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Seed size, shape and persistence in dry Mediterranean grass and scrublands

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Abstract

Seed size and shape, measured as the variance of the three main dimensions, have been proposed as good indicators for predicting seed persistence. We tested whether these variables were robust predictors of seed persistence in the soil for 58 abundant herbaceous species, primarily annuals, in grass and scrubland of central Spain. Seed persistence was estimated from data on germinable seed banks, while seed weight and shape were measured using fresh seeds collected in the study area. There was a significant tendency for species with persistent seeds to have smaller seeds than species with transient seeds. Seed shape was not, however, related to persistence and we did not find any clear seed weight/shape threshold for predicting persistence. The binary logistic model of seed bank type as a function of seed weight was significant and explained 67% of total variability. Supplementary information about dormancy, environmental conditions of habitat, predation and attack by pathogens has to be used to elaborate more accurate general predictive models of seed persistence.

Keywords: annual grasslands, phylogenetic independent contrasts, seed bank, seed shape, seed weight

Introduction

Seed size and shape have been proposed as indicators for predicting seed persistence in the soil for British herbaceous plant species. Thompson *et al.* (1993) found that, among 97 British herbaceous species, small and compact seeds and diaspores tend to persist in the soil, while most large-seeded species have transient seed banks. They also found a threshold of seed weight and shape, below which all diaspores are persistent in the soil and proposed that the main mechanism underlying this pattern could be ease of burial, since buried seeds can escape post-dispersal predation (Fenner, 1985; Thompson, 1987; Westoby *et al.*, 1992; Thompson *et al.*, 1994; Price and Joyner, 1997). However, Thompson *et al.* (1993) also acknowledged the existence of other factors related to persistence, including germination requirements, dormancy mechanisms and resistance to pathogens.

This burial hypothesis has been supported by similar results in other studies of grasslands in northern and central Europe (Bakker *et al.*, 1996; Bekker *et al.*, 1998), temperate subhumid montane grasslands in Argentina (Funes *et al.*, 1999) and species from a wide range of habitats in Italy (Cerabolini *et al.*, 2003). However, the lack of correlation between seed size and shape and persistence in 101 Australian species, over a range of habitats (Leishman and Westoby, 1998), suggests that the mechanisms by which seeds enter the bank may not be universal. The hypothesis has recently been retested on 47 native species in New Zealand lowland forest (Moles *et al.*, 2000) and for 311 species of grasslands and woodlands of north-western Iran (Thompson *et al.*, 2001), yielding a negative relationship between persistence and weight, but no relationship with diaspore shape. There is still, however, little information about the relationship between seed size, shape and persistence in most of the world's ecosystems. The most conclusive relationships between seed size, shape and persistence have been detected in temperate, mesic habitats, where burial of seeds may be facilitated by earthworms (Thompson *et al.*, 1994). It remains unclear as to whether the same rules apply in arid or semi-arid environments, where burial is either predominantly a passive process or associated with granivory (e.g. burial by ants).

This study contributes further information to the debate by testing whether seed weight and shape are related to persistence in the soil for the 58 most abundant herbaceous species in dry Mediterranean grass and scrublands of central Spain.

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Materials and methods

The study area was situated 20 km north of Madrid (central Spain) over siliceous substrata on the pediment of the Guadarrama range. It consisted of *dehesa* grasslands grazed by cattle and horses, and scrubland that has formed following the abandonment of the *dehesa* grasslands. The grasslands were mainly composed of annual species such as *Xolantha guttata, Leontodon taraxacoides* subsp. *longirostris, Hypochoeris glabra, Trifolium* spp., and the cryptophyte *Poa bulbosa,* and were very species-rich (more than 20 species/400 cm²). The scrubland consisted mainly of the sparsely distributed pioneer shrub species *Lavandula stoechas* subsp. *pedunculata,* with a herbaceous layer matrix amidst the scrub, also rich in annuals such as *Crepis capillaris, Jasione montana, Xolantha guttata, Vulpia* spp., *Teesdalia coronopifolia* and *Mibora minima.* The study area had an altitude range of 700–900 m, a Mediterranean climate with a significant drought period in the summer, mean annual temperature of 13°C and 450–500 mm mean annual rainfall with high interannual fluctuations (Peco, 1989).

Data on seed weight and seed shape (seeds or fruits with difficult to detach structures) were taken from Azcárate *et al.* (2002), where fresh seeds were collected between 1996 and 1999 in the same study area from at least 20 individuals. Air-dried seeds were weighed to quantify size, followed by the measurement of seed length, width and depth. Seed shape was calculated, following Thompson *et al.* (1993), as the variance of the three main dimensions after dividing all values by length. Totally spherical seeds would have shape = 0, with this value increasing as they became flatter or elongated.

Seed persistence in the soil was estimated using data from 1997 on germinable seed banks and vegetation in the same area in ten 10 × 10 m plots with similar topographic features (dry, flat areas) outside the influence of trees. We monitored the established vegetation in spring 1997, measuring species frequency in 20 quadrats of 20 × 20 cm placed at random in each plot. The seed bank was quantified in February 1997 before the production of new seeds. In each plot, we extracted a cylindrical soil core (diameter 4 cm, depth 10 cm) from alongside each of the 20 vegetation sampling quadrats. Each soil core was subdivided into two portions (0–5 cm and 5–10 cm deep).

We calculated the density of buried germinable seeds in each layer of the soil cores using greenhouse germination over a period of 16 months, until no new seedlings emerged for 3–4 months. Greenhouse temperatures ranged from 3 to 39°C during the germination test period. We spread the soil subsamples in 1 cm deep layers over 6 cm of vermiculite in individual 6 × 6 cm pots set in trays that were stored in the greenhouse and watered regularly by capillary action. We identified, counted and removed the emerging seedlings as early as possible, after which we checked 5–10% of the soil sample for remaining seeds under a binocular microscope. No additional seeds were detected.

All species were classified as having transient seed banks (species present in the soil seed bank for less than 1 year) or persistent seed banks (species present in the soil seed bank for more than 1 year). We used a slightly modified version of the method described in Bakker (1989) and Thompson *et al.* (1997). Persistent species were defined as those present in the spring seed bank but mostly on the surface (short-term persistent), and species with a similar frequency in both soil layers or species absent from the vegetation but present in the seed bank (long-term persistent). Transient species were those present in the vegetation, but not detected in the spring seed bank. Using a conservative approach to the estimation of persistence by species from the north-west European flora, Thompson *et al.* (1997) proposed in their key that species present in the spring seed banks, but only near the surface, should be classified as transitory. In contrast, we regarded such species as persistent. Our modification to the method used by the above authors was based on the fact that the vast majority of annual Mediterranean grassland species germinate in autumn (Peco, 1989; Peco *et al.*, 1998). We therefore assumed that if a species was present in the spring bank, it could potentially remain for more than a year unless it was winter transient (Thompson and Grime, 1979) – a very uncommon type of bank in our systems (Ortega *et al.*, 1997). Species with insufficient information, i.e. present in fewer than four quadrats in the vegetation and with fewer than three seeds in the seed bank, were not classified.

Differences in seed weight and shape between transient and persistent (short- or long-term) species were evaluated using a *t*-test after seed weight was log transformed to achieve the normality assumption. A binary logistic model (Crawley, 1993) was also fitted to the data, using persistence as the binary response variable and seed weight and shape as explanatory variables. In order to control any possible phylogenetic effect on the patterns detected, we also analysed phylogenetic independent contrasts (PICs), which were obtained as per Felsenstein (1985). Details on the construction of the phylogenetic tree are described in Azcárate *et al.* (2002). A total of ten PICs, representing divergences within individual clades between persistent and non-persistent seed banks, were selected. We used a sign paired sample-test (Zar, 1984) to check whether these divergences tended to be associated with either increasing seed weight or seed dimension variance. SPSS-10 (Version 10.0 for

Windows, SPSS Inc., Chicago, IL, USA) was used in all statistical analyses.

Results

Twenty-one of the species present in the seed banks or vegetation in the study area were classified as transitory, 37 as persistent and 14 were not classified due to insufficient information (low abundance in the seed banks and the vegetation). For the classified species, seed weights ranged between 0.011 and 6.22 mg, and seed shape ranged between 0.01 and 0.27 and included only herbaceous species, mainly annuals (Appendix 1).

The relationship between seed weight, shape and persistence is shown in Fig. 1. Species with persistent seeds yielded significantly lower seed weights than those with transient seeds (one-tailed t-test = 3.04, n = 58, $P < 0.01$), but there was no significant difference in shape between them (one tailed t-test = −0.02, n = 58, $P = 0.99$). There was, however, no threshold in seed weight that clearly segregated persistent from transient species, although all of our species (persistent and transient) were below the threshold established by Thompson et al. (2001) for persistent species. The forward binary logistic model was significant ($P < 0.01$), only included seed weight (persistence = −0.42–1.46 log(seed weight)) and explained 67.2% of total variance.

The difference in seed weight between phylogenetically independent pairs was significant (sign paired test, $n = 10$, $P < 0.05$). Seeds from transitory species (or nodes) were heavier than those from persistent species, while the difference in seed shape was not significant (Fig. 2).

Discussion

The analysed species had shape ranges that matched those found in other herbaceous species data sets (Thompson et al., 1993; Bakker et al., 1996; Funes et al., 1999) or floras that also included shrubs and trees (Leishman and Westoby, 1998; Moles et al., 2000; Thompson et al., 2001; Cerabolini et al., 2003). Generally, however, seeds were much lighter (Table 1). The percentage of species with persistent banks was relatively high (64%), as also found in other research in the same geographical area (Ortega et al., 1997).

Our results from the analysis of both the complete set of species and the PICs suggest that the pattern of small and/or rounded seeds as more likely to persist in the soil than larger elongated or flattened types, as detected by other authors (Thompson et al., 1993; Bakker et al., 1996; Funes et al., 1999), can only be extended partially to annual-dominated grasslands. In our case, seed weight was significantly greater for transient species, but seed shape did not appear to
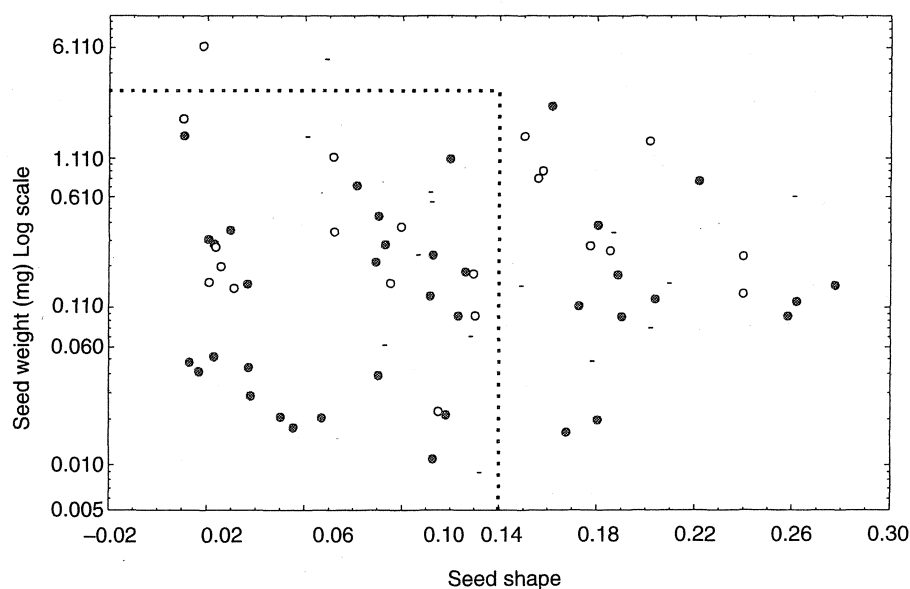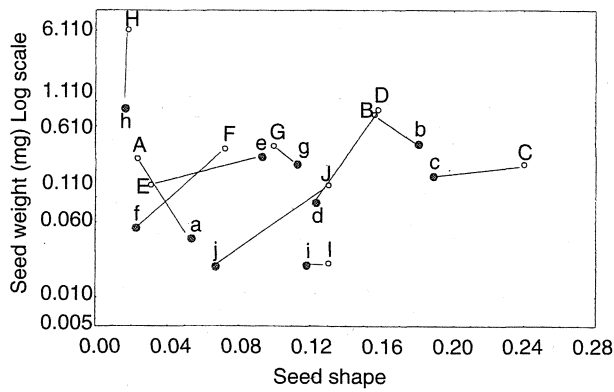

Figure 1. Relationship between seed weight and shape (variance of seed dimensions) in 72 abundant species in dry grasslands and scrublands of central Spain. ●, Species with seeds that persist in the soil for more than 1 year; ○, species with seeds that persist in the soil for less than 1 year; –, species for which the seed bank type could not be determined, due to insufficient information. The dashed line encloses the area suggested by Thompson et al. (1993) to contain the majority of persistent seeds.

Figure 2. Seed weight and shape (variance of seed dimensions) for ten phylogenetically independent contrasts, based on seed persistence in the soil. Each PIC is denoted by a letter (A to J). Uppercase and lowercase letters indicate mean seed weight and shape for transient versus persistent pair components, respectively. Their evolutionary divergence is shown with a line. Each side of a divergence could be an individual species or an average across several species.

Pair name	Transient	Persistent
A–a	*Scleranthus delortii*	*Cerastium semidecandrum, Moenchia erecta*
B–b	*Plantago lanceolata*	*Plantago lagopus*
C–c	*Leontodon taraxacoides* subspp. *longirrostris*	*Crepis capillaris*
D–d	*Festuca ampla*	*Mibora minima*
E–e	*Euphorbia exigua*	*Asterolinon linum-stellatum*
F–f	*Carex divisa*	*Scirpus setaceus*
G–g	*Trifolium dubium*	*Trifolium campestre*
H–h	*Trifolium subterraneum*	Section *Trifolium*
I–i	*Logfia gallica*	*Logfia minima*
J–j	*Spergula arvensis, Spergula pentandra*	*Spergularia purpurea*

have any relationship with persistence. Our data appear to confirm that small-seeded species tend to form persistent seed banks, probably because they bury more easily and they are less subject to predation. In the case of Mediterranean grasslands, seed predation is mainly driven by granivorous ants (genus *Messor*) (López *et al.*, 1993; Cerdá and Retana, 1994), and large seeds appear to be particular targets (Reyes-López, 1987; Baroni-Urbani and Nielsen, 1990; Detrain and Pasteels, 2000). The lack of any relationship between seed shape and persistence could be explained partly by the small seed size of the species in this work compared with other studies (Table 1). The absolute seed dimension is important in preventing burial, but an elongated or flat shape may be less of an impediment to burial in small seeds than in large seeds. The lower value of seed shape in comparison with seed weight for predicting persistence has also been found by Moles *et al.* (2000) and Thompson *et al.* (2001). Finally, the lack of significant relationships between persistence and seed weight and shape detected by Leishman and Westoby

(1998) may be due to the use of seed dormancy as an indicator of seed persistence, as indicated by other authors (Thompson *et al.*, 2001), when these two concepts are not necessarily related (Thompson, 2000).

While the model for seed persistence constructed using seed weight explains 67% of the variability of the data, there is no clear threshold in seed weight that can be used to predict persistence, as in the case of Thompson *et al.* (1993), where compact diaspores with seed weights below 3 mg were all persistent in the soil. Other attempts to construct regression models of persistence on the basis of seed weight and shape for the flora of north-west Europe were also unable to explain more than a small part of the variability of the data (Bekker *et al.*, 1998; Hodkinson *et al.*, 1998).

Why is it that some species with a size and shape that predict a high burial rate in British perennial pastures, and hence a greater capacity to form persistent banks, are transitory in dry Mediterranean pastures with a predominance of annuals? The answer may lie in the different availability of gaps in perennial- and annual-dominated pastures, and the type of dormancy displayed by the species in each system. In annual-dominated pastures, the soil is left almost bare at the end of the summer drought. Despite the paucity of information on dormancy in Mediterranean annual grassland species, we know from indirect evidence that a large proportion of species are ready to germinate when the autumn rains arrive (Table 2), either because they lack dormancy or because they are only dormant in the summer (Baskin and Baskin, 1989). There is also a proportion of species that is not capable of immediate germination. These probably include hard-seeded species, mostly legumes, which need more time to break the testa, and species with other types of dormancy. When the first autumn rains arrive, the immediate-germination species emerge easily, regardless of their size, thanks to the abundance of bare ground, while those that do not germinate immediately have different burial potentials, depending on their size. In northern European perennial pastures, on the other hand, there are relatively few immediate-germination species (Grime *et al.*, 1988), probably due to the lack of gaps. In this case, the seeds have more time to become buried, with more or less effectiveness, depending on their size. Small seeds are therefore nearly always persistent. This explains the case of small-seeded species, such as *Andryala integrifolia*, *Spergula pentandra* and *Logfia gallica*, with rapid germination, which do not form persistent seed banks. It still remains to be explained, however, why small, round-seed species with delayed germination, such as *Trifolium dubium*, do not form persistent banks. The breakdown of dormancy even when deeply buried

Table 1. Number of species, type of species, definition of persistence used, seed weight and shape range and significant relations detected in several papers that link persistence to seed weight (W) and shape (S).

Region	Species type	Number of species	Persistence classes	Seed weight range (mg)	Seed shape range	Significant relationship	Authors
North-west Europe	Herbaceous	44 seeds 53 fruits	Transient + short-term persistent, long-term persistent	0.01–23.6	0.01–0.3	W/S	Thompson et al. (1993)[a]
Sweden	Trees, shrubs, herbaceous	74	Transient + short-term persistent, long-term persistent	0.05–10.66	0.01–0.15	W/S	Bakker et al. (1996)[a,b]
Southern England	Herbaceous	35	Transient + short-term persistent, long-term persistent	0.05–24.55	0.01–0.20	S	McDonald et al. (1996)[a,b]
Australia	Trees, shrubs, herbaceous	101	Transient (immediate germination or seasonal dormancy), persistent (dormant or fire-promoted germination)	0.217– 648.9	0.0–0.2497	None	Leishman and Westoby (1998)
Central Argentina	Herbaceous	71	Transient, short-term + long-term persistent	0.01–11.5	0.01–0.274	W/S	Funes et al. (1999)[a]
New Zealand	Trees, shrubs, herbaceous	47	Transient < 2 years, persistent > 2 years	0.01–1080	0.01–0.25	W	Moles et al. (2000)
Iran	Trees, shrubs, herbaceous	311	Long-term persistent, transient + short-term persistent	0.01–1076	0.001–0.22	W	Thompson et al. (2001)
Italy	Shrubs, herbaceous	259	Transient + short-term persistent, long-term persistent	0.01–105.6	0.0014–0.3298	W/S	Cerabolini et al. (2003)
Central Spain	Herbaceous	58	Transient, short-term + long-term persistent	0.01–6.22	0.01–0.27	W	This paper

[a] In these cases, seed persistence is calculated following Bakker (1989) and Thompson (1992), while in the other papers the authors used their own methods.
[b] In these cases, variance for a population was used for the calculation of seed shape (maximum value 0.2), while the others used the variance for a sample (maximum value 0.33).

Table 2. Species capacity for immediate germination in relation to the type of seed bank. Data taken from fresh seed germination experiments after 2 months of dry storage (Espigares and Peco, 1993). Rapidly germinating species were considered to be those that required <20 days to reach 50% of the seeds germinated in experiments. Delayed germination species were considered to be those that required >20 days to reach 50% of the seeds germinated in experiments

Species with rapid germination	Seed bank type	Species with delayed germination	Seed bank type
Andryala integrifolia	t	*Aphanes microcarpa*	p
Asterolinon linum-stellatum	p	*Astragalus pelecinus*	p
Crepis capillaris	p	*Cerastium semidecandrum*	p
Galium parisiense	p	*Crassula tillaea*	p
Hypochoeris glabra	p	*Erodium cicutarium*	t
Leontodon taraxacoides subsp. *longirostris*	t	*Logfia minima*	p
Logfia gallica	t	*Trifolium arvense*	p
Mibora minima	p	*Trifolium campestre*	p
Spergula pentandra	t	*Trifolium dubium*	t
Spergularia purpurea	p	*Trifolium glomeratum*	p
Veronica arvensis	p	*Trifolium striatum*	p
Vulpia ciliata	p	*Trifolium suffocatum*	p
Vulpia muralis	p	*Veronica verna*	p
Vulpia myuros	p	*Xolantha guttata*	p

p, Species with seeds that persist in the soil for more than 1 year; t, species with seeds that persist in the soil for less than 1 year.

(Cook, 1980), predation and attack by pathogens, and the effect of the abiotic environment (Thompson, 2000), seem the most likely candidates to explain these exceptions.

In summary, small seeds seem to have a greater chance of persisting than large seeds, probably due to their facility for burial, which enables them to escape post-dispersal predation and distances them from conditions that are conducive to germination. In addition to these mechanisms, there may also be a more trivial reason: seed size is negatively related to seed numbers. This increases the probability of detection of small species in the seed bank in comparison with larger sizes, even when their likelihood of burial is the same.

Seed shape seems not to have such a good predictive value in relation to persistence, perhaps because, although seed shape is a dimensionless variable, its effect on burial is presumably dependent on size. Explanatory models constructed using seed size and shape nearly always leave a large percentage of variability unexplained. Supplementary information about seed dormancy, environmental conditions of the habitat and seed survival is still needed to design more accurate, general predictive models.

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Appendix 1

Seed weight (mg), shape (variance of seed main dimensions) and persistence in the soil of the 72 most abundant species in dry grasslands and scrubland of central Spain. Nomenclature follows Castroviejo *et al.* (1986–99), except for taxa yet to be covered, which follow Tutin *et al.* (1964–1980)

Species	Persistence	Seed weight (mg)	Seed shape
Annual species			
Aira caryophyllea	–	0.16	0.21
Andryala integrifolia	t	0.19	0.13
Anthemis arvensis	p	0.72	0.08
Aphanes microcarpa	p	0.13	0.11

Species	Persistence	Seed weight (mg)	Seed shape
Asterolinon linum-stellatum	p	0.29	0.09
Astragalus pelecinus	p	1.09	0.12
Bromus hordeaceus	–	0.61	0.26
Capsella bursa-pastoris	–	0.07	0.13
Carex divisa	t	0.36	0.07
Carlina corymbosa	t	0.29	0.18
Cerastium glomeratum	–	0.06	0.09
Cerastium ramosissimum	–	0.05	0.18
Cerastium semidecandrum	p	0.04	0.09
Convolvulus arvensis	–	0.35	0.19
Crassula tillaea	p	0.01	0.11
Crepis capillaris	p	0.18	0.19
Erodium cicutarium	t	1.45	0.20
Eryngium campestre	–	0.66	0.11
Euphorbia exigua	t	0.15	0.03
Filago lutescens	p	0.02	0.17
Galium parisiense	p	0.16	0.04
Herniaria hirsuta	p	0.05	0.01
Hypochoeris glabra	p	0.78	0.22
Juncus bufonius	p	0.03	0.04
Juncus capitatus	p	0.02	0.05
Leontodon taraxacoides subsp. *longirostris*	t	0.24	0.24
Linaria spartea	p	0.02	0.18
Logfia gallica	t	0.02	0.12
Logfia minima	p	0.02	0.12
Mibora minima	p	0.10	0.12
Moenchia erecta	p	0.04	0.02
Ornithopus compressus	p	2.47	0.16
Parentucellia latifolia	p	0.02	0.06
Plantago bellardii	t	1.13	0.07
Plantago coronopus	t	0.16	0.10
Plantago lagopus	p	0.39	0.18
Poa annua	–	0.15	0.15
Sagina apetala	–	0.01	0.13
Sanguisorba minor	–	5.08	0.07
Scirpus setaceus	p	0.05	0.02
Scleranthus delortii	t	0.28	0.02
Sherardia arvensis	–	1.56	0.06
Silene scabriflora	p	0.32	0.02
Spergula arvensis	t	0.16	0.02
Spergula pentandra	t	0.14	0.24
Spergularia purpurea	p	0.02	0.07
Teesdalia coronopifolia	p	0.22	0.09
Tolpis barbata	p	0.10	0.19
Trifolium arvense	p	0.29	0.02
Trifolium campestre	p	0.25	0.11
Trifolium dubium	t	0.38	0.10
Trifolium glomeratum	p	0.45	0.09
Trifolium scabrum	–	0.56	0.11
Trifolium striatum	p	1.57	0.01
Trifolium strictum	–	0.25	0.11
Trifolium subterraneum	t	6.22	0.02
Trifolium suffocatum	p	0.19	0.13
Veronica arvensis	p	0.13	0.20
Veronica verna	p	0.11	0.17
Vulpia ciliata	p	0.12	0.26
Vulpia muralis	p	0.10	0.26
Vulpia myuros	p	0.15	0.28
Xolantha guttata	p	0.04	0.04

Species	Persistence	Seed weight (mg)	Seed shape
Perennial species			
Agrostis castellana	t	0.26	0.19
Cynodon dactylon	t	0.10	0.13
Dipcadi serotinum	t	1.55	0.15
Festuca ampla	t	0.91	0.16
Merendera pyrenaica	t	2.04	0.01
Poa bulbosa	–	0.08	0.20
Plantago lanceolata	t	0.81	0.16
Ranunculus paludosus	t	0.21	0.03
Rumex acetosella subsp. *angiocarpus*	p	0.36	0.03

Persistence classes: p, species with seeds that persist in the soil for more than 1 year; t, species with seeds that persist in the soil for less than 1 year; –, species for which the seed bank type could not be determined due to insufficient information.