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Assessment of dispersule availability: its practical use in restoration management

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SUMMARY

Seed dispersal and seed banks are crucial to the restoration of plant communities by nature management authorities. Knowledge of seed dispersal and seed survival of species with nature conservation interest is necessary to anticipate measures to enhance their establishment. The interpretation of the results from seed bank and seed dispersal research for conservation purposes is not always easy. In this paper, an overview is given of methods used to estimate the importance of seed bank and seed dispersal during vegetation restoration. The consequences of the methodology of seed bank and seed dispersal research for decision making in nature management are discussed. Qualitative as well as quantitative methods only provide for rough estimations of seed availability. However, such rough estimations could still prove to be very useful in restoration management.

Key-words: nature management, rare species, reintroduction, restoration, seed bank, seed dispersal.

INTRODUCTION

Restoration and development of endangered plant communities have become important aims of nature conservation authorities all over Europe. Its success depends on recreating a suitable environment (Bakker *et al.* 1996). Apart from difficulties with recreating the proper abiotic site conditions and biotic processes, the absence of dispersules may inhibit the re-establishment of plant species (Bakker *et al.* 1996). Restoration areas are often isolated from source populations of rare species (Verkaar 1990) and long-range dispersal by large animals, water or other vectors may no longer occur in the modern landscape (Poschlod & Bonn 1998).

It is useful to know if the availability of dispersules is restricting succession, especially when its success depends on the establishment of certain individual species. Predictions are necessary to anticipate the need for active enhancement of species establishment by additional management, such as creating gaps or restoring the action of dispersal agents. They would also provide the possibility to evaluate the justification of re-introduction of species, which is still controversial for many good reasons, although it is already widely applied (Stevenson *et al.* 1995, 1997; McDonald 1993; Bakker *et al.* 1996; Pywell *et al.* 1996).

Dispersules may originate from two natural sources: the seed bank and seed rain, which are the result of two distinct processes: seed survival and seed dispersal. All plant species have their own specific dispersal 'strategy' including both processes (Klinkhamer

Table 1. Examples of the possibility for qualitative estimation of the chance that seeds will be available for vegetation restoration. ± = high/low chance of seedbank or seed rain availability

	Information needed	
Source of information	Seed bank	Seed rain
Community ecology	Predictability of environment Predictable large disturbance + Unpredictable large disturbance − Little disturbance −	Predictability of environment Predictable large disturbance + Unpredictable large disturbance + Little disturbance −
Species ecology	Life history strategy: Pioneer species + Climax species − Seed longevity index (Thompson *et al.* 1997)	Life history strategy: Pioneer species + Climax species − Dispersability (vector dependent: see Table 2)
Dispersule characteristics	Size (large −, small +) Weight (heavy −, light +) Shape (round +, other −) Physiology	Size (large −, small +) Weight (heavy −, light +) Shape (round −, other +)

et al. 1987; Poschlod & Jackel 1993; Willson 1993) which is adjusted to their ecological surroundings. Plant dispersules may be adapted to long-range dispersal, to long-term seed survival, or to both. In restoration management, plant species with such strategies are usually expected to re-establish easily although it is known that the chance that seeds travel large distances from the seed source are commonly both overestimated and underestimated (Willson 1993; Portnoy & Willson 1993; Bakker *et al.* 1996). Rare species however, which do not specialize in either seed longevity or long-range dispersal, will not establish readily in new suitable sites. Theoretically, this is a serious problem in vegetation restoration (Verkaar 1990). For that reason the practice of nature management requires answers to direct, simple questions, such as 'what is the chance that dispersules of a certain species are available on a specific site?' and 'in what numbers are those dispersules available?'

A whole set of methods exists to solve these questions. First, qualitative methods could be used (Table 1). Many correlations have been found between specific ecological properties of plant communities, plant species and the chance that species will appear in a seed bank or a distant seed rain. In policy making, such correlations are often used for predicting the success of foreseen restoration practices. More specific knowledge on dispersule characteristics can also be used for predicting the chance of seed availability. Distinct relations are known to exist between seed size, seed shape and their dispersal agent. As it is reasonably well known how effective most dispersal agents are in terms of distance (Willson 1993, Table 2) seed shape may predict the chance that seeds are available in the restoration area. Relations between seed size, seed shape and survival in a seed bank have also been found (Thompson *et al.* 1993).

A qualitative approach provides only estimations of the chance of seed availability with low accuracy. More accuracy is expected of the numerical analysis of seed survival and seed dispersal, which generates chance models (Table 3). These models, combined with knowledge of the present and past landscape, can be used to predict the availability of seeds in specific areas. However, there is little numerical information about the seed

Table 2. Potential range of seeds in the seed shadows created by some well known dispersal vectors (based on Willson 1993)

Vector	Potential range
Wind	Large
Water	Large
Grazing animals	Large
Small mammals	Small
Birds	Large
Ants	Small
Vehicles	Large
Autochory (ballistic)	Small

bank and dispersal of most plant species. Especially of rare species, which are of interest in nature management and restoration, more information is needed (Bakker *et al.* 1996; Thompson *et al.* 1997).

In response to this need, much research has been done recently or is in progress on seed banks (Skoglund 1990; Poschlod & Jackel 1993; Jackel & Poschlod 1994; Bekker *et al.* 1998; Bakker *et al.* 1996; McDonald *et al.* 1996; Thompson *et al.* 1997; Bekker *et al.* this issue), dispersal by machinery (Strykstra *et al.* 1996, 1997), wind dispersal (Bakker *et al.* 1996; Strykstra *et al.* 1998), dispersal by water (Kleinschmidt & Rosenthal 1995), and seed dispersal by large animals (Fischer *et al.* 1996; Kiveniemi 1996; Bakker *et al.* 1996) of individual plant species. Much of this research is aimed directly at obtaining information for practical management or restoration (Bakker *et al.* 1996).

Two approaches can be distinguished in numerical seed dispersal and seed bank research. In the first approach, which we will call the 'seed source' approach, research is focused on the pattern of seeds spreading around a single seed source or on the decline of seed numbers in the soil. This type of research often aims at studying processes in dispersal and seed survival (Willson 1993; Rees & Long 1993) but in practical terms it adds to the knowledge of specific dispersal distances or seed longevity. The second approach, the 'target area' approach, is more directly related to the practice of nature management and is focused on investigating the species composition and seed numbers in seed bank and seed rain in a specific area (Aerts *et al.* 1995).

As a consequence of the differences between the two approaches, seed availability on a site can be estimated in either of two ways: through extrapolation of data on specific dispersal distance or seed survival, obtained by the first approach, or by examining and comparing data obtained by the second approach. The interpretation of the results, in terms of seed availability for restoration, is not easy, especially when a policy has to be made on the basis of such interpretations. There is much uncertainty about the possible use of dispersal and seed bank data and the existing information is easily misused. In this paper, we will try to answer the question which possibilities dispersal and seed bank research can offer to back decisions in restoration management. For this purpose some specific methodological characteristics of dispersal and seed bank research will be discussed.

Table 3. Examples of the possibility for quantitative estimation of the chance that seeds will be available for vegetation restoration

Chance models of survival and dispersal based on	Information needed	
	Seed bank	Seed dispersal
(Integrated) dispersule characteristics	Variance of shape Shape/weight index Information on relevant site conditions	Air resistance Terminal velocity Information on relevant site conditions
Experimental or observed seed survival and seed dispersal data curves	Experimental observations of survival in time (burial experiments) Field observations of survival in time Information on relevant site conditions	Experimental observations of dispersal (wind tunnel experiments) Field observations of dispersal Information on relevant site conditions
Measurements of the actual seed bank and seed rain in the system	Field observations of species, seed numbers of densities in the seed bank	Field observations of species, seed numbers numbers or densities in the seed rain
Actual establishment in similar systems	Monitoring vegetation development and species establishment: no distinct information needed on the two possible origins of dispersules	

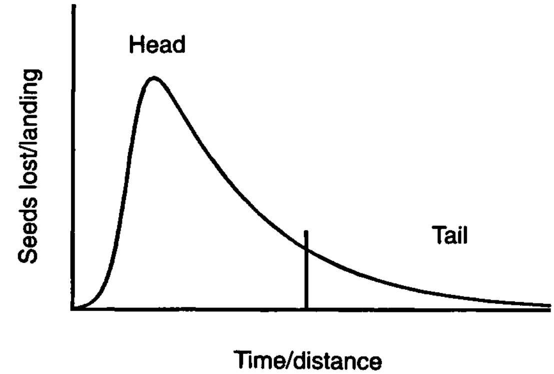

Fig. 1. Leptokurtic curve: general curve of linear seed dispersal distances or seed loss events.

SEED SOURCE APPROACH

Seed dispersal research

From the research available on seed dispersal around a single seed source, it may be concluded that dispersal from a seed source mainly follows the same one-dimensional pattern: close to the seed source small numbers of seeds are found. Further away these numbers increase to a maximum and, beyond this maximum, the number drops continuously until it reaches zero. This pattern is most clearly found and predicted in wind dispersal (Augspurger & Hogan 1983; Augsberger & Franson 1987; Okubo & Levin 1989; Greene & Johnson 1989, 1995), but is also found for animal-dispersed seeds (Willson 1993). Animal-dispersed seeds, however, may also feature quite different distributions because of a highly located deposition of seeds.

Dispersal data can be shown in more than one way. The common leptokurtic linear distribution of seed dispersal distances in wind dispersal is presented in Fig. 1. The curve is skewed to the right and is easily obtained in field and wind-tunnel experiments. This curve can also be generated calculating dispersal trajectories using sophisticated models, incorporating wind speed variation and variation in falling velocity (Burrows 1975; Greene & Johnson 1989). In field studies, seed density may be recorded two-dimensionally. The two-dimensional pattern always shows a certain directionality which is again exemplified most clearly in wind dispersal. It is also possible to record three-dimensional patterns of dispersal which are important, for instance, in epiphytic species, or species growing on slopes (Burrows 1973, 1975).

The majority of dispersed seeds are found mainly near the seed source, regardless of the dispersal vector involved (Willson 1993). The most interesting part of the dispersal distribution for vegetation restoration, however, is often the part beyond the mode of the curve: the tail of the distribution. Examination of this part of the distribution allows estimation of the chance that seeds are dispersed beyond a certain distance, by fitting suitable monotonically declining mathematical models to the data. Mathematical models used for the prediction of dispersal distance approach zero asymptotically with increasing distance. The model that is used most frequently to fit dispersal data is the negative exponential equation, but other models are also used (Okubo & Levin 1989; Willson 1993; Portnoy & Willson 1993). Most frequently used models fit the data reasonably well at the side proximate to the seed source, but the tail of the distribution may 'behave' rather differently (Portnoy & Willson 1993).

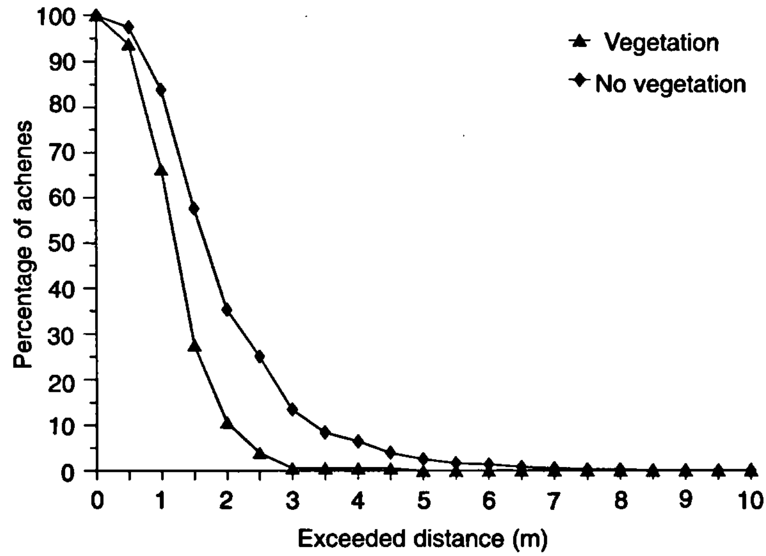

Fig. 2. Influence of vegetation on the horizontal distance, covered by *Arnica montana* achenes in a wind tunnel. Wind speed: 6·5 m/s. Release height of the achenes: 0·35 m (Strykstra, unpublished).

The distribution of seeds within the tail often depends on other factors than that within close range to the seed source. Secondary dispersal may take place, caused by totally different vectors than those active in the primary dispersal trajectory (Bakker *et al.* 1996). The tail may be heavily influenced by small- or large-scale topography (Burrows 1975; Portnoy & Willson 1993). Vegetation structure, for instance, influences seed transport considerably (Fig. 2). The unpredictable behaviour of the tail presents substantial problems for estimation of the proportion of seeds available at large distances from the seed source. Moreover, according to the most frequently used models, there is always a chance, however small, that a seed will travel an extremely long distance. A maximal distance can therefore never be calculated.

Seed longevity research

Seeds may survive in the soil for decades (Thompson & Grime 1979; Thompson *et al.* 1997). After extinction of a plant population, when seed input stops, a seed bank may survive a period of unsuitable conditions for re-establishment. During this period the initial seed bank is depleted gradually when seeds die, for instance by ageing and decay, unsuccessful germination or predation. The death of seeds may show a one-dimensional pattern similar to seed dispersal. The decline is easily shown in burial experiments, or may be derived indirectly from field studies. The same mathematical models which are used to estimate dispersal distances may be used for estimating the chance that seeds survive longer than a certain period. The most used model for seed bank decline is the negative exponential equation. As with dispersal, this model does not always give the best to fit the data, and other models are frequently used (Rees & Long 1993, Table 4). As with dispersal, the asymptotic models mostly fit well to the data obtained within the first period of decline, but may not predict the tail properly. Processes influencing seed survival in the first period of the decline (germination, predation) may be quite

Table 4. Three examples of integrated mathematical functions used for fitting to the unified distribution of measured classes of dispersal distances and time of seed loss. Interval chances are calculated by subtracting $F(t+x)-F(t)$

Probability of occurrence	Distribution	Equation
Constant in time	Exponential distribution	$F(t)=1-\exp(-rt)$
Increases or decreases monotonically in time	Weibull distribution	$F(t)=1-\exp[-(rt)^k]$
Features maximum in time	Log logistic distribution	$F(t)=1-1/[1+(tr)^k]$

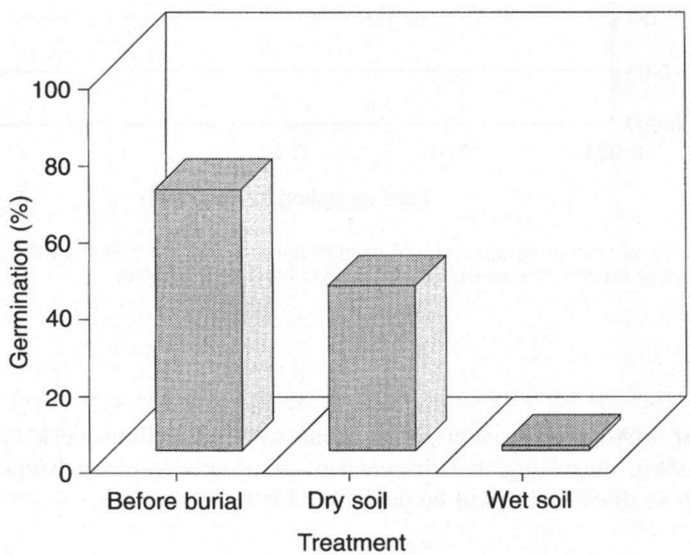

Fig. 3. Influence of soil moisture on survival of seeds of *Filipendula ulmaria* in a burial experiment (Bekker *et al.* 1997).

different from those influencing survival in a later period (Rees & Long 1993). Many of those factors (decay, predation, germination) show density dependence. Differences in the seed storage environment may influence seed survival considerably (Fig. 3). This means that it is as difficult to predict survival chances in the tail of the distribution as it is to predict the chance of being dispersed over a long distance.

TARGET AREA APPROACH

Modelling

It is hard to extrapolate dispersal or seed survival curves to estimate the magnitude of the tail. It is even more difficult to extrapolate experimental observations to any field situation. However, they are applicable in modelling dispersal on a landscape scale. A spatial model, combining the use of dispersal and seed bank data, could predict chances of establishment in specific areas. For animal populations, especially in metapopulation dynamics, such modelling led to the understanding that for species conservation purposes there have to be corridors through the landscape (ecological infrastructure) (Hansson

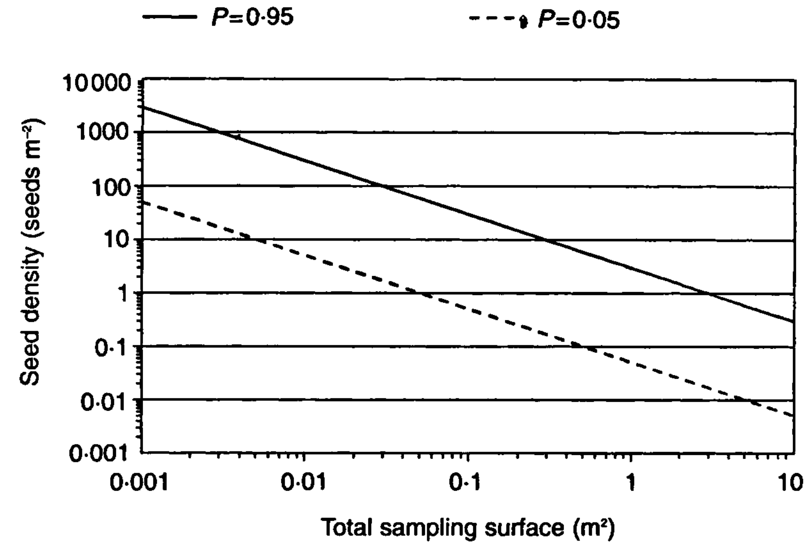

Fig. 4. Relation between sampling area and seed number detection levels at 0·95 and 0·05 level in seed bank or seed rain sampling experiments, assuming the seeds are Poisson distributed.

1991; Verkaar 1990). For seed dispersal alone some modelling work has been done (Van Dorp 1996), suggesting that dispersal of plant species through linear landscape elements such as ditch banks will be negligible for most species.

Target area and seed dispersal: direct measurements

Most target area research is focused on direct measurements of seed rain (Poschlod & Jordan 1992; Jackel & Poschlod 1994) and seed bank (Aerts 1995; McDonald *et al.* 1996; Bakker *et al.* 1996; Bekker *et al.* this issue).

The methods most frequently applied for seed rain measurement are catching seeds on sticky surfaces (Werner 1975; Schenkeveld & Verkaar 1984) and the use of funnels (Jackel & Poschlod 1994; Schott 1995). All catching methods have their advantages and disadvantages, among other things depending on the structure of the environment in which they are placed. After catching the seeds the assessment of species content of the samples may be carried out by sorting by eye, or providing circumstances for germination. The result of such research is always a list of species, in combination with seed numbers or density figures. Ideally for management decisions the whole set of species, invading by means of dispersal, has to be known. However, it is inherent to the method that only species of which the seeds are abundant will be found. The sampled surface is always small for practical reasons (Bakker *et al.* 1996; Thompson *et al.* 1997). A detection level may be calculated on the basis of the Poisson distribution.

For research using funnels the detection level may be defined as the number of seeds per m^2 for which the chance of detection is 0·95. Figure 4 shows the relation between sampling area and the number of seeds at this detection level. It shows that considerable numbers of seeds may not be detected with a reasonable chance.

Target area and seed bank: direct measurements

Seed bank research in a target area is often carried out by taking soil samples, mainly collected from several depths (Thompson *et al.* 1997). Often the sample seed concentration is enlarged by applying washing, sieving or flotation techniques (Ter Heerdt *et al.* 1996). After this the seeds are allowed to germinate. The result of this work is, again, a list of species and seed concentration figures, which may be recalculated into density figures. It is inherent to the method that only the abundant seeds are found with a reasonable chance. Using the same procedure as in seed rain estimations it is possible to calculate a detection level.

EVALUATION FOR PRACTICAL MANAGEMENT

Seed source research and management practice

It is very important that policy makers are aware of the fact that having knowledge of dispersal from a seed source or seed survival in a relict seed bank does not mean that it is easy to estimate chances of seed availability in a specific area. Extrapolation of dispersal or seed bank decline curves to the end of the tail will probably be inaccurate. However, this does not mean that it is impossible to draw any conclusions from seed source research which are valuable as a basis for management decisions.

The virtue of this type of research is that in many cases it gives the possibility to estimate percentile values for most of the seeds (for instance 95%, 99%). With percentile values, in combination with fecundity data or seed density data in the soil, estimates can be made of at least the order of magnitude of the seeds which can possibly reach the tail of longevity or distance distributions. In our opinion, this will be enough to answer most questions about the possibility that species may re-establish from a seed source or a seed bank, especially when it is kept in mind that only a small fraction of seeds actually leads to establishment of adult plants in most species.

Target area research and management practice

In a way, target area research on seed dispersal and seed banks also shows a distribution tail. This tail is formed by species which are present but, due to the methods used, are not found. Another problem related to methodology is the heterogeneity shown by seed rain and seed banks. Sampling seed rain and seed banks may therefore be inaccurate.

The most important result of seed rain and seed bank studies which may be applied to management practice is the knowledge of the ratio between seed numbers of target species and other species. This knowledge, when combined with knowledge of competition between species, may be useful in predicting short-term or even long-term vegetation development. It has often been suggested, and found, that the first species to arrive on a site may determine future trends (Tilman 1994). Knowing this, it may help to anticipate future management of restoration areas or species introductions. Knowledge of the seed bank may be useful, for instance for estimating the best depth for soil stripping, which is often carried out in order to impoverish the soil of former agricultural land for nature development purposes (Aerts *et al.* 1995).

CONCLUSION

The most accurate way to show if dispersal and seed bank contribute to vegetation development and the establishment of certain species is waiting and monitoring. The results of a number of restoration projects in The Netherlands show that there are only a few groups of target species which will emerge readily from a seed bank that was formed decades ago. The most clear examples of these groups are *Carex* and *Juncus* species (*Carex oederi, C. panicea, Juncus effusus, J. squarrosus*) in nutrient-poor grassland systems, *Calluna vulgaris* and *Erica tetralix* in heathland systems, and a number of species from nutrient poor soft water-lakes (*Littorellion uniflorae*) such as *Lobelia dortmanna* and *Littorella uniflora* (Klooker *et al.* 1995; Roelofs 1996; Aerts *et al.* 1995; Bellemakers *et al.* 1996). Except for the common species from the surrounding area, only species which can be dispersed over extreme distances, such as *Senecio, Taraxacum, Typha* and *Epilobium* species, may be found in the restoration area within a short period of time.

For most species, however, it was not found that they established themselves on such a short notice by large seed longevity or long-range dispersal. If dispersal is limited, species may not be able to found new populations in the restoration area. This may be an important problem for rare species conservation. Seed source populations are often threatened. The species as such could become less threatened by creating new populations artificially. Rare species of nutrient poor environments, which are adapted to high light intensity, may be restricted in germination and establishment by competition for light by the established vegetation (Olff *et al.* 1994). For restoration purposes it may be useful to minimize the competition of non target species. On the other hand, species may be facilitated by other species. To anticipate future measures concerning this matter, it is necessary to understand seed dispersal and seed survival of these species. The fact that the interpretation of research on these topics for management purposes is not easy or features uncertainty should not stop people from doing it and using it.

Only for few species is the knowledge on seed bank and seed dispersal so detailed that it is possible to make course predictions of a chance that natural dispersal will contribute to establishment in a restoration area. To show an example of such an estimation, the results of several investigations on dispersal and establishment of *Arnica montana* are combined in Textbox 1. Although *A. montana* is one of the best-known species in this respect, it is obvious that the only possible prediction is a range within which the order of magnitude may be found. However, we feel that in this case (hypothetical, but comparable to the management practice) the conclusion can safely be drawn that without deliberate introduction the chance of establishment in the new area is negligible.

The question remains unanswered how an estimation, such as the one made in Textbox 1, is appreciated by the individual authority in charge of management when they have to decide whether to reintroduce a species or not. In The Netherlands, strong ethical objections against reintroduction of species exist when compared to many other countries. This means that, particularly in The Netherlands, the information provided by research on seed longevity and dispersal is most important for decision making on reintroduction of plant species.

Former farming systems often provided for long-distance dispersal processes initiating and maintaining species richness. Examples of such dispersal processes are large-scale

Textbox 1. Estimation of the chance of establishment for *Arnica montana*

Points of focus	Available data	
Data on the target area	Target area history	Target area intensively used for agriculture for about 50 years. Former heathland.
	Suitability	Suitable for establishment of *Arnica montana*
	Distance from seed source	*c.* 100 m
	Obstacles for wind dispersal	None
	Accidentation	None
	Connections with source population	No obvious connections by machinery or large grazing animals.
	Weather data	Max wind speed (gust) at vegetation height (30 cm) measured in July: *c.* 5 $m s^{-1}$
Seed bank and dispersal of *Arnica montana*	Transient seed bank	
	Seed dispersal primarily by wind	
	Wind tunnel experiment at 6·5 $m s^{-1}$ with vegetation 30 cm tall: 95% of the seeds is deposited within approx. 2·5 m (Fig. 2)	
Source population data	Hypothetical example of demography of a medium sized population of *Arnica montana* in The Netherlands:	
	Number of plants	*c.* 100
	Number of plants flowering	*c.* 40
	Number of flowers per plant	*c.* 5
	Number of seeds per capitulum	*c.* 50
	Total seed production	*c.* 10 000
	Area of the population	*c.* 100 m^2
	Month of seed shed	July
	Germination and seed quality	Strongly declining with distance, on the 95th percentile the chance of germination has dropped to about 10% (Strykstra *et al.* 1998)
	Establishment	Within natural vegetation 5–10% (De Graaf *et al.* 1994)

Conclusion:
Establishment from seed bank: none.
Establishment from seed dispersal: negligible.
Total chance of establishment: negligible.

Motivation:
After 50 years of agricultural use it is extremely unlikely that germinable seeds are still in the soil. Considering the maximum wind speed in July, it seems that the wind tunnel experiment gives a reasonable distance of the 95th percentile. This means that most of the seeds will be trapped in the vegetation within a few metres. Most of the 10 000 seeds will fall within the population itself. In the direction of the prevailing wind most seeds will not travel further than a few metres.

A safe estimation is that several tens of seeds will travel into the tail of the distribution, several metres beyond the population border. These are the seeds with the lowest quality, of which only a small portion will germinate. Considering a reasonable chance of establishment, this would mean that the chance that a seed will actually produce a seedling in a suitable vegetation beyond several metres outside the population is approximately 1% of these several tens of seeds. Considering the spread of this 1% over about a 100 m this chance will be extremely small.

transhumance between grazing areas, or transport induced by hay-making (Poschlod *et al.* 1996; Strykstra *et al.* 1997). Nowadays, restoration can no longer rely on these processes (Poschlod *et al.* 1996; Poschlod & Bonn 1998). Since research has shown already that a large number of species of seminatural communities cannot re-establish from long-term persistent seed banks (Thompson *et al.* 1997; Bekker *et al.* 1998), and most forms of dispersal are ineffective over large distances, dispersal has become a serious bottleneck in restoration management.

Connecting source areas and target areas by a dynamic 'moving ecological infrastructure', such as livestock (Fischer *et al.* 1996; Poschlod *et al.* 1996) or machinery (Strykstra *et al.* 1996, 1997) might offer a solution to this problem. However, such procedures are not always applicable in the modern landscapes of, for instance, The Netherlands in which habitats with nature conservation interest are highly scattered. This may mean that restoration without measures such as reintroductions will be impossible, which renders it difficult and expensive and possibly even impossible to achieve. It should be appreciated that many European countries still contain large areas of low-intensity farming, or 'farming on the edge' systems, which still include the dispersal vectors necessary to maintain species richness (Bignal & McCracken 1996). The maintenance of such systems may be as important or even more important for the conservation of biodiversity in Europe than restoration and deserves more attention than it is given today.

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