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Seed size and shape predict persistence in soil

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Summary

1. An understanding of seed persistence in the soil is important to vegetation management and weed control, but experimental collection of seed bank data is tedious and expensive. We report a rapid, simple method for predicting seed persistence in the soil. The method is tested on a range of British, mostly herbaceous, species.
2. Diaspore (seed or fruit) weight is plotted against variance of the three linear dimensions of the diaspore. All diaspores within an area of the graph defined by a maximum weight and variance are persistent in the soil. The critical weight is the same for fruits and seeds, but the critical variance of diaspore dimensions appears slightly higher for fruits. The great majority of diaspores outside this region are short lived, and the relatively few ambiguous cases can be resolved by reference to habitat.
3. The generality of the suspected underlying mechanism suggests that the method can also be applied to floras outside north-west Europe.

Key-word: seed bank
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Introduction

Informed vegetation management requires accurate and reliable information on the characteristics of many plant species. One of the most important of these relates to seed persistence in the soil. An understanding of persistent seed banks is the key to many aspects of practical land management for agriculture or conservation, and to the effective conservation of many rare species. The world's most pernicious arable weeds all possess a persistent viable seed bank (Holm *et al.* 1977). Furthermore, in the increasingly disturbed environment created by modern land use, soil seed banks are of growing importance in the management and restoration of vegetation (Keddy & Reznicek 1982; Jefferson & Usher 1987; Bakker 1989; Hodgson & Grime 1990), and it is sometimes possible to predict the response of vegetation to various types of management from a knowledge of the composition of the accompanying seed bank (Marks & Mohler 1985; Van Der Valk & Verhoeven 1988). Management which permits intermittent regeneration from a persistent seed bank is crucial to the survival of many rare or declining species (Keddy & Reznicek 1982; Rowell, Walters & Harvey 1982). A persistent seed bank often confers a degree of resilience in the face of modern intensive land use; species which are currently increasing their abundance in Britain are twice as likely to have a persistent seed bank as those which are declining (Hodgson & Grime 1990). Yet even in the comparatively well-studied European flora, data on the persistence of seeds in the soil are available for only a minority of species and are often of uncertain quality. Outside Europe even less information is available, but to offset these deficiencies experimentally is a formidable task. Collection of original seed bank data, either by germinating or extracting the seeds contained in soil samples, is prohibitively labour intensive and expensive, the results of a single investigation are frequently inconclusive, and excavation of soil from beneath rare species is clearly undesirable.

The observation has frequently been made that there is a connection between possession of a persistent seed bank and seed size and shape (Thompson & Grime 1979; Thompson 1987; Leck 1989). For reasons which are almost certainly connected with the probability of burial, persistent seeds tend to be small and compact, while short-lived seeds are normally larger and either flattened or elongate. However, a previous attempt to predict seed persistence required information on germination physiology as well as size and shape (Grime 1989). This paper reports a rapid method of predicting persistence in the soil from measurements of seed size and shape alone.

Materials and methods

Plant diaspores are usually referred to as seeds, even though many of them are in fact fruits. Here we analyse data on seeds and indehiscent, single-seeded fruits separately. Size is quantified as the air-dry weight of 100 diaspores. In order to give quantitative expression to the relationship between diaspore size, shape and persistence, a quantity is required which expresses the extent to which shape differs from sphericity. The quantity we have chosen is the variance of diaspore length, width and depth, after first transforming all values so that length is unity. This variance has a minimum value of zero in perfectly spherical diaspores, a maximum value of about 0·3 in needle- or disc-shaped diaspores, and varies very little between individual seeds of the same species. Five replicate diaspores were measured for each species. In most cases measurements were carried out on the dispersule, rather than the germinule. Thus most grass caryopses were measured with the persistent lemmas and awns with which they are normally dispersed, although the nut of *Carex flacca* was measured without its utricle. *Medicago* fruits rather than seeds were measured for the same reason. The achenes of Compositae, however, were measured without the pappus. In the few examples of species with fleshy fruits (*Arum maculatum* and *Hedera helix*), measurements were made on isolated seeds.

Seed persistence in the soil is frequently classified with respect to both longevity and size of the seed bank relative to annual seed production (Thompson & Grime 1979), but for the purposes of this paper we have adopted a simpler scheme proposed by Bakker (1989), and described in Thompson (1992). In this classification three classes of seed persistence in the soil are described: *transient,* persisting in the soil for less than 1 year; *short-term persistent,* persisting for more than 1 but less than 5 years; and *long-term persistent,* persisting for at least 5 years. In practice, the boundary between the first two classes is often rather blurred, and in this paper we attempt merely to distinguish the third, long persistent, class from the first two. Seed persistence data employed in this paper were abstracted from an unpublished (and as yet unfinished) database of the soil seed banks of the north-west European flora in preparation by K. Thompson and J.P. Bakker. This database presently contains data abstracted from *c.* 200 published sources, and infers seed persistence both from direct estimation of seed longevity and from the depth distribution of seeds in the soil (Thompson 1992). The classification of species into persistence categories in Table 1 must therefore be regarded as provisional, although we are confident that very few, if any, species will eventually turn out to have been misclassified.

Measurements were made for 97 species (44 species of seeds and 53 species of fruits, Table 1). All species are British natives or naturalized aliens, and almost all are herbaceous. The species were chosen in order to provide approximately equal numbers of fruits and seeds and of transient and persistent diaspores, together with a wide range of families, seed sizes and shapes. An additional constraint was that seeds had to be available from the collections held at UCPE.

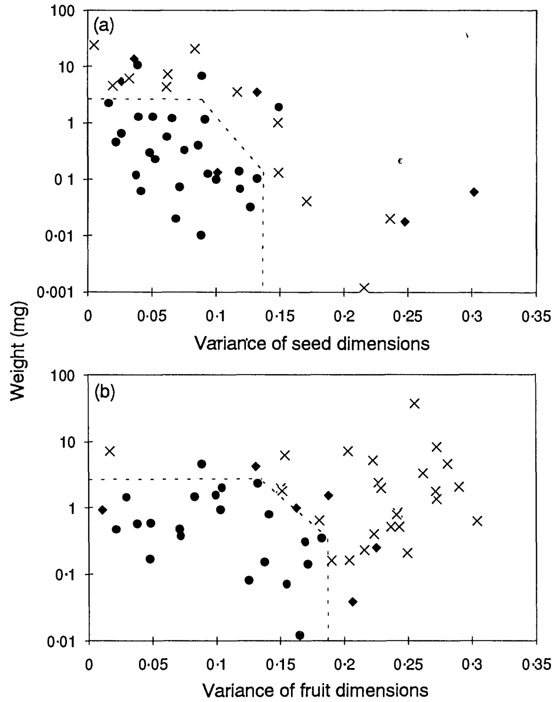

Fig. 1. Relationship between diaspore weight and variance of diaspore dimensions, in (a) 44 species of seeds and (b) 53 species of fruits. Data from Table 1. (●) Species with diaspores which persist in the soil for at least 5 years; (×) species with diaspores which persist in the soil for <5 years; (♦) species whose seed bank type cannot be determined at present owing to insufficient or contradictory data. The dashed line encloses the region within which all diaspores examined are long lived.

Results

Diaspore weight, variance and persistence are shown in Table 1, while weight is plotted against variance in Fig. 1. It is apparent that persistent diaspores, whether seeds or fruits, occupy more or less the same, unique region of the size/shape space. Compact diaspores which weigh less than 3 mg are all persistent in the soil. For more flattened or elongated diaspores, persistence appears to be determined by shape, and all diaspores above a critical variance are short lived. This critical variance was identified by eye from Fig. 1, and is very much a working hypothesis at this stage. The exact location of the line dividing transient from persistent diaspores in the lower part of Fig. 1(a) is particularly uncertain. Nevertheless there is some evidence that the critical variance is slightly higher for fruits than for seeds; the persistent fruits with a moderately high variance [which would place them in the transient region of Fig. 1(a)] are mostly grasses in the genera *Poa, Agrostis* and

Table 1. Diaspore weight, variance of three diaspore dimensions (transformed so that longest dimension is unity) and persistence in the soil for 44 species of seeds and 53 species of fruits. Nomenclature follows Clapham, Tutin & Warburg (1981). Persistence classes: (p) species with diaspores which persist in the soil for at least 5 years; (t) species with diaspores which persist in the soil for <5 years; (u) species whose seed bank type cannot be determined at present owing to insufficient or contradictory data

Seeds					Fruits				
Species	Family	Variance	Weight (mg)	Persistence	Species	Family	Variance	Weight (mg)	Persistence
Arum maculatum	Araceae	0·020	4·540	t	*Achillea millefolium*	Compositae	0·190	0·160	t
Hedera helix	Araliaceae	0·084	20·430	t	*Carlina vulgaris*	Compositae	0·188	1·530	u
Impatiens glandulifera	Balsaminaceae	0·063	7·320	t	*Centaurea scabiosa*	Compositae	0·154	6·174	t
Campanula rotundifolia	Campanulaceae	0·119	0·067	p	*Matricaria matricarioides*	Compositae	0·126	0·080	p
Arenaria serphyllifolia	Caryophyllaceae	0·041	0·061	p	*Erigeron canadensis*	Compositae	0·207	0·038	u
Cerastium fontanum	Caryophyllaceae	0·038	0·120	p	*Gnaphalium uliginosum*	Compositae	0·165	0·012	p
Silene dioica	Caryophyllaceae	0·026	0·646	p	*Hieracium pilosella*	Compositae	0·216	0·232	t
Silene nutans	Caryophyllaceae	0·048	0·298	p	*Leontodon hispidus*	Compositae	0·272	1·358	t
Silene vulgaris	Caryophyllaceae	0·066	1·199	p	*Senecio vulgaris*	Compositae	0·225	0·250	u
Spergula arvenis	Caryophyllaceae	0·022	0·449	p	*Coronopus didymus*	Cruciferae	0·072	0·472	p
Stellaria media	Caryophyllaceae	0·076	0·327	p	*Carex flacca*	Cyperaceae	0·072	0·370	p
Chenopodium album	Chenopodiaceae	0·062	0·560	p	*Agrostis capillaris*	Gramineae	0·155	0·070	p
Helianthemum nummularium	Cistaceae	0·051	1·280	p	*Anthoxanthum odoratum*	Gramineae	0·181	0·640	t
Convolvulus arvensis	Convolvulaceae	0·039	10·420	p	*Arrhenatherum elatius*	Gramineae	0·227	2·390	t
Alliaria petiolata	Cruciferae	0·132	3·451	u	*Avenula pratensis*	Gramineae	0·290	2·080	t
Arabidopsis thaliana	Cruciferae	0·069	0·020	p	*Brachypodium pinnatum*	Gramineae	0·262	3·290	t
Capsella bursa-pastoris	Cruciferae	0·094	0·123	p	*Brachypodium sylvaticum*	Gramineae	0·304	0·618	t
Cardamine hirsuta	Cruciferae	0·132	0·101	p	*Bromus erectus*	Gramineae	0·281	4·530	t
Erophila verna	Cruciferae	0·127	0·032	p	*Bromus sterilis*	Gramineae	0·273	8·370	t
Thlaspi arvense	Cruciferae	0·092	1·163	p	*Dactylis glomerata*	Gramineae	0·242	0·839	t
Drosera rotundifolia	Droseraceae	0·248	0·018	u	*Deschampsia flexuosa*	Gramineae	0·243	0·505	t
Ledum palustre	Ericaceae	0·236	0·020	t	*Desmazeria rigida*	Gramineae	0·204	0·160	t
Juncus effusus	Juncaceae	0·089	0·010	p	*Festuca ovina*	Gramineae	0·237	0·511	t
Origanum vulgare	Labiatae	0·100	0·098	p	*Festuca rubra*	Gramineae	0·241	0·780	t
Anthyllis vulneraria	Leguminosae	0·117	3·529	t	*Holcus lanatus*	Gramineae	0·183	0·350	p
Cytisus scoparius	Leguminosae	0·089	6·734	p	*Koeleria macrantha*	Gramineae	0·249	0·208	t

Table 1. (*Continued*)

Seeds					Fruits				
Species	Family	Variance	Weight (mg)	Persistence	Species	Family	Variance	Weight (mg)	Persistence
Lathyrus pratensis	Leguminosae	0·036	13·688	u	*Lolium perenne*	Gramineae	0·272	1·780	t
Lotus corniculatus	Leguminosae	0·040	1·278	p	*Poa annua*	Gramineae	0·170	0·306	p
Ononis repens	Leguminosae	0·027	5·427	u	*Poa trivialis*	Gramineae	0·172	0·140	p
Trifolium dubium	Leguminosae	0·053	0·227	p	*Ballota nigra*	Labiatae	0·103	0·913	p
Vicia cracca	Leguminosae	0·005	23·661	t	*Galeopsis tetrahit*	Labiatae	0·089	4·600	p
Vicia hirsuta	Leguminosae	0·017	2·190	p	*Stachys sylvatica*	Labiatae	0·030	1·430	p
Allium ursinum	Liliaceae	0·061	4·270	t	*Teucrium scorodonia*	Labiatae	0·011	0·924	u
Hyacinthoides non-scripta	Liliaceae	0·032	6·170	t	*Thymus praecox*	Labiatae	0·048	0·167	p
Narthecium ossifragum	Liliaceae	0·302	0·060	u	*Medicago lupulina*	Leguminosae	0·100	1·556	p
Chamerion angustifolium	Onagraceae	0·171	0·041	t	*Melilotus altissima*	Leguminosae	0·131	4·223	u
Epilobium hirsutum	Onagraceae	0·118	0·138	p	*Polygonum aviculare*	Polygonaceae	0·083	1·450	p
Oxalis acetosella	Oxalidaceae	0·148	1·010	t	*Rumex acetosella*	Polygonaceae	0·022	0·465	p
Plantago lanceolata	Plantaginaceae	0·150	1·891	p	*Ranunculus repens*	Ranunculaceae	0·133	2·320	p
Pyrola minor	Pyrolaceae	0·216	0·001	t	*Dryas octopetala*	Rosaceae	0·224	0·400	t
Digitalis purpurea	Scrophulariaceae	0·072	0·072	p	*Potentilla erecta*	Rosaceae	0·049	0·580	p
Euphrasia officinalis	Scrophulariaceae	0·149	0·130	t	*Filipendula ulmaria*	Rosaceae	0·163	0·990	u
Linaria purpurea	Scrophulariaceae	0·101	0·133	u	*Galium aparine*	Rubiaceae	0·017	7·250	t
Viola arvensis	Violaceae	0·087	0·400	p	*Galium saxatile*	Rubiaceae	0·038	0·560	p
					Anthriscus sylvestris	Umbelliferae	0·223	5·180	t
					Chaerophyllum temulentum	Umbelliferae	0·229	1·989	t
					Conium maculatum	Umbelliferae	0·104	2·027	p
					Daucus carota	Umbelliferae	0·142	0·773	p
					Foeniculum vulgare	Umbelliferae	0·150	1·990	t
					Heracleum sphondylium	Umbelliferae	0·203	7·167	t
					Myrrhis odorata	Umbelliferae	0·256	37·321	t
					Torilis japonica	Umbelliferae	0·151	1·796	t
					Urtica dioca	Urticaceae	0·138	0·152	p

Holcus. While the region of the graph within which all diaspores are persistent is relatively well defined, it is not true that all diaspores outside this region are short lived. Large, more or less spherical diaspores in particular may be either persistent or not. Here habitat seems to be the best guide. Species with large, round, short-lived diaspores (seeds or fruits) are all commonest in woodland, hedgerows or tall herb communities (e.g. *Vicia cracca*, *Hyacinthoides non-scripta*, *Galium aparine*), while those with persistent diaspores are plants of disturbed arable (*Convolvulus arvensis*, *Galeopsis tetrahit*) or fire-prone habitats (*Cytisus scoparius*) (Grime, Hodgson & Hunt 1988).

A strong phylogenetic effect is also apparent in Table 1. Families in which the diaspores are normally small and compact (e.g. Caryophyllaceae, Cruciferae) are generally persistent, while families in which the diaspores are large and either flattened or elongated (e.g. Umbelliferae) are mostly short lived. These trends are also evident within families; small, compact grass and composite fruits are persistent, while their larger relatives are not.

Discussion

DIFFERENCES BETWEEN SEEDS AND FRUITS

Some interesting differences between seeds and fruits emerge from Fig. 1. Seeds, which until shedding are enclosed within the protective walls of the ovary, encompass a rather narrower range of shapes than fruits. However, there are some important exceptions. The four species on the right of Fig. 1(a) are all small-seeded plants of unproductive, infertile habitats (*Pyrola minor, Narthecium ossifragum, Ledum palustre, Dorsera rotundifolia*). The significance, if any, of elongated seeds in these types of habitats is unknown.

The data illustrate that the likelihood of a diaspore persisting in the soil is determined to a large extent not by its developmental origin (i.e. whether it is a seed or fruit), but by its size and shape. Within the sample studied more seeds than fruits formed persistent seed banks simply because seeds, on average, are more compact than fruits. Size seems to differ rather little between the two groups (Fig. 1), although the upper and lower size limits are occupied by a fruit and a seed respectively.

PREDICTING PERSISTENCE

On the basis of the relatively small sample of the British, mostly herbaceous, flora examined here it seems that seed size and shape can predict diaspore persistence in the soil. Additional habitat data seem capable of resolving those few cases where any ambiguity remains. The mechanism underlying the relationship in Fig. 1 is almost certainly ease of burial, linked to the relative freedom from predation conferred by burial (Thompson 1987). Most likely mechanisms of burial (penetrating cracks in soil, being washed into soil by rain, ingestion by earthworms) will operate more effectively on small, compact diaspores. Exceptions include self-burial, e.g. in *Avena* and *Erodium* (Stamp 1984), and ant dispersal. *Avena fatua* is one conspicuous example of a large, elongated diaspore with a persistent seed bank which fails to conform to the relationship in Fig. 1(b). Many genera with an elaiosome (e.g. *Luzula*) have relatively small, round seeds consistent with Fig. 1, while some with large, rounded seeds are also persistent (e.g. *Ulex*). We are not aware of any species which combines ant dispersal with a transient seed bank, but more work is needed to determine the exact relationship between ant disperal and seed persistence. However, outside these small and perhaps atypical groups, the work of Peart (1984) has demonstrated that small diaspores not only become buried more easily, but that they also require burial for successful seedling establishment.

Of course seed persistence in the soil is not wholly determined by seed size and shape. Germination requirements, dormancy mechanisms and resistance to pathogens also contribute to persistence. For example, phenolic defence compounds are implicated in prolonged seed persistence (Kremer 1986; C. Moss, G.A.F. Hendry, K. Thompson & P.C. Thorpe, unpublished observations). Nevertheless seeds do not persist for long periods on the soil surface, and burial is clearly an essential prelude to persistence. Artificial burial nearly always overestimates the potential for persistence in the soil. For instance Pons (1989) commented on the results of a seed burial experiment: 'The results indicate that *Molinia caerulea* seeds can survive for long periods in the soil, but the author knows of no records of persistent seed banks of this species'. Under normal circumstances diaspores of some species frequently become buried, while others do so only rarely. Those diaspores which often become buried consequently experience different selection pressures from those which do not, and thus probability of burial has come to be associated with a suite of other characteristics concerning germination, dormancy and defence chemistry. Measurements of seed shape and size, which admittedly affect only the first essential step in seed persistence, can perhaps therefore prove a surprisingly good guide to subsequent seed persistence. It remains to be determined whether mechanisms whereby seeds become incorporated into a persistent seed bank are similar world-wide, but if so, we anticipate that this method of predicting seed persistence can be easily extended to other floras and climates.

Acknowledgements

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