots represent species whose seeds persist for less than 2 yr. Variance in diaspore dimensions was obtained by transforming the average length, breadth and width for 10 seeds of each species so that length was unity, and calculating the variance of the transformed values (as in Thompson et al. (1993)). Seed mass is the average air dry weight from a sample of 10 seeds. The dashed line shows the threshold drawn by Thompson et al. (1993), below which all species had seeds that could persist in the soil for at least 5 yr.

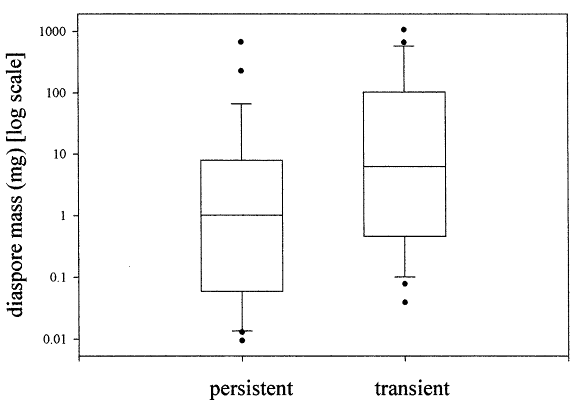

Fig. 2. Seed mass and persistence in the soil. Seed mass is the average air dry weight from 10 seeds. Log seed mass of species with persistent seeds is significantly lower than that of species with transient seeds (one-tailed t-test; $P = 0.01$). Boxes span the 25th to the 75th percentile; whiskers span from 10th percentile to the 90th percentile. Outliers are represented by dots. The bar across the box shows the median seed mass.

soil in New Zealand in the same way as in Britain and Argentina. However, species with transient seeds tended to have larger seeds than species with persistent seeds (one-tailed t-test: $P = 0.01$; Fig. 2). There was no significant difference in seed shape between species with transient seeds and species with persistent seeds (one-tailed t-test: $P = 0.47$).

Discussion

This study provides an example of a flora in which species with persistent seeds tend to have smaller seeds than species with transient seeds. This is a result that is predicted by current theory involving bet-hedging (Venable and Brown 1988), and that has been found in many floras around the world, including the northwest European flora (Thompson 1987, Thompson et al. 1993, Eriksson 1995, Bakker et al. 1996, Bekker et al. 1998), tropical forest in Panama (Dalling et al. 1997), wetlands (Leck 1989), Argentinian montane grasslands (Funes et al. 1999) and the Mojave desert in California (Price and Joyner 1997). However, studies in Australia have failed to find a relationship between seed size and persistence in the soil (Leishman and Westoby 1994, Lunt 1995, Leishman and Westoby 1998).

Although there is a relationship between seed size and persistence in the soil in New Zealand, there are many species with persistent seeds that have large and/or elongate or flattened seeds, and there was no significant difference in diaspore shape between species with persistent and transient seeds. Overall, seed size and shape do not appear to be related to persistence in the soil in New Zealand in the same way as in Europe and Argentina, where there were no species with large and/or irregularly shaped seeds that persisted for more than 5 yr in the soil (Thompson et al. 1993). This result, combined with similar evidence from Australia, shows that using diaspore morphology to predict the ability of a species' seeds to persist in the soil is not appropriate in all floras.

The underlying cause of the patterns observed is unlikely to be ease of burial, since incorporation of seeds into the soil is likely to operate in all countries in a similar manner on seeds without specialised seed burial mechanisms (Thompson et al. 1993). The low rate of seed predation in New Zealand (Moles and Drake unpubl.) could explain the lack of a relationship between seed size and shape and persistence in the soil in this flora. However, a different explanation would need to be invoked for Australia, where levels of seed predation are high (Osunkoya 1994, Yates et al. 1995, Wurm 1998). It may be vegetation structure that determines which studies show a relationship between seed morphology and persistence in the soil. The British and Argentinian studies were conducted in mainly herbaceous floras (dominated by the Asteraceae and Poaceae), whilst the Australian and New Zealand studies contained species with a range of growth forms, from a wide range of families.

None of the species with transient seeds in the British study had small, rounded seeds. In fact, it appears that the threshold in size and shape drawn by Thompson et al. (1993) is better interpreted as a line below which a species cannot have transient seeds than as a threshold above which a seed may not persist for long periods in the soil. This pattern was also found in the present study, where there were no species with transient seeds that had a seed mass of below 0.5 mg and a variance of below 0.1; and in the Argentinian study, where there were only two species with transient seeds which had a seed mass below 0.2 mg and a variance below 0.125. We therefore suggest a shift in focus away from the question "Why are large-seeded species unable to form persistent seed banks?" (the question most commonly asked, and that which is readily answered by the burial hypothesis) to "Why are there so few species with small, round seeds and transient seed banks?". The most logical answer to this question seems to be that species with small, rounded seeds cannot help but be incorporated into the soil, and are only ecologically viable if they have the ability to persist until such time as a disturbance event brings them back to the surface. However, there were several Australian species with small round, transient seeds. Importantly, all of these species have immediate germination. So, it would seem that species with transient seeds that germinate immediately after dispersal may have large or small, rounded or elongated diaspores, but any species with small, rounded seeds that do not germinate immediately must have the ability to survive periods of burial.

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