REVIEW

Seed banks and seed dispersal: important topics in restoration ecology[§]

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INTRODUCTION

Restoration ecology deals with the scientific and ecological background of nature management practices aiming at the re-establishment of plant species which have disappeared. As we focus on semi-natural landscapes, these disappearances can be

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caused by intensification of agricultural practices or cessation of human interference. Nature management practices attempt to re-establish the often species-rich original plant communities by the removal of nutrients (sod cutting, hay-making, grazing) after eutrophication (Schiefer 1984; Bobbink & Willems 1991; Oomes 1992; Bakker & Olff 1995), rewetting after severe drainage (Grootjans & Van Diggelen 1995; Koerselman & Verhoeven 1995), scrub and woodland removal (clear cutting, grazing) after bush encroachment (Willems 1988; Poschlod & Jordan 1992).

The re-appearance of plant species may depend on their persistence in the soil seed bank as a 'memory' of the original plant community. If the species has been lost from the persistent soil seed bank, it has to be transported to the site of re-appearance by some vector, e.g. wind, water, animals, man, and incorporated into the fresh seed bank. The site of re-appearance after emerging either from the old seed bank or from the fresh seed bank has to be proven to be a safe site from the point of view of abiotic and biotic conditions (Harper 1977). Without the presence or arrival of seeds no re-appearance in the established vegetation will be possible. For this reason we focus on seed bank dynamics and seed dispersal in restoration ecology. We will present (i) a review of current methods of seed bank analysis including estimations of longevity and density, and (ii) the state of the art on methods and results of seed dispersal.

SEED BANKS AND SEED DISPERSAL

The written evidence on soil seed banks begins with the observations of Darwin (1859): 'I took in February three table-spoonfuls of mud from three different points, beneath water, on the edge of a little pond; this mud when dry weighed only 6 3/4 ounces; I kept it covered up in my study for six months, pulling up and counting each plant as it grew; the plants were of many kinds, and were altogether 537 in number; and yet the viscid mud was all contained in a breakfast cup'. Since that time very many papers on seed bank studies have appeared, and Harper (1977) made some generalizations suggesting that (i) long-lived seeds are characteristic of disturbed habitats, (ii) most long-lived seeds are annuals or biennials, (iii) small seeds tend to have much greater longevity than large ones, (iv) aquatic plants may have great seed longevity, and (v) seeds of mature tropical forests have very short lives. For the purpose of this review we will mainly deal with longevity of seeds of temperate plant species.

There are a few recent reviews on the ecology of seed banks (Roberts 1981; Leck *et al.* 1989; Thompson 1992), and some compilations of seed bank references (Vyvey 1989a,b; Bernhardt & Poschlod 1993) and a compilation on seed longevity (Milberg 1990). These compilations feature a recent explosion of new data on buried seed banks. There is hardly a single area of modern plant ecology in which seed banks are not implicated, many of them (e.g. recolonization after forest fire and volcanic eruption, prediction of marsh vegetation after a drawdown, succession, endangered species conservation and spread of invasive aliens) with direct relevance to restoration ecology.

There are some classifications of seed dispersal derived from a morphological point of view (Müller-Schneider 1977, 1986; Luftensteiner 1982; Van der Pijl 1982). The pity of these systems is that in most cases they do not include the fact that there are many ways of dispersal of one seed and they lack data on dispersal distances. However, this is important to know with respect to restoration management even though Silvertown & Lovett Doust (1993) remark: 'Like the end of the rainbow, the tail of the seed dispersal curve is impossible to reach' and further 'The occasional seed is carried by chance events

quite extraordinary distances, but these seeds are so few that we can only ever know where they end up when they attract attention by starting a new population in an alien site'. Furthermore, we lack information about if and how a distinct management does disperse seeds (Poschlod 1996b). Seeds can be dispersed by grazing animals and cutting machineries, but this knowledge is not yet incorporated into restoration management. Therefore a classification on dispersal with respect to restoration management has to be developed in the future.

Poschlod *et al.* (1995) used a classification which included type of diaspore (seed, type of fruit), type of structure, type of dispersal and possible long-distance dispersal by different means to analyse the viability and regeneration of populations after clear-cutting on fallow or afforested calcareous grassland sites. They showed, in an analysis of a regional calcareous grassland flora of 187 species, that only four species are regarded as adhesive or 'acanthochoric' according Dansereau & Lems (1957), which is the most likely long-distance dispersal possibility apart from wind dispersal. However, field studies showed that 54 species of this flora were transported on the wool of sheep and 37 species by hoofs (see also Fischer *et al.* 1995, 1996). Only a few studies compare the structure and derived dispersal type of seed with the real dispersal in the field. Therefore, we need more ecological field studies in the future.

SEED BANK CLASSIFICATION

Naturally buried seeds

Until now there has been no single source of data on seed persistence in individual species. Recently Thompson *et al.* (1996) published a database on seed banks for North West Europe, and many of the topics mentioned in this review are covered in more detail there. The first problem to be solved in comparing literature on soil seed banks is a standardized classification of persistence. It has become customary for seed banks to be classified with reference to the scheme proposed by Thompson & Grime (1979). There are good reasons for not doing so, however. The Thompson & Grime scheme was proposed on the basis of the observed behaviour of seeds in the soil as revealed by a programme of seasonal sampling over a period of 1 year. This approach suffers from a number of disadvantages, but for the purposes of restoration ecology the chief one is that the two transient and two persistent seed bank types distinguished tell us too little about longevity. For practical purposes, as Vyvey (1986), Pfadenhauer & Maas (1987) and Bakker (1989) have pointed out, we would like to know whether seeds are likely to persist beneath plant communities which have been destroyed or degraded at some time in the past. We have therefore adopted a modified version of the seed bank classification proposed by Bakker (1989; Bakker *et al.* 1991) and described in Thompson (1992, 1993), which defines three types:

Transient. Species with seeds which persist in the soil for less than 1 year, often much less. This corresponds directly to Thompson & Grime's transient types I and II, and acknowledges that for many species the two types are inseparable.

Short-term persistent. Species with seeds which persist in the soil for at least 1 year, but less than 5 years. This type, originally described by Bakker (1989) as 'persistent', may play a role in the maintenance of plant populations after poor seed setting in a dry year or after cutting too early.
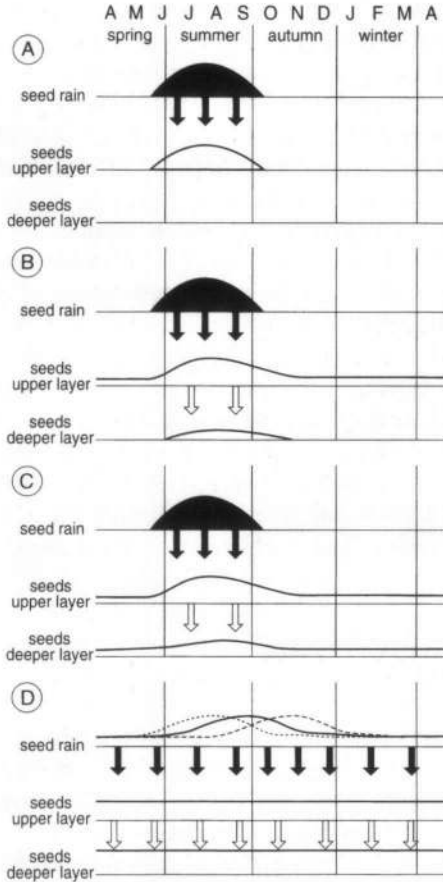
Fig. 1. Four types of seed bank (after Poschlod & Jackel 1993), defined on the basis of seasonal dynamics of the seed rain and seeds in the upper and deeper soil layers. For more detailed description see text.

Long-term persistent. Species with seeds which persist in the soil for at least 5 years. This type, originally termed 'permanent' by Bakker (1989), is the only one likely to contribute to the regeneration of destroyed or degraded plant communities in the framework of restoration ecology.

The cut-off point of 5 years between the latter two types is admittedly arbitrary, and was chosen largely because it is the end point of a significant number of burial experiments.

The above classification is admittedly very crude, and Poschlod & Jackel (1993) published a further elaboration of the classification into transient, short-term persistent and long-term persistent types, which relies on the dynamics of the seed bank and seed rain (Fig. 1). They recognize four types:

A *Transient.* Seeds confined to the upper soil layer, and only for a short period after seed rain (persistent for <1 year).

B *Transient.* Seeds in the surface soil all year, with a distinct peak following seed rain, and some seeds in the lower soil layer (persistent for 1 or 2 years).

C *Persistent.* Many seeds in the surface soil and some seeds in the lower layer all year, with a distinct peak following seed rain in the upper layer and a much smaller peak in the lower layer (persistent for some years to some decades).

D *Persistent.* At least as many seeds in the lower soil layer as in the upper layer all year, and no distinct peak after seed rain (persistent for several decades).

This scheme, by combining seasonal behaviour with depth distribution, is certainly a refinement of previous seed bank classification systems. Unfortunately, like all such systems, it suffers from the drawback that the data needed to apply it to most species are simply not available.

Studies of naturally buried seeds may provide direct evidence of seed longevity. This evidence usually takes the form of species which are no longer present in the community but are still present as seeds in the soil. Provided the last time the species grew at the site can be ascertained with reasonable certainty, buried seeds can often be dated with moderate accuracy. Two common examples of communities in which this is normally possible are weed seeds beneath formerly arable grasslands, and seeds of light-demanding species beneath woodlands and plantations of known age. Other direct sources of evidence of seed longevity include seeds buried beneath volcanic ash or buildings of known age, seeds in stored topsoil and prevention of fresh seed input by close cutting or the application of herbicides. All these sources, of course, normally provide evidence only of *minimum* potential longevity.

Another valuable but less direct source of evidence is the vertical distribution of seeds in the soil. There is abundant evidence that deeply buried seeds are older than shallow ones, allowing the ratio of deeply buried to shallow seeds to be used as an index of seed longevity. This approach, used with care, has been shown to produce results which are broadly comparable with those of more direct measures of longevity (Bakker 1989), although it is not without its critics (Poschlod 1993). A potential obstacle to the general application of the method is the wide variety of soil depths employed by different investigators. Thompson *et al.* (1996) took the top 5 cm as surface soil, as 4 cm or 5 cm are the most popular sampling depths of the top layer in those cases where more than one layer is sampled. It is worth mentioning that in 80% of studies on seed banks the authors sampled only one layer.

In an attempt to formalize the above criteria into a more usable form, Thompson *et al.* (1996) have devised a key to seed bank types (Fig. 2). The key applies only to naturally buried seed data of the most common type; that is, an enumeration of seeds in soil sampled on a single occasion. The key uses both direct and indirect evidence of longevity, but gives priority to direct evidence. Further conservative estimations on criteria to use publications for a review and details and comments on the usage of the key are given by Thompson *et al.* (1996).

Artificially buried seeds

Why can the problems concerning seed bank classification not simply be solved by taking the results of artificial burial experiments? The results of artificial burial experiments have a beguiling air of authority and precision, but must be interpreted with caution. Artificial burial bypasses the crucial role of natural burial mechanisms, and therefore is prone to serious exaggeration of seed longevity. It is probably safe to say that if a species proves to be short-lived when artificially buried, then it will also be short-lived under more natural conditions. The converse, however, cannot be relied
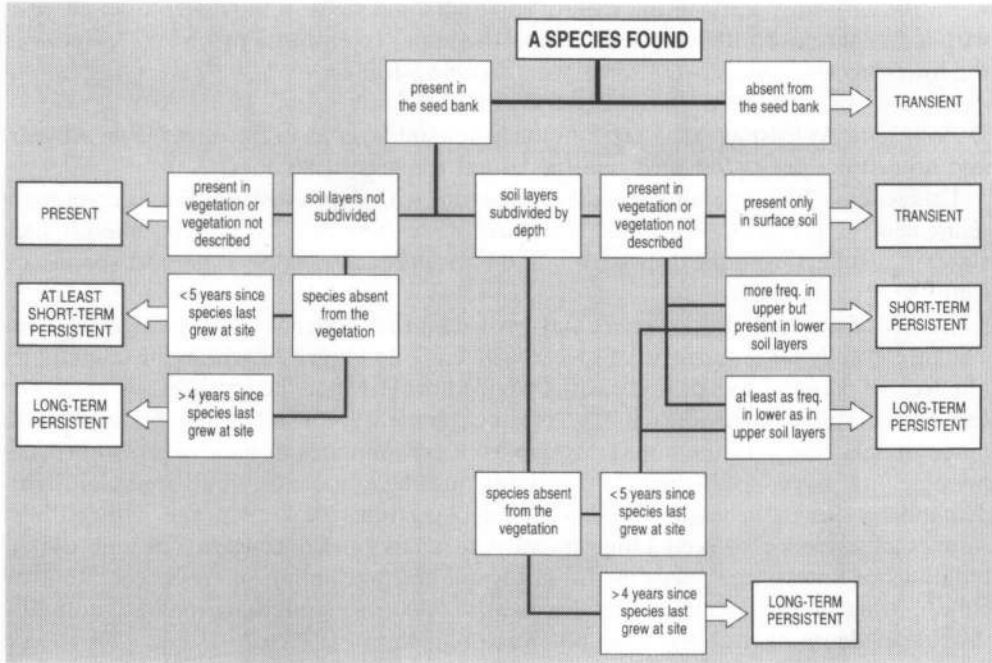
Fig. 2. A dichotomous key to the three seed bank types employed in the database of Thompson *et al.* (1996): transient, short-term persistent and long-term persistent. For definitions of seed bank types see text.

upon, and it is generally true that the results of long-term burial experiments are close to the upper limit of longevity recorded for many species.

A second difficulty with artificial burial experiments is that, with a very few notable exceptions, the period of burial is relatively short. This is inevitable; the funding problems encountered by seed burial experiments are no different from those which beset all long-term ecological research. For many species, meaningful burial experiments need to continue beyond the working life of a single experimenter. For these reasons, burial experiments are much better at separating short from long-lived seeds than they are at determining the potential longevity of the latter.

Artificially buried seeds are also, to varying degrees, protected from the attentions of potential predators. It is known that seeds on the soil surface are eaten or dispersed by animals such as mice (Leutert 1983), birds (Kollmann 1994) or beetles (Bernhardt 1995). However, it is uncertain how far seed banks are depleted by predation, but buried seeds are ingested in large numbers by earthworms, and many are either killed by this treatment, are exhumed and stimulated to germinate (Van Tooren & During 1988; Thompson *et al.* 1994), or are transported vertically (Willems & Huijsmans 1994).

SEED BANK DENSITY AND LONGEVITY

Seed bank analysis

Two categories of methods are commonly used to analyse the composition of the soil seed bank; seed separation and seedling emergence. Seeds can be separated by flotation, by washing and sieving, or by both. The extraction of seeds by washing and sieving

includes the concentration of seeds by washing soil samples through sieves of various mesh sizes (Barralis *et al.* 1988; Bernhardt & Hurka 1989; Gross 1990; Ter Heerdt *et al.* 1996). In seedling emergence methods, the samples are spread in trays and kept under conditions known (or suspected) to promote the germination of as many species and individuals as possible. The period of seedling emergence in the trays largely depends on the thickness of the layer spread on the sterilised subsoil, which can vary from one cm (or less) up to 5 cm. The period of seedling emergence is prolonged by thick sample layers. Such long seedling emergence periods also imply large glasshouses or open cages, which are not always available. The space problem can be countered by a reduction of the bulk of the sample by sieving (Brenchley & Warington 1930; Kropác 1966; Barralis & Chadoeuf 1980). Ter Heerdt *et al.* (1996) showed that sieving with a 0·2 mm mesh reduced the bulk of the soil by 55–85% depending on soil type, indicating the potential area saving in the glasshouse. Some authors compare the results of seedling emergence from soil samples in the glasshouse or in an open cage with the results from seedling emergence in the field, after removing the vegetation by various means (Pfadenhauer & Maas 1987; Graham & Hutchings 1988; Bakker *et al.* 1996). Several authors cited by Hutchings (1986) recommended that, if the objective is to determine the species composition of the seed bank, 0·8 litre was necessary for early successional vegetation, 1–1·2 litres for grasslands, and 8–12 litres for climax woodland, reflecting the generally much lower seed density beneath the latter community. In every case the number of samples required is strongly influenced by the mean density; sparse species require more samples for any given level of precision.

In summarizing recommended methods of seed bank sampling, Thompson *et al.* (1996) largely follow the conclusions of Ter Heerdt *et al.* (1996), who used a combined method of concentrating soil samples and germination in the glasshouse. The advantage of standardized sampling of the seed bank is the possibility of comparing the results from different studies. Details about methods on seed bank sampling can be found in the North West European seed bank database (Thompson *et al.* 1996).

Many of the publications in the database from Thompson *et al.* (1996) include data from more than one site, the same site sampled in different years, or burial experiments at various depths or in different soils. They treat each such record separately, and thus their total of 275 publications contains 1936 *source records*. Since each source record normally contains data on more than one species, the database contains a total of 21 071 *species records*.

The majority of seed bank studies were carried out in grassland (75% of which were unfertilized), and the majority of these records concern managed grassland, most often by grazing and less often by hay-making. Arable fields comprise the only other large habitat category, reflecting the continuing interest in the behaviour of buried weed seeds. There are relatively few data available from woodland, heathland, dunes, (salt) marshes, arctic/alpine and aquatic communities.

Taxonomic relationships

The North West European region harbours species from 120 higher plant families, of which 98 are represented in the database (Thompson *et al.* 1996). About half the 22 families without any information are primarily woody. The Orchidaceae were omitted from the database as members of this family are not recorded by any source. Whether this reflects the genuine absence from the seed bank, or a failure to provide the

right germination conditions, is unknown. Otherwise no large family is absent from the database. For a typical large family, data for about half the species present in North West Europe are available. This is true, for instance, of the Caryophyllaceae, Compositae, Gramineae, Leguminosae, Ranunculaceae, Scrophulariaceae and Umbelliferae. Representation of smaller families depends to a large extent on their abundance in the agricultural habitats which have been the main focus of seed bank investigation. Not surprisingly, therefore, the Urticaceae, Plantaginaceae and Polygonaceae are the top three families in terms of records per species. In contrast, some medium-sized families which are mostly confined to semi-natural, unproductive habitats, such as the Liliaceae, Gentianaceae and Saxifragaceae, are under-represented in the database. Aquatic families, such as the Alismataceae and Potamogetonaceae, are generally poorly represented. There is a clear tendency for small-seeded families as Juncaceae to have the highest proportion of long-term persistent records (Table 1).

The list of species of the North West European flora includes 2568 taxa, but seed bank data are available for only 1189 (Thompson *et al.* 1996). The quantity of data available for individual species also varies enormously; 250 species are represented by a single record. The top 100 species ranked by their number of records in the database consist almost entirely of species from productive grassland and arable habitats. The top 30 species are shown in Table 2. Extremely few species from heathland and woodland are represented in the top 100, and one has to travel to number 45 before encountering the first of these (*Calluna vulgaris*) (Thompson *et al.* 1996). The great majority of species in the top 100 tend to have a long-term persistent seed bank.

Restoration ecologists are often interested in rare and endangered species. For the Dutch flora we calculated that seed bank records exist for only about 25% of the 600 Red List species. Hence we have no information at all on seed bank longevity of about 75% of the Red List species in The Netherlands. The situation is very similar for the British flora. The relationship between abundance in the landscape and available seed bank data (Thompson *et al.* 1996) is quantified in Fig. 3; clearly, species are abundant in the database because they are abundant in the landscape, and we cannot rely on the present pattern of seed bank studies to tell us much about rare plants.

Seed density

Data on seed density show a large variation (Thompson *et al.* 1996). The majority of species have seed densities below 500 seeds m^{-2} (Fig. 4). Average densities up to 5000 seeds m^{-2} are, however, not exceptional, and maximal densities of 300 000–500 000 seeds m^{-2} of a single species have been reported. A summary of the top 15 species according to their average seed densities is given in Table 3. Thompson *et al.* (1996) present the summary for three frequently sampled depths (0–3 cm, 0–5 cm, 0–10 cm) since density obviously depends on the total volume sampled. Not surprisingly, therefore, the average densities of the top 25 species tend to increase if a greater depth is taken into account. Also the lowest and highest densities recorded for a particular depth can vary enormously, e.g. 88–17 750 m^{-2} for *Agrostis capillaris* and 38–89 063 m^{-2} for *Juncus bufonius* in the 10 cm layer (Table 3). This variation is an inevitable consequence of the compilation of records with varying seed rain, soils and different storage conditions for the survival of seeds. Most of the species in Table 3 have small or very small seeds.

Table 1. Example of the representation of complete families in the database

Family	Total number of species in NW Europe	Number of species represented in the database	Number of transient records	Number of short-term persistent records	Number of long-term persistent records	Total number of records in the database
Campanulaceae	27	17	55	23	7	138
Compositae	244	134	1029	517	218	2249
Juncaceae	53	29	151	344	225	968
Umbelliferae	105	46	324	98	34	525
Violaceae	24	11	49	37	19	182

Table 2. Top 30 species ranked after the number of records in the database

| Species	Total number of records	Species	Total number of records
Trifolium repens	326	*Agrostis capillaris*	187
Juncus effusus	278	*Agrostis stolonifera*	180
Holcus lanatus	267	*Juncus bufonius*	179
Cerastium fontanum	265	*Anthoxanthum odoratum*	172
Poa trivialis	254	*Dactylis glomerata*	166
Ranunculus repens	250	*Urtica dioica*	164
Stellaria media	247	*Capsella bursa-pastoris*	146
Poa pratensis	233	*Anagallis arvensis*	140
Festuca rubra	224	*Polygonum aviculare*	139
Taraxacum officinale	221	*Sagina procumbens*	135
Chenopodium album	207	*Achillea millefolium*	129
Rumex acetosa	204	*Ranunculus acris*	127
Plantago major	198	*Cirsium arvense*	125
Poa annua	197	*Trifolium pratense*	120
Plantago lanceolata	194	*Lolium perenne*	119
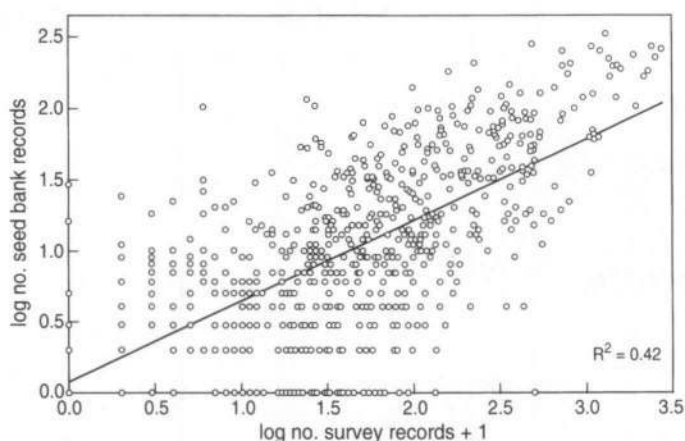
Fig. 3. Relationship between number of records in the seed bank database published by Thompson *et al.* (1996) and abundance in central England. Abundance data are derived from Hodgson *et al.* (1995) and unpublished UCPE survey data, and represent frequency of occurrence in a survey of over 10 000 quadrats. *n*=670 species.

Seed longevity

The maximum longevity of seeds is known to exceed 100 years for only a few species (Thompson *et al.* 1996). It must be emphasized, however, that data on longevities measured in centuries or many decades are available only exceptionally, and do not always seem to be reliable. Some sources occasionally provide evidence of apparently very great longevity in buried seeds, and great care must be taken to guarantee that such reports are not the result of contamination by seeds of more recent origin. Contamination of soil samples by wind-borne or surface seed is always a potential problem, of course, but it becomes much more serious when, as with very old seeds, the likely density
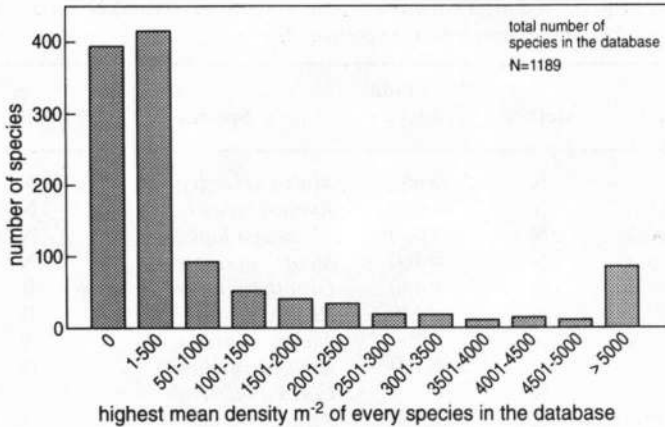
Fig. 4. Distribution of highest mean density of seeds m^{-2} irrespective of volume sampled.

Table 3. Species ranked after higest average density per metres squared

Depth: 10 cm	Lowest density (m^{-2})	Highest density (m^{-2})	Average density (m^{-2})	Number of records
Spergularia marina	488708	488708	488708	1
Juncus effusus	2444	97032	41522	8
Calluna vulgaris	26702	26702	26702	1
Urtica dioica	526	67979	23819	5
Bromus hordeaceus	18110	18110	18110	1
Glyceria fluitans	1248	38376	17957	6
Cardamine pratensis	468	32448	11249	3
Lolium multiflorum	11200	11200	11200	1
Salicornia europaea	3360	18600	10980	2
Typha latifolia	9510	9510	9510	1
Hypericum maculatum	1052	31944	7806	10
Hypericum perforatum	1404	12090	6747	2
Poa trivialis	2704	11180	6479	5
Alopecurus geniculatus	1508	16328	6023	6
Agrostis capillaris	88	17750	5237	34

of genuine seed is low. A good discussion of records of great longevity in buried seeds can be found in Priestley (1986). The top 100 species ranked by their maximum longevity in the database indicates that only 27 data are derived from burial experiments. The top 30 species are shown in Table 4. The majority of data have been derived from historical records, frequently from soil underneath buildings, requiring an assumption that no fresh seed input has taken place. If we accept this assumption, the maximal longevity of many species is greater than presented in the review by Milberg (1990).

Thompson *et al.* (1996) do not consider interspecific variability in viability of seeds after exhumation, but this can be very high, e.g. *Verbascum blattaria* had 42% viable seeds after 100 years of burial, whereas for *Verbascum thapsus* this was only 2% (Kivilaan & Bandurski 1981); *Datura stramonium* had 91% viable seeds after 39 years of burial, *Apium graveolens* only 1% (Toole & Brown 1946). Different authors often report

Table 4. Top 30 species ranked after their maximum longevity (method N, data from soil samples of field sites; method B, data from burial experiments)

Species	Method	Maximum longevity	Species	Method	Maximum longevity
Lamium album	N	>660	*Malva sylvestris*	N	>90
Lamium purpureum	N	>660	*Rubus idaeus*	N	>87
Taraxacum officinale	N	>660	*Medicago lupulina*	N	>80
Glechoma hederacea	N	>460	*Sinapis arvensis*	N	>80
Trifolium repens	N	>460	*Oenothera biennis*	B	80
Carex bigelowii	N	>200	*Rumex crispus*	B	80
Luzula parviflora	N	200	*Juncus effusus*	N	>73
Sambucus nigra	N	>160	*Calluna vulgaris*	N	>68
Galium saxatile	N	>120	*Carex pilulifera*	N	>68
Juncus conglomeratus	N	>100	*Atriplex patula*	N	>58
Malva pusilla	B	>100	*Chenopodium rubrum*	N	>54
Verbascum blattaria	B	>100	*Elatine triandra*	B	>50
Verbascum thapsus	B	>100	*Gnaphalium uliginosum*	N	>50
Veronica officinalis	N	>100	*Ranunculus sceleratus*	B	>50
Hyoscyamus niger	N	>90	*Rorippa islandica*	N	>50

Table 5. Species records of *Viola canina* (Violaceae). Information known about 11 species of 24 in this family (method N, data from soil samples of field sites; method B, data from burial experiments)

Number of species records	Seed bank type	Longevity	Minimum density (m⁻²)	Maximum density (m⁻²)	Mean density (m⁻²)	Depth (cm)	Method
1	Transient		0	0	0	6·5	B
1	Transient		0	0	0	10	N
1	Transient		0	0	0	12	N
2	Transient		0	0	0	10	N
1	Short-term persistent		32	32	32	30	N
2	Short-term persistent		263	1113	688	10	N
5	Short-term persistent		1	23	7	5	N
1	Long-term persistent	>40	80	80	80	20	N
2	Long-term persistent		205	292	249	10	N
2	Present		526	1169	848	10	N
6	Present		50	1525	648	10	N

wide variability in the longevity of a single species, e.g. 4% after 11 years (Salzmann 1954) and 83% after 39 years (Toole & Brown 1946) for *Solanum nigrum*.

The seed bank database presented by Thompson *et al.* (1996) reveals many apparent inconsistencies, as shown in the example of *Viola canina* (Table 5). This variability is the main reason why the authors did not classify each individual species with a definite label of 'transient', 'short-term persistent' or 'long-term persistent'. Moreover, they wanted to present the original data of individual species to give the readers the opportunity to draw their own conclusions. We will make an attempt to integrate the individual data of a species applied for whole plant communities by adding the number of records of all
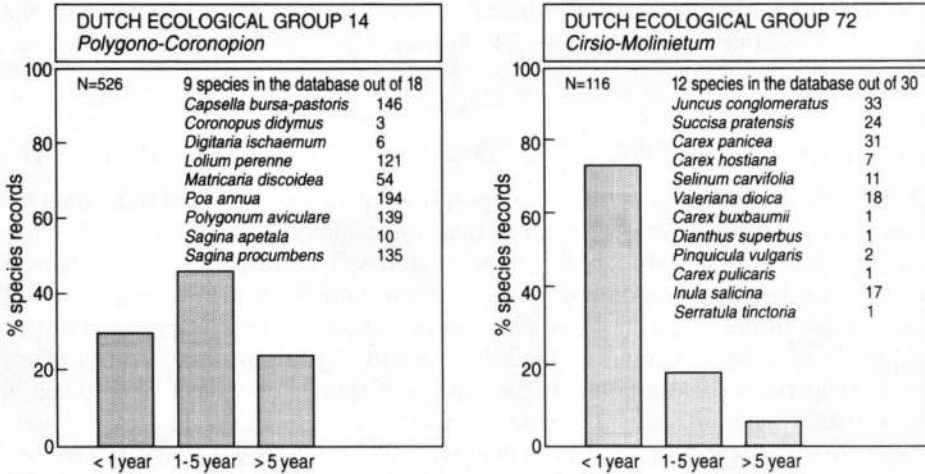
Fig. 5. Spectra of percentages of species records indicating various types of seed bank derived from the database by Thompson *et al.* (1996) of the pioneer community *Polygono-Coronopion* and the species-rich semi-natural grassland community *Cirsio-Molinietum*.

individual species available in that plant community. Examples are presented for the common *Polygono-Coronopion* (including relatively more species and records) and rarely occurring *Cirsio-Molinietum* (including relatively fewer species and records) in The Netherlands. The message for restoration ecologists is that the rare and endangered *Cirsio-Molinietum* community contains a high proportion of species having a transient seed bank (Fig. 5).

Seed shape and weight

The longevity of seeds may also be assessed by their size and shape (Harper 1977; Thompson & Grime 1979; Leck 1989; Thompson *et al.* 1993). Persistent seeds tend to be small and compact, whereas transient seeds seem to be larger (heavier) and either flattened or elongate. The proposed basis of this relationship is that larger seeds do not penetrate into the deeper soil layers, whereas small and rounded seeds do so easily.

Species can be classified according to diaspore (whether true seed or fruit) size and shape. The general principle is that the diaspore is measured with all its permanent attached structures, i.e. those which may reasonably be expected to influence its burial. Thus *Carex* spp. are measured without their utricles and Composites are measured without their pappus. Grass lemmas and awns are included if firmly attached to the caryopsis. The size of a diaspore is quantified as the air-dry weight. The shape is quantified by the extent to which it differs from a sphere, using the variance of diaspore length, width and height, after transforming all values so that length is unity. This variance has a minimum value of zero in perfectly spherical seeds, and a maximum of 0·2 in needle or disk-shaped diaspores. Variance is the square of the standard deviation. The standard deviation is calculated using *n*, being the whole population of length, width and height of seeds, and not *n*-1, being a sample of the population. Thompson *et al.* (1993) used *n*-1, and hence calculated a maximum value of 0·3 of the diaspores. The variance varies little between individual seeds of the same species. The variance in shape of diaspores of each species is estimated on the basis of measurements of five diaspores. Species classified as having a transient or short-term persistent seed bank are

found to have seeds which are significantly heavier, with a larger variance of shape than species reckoned among the long-term persistent seed bank type (Bakker *et al.* 1996).

RELATIONSHIP BETWEEN SEED LONGEVITY AND DISPERSAL

Both dispersal in space and in time (incorporation into a seed bank) of individual plant species may determine the success of management aimed at restoration of a target vegetation. Knowledge about both temporal and spatial dispersal of a species will probably give the best estimation of chances of re-establishment (Poschlod *et al.* 1995). Moreover, for future maintenance of restored vegetation the relation between dispersal strategies in relation to habitat dynamics of certain vegetation types may be of great interest. Dispersal and seed bank characteristics of species may have to be taken into account within the management regime.

There are some generalizations to be made regarding dispersal strategy, related to the extent to which the environment for establishment can be 'predicted' (Harper 1977, Fenner 1987, Chapin 1993). If the environment is spatially unpredictable and rare, species have to feature long-distance dispersal, which can be examplified by pioneer species in primary or secundary successions, such as *Senecio congestus* colonizing mud flats in newly formed polders in The Netherlands (Bakker 1960), *Salix* spp. which colonize river flood plains (Chapin 1993) and *Chamerion angustifolium*, which colonizes gaps in woods (Van Andel & Ernst 1985). If the environment is moderately predictable on a time scale and confined spatially, building a persistent seed bank is a common strategy, e.g. for pioneer species in secondary successions such as many weed species in arable fields (Fenner 1987), but also species such as *Calluna vulgaris* and *Erica tetralix* in heathlands, or species such as *Digitalis purpurea* reacting on the opening of the canopy in woodlands (Van Baalen & Prins 1983; Thompson 1992).

Many species are specialized on either good dispersal capacity or building a persistent seed bank. Adaptation to long-range dispersal may even predict a small chance of seed bank formation. Klinkhamer et al. (1987) found a negative correlation between seed bank formation and dispersal ability in their species set. Poschlod & Jackel (1993) found in calcareous grassland that Asteraceae seeds with a pappus had transient seed banks *sensu* Thompson *et al.* (1996) and those without pappus had persistent seed banks which suggests a separation of the two types of dispersal strategy within this group of Asteraceae.

Some species can disperse over very long distances, and can also build large persistent seed banks. With respect to environmental predictability these species are adapted to spatially rare environments which may not provide much opportunity for germination and establishment in time as well. A good example is *Typha angustifolia*, which germinates on lake bottoms on the rare occasions that they are dry (Ter Heerdt & Drost 1994). Other examples are found within the group of species colonizing gaps in woodlands (Thompson 1992).

Other species (apparently) have little long-distance dispersal capacity and build no persistent seed banks. These species may occur in environments which produce predictable circumstances for establishment in space as well as in time, for instance wet grasslands, probably relying on clonal colonization. The latter are species which are not likely to re-establish easily during nature regeneration and may need deliberate reintroduction by man.

Seed characteristics such as weight, size and shape may be linked to both seed longevity and dispersal distance. Small, light and round seeds are more likely to build persistent seed banks than large, heavy, flattened and/or elongated seeds (Thompson *et al.* 1993). The influence of seed form on seed bank formation may be illustrated by the behaviour of dimorphic seeds of *Spergularia salina*. After being dispersed by wind, vertical transport of unwinged seeds in dense vegetation was higher than that of winged seeds. Hence under dense vegetation unwinged seeds disappeared quicker into the ground, and showed a higher proportion in the seed bank than winged seeds (Redbo-Torstensson & Telenius 1995). Differences in longevity of winged and unwinged seeds in the seed bank, however, were not studied. In wind dispersal, the same type of seed characteristics influence wing loading and are therefore linked to dispersal distance (Augspurger & Franson 1987). Seeds of species with a more specialized form disperse further than of species without such form (Sheldon & Burrows 1973). With a given morphology lighter seeds have smaller falling velocities and are therefore more effectively dispersed (McGinley & Brigham 1989).

A certain combination of seed traits may therefore point to a comprehensive dispersal strategy in terms of both dispersal distance and seed longevity. This may lead to conclusions seeming contradictory to the conclusion of Klinkhamer *et al.* (1987) that dispersal ability is negatively correlated with seed bank formation. For instance, within a specialized group of wind dispersed species producing seeds with specialized extensions, the formation of a persistent seed bank would be expected usually among those producing small seeds. Small seededness in specialized wind dispersed seeds mostly means a very low terminal velocity. As a result, within a group of wind dispersed species persistent seed bank formation is found significantly more in species with low terminal velocity and hence long-distance dispersal than in species with higher terminal velocity (Mann-Whitney $P<0.05$, see Table 6). The relationship between seed characteristics and dispersal strategy is not always immediately clear, when knowledge on the actual process of seed dispersal is limited. For instance, small seeds without specialized extensions, like those of *Juncus squarrosus*, *Drosera intermedia*, *Erica tetralix* or *Calluna vulgaris* are still often considered to be wind dispersed (Fenner 1985) apart from forming large persistent seed banks, which can survive in the soil for decades (Thompson *et al.* 1996). However, wind tunnel experiments show that seeds of these species, considering their seed release height, feature flight distances (primary trajectory) in the same order of magnitude as species which are never considered to be wind dispersed (R. J. Strykstra, unpublished). Within vegetation this most certainly leads to very limited dispersal distances. Nevertheless, the terminal velocity of small seeds may be comparable to those of species which are considered to be wind dispersed (Askew *et al.* 1996; R. J. Strykstra, unpublished). In this example considering only the terminal velocity may lead to an overestimated impression of dispersal ability and misconceiving specific dispersal strategy, resulting in wrong expectations on re-establishment.

Examples of underestimating dispersal ability due to the assumption that seeds lacking any obvious specializations for wind dispersal will have limited dispersal distances are as easily given. Sernander (1901) showed that *Calluna vulgaris* is well dispersed by wind along bare soil surface if the capsule is still around the seeds. This also applies to a number of *Juncus* species (Bernhardt 1993). Moreover, the examples of the machine dispersed flora in a grassland reserve mentioned earlier (Strykstra & Verweij, in press) and sheep dispersed flora in calcareous grasslands (Fischer *et al.* 1996) indicate

Table 6. Terminal velocity of the seeds and seed bank type of 22 specialized wind dispersed species. Terminal velocity derived from Sheldon & Burrows (1973), Matlack (1987), Schenkeveld & Verkaar (1983) and from windtunnel experiments by Strykstra *et al.* (unpublished). Seed bank type was derived from Thompson *et al.* (1996)

Species	Terminal velocity (m/s)	Seedbank type
Chamerion angustifolium	0·07	Persistent
Typha latifolia	0·13	Persistent
Tussilago farfara	0·19	Transient
Cirsium arvense	0·21	Persistent
Erigeron acer	0·22	Transient
Sonchus arvensis	0·24	Persistent
Senecio vulgaris	0·28	Persistent
Senecio viscosus	0·31	Persistent
Cirsium palustre	0·34	Transient
Taraxacum sp.	0·35	Transient
Sonchus oleraceus	0·35	Persistent
Cirsium vulgare	0·36	Transient
Eupatorium cannabinum	0·39	Transient
Hypochaeris radicata	0·40	Transient
Senecio jacobea	0·42	Transient
Leontodon autumnalis	0·51	Transient
Hieracium umbellatum	0·55	Persistent
Carlina vulgaris	0·58	Transient
Drosera rotundifolia	0·58	Transient
Narthecium ossifragum	0·77	Transient
Arnica montana	1·08	Transient
Leontodon hispidus	1·73	Transient

that lack of specialized form does not always prevent long travelling distances. For many species the way of seed dispersal is simply unknown, which provides a challenge for future investigations.

Finally, it is very important to realize that seed dispersal distance and seed bank formation, which are discussed here, form only part of the total dispersal strategy of a species. Other parts of this strategy, such as seed release time and duration and, after establishment, clonal and sexual reproduction speed may be equally important in restoration. The arrival of a certain species before others may determine succession through shifts in competition between species (Lawton 1987; Grace 1987). Timing of restoration measures may therefore be important.

SEED RAIN AND LONG-DISTANCE DISPERSAL

Seed dispersal analysis

A large variety of structure and dispersal types of diaspores exist among plant species (Poschlod *et al.* 1995). To what extent these types are related to dispersal in field conditions is hardly known. Several categories of methods are used to analyse dispersal and seed rain depending on the dispersal agents, such as wind and animals. Only in the case of water and man or machines as dispersal agents has dispersability of species been

mainly derived, until now, by the description of single observations (Ridley 1930; Müller-Schneider 1977; Van der Pijl 1982; Willson 1992).

Potential dispersal distances by wind can be derived from fly characteristics and fall velocity (Schmidt 1918; Sheldon & Burrows 1973; Luftensteiner 1982; Burrows 1986; Matlack 1987). Flying distances are investigated in wind tunnels (Augspurger 1986; Augspurger & Franson 1987; Johnson & West 1988; Kadereit & Leins 1988). Measurements of the diaspore rain in the field can be carried out using diaspore traps (Fischer 1987; Poschlod & Jordan 1992; Poschlod & Jackel 1993; Poschlod 1995). Whereas the first method is only a rough estimation of the possible dispersal distance by wind, both the wind tunnel experiments and the method trapping the diaspore rain are more exact but have also disadvantages. Results of wind tunnel experiments are not applicable to field conditions and to a distinct landscape. Also they ignore that seeds can be secondarily dispersed once fallen. The type of seed trap has a great influence on the result. Fischer (1987) made a review on the type of traps and stated that 'wet' and 'sticky' traps are not as suitable as 'dry' traps. Finally, the total area of seed traps in the field, which can be analysed within a justifiable time, is not big enough to catch the whole quality and quantity of seed rain (Jackel & Poschlod 1994). Johnson & West (1988) mentioned another disadvantage of funnels. Funnel traps would be more likely to lose seeds again as a result of flooding, resuspension by winds or seed predation. Another method is to mark diaspores with fluorescent powders (McEvoy & Cox 1987) or radioactive tracers (Lawrence & Rediske 1960; Watkinson 1978a) and to recapture them. The aforementioned methods do not address complications which may occur during seed dispersal. Other factors such as structure of the soil surface (Feldman & Lewis 1990; Andersen 1991), movement on the ground (Watkinson 1978b), vegetation structures as dispersal barriers (Feldman & Lewis 1990) and structures which catch seeds (ditches, Burrows 1986) are also important for the dispersal after landing.

Seed acquisition and transport by animals is passive by attachment to fur or feet or by foraging. Seeds and fruits are also collected actively for storage or food (Stiles 1992). The passive transport of seeds on fur can be studied on dead (Agnew & Flux 1970; Luftensteiner 1982; Shmida & Ellner 1983; Sorensen 1986; Milton et al. 1990) and living animals (Hillegers 1985; Fischer et al. 1995, 1996). Dispersal distances can be determined by attachment experiments (Bullock & Primack 1977; Fischer et al. 1996; Kiviniemi 1996). The same methods can be applied to study dispersal by hoofs. Seeds which are attached to the hoofs together with soil can be removed by cleaning (Fischer et al. 1995). Dispersal by herbivores can be studied by feeding cattle with seed containing material and testing the viability of seeds in the dung after excretion (Kempski 1906; Gardener et al. 1993). However, collecting dung in the field (Welch 1985; Fischer et al. 1995; Malo & Suárez 1995) is also practicable. Dispersal distances can be determined by the knowledge of the movement during digestion and time period of digestion (e.g. 24 to more than 96 hours at sheep, Özer 1979).

In summarizing methods to assess wind dispersal it is recommended to combine measurements in the field and in the wind tunnel together with fly characteristics to acquire a distinct picture of dispersability by wind in a landscape. As a standardized method of measuring the seed rain in the field, dry seed traps of small and large size are recommended to catch the seed rain within a vegetation stand and from outside, respectively (see Figs 6, 7; Jackel & Poschlod 1994; Poschlod 1996a). To study dispersal distances by animals attachment experiments proved very worthwhile, as well as seed analysis of the dung, including germination tests.
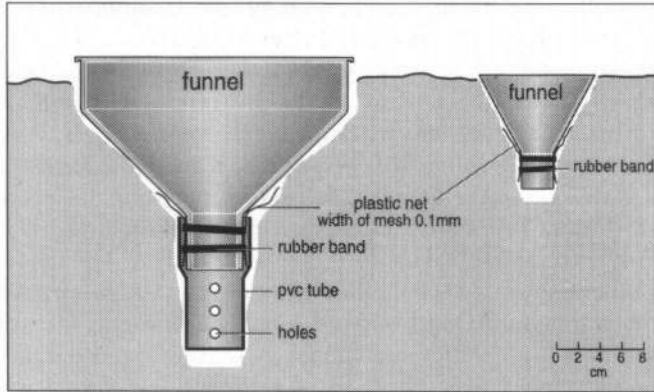
Fig. 6. Shape, size and configuration of dry seed traps (after Jackel & Poschlod 1994).
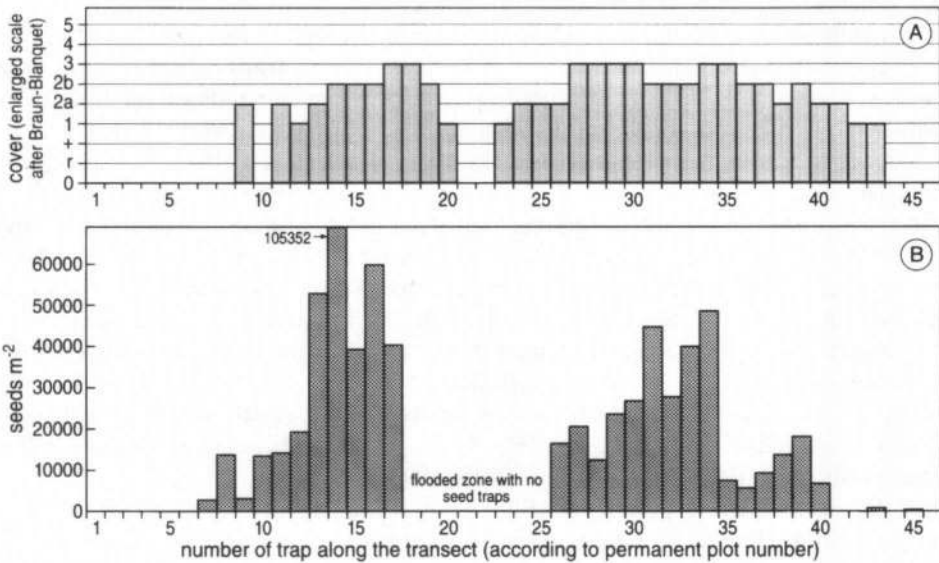

Fig. 7. Spatial distribution of (A) cover and (B) seed rain (caught by the dry seed trap type after Jackel & Poschlod 1994) of *Carex bohemica* in a pond (Gloggere Weiher, Oberschwaben, Southwest Germany) after drainage during the vegetation period 1993. Studied seed rain period: 29.4.–19.10.1993. From Poschlod (1996).

Seed dispersal by wind

Wind dispersal occurs in almost all species. However, only seeds with small Reynolds numbers (index without dimension for the relationship between inert and viscous forces: if the Reynolds number is small movement in the air is dominated by viscous forces) or a mass less than about 0·05 mg (tiny dust seeds such as those of many species of the families Orchidaceae and Pyrolaceae) have the potential to be dispersed over long distances by wind (Harper 1977; Burrows 1986; McCartney 1990). Therefore, it is not surprising that species of these families are characteristic of pioneer sites such as quarries (Tränkle 1995) and often appear on restoration sites very quickly if conditions are suitable (unpublished observations of the authors). Larger seeds are only effectively

dispersed by wind if their shape reduces fall speed (Burrows 1986). *Spergularia salina* features heteromorphic seeds. The winged seed type was slightly further dispersed than the winged type, but neither travelled more than about 1 m (Redbo-Torstensson & Telenius 1995). Seeds which have a pappus or plume can also be carried over long distances by the wind, although calculations from Sheldon & Burrows (1973) resulted only in a few meters dispersal distances. However, field experiments on *Senecio jacobea* (McEvoy & Cox 1987) and *Solidago canadensis* (Grunicke 1995) showed that the majority of seeds dispersed short distances but some of them could be transported up to 14 or 50 m. It is important to state here that only a few studies also examined the viability of dispersed seeds (Salonen 1987). Strykstra (unpublished data) measured in a wind tunnel experiment that 95% of seeds of *Arnica montana* reached the floor within 3 m. Of the seeds travelling more than 3 m only 5% turned out to be viable, compared with 60% of the seeds at 1 m distance.

Other authors also tried to model flight properties of seeds considering aerodynamic characteristics. McCartney & Fitt (1985) and McCartney (1990) included in their models particle size, fall speed, wind profiles and other factors. Greene & Johnson (1989) discussed a similar model for winged and plumed seeds. Further modelling approaches were done by Okuber & Levin (1989) and Verkaar (1990). Okuber & Levin (1989) showed the theoretical base for a prediction model. Verkaar (1990) discussed maximal wind dispersal distances to implicate corridors as tools to conserve plant populations. He included the vertical and horizontal movement of seeds, the density of reproducing plants and the number of seeds produced in the model and simulated maximal dispersal distances. Then he estimated the time needed to disperse five plant species (*Betula, Acer, Lathyrus, Tragopogon, Viola*) over 500 m by wind in optimal habitat and non-habitat. All herbs, including *Tragopogon*, would need more than one century to cover 500 m distance by the wind. All these models, however, do not include different meteorological conditions or thermal convections and are not related to distinct landscapes.

There are such dispersal models on small particles such as dusts, spores and pollen (Mukammal *et al.* 1968; Mandrioli *et al.* 1984; Belmonte & Roure 1986; Cesari *et al.* 1986; Pedgley 1986; Peters 1986) which take landscape features into account. However, they can be applied only in a limited way, because seeds have different forms and sizes. Because of their mass most seeds follow aerodynamic laws. Therefore, the manner of flight differs from that of dusts and aerosols (Burrows 1986).

Wind dispersal also can occur along the soil surface. Seeds which move along the ground after landing (secondary dispersal) can cover distances from several centimeters (Mortimer in Harper 1977, Watkinson 1978b) to several meters (Feldman & Lewis 1990). Seeds of *Spergularia salina* were further transported on bare soil than in dense vegetation. They travelled no further than 1 m, and could be dispersed secondarily some extra centimeters by water (Redbo-Torstensson & Telenius 1995). Further, wind dispersal can also be combined with other dispersal possibilities. Pappus-bearing seeds were often found in the wool of sheep (Fischer *et al.* 1996).

Seed dispersal by animals

Passive transport by attachment to fur or wool is believed to cover very long dispersal distances depending on duration of attachment, movement and speed of the animal. Possibly, herbivore mammals are one of the most important seed movement vectors with respect to restoration management (Poschlod *et al.* 1995; Poschlod 1996b).

However, until now most studies regard only single observations (Shmida & Ellner 1983; Hillegers 1985; Milton *et al.* 1990). Kiviniemi (1996) reported that seeds attached to the hair of fallow deer and cattle might be dispersed 1 km. Species with hooks (*Agrimonia eupatoria*) revealed better adhesive properties than species with smooth seed surfaces (*Triglochin palustre*). For the first time, Fischer *et al.* (1996) investigated seed dispersal on wool during a whole vegetation period on a tamed sheep. Seeds were dispersed over very long distances. More than 8% of artificially attached seeds both with hooks (*Bromus erectus*) and smooth surface (*Helianthemum nummularium*) were transported by the sheep over more than 40 days. During this time period sheep could cover distances over more than 100 k. Above all, small seeds were transported by the hoofs (Fischer *et al.* 1995).

However, most grazing animals disperse seeds by dung. Hansen (1911) reported huge amounts of seeds from *Matricaria chamomilla* (198 000, 27% germination capacity) and *Plantago* species (85 000, 58% germination capacity) dispersed by the dung of a cow. Heintze (1915) found more than 15 species in the dung of reindeer. Welch (1985) studied the dung of six herbivore species grazing heather moorland in north-east Scotland and found 55 species of moorland communities and 18 species absent or scarce in moorland. Twenty-one calcareous grassland species and five species absent or scarce in calcareous grasslands were dispersed by the dung of sheep (Fischer *et al.* 1995). However, until now there exists no study or experiment which really shows the positive effect of passive seed dispersal by animals on restoration management. Therefore, it is necessary to include such experiments in future management practices.

Active seed acquisition concerns either birds or mice, beetles and ants. Birds collect seeds and fruits of trees and shrubs. This phenomenon is well investigated in *Pinus cembra* (dispersal by nutcracker, Mattes 1978), *Quercus* spp. (dispersal by jays, Bossema 1979) and other species (Stiles 1992). Kollmann (1994) and Grunicke (1995) studied the dispersal of shrub and tree species invading fallow grassland areas. Since the invasion of shrub and tree species is a problem in most restoration management sites, it is important to know the structure of landscape and vegetation which attract hoarders to avoid their invasion. Kollmann (1994) showed that dispersal of shrub species depends on the movement of frugivore birds between shrub groups and their period of stay in these groups. Introduction of diaspores by birds is very rare on treeless sites or under pioneer trees but increases with increasing shrub size (see also McDonnell & Stiles 1983). Also long-distance dispersal (>100 m) occurs very rarely.

Mice, beetles and ants collect seeds of grasses and herbs (Sernander 1906; Leutert 1983; Bernhardt 1993). Additionally mice also disperse vegetative diaspores (Leutert 1983). However, there is no long-distance dispersal possible. Both ants and seed collecting beetles (Den Boer 1970) transport seeds only over a distance of a few meters. Also mice only collect seeds within a radius of several meters (Leutert 1983). Therefore, these dispersal agents are important within a community but not for restoration management unless restoration sites are adjacent to sites which still possess a potential of species worth striving for.

Seed dispersal by man and his machines

Direct transport by attachment on clothes and footwear was investigated by Clifford (1956). Possibly this factor will become increasingly important because behaviour during leisure time has changed drastically during the last years.

In some ecosystems man has strongly influenced seed dispersal and establishment of species, especially by agricultural practices. In former times weeds were sown each year with uncleaned seeds. Species with a transient seed bank such as *Agrostemma githago* and *Melampyrum arvense* are now extinct on arable fields in Central Europe because of cleaned seeds today (Schneider *et al.* 1994; Poschlod 1996b). In fact, rare species were not only unconsciously dispersed. Some vegetation types such as the litter fen type *Molinietum* with many rare and endangered species were sometimes artificially created by sowing and hay spreading (Stebler 1898) at the end of the last and the beginning of this century to produce more litter in regions where litter was rare (Switzerland, German foothills of the Alps). Today, sowing and hay spreading are used for nature conservation purposes to create species-rich grassland (Biewer & Poschlod 1995; Tränkle 1995).

Due to agricultural practices in historical times there were many possibilities for plants to migrate. Some of these are reported in a review from Poschlod (1996b) of metapopulations. There are many examples which cannot be reported here, but it is obvious that in many regions we have lost a great deal, e.g. by spreading dung from cattle, seeds were dispersed on arable fields (Salzmann 1939; Müller-Schneider 1977).

Vehicles often cover large distances and may therefore be very effective agents for long distance seed dispersal, such as the rapid spreading of *Puccinellia distans* along road verges (Krach & Koepff 1980). Of many plant species seeds have been found in dirt, soil or adhering plant material on vehicles, for instance on cars (Clifford 1959; Schmidt 1989; Lonsdale & Lane 1990; Milberg 1991; Zwaenepoel 1993). Recent work has shown that cars transport mostly fast-growing weeds, and therefore while undoubtedly a major dispersal vector in the modern European landscape, cars probably contribute little to restoration of vegetation of significance to conservation (Hodkinson & Thompson, in prep.). Harvesting machinery (Mesa Garcia *et al.* 1986; Maxwell & Ghersa 1992; Mortimer *et al.* 1993; Howard *et al.* 1993; Ghersa *et al.* 1993) is also known to contribute to seed dispersal. Hay-making machinery was also expected to disperse seeds, which might contribute to grassland restoration in nature reserves (Bakker & De Vries 1988; Bakker 1989; Willems & Bobbink 1990; Bakker & Olff 1995).

Seed dispersal by hay-making machinery was investigated within the Drentse A grassland reserve in The Netherlands by Strykstra & Verweij (in press). A single tractor disk mower combination moving between fields can transport up to hundreds of thousands of seeds of many species (Strykstra & Verweij, in press). It was shown that seeds are actually exported from species-rich fields and imported into species-poor fields. This means that new areas can be colonized by means of dispersal by machinery, which may be important for regeneration. In an other experiment in the Drentse A reserve the import of *Rhinanthus angustifolius* seeds by machinery in a hayfield followed by establishment in the next year was shown (Strykstra *et al.* 1996).

The way machinery is built may influence its capacity to transport seeds. This has been shown for harvesting machinery (Ballare *et al.* 1988) but this will also apply to hay-making machinery. It is also conceivable that machinery may be positively or negatively selective towards certain species, as has been established for cars, where the mean seed size in dirt samples is much smaller than that in the road verge vegetation where the seeds come from (Clifford 1959; Zwaenepoel 1993). However, in the Drentse A experiment seeds of very different sizes were found, varying from tiny orchid seeds to the large seeds of *Rhinanthus angustifolius*. Most species were caught proportionally to their abundancy in the field, and were, therefore, not selected.

However, for a few species a large discrepancy between field abundance and seed transport by machinery was found, which was attributed to plant phenology at the cutting date. Some selection of plant height also took place on different machinery parts where seeds accumulated. The results of the Drentse A experiments suggest an important role of seed dispersal by hay-making machinery in restoration of species rich vegetation in grassland reserves (Strykstra & Verweij, in press).

Seed dispersal by water

Seeds can also cover long distances by water, which is known above all by drifting seeds along sea streams (Van der Pijl 1982, Murray 1986) by flooding. Koutstaal *et al.* (1987) demonstrated that propagules of salt marsh species may travel over a net distance of 60 km by tidal currents within a week. Huiskes *et al.* (1995) found that the transport of propagules in salt marshes was mainly determined by the tidal currents: neither wind direction nor speed nor the height of high tides played a significant role. Few propagules were transported into the marsh from elswhere by incoming tide; many propagules were transported out of the marsh with the ebb currents.

In rivers dispersal can occur by drifting with the water or together with the sediment (e.g. Skoglund 1990). However, transport by water mostly is derived by floristical mapping and not by trapping seeds in the water or sediment body except single observations (Van der Pijl 1982). First reports on the quality of seeds transported by different rivers during longer time periods are given by Poschlod (1996b). Kleinschmidt & Rosenthal (1995) showed the importance of drifted seeds for the restoration of wet meadows by flooding.

IMPLICATIONS FOR RESTORATION MANAGEMENT AND ESTABLISHMENT OF SPECIES

In many short- and long-term studies in restoration management aiming at the restoration of species-rich grassland types, most of the 'target' species did not establish still after years (Poschlod & Jordan 1992) and decades (Kapfer 1988, 1994; Bakker 1989; Rosenthal 1992). As shown above there exists no potential in the soil, because the majority of these species has a transient or short-term persistent seed bank. Therefore, these species have to come from outside by dispersal of diaspores.

Restoration management has only recently taken into account that dispersal is an important key for the establishment of 'target' communities or species (Salonen 1987; Poschlod & Jordan 1992; Poschlod 1995; Tränkle 1995). Although only seed rain was investigated in these studies, these experiments showed that dispersal is the most important factor in a second phase of restoration, after activating the present seed bank. However, they also showed that even species occurring close to restoration sites were absent from the seed rain.

Disturbance is often necessary to activate a seed bank of 'target' species. Fix & Poschlod (1992) showed that rotivation at the beginning of a reduction of an intensive land use can favour extinct species to germinate and establish from a long-term persistent seed bank, e.g. *Campanula patula* and *Lychnis flos-cuculi* in dry to moist grassland types. The establishment of heathland species in dry grassland after cessation of fertilizer application was very little in sites grazed or cut for hay, but the 'target' species spread rapidly from the seed bank after sod removal (Bakker 1989). In many cases 'target' species, however, do not appear as they are lacking from the seed bank, e.g. if reclamation

was too long ago or the 'target' community mainly includes transient or short-term persistent seed bank species (Klooker *et al.* 1995). Species that do emerge from the seed bank after sod removal are not always wanted, e.g. large amounts of *Juncus effusus* or grasses, as they are no 'target' species. Moreover, they can also be a problem being a competitor for 'target' species, which do not always emerge in large quantities.

Restoration of the plant communities of soft-water lakes demonstrated that *Littorellion* species (e.g. *Lobelia dortmanna*, *Littorella uniflora*, *Isoetes echinospora*, *Pilularia globulifera*) have long-term persistent seed banks and can emerge after removal of the acidifying mud layer (Bellemakers *et al.* 1993). A necessary prerequisite after mud removal seems the gradual seepage of calcium-rich groundwater. Attempts to reduce acidification at once by artificial liming resulted in mass spreading of *Juncus bulbosus*, and subsequent competing out of the just-returned Red List species (Roelofs *et al.* 1995). A seed bank can thus be activated, but if the right conditions for establishment are not fulfilled it may result in exhaustion of a long-term persistent seed bank.

In a review about metapopulations of plants Poschlod (1996b) emphasized that dispersal of plant species has totally changed during the last decades. In a historical man-made landscape dispersal events were much more diverse than today. Studies on dispersal by herbivores showed that they can disperse enormous numbers of seeds per year. Fischer *et al.* (1995, 1996), studying dispersal of seeds by sheep, calculated that at least more than three million seeds are dispersed by the wool of a flock of sheep of 350 individuals during one vegetation period. However, grazing livestock have been declining in all man-made landscapes in Central Europe for decades because of cheaper imports of wool, leather and meat from other countries. So far, we do not know which possible dispersal agents we have lost. The literature review also showed that there is a huge gap of knowledge especially on field studies (Poschlod 1996b and unpublished data). We do not know if dispersal by former management can be displaced by any actual management or, if not, by wind dispersal. These will be some of the main tasks in restoration management in the future.

The success of establishment not only depends on possible long-distance transport of seeds by animals; this is most important if there are good conditions for germination in the place or microhabitat where seeds were dispersed (Webb 1966; Fenner 1987; Poschlod 1996b). For example, Sarukhan (unpublished data in Harper 1977) showed that the distribution of seedlings of *Ranunculus bulbosus* in a permanent grassland were closely related to cattle hoof-marks. In another example it was demonstrated that species which were absent from both the established vegetation and the seed bank did germinate in a hay-field with various cutting regimes. Subsequent early establishment was, however, only found in sites with an open sward; a dense canopy apparently competed out the emerged seedlings (Bakker 1989). Therefore, further studies on restoration management should also investigate if seed dispersing agents are creating germination niches by disturbing vegetation structure and soil surface (wallowing, hoof-marks). Biewer & Poschlod (1995) showed that the number of established individuals after spreading species-rich hay is much higher on sites where soil surface was artificially disturbed.

CHALLENGES FOR FURTHER RESEARCH

Apart from an overview of principal features of seed bank and dispersal research, this review draws attention to the more obvious lacunae in the data and suggests challenges

for further research. The gaps in our knowledge on longevity of seeds, even for a flora as small and well-studied as NW Europe, are remarkable. The seed bank data suggest that attention has been concentrated on the productive agricultural habitats which make up most of the landscape, while semi-natural habitats have received much less attention. This undoubtedly reflects the relative abundance of the habitats, but has led to a serious imbalance in our knowledge. We know a great deal about a handful of important species of arable fields and fertile grassland, and almost nothing about most species (which are often declining or endangered) of less productive, semi-natural habitats. Given the importance of the latter for nature conservation and habitat restoration, it would be helpful if future seed bank studies could begin to redress the balance.

Even less is known about the ways of dispersal of many plant species and the realized dispersal distance of diaspores.

In addition to the obvious taxonomic gaps in our knowledge, we suggest the following as topics worthy of future study:

1. Seed bank sampling in rare and endangered plant communities.

2. The relationship between seed rain and seed bank.

3. Mechanisms of incorporation of seeds into the different layers of the seed bank.

4. Effects on seed viability and longevity of storage in different types of soil, e.g. sand versus peat, and under different types of management, e.g. drained versus waterlogged, fertilized versus unfertilized.

5. The physiological basis of seed longevity in soil.

6. Seed rain sampling in rare and endangered plant communities.

7. Wind dispersal experiments including studies of seed rain in field conditions, especially of rare and endangered species.

8. Improvement of methods to catch seed rain in the field.

9. Seed dispersal experiments on living animals including all possibilities (fur, wool, hair, hoofs, dung).

10. Dispersal and germination niches created by dispersal agents.

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