Field experiments on seed dispersal by wind in ten umbelliferous species (Apiaceae)

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Abstract

This report presents data from experiments on seed dispersal by wind for ten species of the family Apiaceae. Seed shadows were obtained in the field under natural conditions, using wind speeds between four and ten m/s. The flight of individual seeds was followed by eye, and seed shadows were acquired, with median distances varying from 0.7 to 3.1 m between species. Multiple regression models of wind speed and seed weight on dispersal distance were significant for six out of ten species; wind speed had significant effects in seven cases, but seed weight only once. A good correlation between mean terminal falling velocity of the seeds of a species and median dispersal distance, indicates the promising explanatory power that individual terminal velocity data might have on dispersal distance, together with wind speed and turbulence. The theory that seeds that seem to be adapted to wind dispersal travel much longer distances than seeds that have no adaptation was tested. Flattened and winged seeds were indeed found to be transported further by wind, but not much further. Moreover, the species with wind-adapted seeds were also taller, being an alternative explanation since their seeds experienced higher wind speeds at these greater heights. Furthermore, flattened and winged seeds were disseminated from ripe umbels at lower wind speeds in the laboratory. This means that the observed difference in dispersal distance would have been smaller when species specific thresholds for wind speed were incorporated in the field experiments. We argue therefore, that seed morphology is not always the best predictor in classifying species in groups with distinctly different dispersal ability.

Introduction

Among the factors that govern plant distribution and abundance, the processes of propagule dispersal under natural conditions, and the ensuing recruitment are among the most difficult to examine. Attempts have been made to link overviews of frequencies of different modes of dispersal with patterns of distribution and abundance (Willson et al. 1990; Hughes et al. 1994; Quinn et al. 1994; Hovestadt et al. 1999), and a body of theoretical and experimental investigations exists on seed shadows and transportation of propagules (Andersen 1991; van Dorp et al. 1996; Kiviniemi & Telenius 1998; Jongejans & Schippers 1999), but

investigations in the field or experiments carried out under natural conditions are scarce (Morse & Schmitt 1985; Casper 1987; Redbo-Torstensson & Telenius 1995; Kiviniemi 1996). The main reasons are that practical difficulties in tracing individual propagules during dissemination, monitoring their fate and keeping record of new recruits are almost insurmountable.

It is generally assumed that the anticipated mode of dispersal indicated by the morphology of the diaspores, is reflected in the distribution and abundance of plant species (Quinn et al. 1994). Thus, endozoochorous diaspores travel long distances – as long as they are retained in the digestive tract of the moving disperser – in a directed fashion. Ectozoochorous di-

aspores are expected to become transported slightly shorter, and end up less specifically, and water dispersal confers long distances of transportation in restricted habitats. Finally wind dispersed propagules are assumed to travel further and again, not in a directed way, than those lacking any particular morphological features that may enhance dispersal (Matlack 1994). The evidence behind these assumptions has weak underpinnings as they are often inferential and theoretical rather than experimental. The present investigation was undertaken to evaluate the significance of one of the major vectors during dispersal, wind, among diaspores of six plant species that are expected to be primarily dispersed by wind, and four that are not.

The investigated species all belong to the same family (Apiaceae), and the propagules are all held in a similar type of umbel. The major variables affecting primary dispersal are presumed to be diaspore morphology (presence of increasing surface area exposed to the wind) and weight, that together determine the terminal falling velocity, and the force of the wind (Greene & Johnson 1993). Wind speed of course is expected to have a positive effect on dispersal distance, while in general increasing diaspore weight will reduce it (Morse & Schmitt 1985; Strykstra et al. 1998). Diaspores were exposed to natural wind conditions. The range of wind speeds used was compared with wind speeds needed to detach seeds from umbels (Maier et al. 1999). We examine the following questions:

— What seed shadows (density curves of arrival probabilities (Willson 1993)) are found after primary dispersal of these species under natural conditions?
— What is the predictive power of wind speed, diaspore weight and terminal velocity for dispersal distance?
— Is assigning to dispersal modes based on diaspore morphology justified?

Methods

Species and seed selection

For the experiment on dispersal by wind ten species belonging to the family Apiaceae were selected, that occur near Tullbotorp field station (60 km SW of Stockholm, Sweden, 58°57′ N, 17°36′ E) (Table 1,

nomenclature follows Lid & Lid 1994). By choosing species from the same family and with reasonably similar appearance and height (all are over half a meter tall), interspecific variation was considerably limited to variables of interest to dispersal.

The fruit (a schizocarp) of the Apiaceae consists of two one-seeded mericarps that separate during ripening (Hendrix et al. 1991). In this report each of these mericarps will be referred to as a seed. Seeds from each of the ten species were collected and their viability was determined by cutting 50 weighed seeds per species in halves to check for a healthy endosperm. As a threshold weight for viable seeds of each species the mean was subsequently used of the lightest seed which seemed to be viable and the heaviest of those that did not. However, when the weight ranges of both seeds with healthy and seeds with unhealthy endosperm overlapped, the weight of the lightest approved seed was used.

Hundred seeds of each of the ten species were weighed within the weight range of viable seeds. These 100 seeds were subdivided into two groups of 50, each with similar weight distribution. In one of the groups the seeds were painted using a small paint brush, and used for the field experiments on dispersal by wind; while the second group was later used for measuring terminal velocities.

Site and vegetation selection

For each species the location of the field experiments was chosen within vegetation where the particular species did or could occur. These vegetation types included dry and wet meadows, forest edges, a raised bog and a seashore (Table 1). In each location a 1 m^2 vegetation description was made using the Braun-Blanquet (Westhoff & van der Maarel 1973) system of abundance (Appendix 1).

Seed dispersal by wind

During experimentation seeds were released individually from a raised platform and followed by eye until they arrived within the vegetation. The round horizontal platform had a radius of 4.2 cm and was placed on top of a long tube, diameter 1 cm. The height of the platform above ground was adjusted to maximum vegetation height (Table 1) by using a previously determined species specific relationship between plant height and maximum vegetation height (Telenius, unpubl.). A transparent lid on top of the platform kept the seeds in place until the lid was taken off (from a

Table 1. Vegetation type, heights (m) of platform and vegetation, wind speed (m s^{-1}) at platform height (calculated from 5 m s^{-1} at height 1.65 m, see text for formulae), seed number, seed morphology and seed weight (mg) (both mean as range) per species as in the primary dispersal experiments. The mean and range (*n*=25) of terminal velocities [m s^{-1}] measured in the fall tower. The first four species have seeds without obvious adaptation for dispersal, the latter six have winged or flattened seeds. Besides, the resulting median dispersal distance (m) is shown.

Species	Vegetation	Platform height	Vegetation height	Wind speed at platform height	Seed number	Seed morphology	Seed weight		Seed terminal velocity		Dispersal distance
			max.				mean	range	mean	range	median
Aegopodium podagraria L.	Forest edge	1.17	0.47	3.7	47	Cylinder	2.23	(1.10–3.47)	4.32	(2.76–5.34)	0.58
Myrrhis odorata (L.) Scop.	Forest edge	1.00	0.50	2.8	49	Cylinder	52.47	(18.13–71.49)	4.94	(4.27–5.54)	0.65
Aethusa cynapium L.	Dry meadow	0.91	0.41	2.9	46	Half sphere	0.81	(0.25–1.29)	2.48	(1.17–5.42)	0.72
Seseli libanotis (L.) Koch	Dry meadow	0.96	0.36	3.3	48	Cylinder	2.01	(1.12–2.51)	2.90	(1.87–3.37)	0.76
Selinum carvifolia (L.) L.	Shore	0.69	0.29	2.6	46	Winged half sphere	1.29	(0.43–1.81)	2.10	(1.38–3.63)	0.79
Peucedanum palustre (L.) Moench	Raised bog	0.90	0.30	3.4	47	Winged half sphere	1.99	(0.93–2.73)	1.84	(1.42–4.03)	1.31
Laserpitium latifolium L.	Forest edge	1.46	0.66	4.3	47	4 wings	6.36	(2.64–12.26)	2.29	(1.40–2.91)	1.90
Angelica sylvestris L.	Wet meadow	1.72	0.72	5.3	49	Flattened	1.93	(1.02–2.56)	1.53	(1.09–2.75)	2.29
Pastinaca sativa L.	Dry meadow	1.52	0.52	4.7	44	Flattened	3.12	(1.23–5.27)	2.06	(1.30–5.31)	3.05
Heracleum sphondylium L.	Dry meadow	1.58	0.68	4.7	50	Flattened	3.47	(1.73–6.10)	1.51	(1.09–1.82)	3.12

distance of about 60 cm with the use of stick, in order not to disturb air flow around the platform too much) at an occasion with a desired wind speed.

The lid was only removed, and the seed offered to the wind, when the wind speed was at least 4 m s^{-1}. Wind speed was measured with a simple rotating anemometer at 1.65 m height to 0.28 m s^{-1} (= 1 km h^{-1}) accuracy. When the wind speed during gusts stayed over 4 m/s for more than ca five seconds, seed release was restricted to every 10th or 15th second, in order to get a representative distribution of available wind speeds. Afterwards the wind speed at platform height was calculated using the following equations (Goudriaan 1977, Okubo 1980; Monteith & Unsworth 1990):

$$u_w = (u_*/k) * \log((z - d)/z_0) \text{ for } z \geq d + z_0,$$
$$\log d = 0.9793 \log z_v - 0.1536,$$
$$\log z_0 = 0.997 \log z_v - 0.883,$$

in which u_w is the wind speed at a certain height z, u_* is the friction velocity, k the von Kármán constant (0,41), z_v vegetation height, z_0 a measure for the roughness of the vegetation and $d + z_0$ the height at which the wind speed is zero. In practice, only vegetation height, and wind speed at a certain height are required. With those measured values parameters d, z_0 and u_* can be determined, and eventually wind speed at platform height calculated.

The arrival location on the ground was marked for each seed and the distance to the platform measured to the nearest cm. Per species wind speed at platform height and seed weight were used as independent variables in a multiple regression on dispersal distance.

Terminal velocities

Terminal velocities were determined by dropping seeds (per species $n=25$, randomly selected from the 50 seeds mentioned above) from a height of 15.83 m in a fall tower, which had a cross-section of 42 × 42 cm (Hofstee 1992; Grift et al. 1997; Jongejans & Schippers 1999). The falling speed the seeds eventually reached was calculated from the time seeds needed to fall over this height, taking acceleration into account.

Dissemination

Wind speeds needed to detach seeds from umbels were experimentally determined by exposing ten intact, ripe, umbels from each of 18 Apiaceae species, ten of which were subject to the investigation referred to above, during 60 s to a constant stream of air produced by a fan. The proportions of seeds released at successively greater distances from the fan, representing wind velocities of 1 m s^{-1}, 5 m s^{-1} and 10 m s^{-1}, respectively were estimated.

Results

Seed dispersal by wind

The cumulative distribution of wind speeds measured differed only slightly between species (Figure 1). *Angelica* seeds experienced the weakest wind speeds, *Pastinaca* seeds the hardest. The differences in wind speed calculated at platform height are considerably larger (Table 1).

Due to losses of seeds during the preparation of single measurements (i.e., while placing a seed on the platform), the actual number of measured distances is in many cases smaller than 50 (Table 1). However, it never occurred that a seed was lost out of sight during measurement, hence data are not biased, for instance towards shorter distances

The duration of the flight of most seeds was less than one or two seconds. Wind speed could sometimes change in that period with a magnitude of up to 1 m s^{-1}. The measured dispersal distances were used to produce cumulative seed shadows (Figure 2). Heterogeneity in neighboring plant heights sometimes caused some minor aggregation of seeds especially in taller vegetation; once a seed hit a plant and was within the vegetation, its primary journey was over: it fell to the ground or sometimes ended up on a leaf. However, since the vegetation height was homogeneous on the scale of the dispersed distances, this had no effect on the global seed shadow curves.

Median distances (Table 1) increased as follows: first a cluster of *Aegopodium*, *Myrrhis*, *Aethusa*, *Seseli* and *Selinum* around 0.7 m, than *Peucedanum* at 1.3 m, *Laserpitium* at 1.9 m, *Angelica* at 2.3 m and finally *Pastinaca* and *Heracleum* at 3.1 m. The median dispersal distance of the six wind adapted species is significantly higher than that of the other four ($F=8.592$, $p<0.05$, d.f.=1). All species (except *Peucedanum* and *Laserpitium*) have a seed shadow with a 'tail', that is a few seeds with considerably greater dispersal distance than the majority. One *Pastinaca* seed reached a distance of 13.9 m.

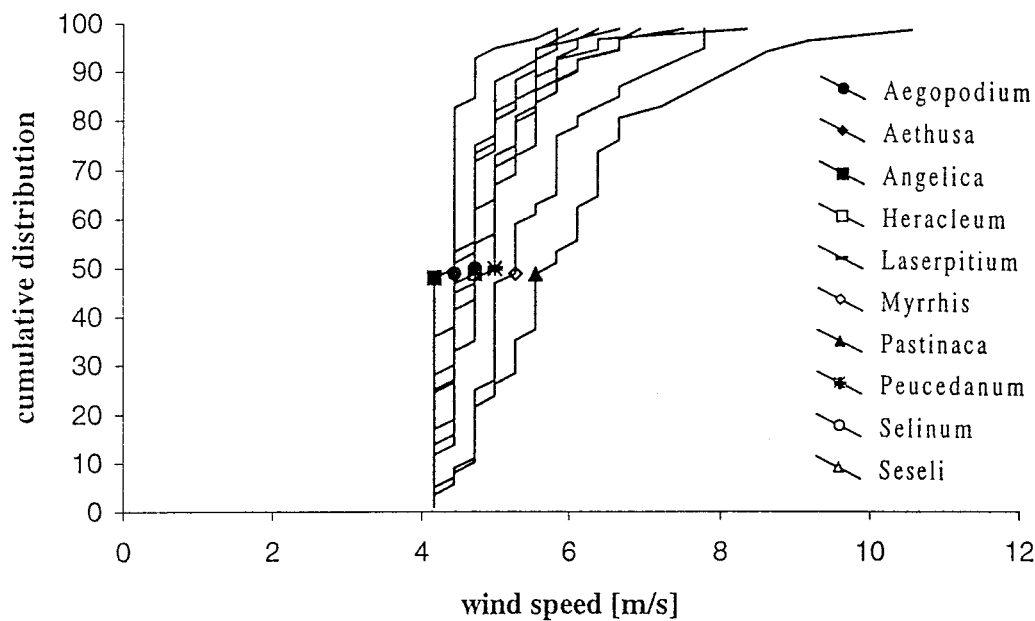When analyzing the data, three outliers (data that differed much from the normal range of values and

Figure 1. Cumulative distribution of used wind speeds per species. Measuring height is 1.65 m. The curve to the left represents *Angelica*, the two curves to the right *Pastinaca* and *Myrrhis*. The rest are indistinguishable.
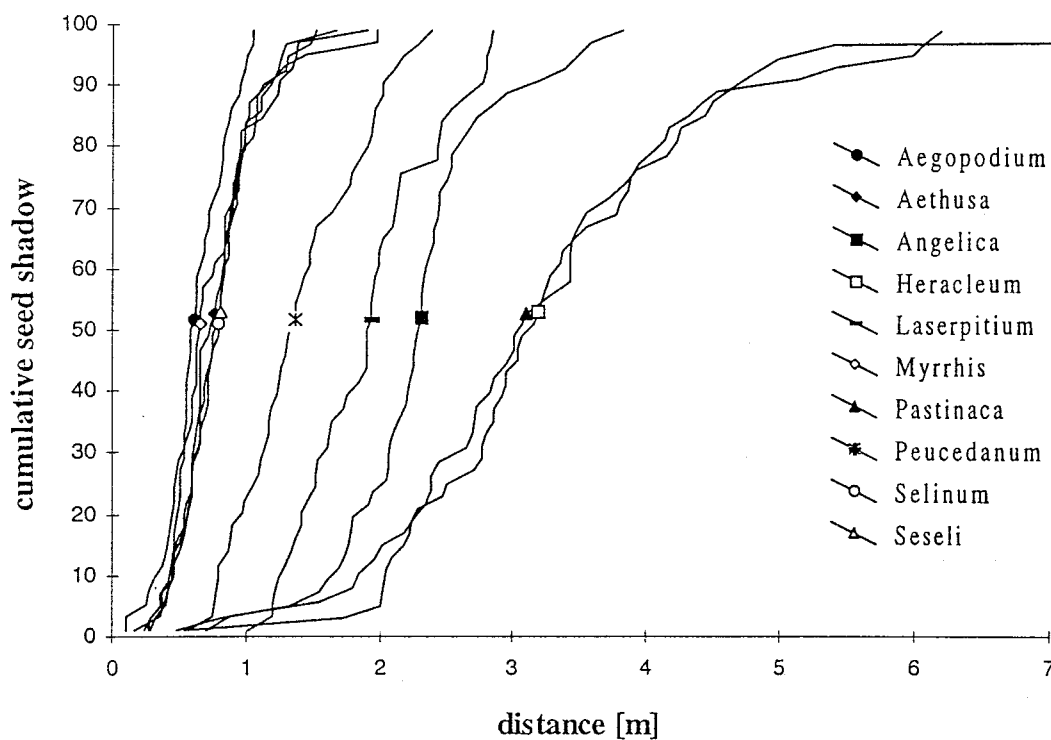

Figure 2. Cumulative seed shadows of ten Apiaceae species under field conditions. Wind speed was at least 4 m s^{-1} at a height of 1.65 m. See Table 1 for number of seeds, and release and vegetation heights. One *Pastinaca* seed reached a distance of 13.9 m.

Table 2. Multiple regression models for dispersal distances (distance [m] $= B_0 + B_1$ wind speed [m s^{-1}] $+ B_2$ weight [mg]).

Species	B_0	B_1	B_2	R^2	F	p
Aegopodium	−0.090	0.249**	−0.069	0.23	6.70	<.0029
Myrrhis	−0.170	0.377***	−0.006	0.47	20.40	<.0000
Aethusa	0.252	0.204*	−0.065	0.10	2.42	<.1010
Seseli	−1.563***	0.735***	0.031	0.62	35.17	<.0000
Selinum	0.623	0.161	−0.180	0.07	1.63	<.2078
Peucedanum	−0.644	0.469***	0.220	0.31	9.69	<.0003
Laserpitium	0.681	0.376**	−0.068	0.21	5.71	<.0062
Angelica	2.090	−0.033	0.173	0.01	0.29	<.7509
Pastinaca	1.860*	0.367**	−0.284*	0.25	6.80	<.0029
Heracleum	1.683	0.480	−0.192	0.10	2.72	<.0759

Note: Significance levels are: *, $p<0.05$; **, $p<0.01$; ***, $p<0.001$.

which therefore would have a disproportionally great impact on regressions) were detected with residual analysis and excluded from further regression analysis (Anonymous 1994): one light-weight *Myrrhis* seed reaching almost 2 m on a relatively weak wind, one light *Pastinaca* seed carried by a relatively strong wind (13.9 m), and one average weighted *Seseli* seed that did not travel far even on a strong wind. Furthermore, though staining the seeds slightly increased their weight (on average 4.3%), only unpainted seed weights were used in the analysis. Linear regression of dispersal distance on seed weight shows almost none or only a weak negative correlation between these two variables (*Aegopodium*, *Pastinaca*, *Selinum* and *Laserpitium*) (Table 2). Regression on wind speed at platform height (Figure 3) reveals much stronger (positive) correlations (except for *Heracleum*, *Selinum* and *Angelica*). When both independent variables are used to explain the variation in dispersal distances multiple regression models were highly significant for *Aegopodium*, *Laserpitium*, *Myrrhis*, *Pastinaca*, *Peucedanum* and *Seseli*, but not significant for the other four species. Within these models it was mostly wind speed that contributed significantly (Table 2). ANOVA between species with wind speed and seed weight as covariates was not possible due to the lack of parallel correlation with these variables (Anonymous 1994).

Terminal velocities

Mean terminal velocities differed significantly between species (Figure 4). When the species order of terminal velocities is compared with that of the median dispersal distances a highly significant, neg-

Table 3. Variation in terminal velocity per species explained by individual seed weights ($n=25$). The first four species have seeds without obvious adaptation for dispersal by wind, the latter six have winged or flattened seeds.

Species	R^2
Aegopodium podagraria	0.598***
Myrrhis odorata	0.237*
Aethusa cynapium	0.110
Seseli libanotis	0.198*
Selinum carvifolia	0.203*
Peucedanum palustre	0.012
Laserpitium latifolium	0.047
Angelica sylvestris	0.004
Pastinaca sativa	0.099
Heracleum sphondylium	0.440***

*Correlation is significant at the 0.05 level.
***Correlation is significant at the 0.001 level.

ative correlation is found (Kendall's tau_b$=-0.733$, $p<0.01$). Mean seed weight does not correlate significantly with dispersal distance nor with terminal velocity (Kendall's tau_b$=0.111$, $p=0.66$ and Kendall's tau_b$=0.156$, $p=0.53$, respectively).

Individual seed weights within species explained a significant part of the variation in terminal velocities for *Aegopodium*, *Heracleum*, *Myrrhis*, *Selinum* and *Seseli*. However, even for these species most variation was unexplained (Table 3).

Dissemination

A one-way ANOVA showed a strongly significant difference in dissemination at low wind speed between
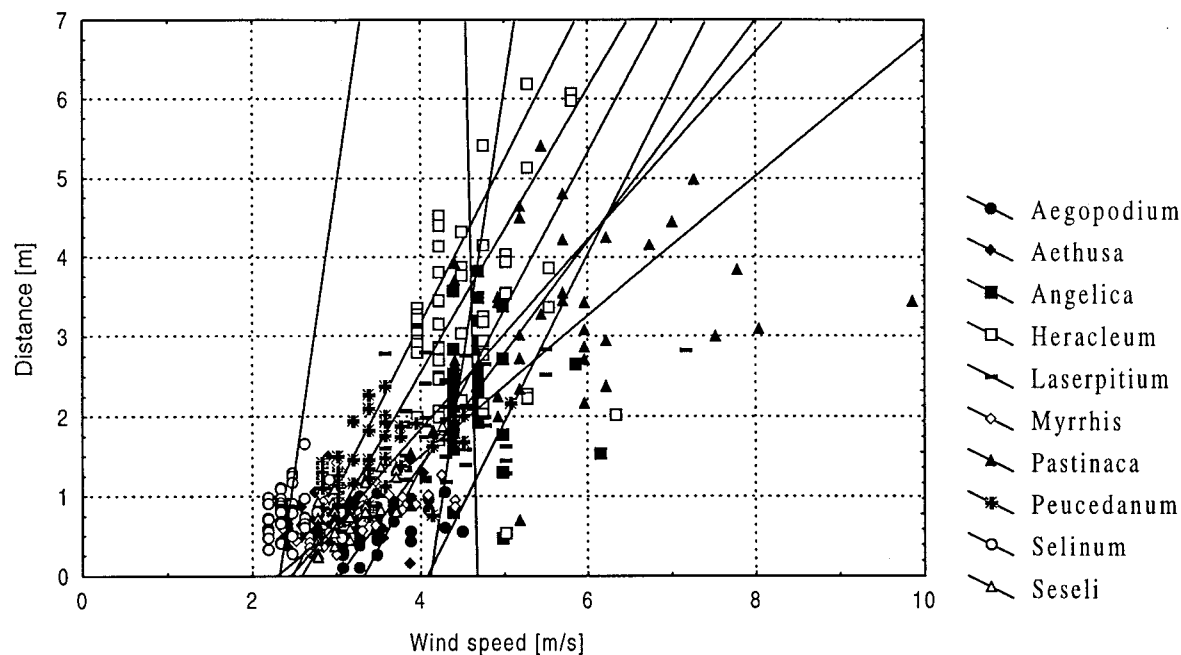
Figure 3. Linear regression per species of dispersal distance on wind speed (at platform height) only. Three outliers (see text) are left out of the figure and regressions.
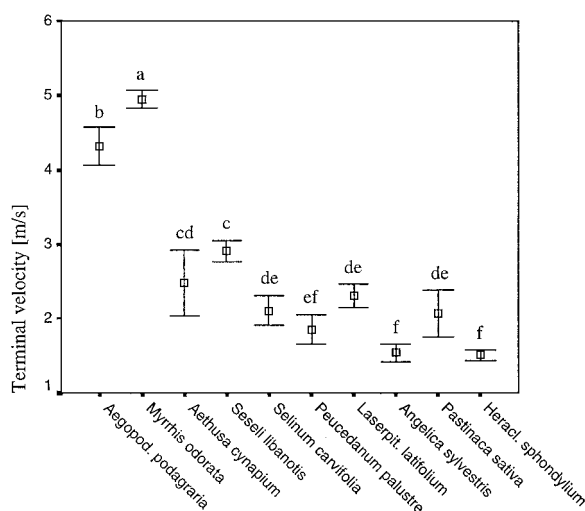

Figure 4. Mean (± standard deviation, $n=25$) terminal velocity [m s^{-1}] of seeds per species. Terminal velocities were calculated from the time needed to fall over a height of 15.83 m in a fall tower, adjusting for initial acceleration. Species are ordered by median dispersal distance as found in the field experiment (Table 1). Mean values with the same superscript letters are not significantly different at $p<0.05$ according to Tukey's test.

species with seeds that are assumed to be wind dispersed and species that do not have wind adapted seeds. Umbels with wind adapted seeds lose a higher

percentage of seeds when exposed to wind speeds below 10 m s^{-1} in the laboratory (Table 4).

Discussion

Species with flattened seeds have higher median dispersal distances than seeds without adaptations for wind dispersal, while winged seeds are intermediate (Table 1). Thus, at first glance it seems possible to separate the groups of species in their dispersal ability. However, other factors, i.e. wind speed, turbulence, plant and seed characteristics, may play an important role on dispersal distance, occasionally overwhelming the effect of seed morphology, as will be discussed below.

Wind

Although wind speeds can change during the flight of a seed, wind speeds measured explain a considerable part of the variation of the individual seed dispersal distances for seven of the investigated species. Of course, average wind speeds during individual flights are expected to be even better predictors. Within most species, a clear trend of greater dispersal distances with increasing wind speeds was found (Table 2),

Table 4. Percentage of seeds disseminated from a ripe umbel when held in front a fan at wind speeds lower than 10 m s^{-1}. Assumingly wind dispersed seeds detach significantly easier ($F=14.474$, $p=0.002$). Species with an asterix are used in the field experiment.

Species	Percentage of seeds disseminated at wind speed below 10 m s^{-1}
Wind dispersed seeds assumed:	
* *Angelica sylvestris*	89
* *Heracleum sphondylium*	92
* *Laserpitium latifolia*	49
* *Pastinaca sativa*	78
* *Peucedanum palustre*	40
* *Selinum carvifolia*	50
Heracleum sibiricum	89
Not wind dispersed seeds assumed:	
* *Aegopodium podagraria*	12
* *Aethusa cynapium*	97
* *Myrrhis odorata*	0
* *Seseli libanotis*	20
Carum carvi	3
Cicuta virosa	45
Daucus carota	27
Pimpinella major	1
Pimpinella saxifraga	3
Sanicula europaea	4
Sium latifolium	16

though it was not possible to distinguish whether the relationship was truly linear or quadratic as predicted by Hensen & Müller (1997), or whether distances of far blown seeds were related exponentially as found in wind tunnel experiments by van Dorp et al. (1996). *Angelica* was the only species in which no correlation could be found as a result of the small range of wind speeds.

Regarding the percentages of seeds disseminated at wind speeds below ten m s^{-1}, the wind speeds used in the field experiment are realistic for most species. Strong gusts of wind are available in the autumn, and field investigations show that these species spread their dissemination at least over several weeks (Lacey 1982). The turbulent character of wind is probably another important cause of the unexplained variation in dispersal distance (Morse & Schmitt 1985). Telenius & Torstensson (1989) did find that stronger winds decreased the influence of seed morphology on dispersal distances.

Plant characteristics

The species with morphological adaptations for wind dispersal tended to be taller (Table 1). Furthermore, their umbels present seeds to the wind higher above the surrounding vegetation. This means that for comparable winds their seeds experience stronger wind speeds at the height of the inflorescence. Thus, besides seed morphology, plant height can be a second explanation for the observed difference in dispersal distance.

The dissemination results weaken too the separation of species in dispersal ability groups on seed morphological characteristics only. Flattened or winged seeds are found to be detached by lower wind speeds than seeds that are cylinder shaped, probably because they expose a larger surface area to the wind. When during field experiments species specific thresholds for wind speed are used instead of a constant threshold wind speed for all species, dispersal distances are expected to differ less between seed morphological groups. Considering the process of dissemination, flattened seeds are a drawback, rather than an advantage for further dispersal.

Seed characteristics

Both seed morphology and seed weight are expected to contribute to the overall dispersal parameter of a seed: its terminal falling velocity. For a given size and shape, an increase in weight would increase seed terminal velocity (Augspurger & Franson 1987; Greene & Johnson 1993). One would expect that the relative importance of weight for the characteristic terminal velocity is greater for cylinder shaped seeds than for winged or flat seeds. This is confirmed by our results which show higher correlations between terminal velocity and seed weight for species with seeds that are not adapted for wind dispersal (Table 3). Only within the species with the highest terminal velocity, *Aegopodium*, having cylinder shaped seeds, seed weight can explain a significant part of variation in field dispersal distance (Table 2).

Terminal velocity itself is, in contrast to seed weight, significantly correlated with measured dispersal distance at the species level. Therefore, one may expect that individual terminal velocity data will probably have a much stronger predictive power of actual dispersal distance than seed weight, unless considering uniformly cylinder or ball shaped seeds. Seed weight should not be disregarded though, since it contains more than dispersal information only, like

Table 5. Factors affecting median dispersal distances for six species with seeds assumingly wind dispersed and four species without flattened or winged seeds. For each of these two groups averages of species means are calculated for wind speed at dissemination height (Table 1), for seed terminal velocity (Table 1) and for the part of the variation in terminal velocity that is explained by seed weight (Table 3). The observed difference in median dispersal distance (calculated from Table 1) would have been smaller when species specific thresholds for wind speed (Table 4) were taken into account.

Factors affecting dispersal distance	Assumingly wind dispersed seeds	Assumingly not wind dispersed seeds
Wind speed at dissemination height (m s^{-1})	4.17	3.18
Seed terminal velocity (m s^{-1})	1.89	3.66
Partly explained by seed weight (R^2)	0.134	0.286
Percentage dissemination at wind speeds lower than 10 m s^{-1}	66.3	32.3
Observed median dispersal distance	2.08	0.68

investment of the mother plant, or likelihood for successful germination and establishment (Strykstra et al. 1998, Eriksson 1999).

Conclusions

The dispersal distances reached by seeds in these field experiments were 14 m at the most. These distances are probably not enough to account for real colonization of new patches. However, further dispersal may still arise when the lifetime seed output of a plant is considered: the probability of some seeds travelling far increases with the total number of seeds produced.

Although the seeds that were *a priori* recognized as being adapted to wind dispersal were transported slightly further than those without obvious adaptations, this might be subscribed to plant height as well. Together with the finding that winged seeds detach at lower wind speeds, which would have reduced the observed difference in dispersal distance when taken into account, there seems to be little evidence to justify a clear differentiation between apparently wind-adapted seeds and seeds with no obvious adaptation (Table 5). The results rather support a gradual change between the extremes and great importance of stochastic processes like air turbulence.

For future field experiments we recommend the additional use of data on average wind speed during the flight of a seed, on air turbulence and on seed terminal velocities for interpreting dispersal distances. The use of natural habitats for field experiments has the advantage that less assumptions are needed for the discussion on natural seed dispersal. Wind tunnels are more suitable to investigate the effect of separate factors under controlled (but unnatural) circumstances. For investigating long-distance dispersal by rare events like storms, a modeling approach is most useful (Cain et al. 1998), but again, field experiments are needed to determine the range of occurring dispersal conditions and distances, and to test the modeling of dispersal processes.

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Appendix 1

Description of plant species occurrence and abundance in a 1 m^2 plot on the ten field experiment locations. Abundance is recorded using a renumbered Braun-Blanquet scale. Nomenclature follows Lid & Lid (1994). Location codes are: A, *Pastinaca*; B, *Heracleum*; C, *Aethusa*; D, *Angelica*; E, *Aegopodium*; F, *Seseli*; G, *Laserpitium*; H, *Myrrhis*; I, *Peucedanum* and J, *Selinum*.

Locations	A	B	C	D	E	F	G	H	I	J
Dead organic material (covering%)	90	70	60	100	90	30	95	80	15	95
Herb layer (covering%)	80	95	80	100	95	80	70	75	20	3
Moss layer (covering%)	20	0	10	0	0	20	5	10	100	0
Canopy (covering%)					90		60	40		
Bare (covering%)	0	5	0	0	0	5	0	25	0	5
Poa pratensis L.	3	5	3	2	3	5	8			
Dactylis glomerata L.	2	5	3		5	2	5			
Achillea millefolium L.	5	3	5		1	5				
Festuca pratensis Hudson	7		2			7				
Lathyrus pratensis L.	3	5	6							
Phleum pratense L.	5	2						2		
Deschampsia flexuosa (L.) Trin.	2	6						5		
Taraxacum sp. Weber	3		1			5				
Trifolium pratense L.	5									
Ranunculus acris L.	3									
Luzula pilosa (L.) Willd.	2						2	1		
Poa compressa L.	1									
Cirsium arvense (L.) Scop.		2		2						
Myosotis arvensis (L.) Hill		2								
Vicia tetrasperma (L.) Schreber		1								
Festuca rubra L.		5	5							
Galium album Miller		5	5							
Galium verum L.		3	2						2	
Tragopogon pratensis L.		2	3	1						
Avenula pubescens (Hudson) Dumort.			3							
Stellaria graminea L.			2							
Alopecurus pratensis L.			3	5	3	1				
Anthriscus sylvestris (L.) Hoffm.			2	2	2	1				
Urtica dioica L.				7						
Equisetum palustre L.				2						
Lolium perenne L.				8	3					
Aegopodium podagraria L.					8					
Equisetum arvense L.					3					
Filipendula ulmaria (L.) Maxim.					2					
Oxalis acetosella L.					2					
Viola riviniana Reichenb.					2		2			
Vicia cracca L.					2		1			
Veronica chamaedrys L.					2		2	2		
Trifolium repens L.						7				
Leucanthemum vulgare Lam.						3				
Agrimonia eupatoria L.						2				
Centaurea jacea L.						2				
Plantago major L.						2				
Fragaria vesca L.							7			
Hepatica nobilis Schreber							5			
Fraxinus excelsior L.							2			

Locations	A	B	C	D	E	F	G	H	I	J
Dead organic material (covering%)	90	70	60	100	90	30	95	80	15	95
Herb layer (covering%)	80	95	80	100	95	80	70	75	20	3
Moss layer (covering%)	20	0	10	0	0	20	5	10	100	0
Canopy (covering%)					90		60	40		
Bare (covering%)	0	5	0	0	0	5	0	25	0	5
Veronica serpyllifolia L.							2			
Geum rivale L.							1			
Melica nutans L.							1			
Saxifraga granulata L.							1			
Sedum telephium ssp maximum (L.) Krocker							1			
Anemone nemorosa L.							3	2		
Lathyrus linifolius (Reichard) Bässler							2	5		
Quercus robur L.							1	1		
Acer platanoides L.								1		
Sphagnum spec									9	
Eriophorum vaginatum L.									6	
Andromeda polifolia L.									4	
Vaccinium oxycoccos L.									4	
Carex limosa L.									3	
Drosera rotundifolia L.									3	
Phragmites australis (Cav.) Trin. ex Steudel										3

Note: The canopy consisted in all three cases of *Quercus robur* and on the *Laserpitium* and *Myrrhis* location also of *Fraxinus excelsior*.

Code	Covering percentage or number of plants	Braun–Blanquet code
9	75–100%	5
8	50–75%	4
7	25–50%	3
6	12.5–25%	2b
5	5–12.5%	2a
4	>100	1m
3	20–100	1
2	3–20	+
1	1–3	r