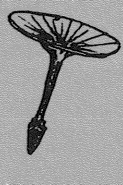
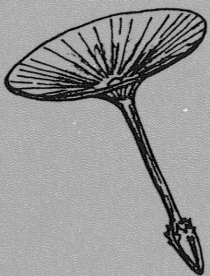


Seed Dispersal by Wind in Herbaceous Species



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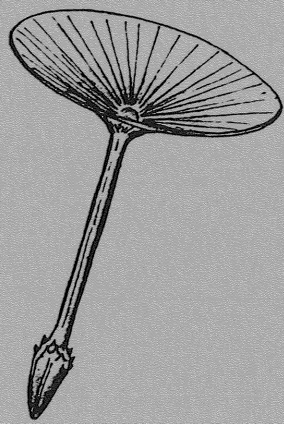

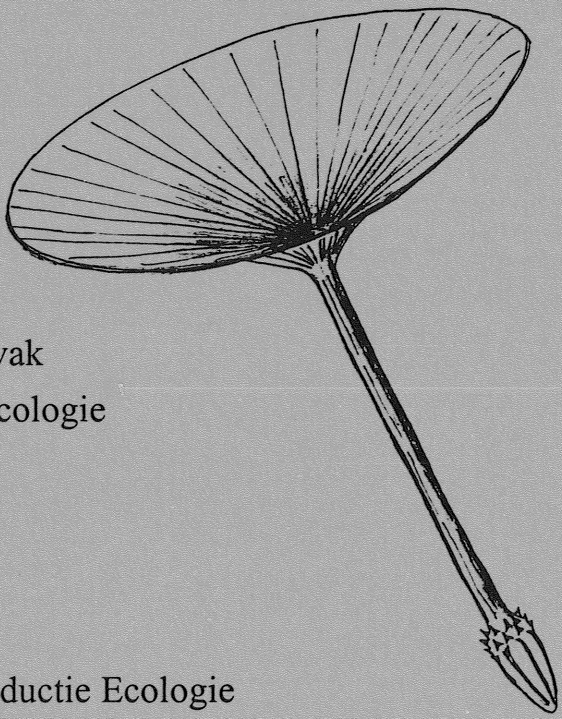

Maart 1998

Verslag in het kader van een afstudeervak
Onkruidkunde en Toegepaste Plantenecologie

Begeleider: Peter Schippers

Theoretische Productie Ecologie
Landbouwuniversiteit Wageningen

Voorwoord

Dit onderzoek naar windverspreiding van zaden van grasland kruiden is gedaan als afstudeervak in de Wageningse studie biologie aan de vakgroep Theoretische Productie Ecologie. Hoe meer ik in het onderwerp van zaadverspreiding kwam, hoe intrigerender het werd. Het enthousiast samenwerken met begeleider Peter Schippers heb ik als zeer leerzaam en prettig ervaren. Dit verslag is het resultaat van die samenwerking. David Kleijn was mijn leermeester in het herkennen van kiemplantjes in zijn akkerrand proefstroken en in het verwerken van die gegevens in GENSTAT.

Verder hebben Jan Goudriaan en Johan Grasman (vakgroep Wiskunde) geholpen bij het doorgronden van de wiskundige formules; heeft Bram de Vos (AB-DLO te Haren) de horizontale windtunnel, en heeft Jan van Kleef (AB-DLO te Wageningen) vele malen een hittedraad anemometer ter beschikking gesteld. Jan Willem Hofstee en Michel Govers hebben (vakgroep Agrotechniek en -fysica) enthousiast hun valtoren voor gebruik aangeboden en de benodigde apparatuur geïnstalleerd. Medestudenten Linda Haartsen, Jasper van der Hout, Linus Franke en Joost van Heerwaarden hielpen bij de metingen in de valtoren. Eenieder bedankt voor de hulp, die het mogelijk maakte dit onderzoek te doen.

Eelke Jongejans
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Zaadje

Daar zweeft een zaadje door de lucht
hoe grillig is zijn baan.
Dan denk ik met een diepe zucht
Waar komt dat zaad vandaan.

Er krimpt iets samen in mijn maag
dan moet ik bijna wehenen.
Nooit krijg ik antwoord op de vraag
Waar gaat dat zaadje hehenen

Waarheen, waarheen, wahaarheen?

Crackerhash

Table of Contents

Abstract

The first objective was to evaluate an individual-based seed dispersal model presented by Andersen (1991) for different kinds of herbaceous seeds which differ in seed weight and presence of plumes. Simulation results of the seed dispersal model were compared with observations in a horizontal windtunnel. Considering the large variation in seed morphology and mass, the simulation results fitted wind tunnel results reasonably well indicating the generality of the model for herbaceous species. Model sensitivity was evaluated with respect to wind speed, vegetation height and terminal velocity range. Furthermore, the model was elaborated to account for seed acceleration processes. This elaboration, however, did not produce better results.

The second objective was to compare two methods to estimate terminal velocity, the most import species specific parameter of the model. Terminal velocities were estimated with a dropping method and a method to float seeds in an upward air stream. Although both methods have their advantages and disadvantages simulations with results of the dropping method gave better resemblance to seed shadows generated with results of the horizontal windtunnel.

Key words: connectivity; Crepis capillaris; *dispersal model; fall tower;* Leucanthemum vulgare; Picris hieracioides; *seeds;* Silene latifolia ssp. alba.; *terminal velocity; vertical windtunnel; wind dispersal.*

1. Introduction

In densely populated areas plant habitats are becoming more and more fragmented because of urban, infrastructural and agricultural expansions (Verkaar, 1988). Local plant populations living in such a landscape are often small and contain few individuals which makes the risk of extinction high. The survival of the meta-population, a group of local populations connected by inter patch dispersal, in such landscapes is strongly dependent on the recolonisation probability or connectivity (Mac Arthur and Wilson, 1967; Fahrig and Merriam, 1985; Tilman, 1994). Reduction of this connectivity may lead to extinction of species in such a landscape. One of the bottlenecks when analysing the meta-population dynamics of species is knowledge about dispersal (Primack and Miao, 1992; Schippers et al., 1996). Seed dispersal can be considered as a key process in determining the survival of these populations.

Seeds are dispersed in many different ways (by wind, water, ballistic mechanisms, animals), in open grasslands, however, wind can be regarded as one of the most important vectors (Ridley, 1930; Van der Pijl, 1982). The dispersal distances of all seeds of a certain plant displaced by the wind form a seed shadow, a probability density curve of arrival probabilities (Willson, 1993). The tail of this seed shadow, representing the furthest blown seeds, can be regarded as important as the median for an estimation of the recolonisation rate (Portnoy and Willson, 1993; Van Dorp et al., 1997).

1.1. Seed dispersal models

It is difficult to estimate seed shadows of wind dispersal experimentally because the tail of these functions is characterised by very low probabilities. This problem may be overcome when there are good explanatory models to describe the wind dispersal process. Two kinds of mechanistic seed shadow models have been described (Greene and Johnson, 1989; Okubo and Levin, 1989; Andersen, 1991): (1) Seedflux models, that describe seed densities in z,x space analytically and (2) individual-based models, that simulate the flight of one seed in time and produce seed-shadow curves by combining many simulated dispersal distances. In both models the displacement rate of the seed in horizontal direction equals the wind speed and in vertical direction is determined by the terminal velocity, which is the speed finally reached when a seed is falling in motionless air (Verkaar et al., 1983). Gaussian functions describe air turbulence in these models.
An advantage of individual-based models is the possibility to add extra processes like vegetation-roughness dependant windprofiles or acceleration of seeds. Furthermore,

Andersen (1991) showed that an individual-based model gives better results than seedflux models when predicting seed-shadow curves. Although the individual-based model of Andersen is promising it is only tested for plumed seeds of one species using the mean terminal velocity.

1.2. Methods to determine terminal velocity

The most important species specific characteristic used in dispersal models is the terminal velocity (V_t), The terminal velocity is determined by seed morphology and -weight, and can be obtained by two methods (Browder and Schroeder, 1980): (1) A dropping method, using a fall tower in which seeds are dropped from a certain height in motionless air (Schulz et al., 1991; Askew et al., 1997) and (2) a floating method, using a vertical windtunnel in which seeds float and the necessary upward windflow is determined (Bilanski and Lal, 1965; Law and Collier, 1973; Hofstee, 1992). Both methods have their advantages and problems. The advantage of the floating method compared to the dropping method is that the terminal velocity can be obtained directly and that the apparatus can be relatively small. A disadvantage is that it is difficult to obtain a smooth windflow with little turbulence. A good comparison between the two methods has never been made.

1.3. Dispersal in field margins

As said, seed dispersal is supposed to be the most crucial factor in colonisation of plant species. If this is true there should be a direct correlation between the most important species specific character influencing seed dispersal and the relative species colonisation rate.

1.4. Objectives

A promising seed-shadow model found in literature is Andersen's individual-based model incorporating turbulence. However this model has never been tested for more than one species with plumed seeds. Therefore our first objective is to test the generality of this model for various seeds that differ with respect to seed weight and the presence of plumes. Andersen's model assumes that seeds reach the wind speed and terminal velocity instantaneously. This may be a proper assumption for plumed seeds but when using other seeds, acceleration processes might be crucial. To overcome this problem we develop an elaborated version of Andersen's model incorporating acceleration and compare this model to the original model. Furthermore we want to test model sensitivity with respect to wind speed, vegetation height and intraspecific terminal velocity range.
V_t can be regarded as the most important species specific model parameter for determining the seed shadow caused by wind. Two methods have been used to obtain V_t. However a

good comparison between the two methods for estimating terminal velocities has never been made. Therefore the second objective of this paper is to evaluate these methods. And finally we test the theory that terminal velocity is the most important characteristic for dispersal by measuring median colonisation distances from a known source in field boundary margins and comparing these with seed characteristics.

2. Material and Methods

2.1. Terminal velocity measurements

2.1.1. Dropping method

For the terminal velocity measurements 21 grassland species (collected in the Netherlands) were chosen (table 1). Seeds were released in a fall tower consisting of a square tube of 42 by 42 cm in a stairwell, and had a free fall over a height of 15.83 m. The time needed for this fall was measured electronically by use of a photo sensor just below the point of release and by a piezo element (which senses vibrations) in the plate on which the seeds landed (Hofstee, 1992; Grift et al., 1997). For seeds with a low rate of descent and thus too little impulse to trigger the piezo element, the time was stopped manually, and corrected for the reaction time of the observer. For each species the falling time was thus measured for 20 seeds. The terminal velocity was calculated by dividing the height of the fall tower by the duration of the fall, with a correction for the acceleration process. For *Crepis capillaris* and *Hypochaeris radicata* no measurements were made because seeds were not collected at the time.

2.1.2. Floating method

A vertical windtunnel (figure 1) was constructed using a transparent tube of 5.2 cm diameter. A fan caused an upward airflow, which was stabilised by a box in which the flow rate was very low, resulting in an even distribution of the underpressure over the cross-section of the tube. Underneath the tube, where the air was sucked in, a funnel with a grid was placed to minimise air turbulence. The grid, 7 cm high, consisted of adjoining holes with a diameter of 6 mm.

In the tube a section of 50 cm was enclosed by 2 sieves in which the seeds were released. The flat metal sieves, necessary not to lose the selected seed, had holes of 0.7 mm. The flow rate was measured with a hot-wire anemometer. The measurements 7.4 cm above the upper grid (to keep from disturbing the air flow in the section), were adjusted for the small difference in measured flow rates above and in the section.

Seeds were released through a hole in the measuring section of the tube. The flow rate was recorded at which a seed floated in the middle of the section. *Campanula rotundifolia* seeds were too small as they were able to penetrate the sieves of the vertical windtunnel making measurements impossible.

Table 1. The morphology, weight and terminal verlocity of seeds used. Besides the mean also the range of terminal velocity values is given. In the last column the mean field medians are presented.

species	family	seeds						field median
		morphology	weight	terminal velocity				
				dropping method		floating method		
			[mg]	[m/s]	[m/s]	[m/s]	[m/s]	[m]
			mean	mean	range	mean	range	mean
Species used for the model evaluation								
Crepis capillaris	Asteraceae	plume	0.09			0.39	(0.20 - 0.93)	2.83
Picris hieracioides	Asteraceae	plume	1.11	0.83	(0.27 - 1.79)	0.58	(0.26 - 1.19)	1.87
Leucanthemum vulgare	Asteraceae	cylinder	0.39	2.62	(1.84 - 3.26)	2.32	(1.73 - 2.68)	0.45
Silene latifolia subsp. alba	Caryophyllaceae	ball	1.04	4.35	(3.30 - 5.04)	3.43	(2.97 - 3.84)	0.68
Species only used for measurements								
Taraxacum officinale	Asteraceae	plume	0.78	0.43	(0.36 - 0.54)	0.32	(0.13 - 0.45)	
Hypochaeris radicata	Asteraceae	plume	1.05			0.49	(0.28 - 0.86)	1.76
Hieracium pilosella	Asteraceae	plume	0.17	0.98	(0.36 - 1.81)	0.64	(0.22 - 1.01)	
Holcus lanatus	Poaceae	caryopsis/lemma	0.22	0.84	(0.63 - 2.02)	0.81	(0.54 - 1.51)	
Linaria vulgaris	Scrophulariaceae	winged disk	0.15	0.92	(0.47 - 1.19)	0.85	(0.63 - 1.02)	
Tanacetum vulgare	Asteraceae	cylinder	0.12	1.04	(0.67 - 2.06)	0.94	(0.64 - 1.34)	1.15
Leontodon autumnalis	Asteraceae	plume	0.66	1.33	(0.43 - 3.20)	1.00	(0.62 - 1.90)	2.33
Campanula rotundifolia	Campanulaceae	ball	0.07	1.53	(1.24 - 1.78)			
Anthoxanthum odaratum	Poaceae	caryopsis/lemma	0.58	1.86	(1.02 - 2.99)	1.43	(0.89 - 1.90)	
Festuca ovina	Poaceae	caryopsis/lemma	0.31	1.62	(0.80 - 2.66)	1.75	(1.16 - 2.11)	
Daucus carota	Apiaceae	cylinder	0.85	2.01	(1.38 - 3.41)	1.51	(0.86 - 2.61)	1.53
Poa annua	Poaceae	caryopsis/lemma	0.45	2.34	(1.81 - 2.95)	2.16	(1.59 - 2.91)	
Rumex obtusifolius	Polygonaceae	ball/perianth	3.19	2.72	(1.71 - 3.57)	2.23	(1.86 - 2.54)	
Chenopodium album	Chenopodiaceae	ball in capsule	0.78	2.71	(1.55 - 3.90)	2.26	(1.40 - 2.71)	
Plantago lanceolata	Plantaginaceae	cylinders in capsule	2.92	3.41	(1.44 - 4.95)	2.71	(1.46 - 4.02)	
Galium mollugo	Rubiaceae	ball	0.62	3.62	(2.19 - 4.32)	2.94	(2.46 - 3.81)	0.25
Centaurea jacea	Asteraceae	cylinder	2.06	4.13	(3.32 - 4.79)	2.99	(2.27 - 3.44)	0.84

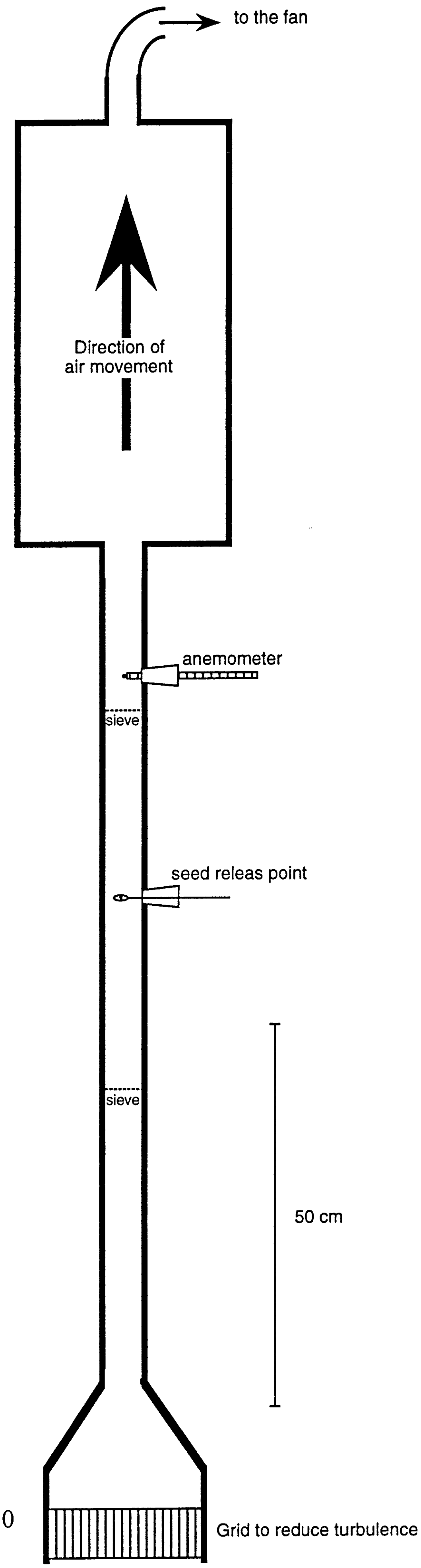

Figure 1.
A schematic picture of
the used vertical windtunnel.

2.2. Model and Test

A stochastic model incorporating turbulence was constructed according to Andersen (1991). The model calculated the flight of an individual seed from the seed source at a height z in a x,z space until it reached the ground. A seed shadow was obtained by adding the arrival distances of many simulations. The mean process, the velocities in downwind (X) and vertical (Z) direction, is described by:

(1a) $$dZ/dt = - V_t$$

(1b) $$dX/dt = u_w$$

in which u_w is the strength of the wind at height Z. If there is a homogenous windprofile, a seed will fall with velocity V_t and move a distance of $u_w * Z / V_t$ in X direction (Matlack, 1987; Ernst et al., 1992; Greene and Johnson, 1992). A logarithmic profile above a vegetation is a more realistic distribution of wind speeds when there is no thermic updraft (Goudriaan, 1977; Okubo; 1980; Monteith and Unsworth, 1990):

(2a) $$u_w = u_*/k * \log((z-d)/z_0) \qquad \text{for } z \geq d + z_0$$

(2b) $$u_w = 0 \qquad \text{for } z < d + z_o$$

in which u_* is the friction velocity, k the Von Karman constant (0,41), z_0 a measure for the roughness of the vegetation and $d + z_0$ the height at which the wind speed is zero. The effect of turbulence on vertical seed flight can be seen as an additional, stochastic process affecting vertical seed position. This was modelled by considering the distance of falling as caused by Brownian motion with mean $M = - V_t$ and diffusion coefficient $V = k\, u_*\, Z\, t$. Andersen (1991) used the generalised derivative of this Brownian motion, Gaussian white noise (W), to get a stochastic differential equation describing the change in vertical seed position in time. This equation was described in Andersen's (1991) article as:

(3a) $$dZ = 1/2\ (k\, u_*\, t - V_t)dt + (2\, k\, u_*\, Z\, t)^{1/2}\, dW$$

This equation however included a misprinted bracket, and should be:

(3b) $$dZ = (1/2\ k\, u_*\, t - V_t)dt + (2\, k\, u_*\, Z\, t)^{1/2}\, dW$$

The (1/2 k u_*t)-part (Gardiner, 1990) may be neglected because it was very small compared to V_t. The above equation can be modelled in discrete timesteps ($\Delta t = 0.001$s in our case) with this formula:

(4a) $$\Delta Z = - V_t \Delta t + (2 k u_* Z \Delta t)^{1/2} \Delta W$$

(4b) $$\Delta X = u_w (Z) \Delta t$$

Gaussian white noise (ΔW) can be modelled by drawing randomly from a normal distribution. Throughout the text we will refer to the model described above as the standard model. Figure 2 illustrates how trajectories were simulated by this model.

For slowly falling seeds, in the model, complete momentum transfer (seeds reach terminal velocity and wind speed instantaneously) was assumed. But for seeds with higher values of V_t this might not be acceptable. Therefore the model was elaborated with an acceleration process. To do this it was necessary to calculate the resistance (K) of a seed falling in air, using (Burrows, 1975; Hofstee, 1992):

(5) $$K = g / (V_t)^2$$

in which g is the gravitation constant. It was assumed that the resistance of the seed in the horizontal direction is the same as in the vertical direction. The acceleration (a) in Z and X direction can be modelled with:

(6a) $$a_z = - K u_z (u_z^2 + (u_w - u_x)^2)^{0.5} - g$$

(6b) $$a_x = K (u_w - u_x) (u_z^2 + (u_w - u_x)^2)^{0.5}$$

where u_z en u_x are the velocities of the seed in Z and X direction respectively. Notice that when $u_z = V_t$, $a_z = 0$. Throughout the text we will refer to the above described model as the elaborated model.

Four species were selected on basis of seed weight and the presence of plumed seeds for testing the model. *Crepis capillaris* and *Picris hieracioides* have plumed seeds; *Leucanthemum vulgare* and *Silene latifolia ssp. alba* have no wind adapted seeds. *Picris* and *Silene* have heavy (>1 mg) and *Crepis* and *Leucanthemum* light (<0,4 mg) seeds. Seed shadows of these species were measured in a horizontal windtunnel at different wind speeds (2, 3 and 6.5 m/s). The windtunnel was a closed circuit and had a measuring compartment of 13 m long and a cross-section of 75 cm x 75 cm. Van Dorp et al. (1996) used the same windtunnel for their experiments. Seeds were released at a height of 40 cm. With a flexible

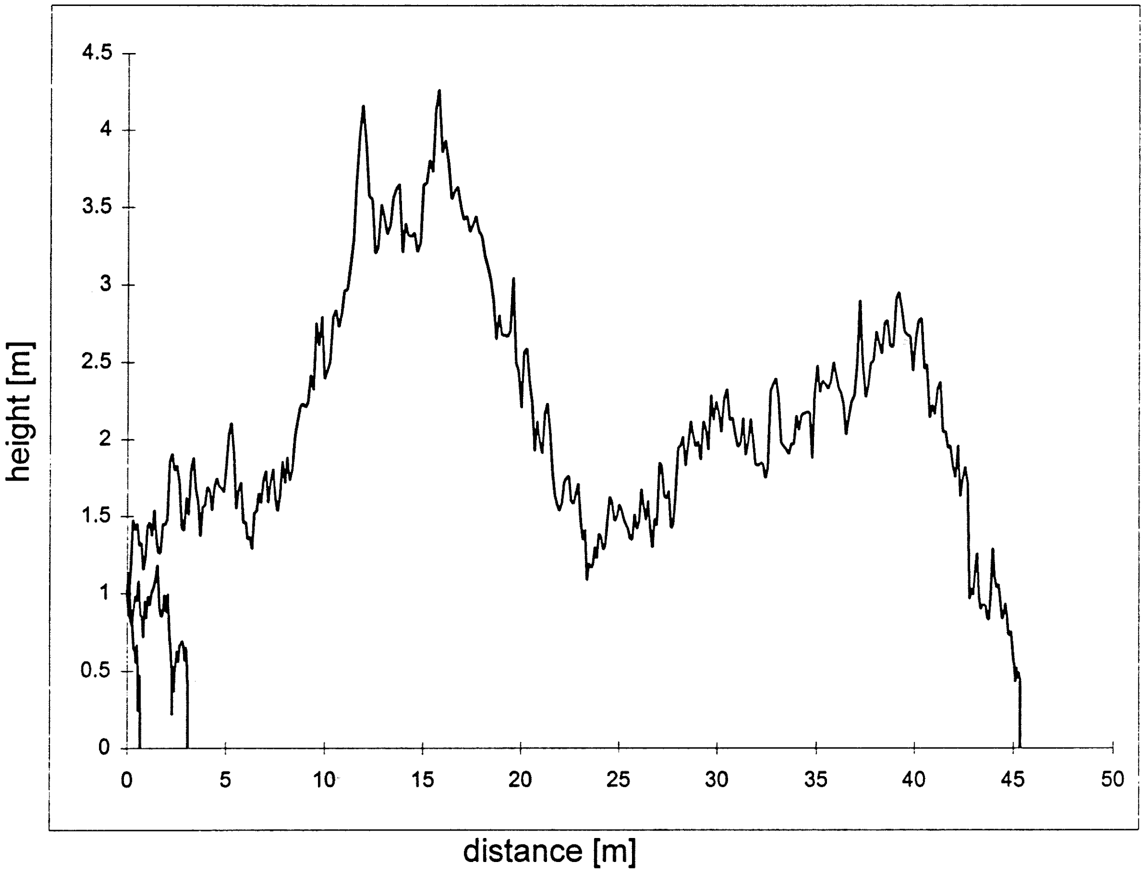

Figure 2.

3 illustrative flight trajectories, selected from standard model simulations (terminal velocity 1 m/s; flowering and vegetation height respectively 1 and 0.5 m; wind speed 20 m/s at reference height of 10 m).

tube seeds were brought from outside the windtunnel to the release point in a perpendicular direction to the wind flow. The surface of the tunnel was covered with sticky wallpaper to trap the seeds at the point they reached the ground. The dispersal distance along the length of the windtunnel was measured for each seed with an accuracy of 13 cm. The plumed seeds were not released at a wind speed of 6.5 m/s because of the limited length of the measure compartment.

Both the standard as the elaborated (for not-plumed seeds only) model were used to produce seed shadows of the selected species under the conditions of the horizontal windtunnel. The windprofile parameters were fitted to a measured windprofile. To produce 1 seed shadow all 20 V_t-values (resulting from the dropping or floating methods) were used 50 times per species. Thus a seed shadow was constructed with a thousand simulated dispersal distances. The simulated trajectories started 40 cm above ground and were not allowed to exceed the height of the windtunnel (75 cm).

2.3. Model sensitivity

The standard model was used to derive seed shadow predictions for the four species under grassland circumstances. For two species, with approximately equally heavy seeds, *Picris* and *Silene*, three different aspects of the model were studied: wind speed, vegetation height and terminal velocity input. Starting with basic conditions: flowering height of 80 cm for both species, vegetation height of 60 cm, wind speed of 12 m/s and all 20 V_t-values of the dropping method. First the wind speed (u_w) was varied (6, 12 and 24 m/s, corresponding with forces of 4, 6 and 9 on the Beaufort scale), secondly vegetation height (z_v) (20, 40, 60, 80 and 100 cm) and finally terminal velocity per species (all data, mean, minimum and maximum of the results of the dropping method). The flowering height was estimated using known height ranges (Van der Meijden, 1996). Goudriaan (1977) gives formulas to estimate z_0 and d with vegetation height (z_v):

(7) $$\log d = 0.9793 \log z_v - 0.1536$$

(8) $$\log z_0 = 0.997 \log z_v - 0.883$$

The friction velocity was calculated from (2a), when z_0 and d were estimated and u_w chosen at a reference height of 10 m, which is a normal height in meteorology.

2.4. Dispersal measurements in field margins

In spring 1993 the original field boundary along three arable fields in the vicinity of Wageningen were extended with a four metre wide vegetation strip. The vegetation strip was created by taking the outer four metres of the arable field out of production and in these strips 4 x 8 m large plots were created by (1) sowing a mixture of 30 grassland forbs, (2) sowing *Lolium perenne* and (3) allowing the vegetation to regenerate naturally. These boundary plots were replicated three times on each field in a randomised block design (for details see Kleijn et al., 1997). Plots were mown annually in autumn and cuttings were removed for each plot separately to avoid dispersing seeds by mowing activities. The introduced species did not occur in the original boundary, therefore, the occurrence of introduced species in the grass and regeneration plots gives an estimate of the realised dispersal distance of the introduced species into these plots. Hereafter plots sown with the forbs mixture will be referred to as source plot, the grass and regeneration plots as colonisation plots.

In April 1997 the distance of each seedling of the introduced species in the plots next to a source plot was measured up to the border of the source plot, with an accuracy of 10 cm (figure 3). Each colonisation plot was divided in 5 strips from the field edge to the arable field. Four strips were 1 m wide and the last, a safety margin next to the arable field, varied in width up to about half a meter.

The distance medians of the 10 most abundant species per plot per strip were used to analyse the effect of species, location, treatment and orientation (east or west), using ANOVA (GENSTAT, 1993).

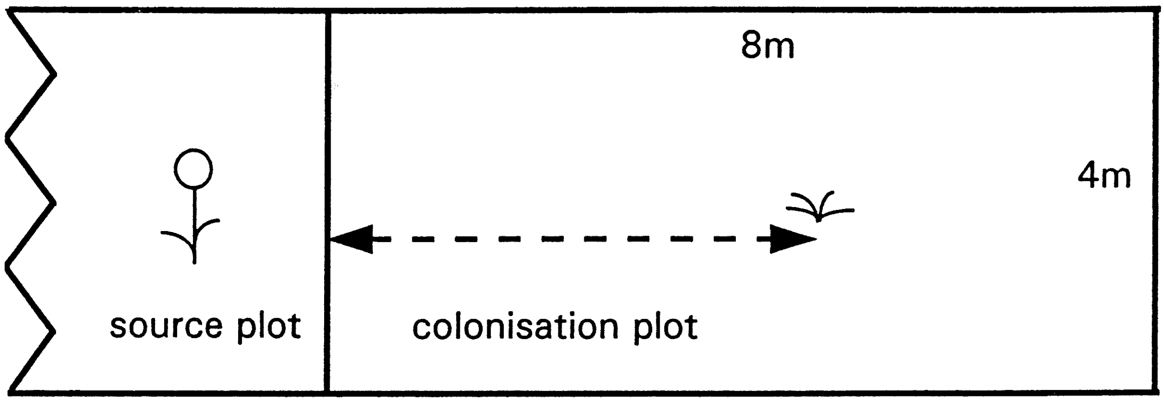

Figure 3.
Schematic picture of the measurements in the field margins.

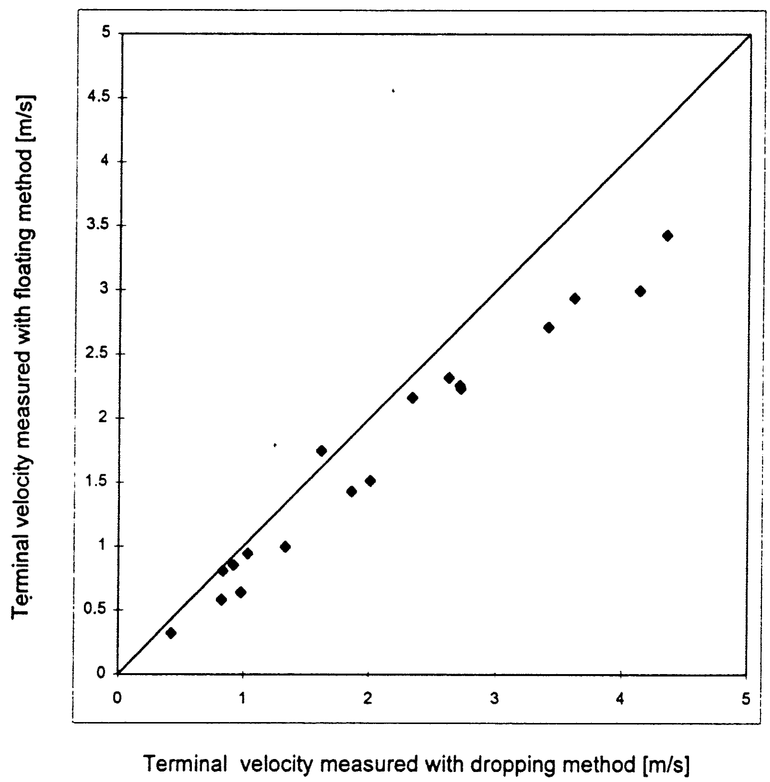

Figure 4.
The relationship between the mean average V_t-values [m/s] resulting from the dropping method and the floating method per species plotted against these values from the fall tower.

3. Results

3.1. Terminal velocities

The averages and ranges of V_t-values measured with the fall tower and the vertical windtunnel are listed in table 1. The mean weight (n=20) of the used seeds are also shown. In figure 4 the V_t-values of the floating method are plotted against the V_t-values of the dropping method per species. With one exception (*Festuca ovina*) the vertical windtunnel produced lower V_t-values. The dropping method V_t values were on average 1.23 times larger than for the floating method.

3.2. Model and Test

The cumulative seed shadow curves constructed with the measured and simulated dispersal distances are shown in cumulative frequency diagrams (figures 5, 6 and 7). Figure 5 depicts these curves for *Crepis* and *Picris* resulting of the standard model (without acceleration). For *Picris* the median, slope and tail of the measured curve were approached closely by both simulated curves. At 2.0 m/s the median of the curve (note the different scales on the X-axes) of the floating method curve seemed better, while at 3.0 m/s the tail was closer to the dropping method curve. For *Crepis* there were only simulated curves with floating method data. These met the measured medians well at 2.0, however at 3.0 m/s rather badly. The slopes fit well in both cases. But the tail of the measured curves at 2.0 m/s was lower than simulated.

The simulated and measured curves of *Leucanthemum* and *Silene* are plotted in figure 6. Except for *Leucanthemum* by 6.5 m/s, the measured curves were best approached by the simulated curve with dropping method data. For *Leucanthemum* the median distances of the simulations fitted very well, for *Silene* there was a slight, persistent overestimation of median distances. The slope of the simulated curves resembled that of the measured ones rather well for *Silene*, though for *Leucanthemum* they were a bit steeper at 2.0 m/s. The tails of the *Silene* simulation curves fit the experimental results better than the simulation curves of *Leucanthemum*, where especially at 2.0 and 6.5 m/s the measured curve tail lay lower. This means that relatively more seeds are dispersed a relative great distance.

Figure 7 depicts the comparison between the windtunnel experiment and the simulation results generated by the elaborated model (with acceleration). By comparing figures 6 and 7, the effect of introducing acceleration can be observed. The simulted curves differ in that they have a less steep slope than the simulated curves generated by the model without acceleration. Moreover their median distance in relation to that of the measured curves clearly shifts with changing wind speeds: at higher wind speeds curves changed from lesser to greater median distances compared with the measured medians. Therefore these last medians were best approached for low (2.0 m/s) wind speeds with floating method simulations, and best approached for higher wind speeds with dropping method simulations. The simulated slopes fit measurements best where the simulations without acceleration did worst (*Leucanthemum* by 2.0 m/s). In the other cases the curves in figure 6 fit the slopes better, though for *Silene* at 2.0 and *Leucanthemum* at 6.5 m/s there is no preference. However, in figure 7 the curve tail forms are rather good for all cases.

3.3. Model sensitivity

The model simulations with varied field parameters resulted in the cumulative frequency seed shadows shown in figures 8, 9 and 10. These diagrams have logarithmic scales on the distance-axis and are therefore not directly comparable with the model-test diagrams. Not surprisingly the windspeed diagram (figure 8) illustrates that higher wind speeds resulted in greater dispersal distances for both *Picris* and *Silene*. At double wind speed the median dispersal distance also doubled. Tail distances (95 and 99 percentiles in table 2) on the other hand were more affected by wind speed. For both species the tail distances increased about 3.3 times at a doubled windspeed.

Figure 9 shows the results of the model simulations at varying vegetation heights. Taller vegetation led to smaller median dispersal distances in all cases. In the case of a vegetation height of 100 cm (20 cm higher than the release height), about 20% of the simulated *Picris* seeds and 60% of the *Silene* seeds did not come further than 1 mm. In contrast to the trend in median dispersal distances, the tail distances (95 and 99 percentiles in table 3) show increasingly less differences by differing vegetation height.

The effect of using different V_t-values is plotted in figure 10. For both species the median dispersal distances generated with the total range of V_t-values are best approached by the medians generated with the mean V_t-value (table 4). When only the minimum V_t-value was used the median was higher, and when only the maximum V_t-value was used the median was lower. The tail dispersal distances of the four curves are all different for *Picris*, with increasing distances in the order: maximum, mean, range and minimum of the V_t-values. *Silene* shows the same pattern, but here the mean-curve approaches the all data-curve in the tail very well too.

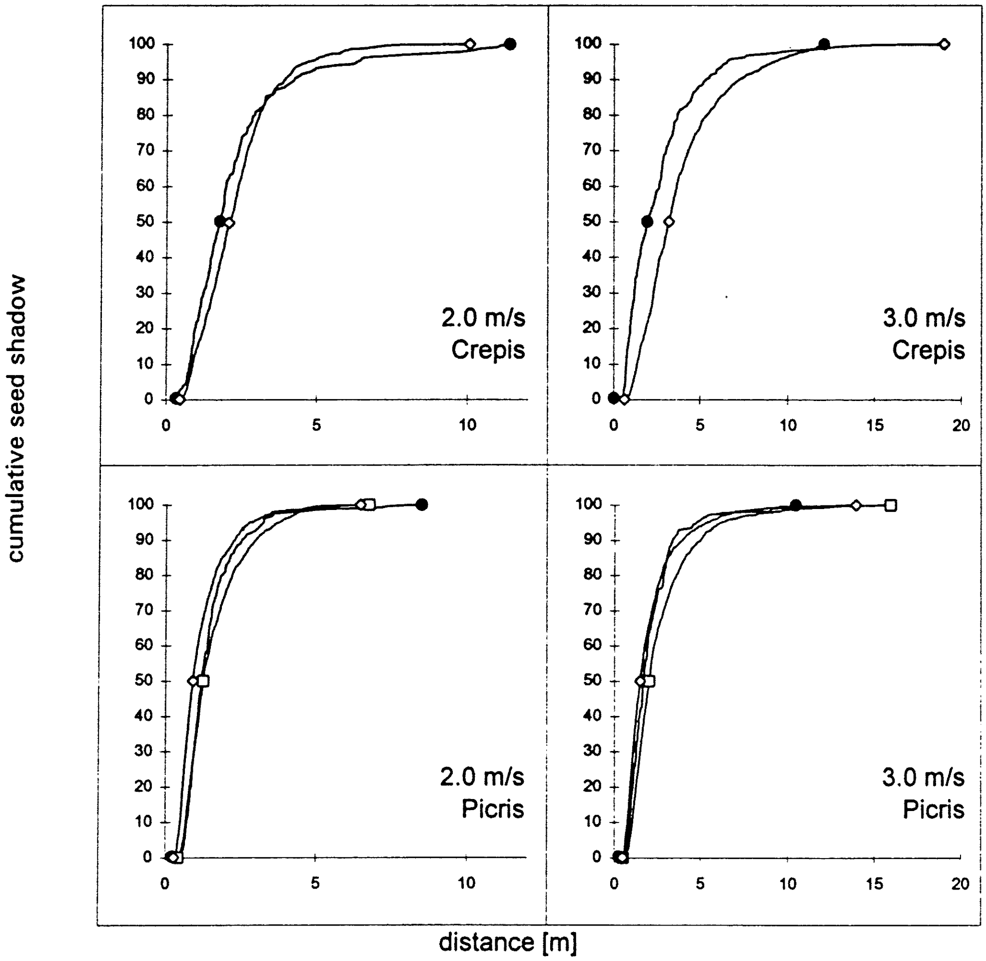

Figure 5.

Cumulative seed shadows resulting from the horizontal windtunnel experiment (n<=300; closed circles) and the model simulations without acceleration (n=1000; dropping method, open diamonds; floating methods, open squares), for different windprofiles (2 and 3 m/s) and species (*Crepis capillaris* and *Picris hieracioides*).

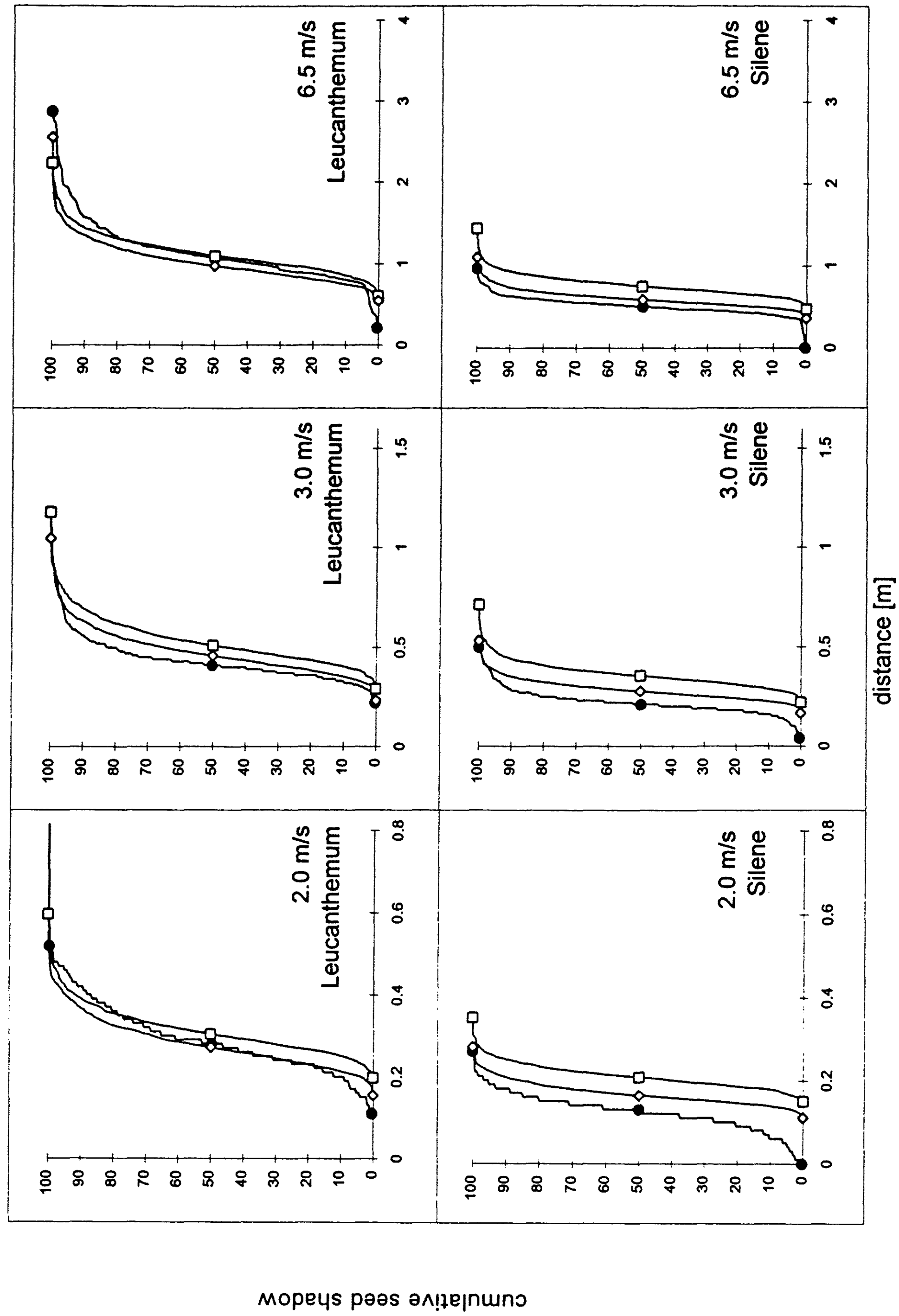

Figure 6.
Cumulative seed shadows resulting from the horizontal windtunnel experiment (n<=300; closed circles) and the model simulations without acceleration (n=1000; dropping method, open diamonds; floating methods, open squares), for different windprofiles (2, 3 and 6.5 m/s) and species (*Leucanthemum vulgare* and *Silene latifolia ssp. alba*).

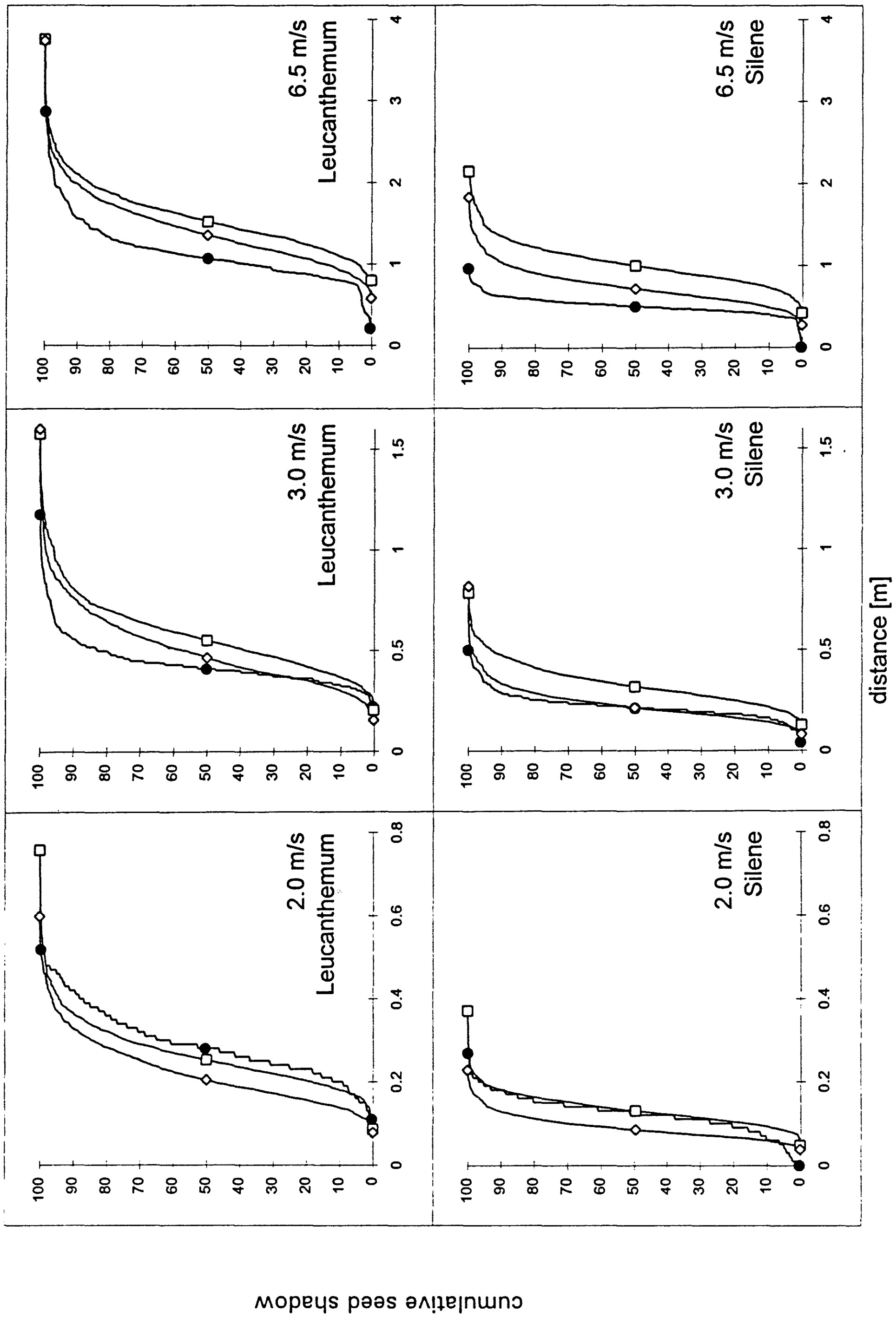

Figure 7.

Cumulative seed shadows resulting from the horizontal windtunnel experiment (n<=300; closed circles) and the model simulations <u>including</u> acceleration (n=1000; dropping method, open diamonds; floating methods, open squares), for different windprofiles (2, 3 and 6.5 m/s) and species (*Leucanthemum vulgare* and *Silene latifolia ssp. alba*).

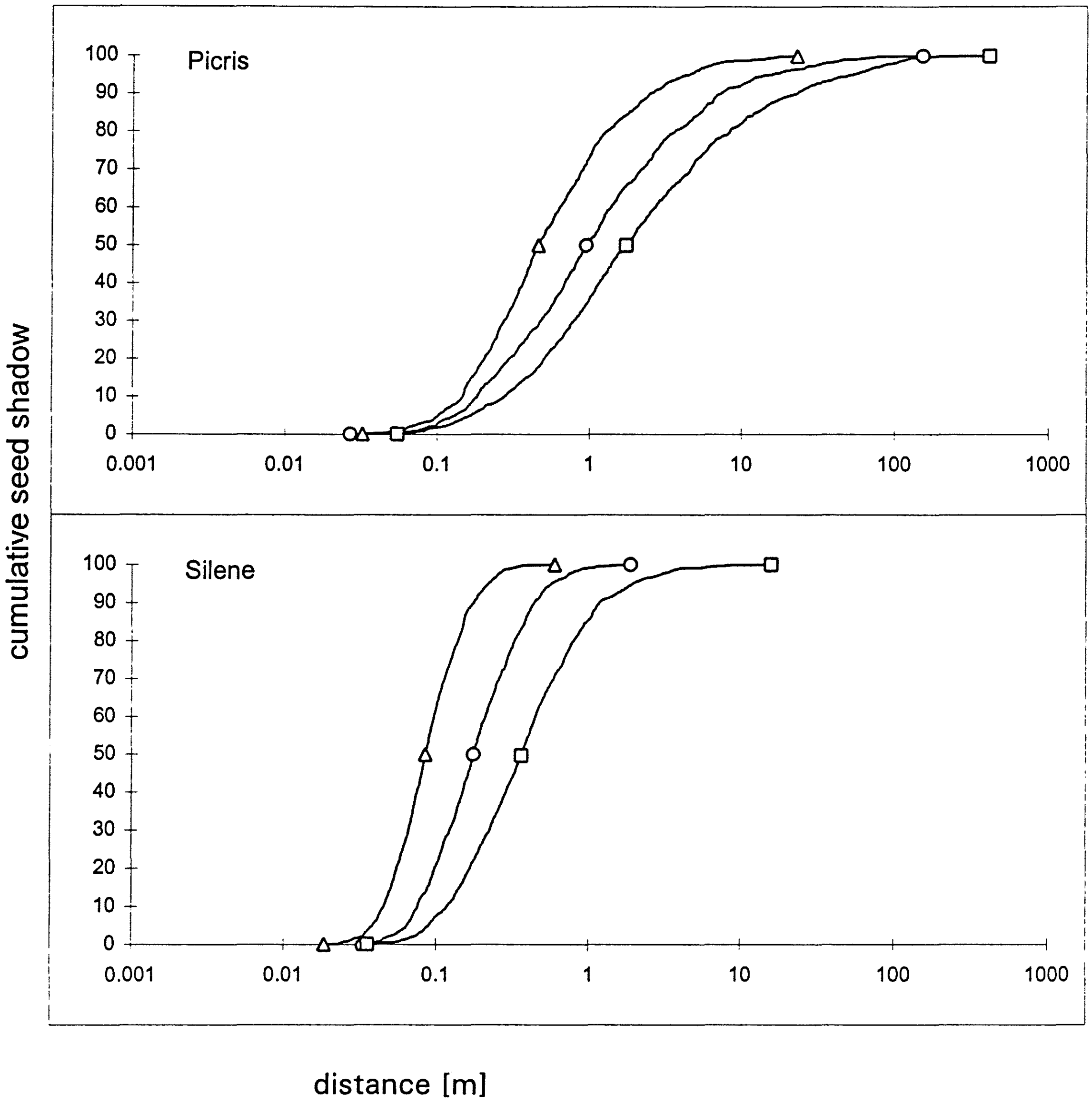

Figure 8.
Cumulative seed shadows for *Picris hieracioides* and *Silene latifolia ssp. alba* resulting from model simulations without acceleration. Wind speeds are varied from 6 (triangles) to 12 (circles) and 24 (squares) m/s, at a reference height of 10m. Flowering and vegetation heights are 80 and 60 cm respectively.

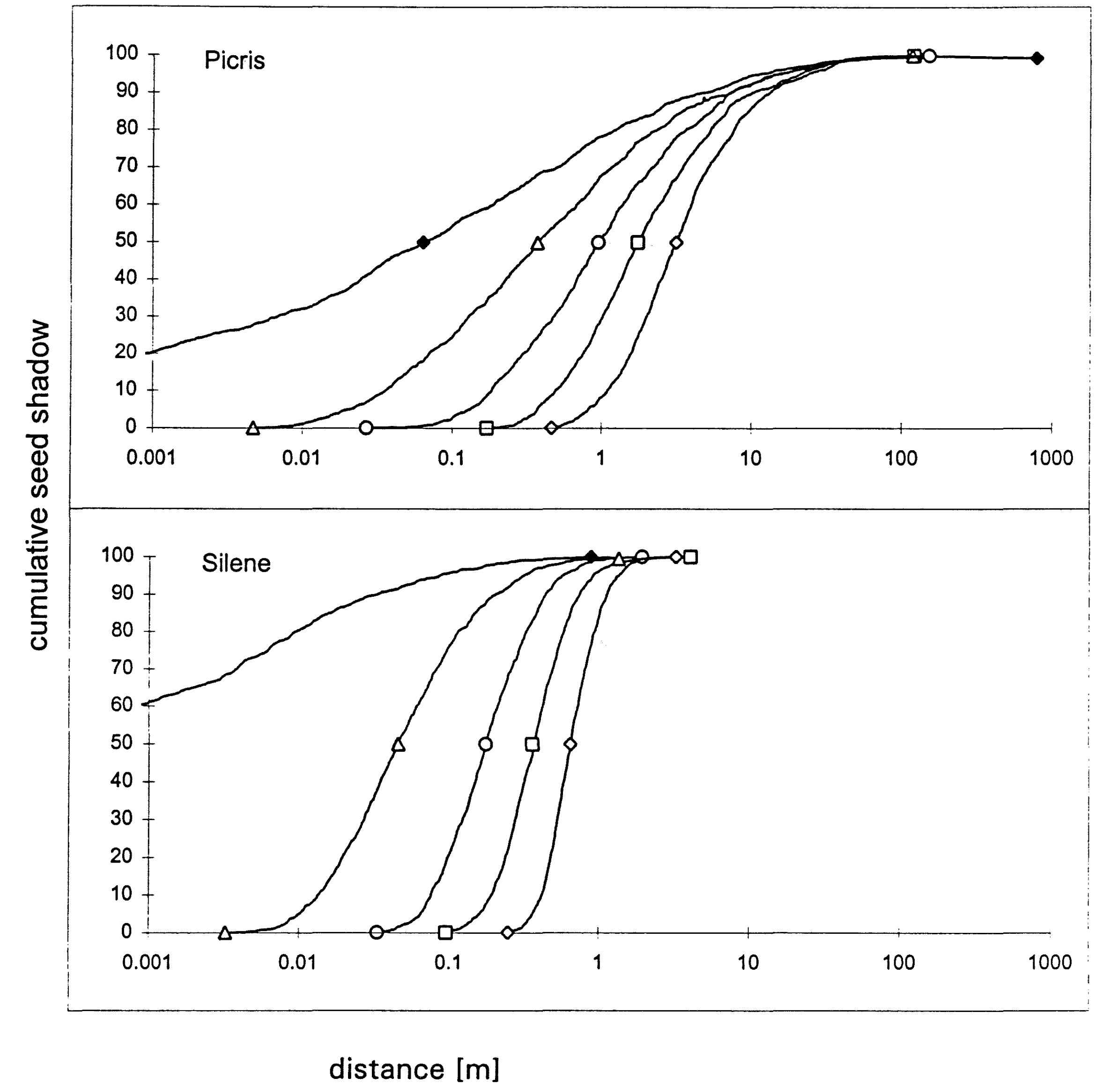

Figure 9.

Cumulative seed shadows for *Picris hieracioides* and *Silene latifolia ssp. alba* resulting from model simulations without acceleration. Vegetation heights are varied from 20 (open diamonds) to 40 (open squares), 60 (open circles), 80 (open triangles) and 100 (closed diamonds) cm. Flowering height is 80 cm and wind speed 12 m/s at a reference heights of 10 m.

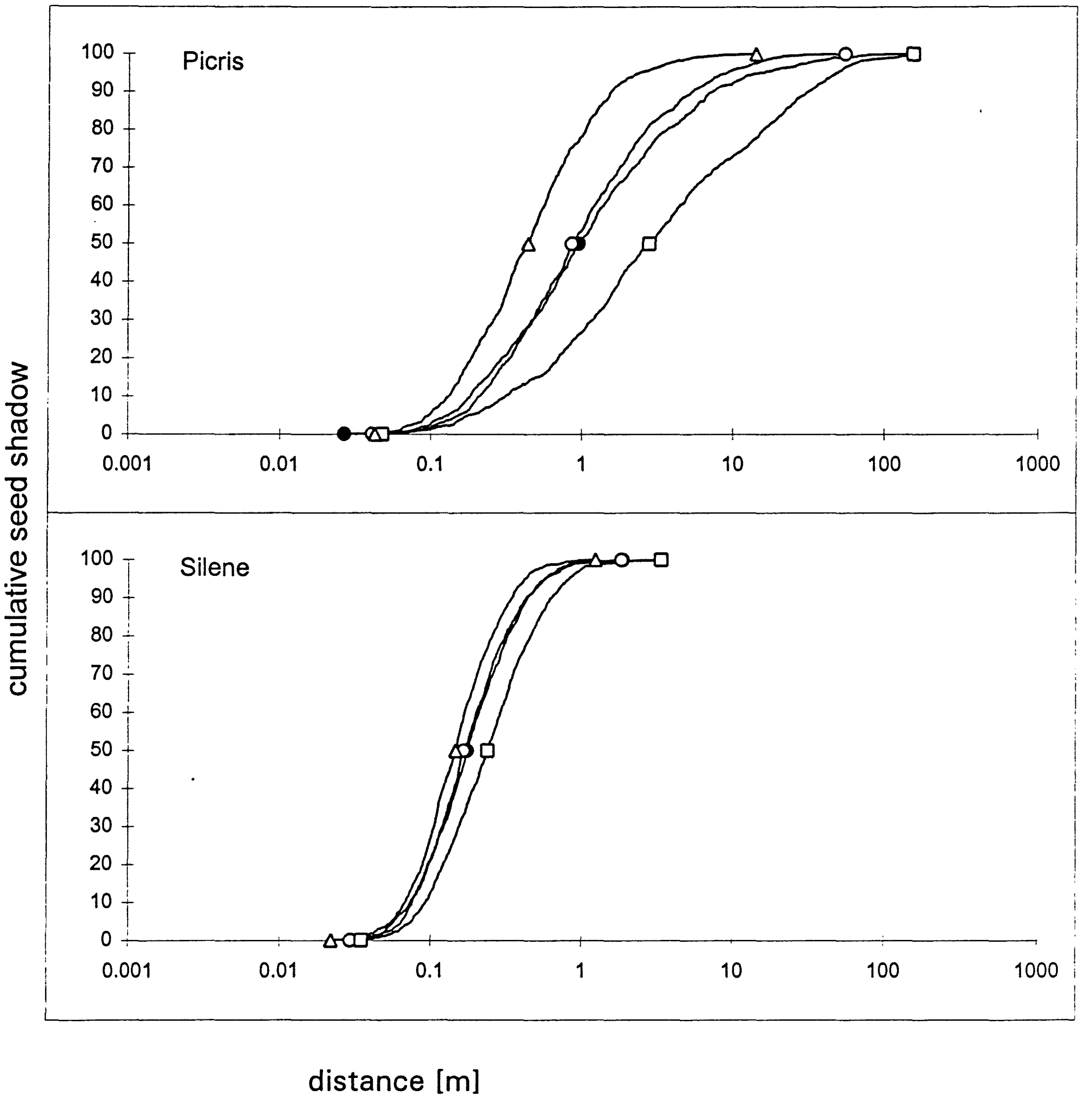

Figure 10.

Cumulative seed shadows for *Picris hieracioides* and *Silene latifolia ssp. alba* resulting from model simulations without acceleration. V_t-inputs are varied (maximum, open triangles; mean, open circles; all data, closed circles; minimum, open squares). Flowering and vegetation heights are 80 and 60 cm respectively. The wind speed is 12 m/s at a reference heights of 10 m.

Table 2. The 50, 95 and 99 percile distances [m] per Species and wind speed (6, 12 and 24 m/s at a reference height of 10 m), of the simulated seed shadows plotted in figure 6. Flowering- and vegetation height are 80 and 60 cm respectively.

Species	Percentile	Wind speed 6	12	24
Picris	50	0.47	0.96	1.76
	95	4.37	14.31	51.60
	99	11.91	46.01	118.46
Silene	50	0.09	0.18	0.36
	95	0.22	0.57	1.98
	99	0.31	0.91	3.96

Table 3. The 50, 95 and 99 percile distances [m] per Species and vegetation height (20, 40, 60, 80 and 100 cm), of the simulated seed shadows plotted in figure 7. Flowering height is 80 cm. Wind speed is 12 m/s at a reference height of 10 m.

Species	Percentile	Vegetation height 20	40	60	80	100
Picris	50	3.21	1.77	0.96	0.38	0.06
	95	23.79	20.82	14.31	14.82	10.88
	99	42.50	47.96	46.01	52.93	51.07
Silene	50	0.65	0.37	0.18	0.05	0.00
	95	1.37	0.91	0.57	0.31	0.09
	99	1.81	1.66	0.91	0.68	0.29

Table 4. The 50, 95 and 99 percile distances [m] per Species and Vt-input ('all data' denotes all 20 values used 50 times, 'mean', 'max' and 'min' denote respectively that the mean, maximum and minimum of the range is used 1,000 times), of the simulated seed shadows plotted in figure 8. Flowering- and vegetation height are 80 and 60 cm respectively. Wind speed is 12 m/s at a reference height of 10 m.

Species	Percentile	Vt input all data	mean	max	min
Picris	50	0.96	0.86	0.44	2.81
	95	14.31	9.09	2.37	47.85
	99	46.01	18.23	5.26	115.52
Silene	50	0.18	0.17	0.15	0.24
	95	0.57	0.58	0.42	0.83
	99	0.91	0.85	0.73	1.44

3.4. Dispersal measurements in field margins

The median displacement from the border of the source plot was not significantly different between the three fields ($p=0.285$), between the east and west orientation ($p=0.300$) or between the grass and regenereation plots ($p=0.550$). There were significant differences between species however ($p<.001$). Since only the difference between species turned out to be significant all medians per species could be averaged to give an overall mean median per species (table 1). The mean V_t-value and the seed weight are plotted against these medians per species (figure 11). Also linear regression lines are shown. The correlation between mean V_t and field median is much greater than the correlation between seed weight and field median.

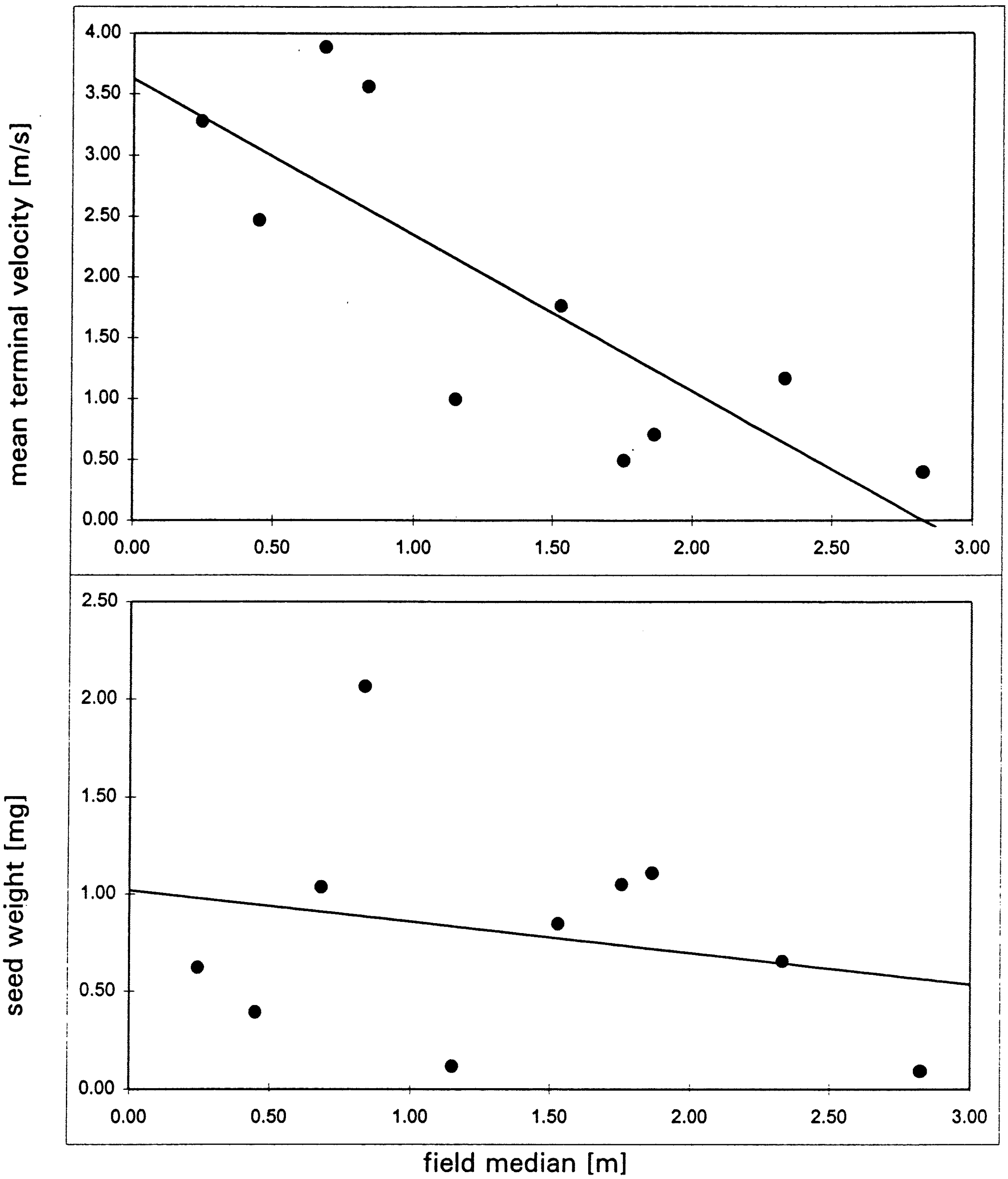

Figure 11.

Mean (of both dropping and floating methods) terminal velocity [m/s] and seed weight [mg] plotted against field median [m] for the 10 most abundant species in the field margin plots: *Centaurea jacea, Crepis capillaris, Daucus carota, Galium mollugo, Hypochaeris radicata, Leontodon autumnalis, Leucanthemum vulgare, Picris hieracioides, Silene latifolia ssp. alba* and *Tanacetum vulgare.*

4. Discussion

4.1. Terminal velocity

4.1.1. Comparison of methods to determine V_t

For five of our species comparison with V_t-values in literature is possible (table 5). In general our results resemble V_t-values found by others. However no conclusions can be made about which method is preferable, also because different authors used different seed samples.

The comparison between V_t-values from the different methods (table 1) indicates some systematic difference. A possible overestimation of V_t-values from the fall tower is difficult to explain. An underestimation of V_t-values from the vertical windtunnel is more probable, since it is very difficult to create a totally laminar windflow in the windtunnel. Aberrant turbulence from the measured average may lift the seeds when a laminar windflow of the same average wind speed is not able to do so (Hofstee, 1992). Results from the horizontal windtunnel also indicate that the simulations with fall tower data produce more realistic values, since the simulations with fall tower data fit better on the whole than those with the vertical windtunnel. Although the V_t-values differ a lot (1.23 times), this should be viewed in light of the great ranges within the data set (see table 1; Andersen, 1992; Geritz, 1995).

4.1.2. Comparison of V_t-values between species

Fenner (1985) stated that heavier seeds are dispersed less far. Results show that morphologic wind-dispersal adaptation has more influence on V_t-values than seed weight for the four species. A crude sequence from low to high V_t-values can be seen when all 21 species are taken into account: plumed and winged seeds → grass seeds with lemma's → other not wind adapted seeds. An overall relation between mere seed weight and V_t-value is not present. It can be said that 3 species with seeds heavier than 2 mg, all have high (>2.5 m/s) V_t-values. This leads to the conclusion, that terminal velocity and thus wind dispersal, within the range of herbaceous plants (with seeds of 0.1 to 2.0 mg), is determined more by seed morphology than by seed mass.

4.2. Seed dispersal model

4.2.1. Standard versus elaborated model

The elaborated model (with acceleration) does not resemble the measured seed shadows better than the standard model. On the contrary, the standard model simulations seem slightly better. Because of that and for the sake of simplicity the standard model is preferable. The flatter slopes of the elaborated model curves can be explained by the fact

Table 5. Comparison of terminal velocities [m/s] between new and published measurements

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Species	Dropping method	Floating method	Literature
Daucus carota	2.01	1.51	1.16[8]
Hypochaeris radicata		0.49	0.32[5], 0.41[7], 0.43[2], 0.67[3]
Picris hieracioides	0.83	0.58	0.13[8], 0.47[6]
Rumex obtusifolius	2.72	2.23	1.26[4]
Taraxacum officinale	0.43	0.32	0.31[1], 0.33[6], 0.36[7], 0.42[4] 0.45[3], 0.66[2]

(1) Andersen, 1992
(2) Andersen, 1993
(3) Askew et al. 1997
(4) Matlack, 1987
(5) Ridley, 1930
(6) Schulz et al., 1991
(7) Sheldon and Burrows, 1973
(8) Verkaar et al., 1983

that the acceleration process has more impact on faster falling seeds, thus causing a greater variation within the simulated distances from one V_t-data set. The acceleration process has two antagonistic effects on dispersal. Because seeds have to 'build up' their falling velocity, they fall longer so they are exposed longer to wind, which increases their dispersal. On the other hand they do not obtain wind speed at once and are thus less far dispersed. Which of these two acceleration delays has the greatest effect on the dispersal distance depends on the numerical relation between its V_t-value and the average windspeed a seed experiences during its flight. When the absolute V_t-value is greater than the experienced average windspeed the vertical acceleration process will have more influence and the seeds will be dispersed less far than in the case of no acceleration (compare *Leucanthemum* by 2.0 and *Silene* at 2.0 and 3.0 m/s in figures 6 and 7). When the absolute V_t-value is smaller than the experienced average windspeed, seeds are dispersed further (compare *Leucanthemum* and *Silene* at 6.5 m/s in figures 6 and 7).

4.2.2. Generality of Andersen's model

The overall impression is that the standard model simulations make sense. The median and tail of the seed shadows were of the same order and the slopes of the curves of the simulated distances also seem realistic. This confirms that this kind of individual-based model with stochastic turbulence can be used to give reliable estimations of seed shadows. But it should be noted that flight trajectories as shown in figure 2 are not very realistic physically. The vertical accelerations, needed for these Brownian displacements, are too high, which is caused by the small timesteps. On the overall outcome it has, however, little effect. Another note concerns windtunnels which are a limited representation of field circumstances, where other processes may occur. However, Andersen (1991) showed already good performance of the model under field conditions. Now, someone interested in the seed shadow of a plant only needs V_t-values, wind speed at a certain height and plant- and vegetation heights.

4.3. Effect of wind speed, vegetation height and intraspecific terminal velocity range

The results of the sensitivity analysis show that the increase in median distance is proportional to the increase in wind speed. This is in agreement with the simple estimation of the dispersal distance: $X = u_w * Z / V_t$ (Matlack, 1987; Ernst et al., 1992; Greene and Johnson, 1992), and field experiments done by Augspurger and Franson (1987) with artificial fruits. However the tail behaved differently. An increase of the windspeed with a factor 4, causes an increase in the tail distances (95 and 99 percentiles) of about 11 times as far. An explanation for this phenomenon can be found in the fact that the friction velocity grows linearly with windspeed (equation 2a), implicating stronger turbulence (equation 4a) and greater variance in dispersal distances. Van Dorp et al. (1996) also found an exponential relation between windspeed and 99 percentile distances. The highest windspeed of 24 m/s (7.8 m/s at flowering height) is still an underestimation of wind speeds that can occur annually (Van Dorp et al., 1996).

The increase of vegetation height resulted in smaller dispersal distances for both *Picris* and *Silene.* The tails of the seed shadows, however, are less affected by the height of the vegetation. The 99 percentile of *Picris* even showed a small increase with vegetation height. Less median dispersal can be accounted for by the fact that the chance that a seed is 'captured' by vegetation almost directly, increases for higher vegetation. On the other hand higher vegetation increases friction velocity slightly. This means that 'escaping' seeds above a high vegetation experience more turbulence, which, as we have seen, can result in an increasing 99 percentile of the seed shadow. Most realistic, though, is the situation where seeds are released above the surrounding vegetation (Verbeek and Boasson, 1995).

The results of the V_t-range analysis show that using the mean value of V_t instead of all V_t-data gives a good estimation of median distances, but underestimates the tail when slowly falling seeds are studied. This indicates that the spread in seed shadow is not only determined by turbulence, but also by variation in terminal velocities of seeds. Intraspecific variation in seed characteristics, and thus dispersal potentials, can therefore be subject to evolutionary selection (Andersen, 1993; Geritz, 1995). However it should be noted that seed characteristics leading to good dispersal, may be disadvantageous for other survival strategies such as long dormancy (Venable and Brown, 1988).

4.4. Dispersal in field margins

One must realise that median displacement in the field is not only the result of seed dispersal. Seed survival, seedling emergence, vegetative dispersal and competition all play their crucial part in determining the occurrence of species in the plots. Furthermore the median distances cannot be compared with model simulations since they are the result of more than one dispersal event and of a non-point source. Plants from all over the mixture plot could have contributed to the dispersal, not only those on the borderline. Still, when the mean V_t-value of the 10 species used in the analysis is plotted against their field median (figure 11), there is a clear trend: for V_t-values getting lower, the median distances are growing. Thus despite the fact that other processes might have obscured the dispersal pattern, this result nevertheless points at the importance of seed morphology for the species specific terminal velocity and dispersal over mere seed weight.

4.5. Finally

Two methods were compared to obtain terminal velocity values. Both methods have their advantages and disadvantages. However, the dropping method over 15.83 m was found to be more reliable, and simulation results, generated with V_t-values obtained by this method, gave in general better resemblance with experimentally obtained seed shadows.

Andersen's (1991) individual-based model was only tested for one species with plumed seeds. Now this model has been tested for four different herbaceous species which differ with respect to seed weight and presence of plumes. The model simulations showed remarkable resemblance with windtunnel results given the different seed characteristics and windspeeds used. This indicates the generality of this model for herbaceous species. The model can easily be elaborated with a third dimension, wind speed fluctuations (in strength and direction), non-point sources, threshold release windspeed probability density of seed release changes over windspeeds (Sharpe and Fields 1982; Greene and Johnson, 1989; Andersen, 1991) or other meteorological aspects like thermic updraft, which indicates a wide range of possible applications which may lead to more insight in wind dispersal of herbaceous seeds. This on its turn will contribute to the increase of knowledge of meta-population dynamics of herbaceous species in fragmented landscapes.

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Appendix 1, program listings

seed dispersal program in FORTRAN

```
      PROGRAM SEEDTRIP

c explanation of the variables
c   ACCEL      = acceleration option (1 = yes, 0 = no)                          [-]
c   AX         = acceleration in X direction                                    [m s-2]
c   AZ         = acceleration in Z direction                                    [m s-2]
c   D          = zero plane displacement                                        [m]
c   DELT       = timestep                                                       [s]
c   FILENAME   = name of file with terminal velocity data                       [-]
c   FINTIM     = time at which the simulation is stopped anyway                 [s]
c   GRAV       = gravitation acceleration                                       [m s-2]
c   H          = height at which wind speed is measured                         [m]
c   IDUM       = random number                                                  [-]
c   K          = air resistance                                                 [m-1]
c   KARMAN     = von Karman constant                                            [-]
c   NUL        = zero                                                           [-]
c   PLAF       = height of the windtunnel (0. means no upper limitation)        [m]
c   PRINTER    = time interval between outputs                                  [s]
c   PROF       = known wind profile option (otherwise general wind profile)     [-]
c   PRTIME     = printer clock                                                  [s]
c   S          = logarithmic part of the wind profile formula                   [-]
c   SEED       = terminal velocities (array)                                    [m s-1]
c   SEEDS      = number of different terminal velocity values in input file     [-]
c   SIM        = number of simulations per terminal velocity value              [-]
c   TIME       = seed flight clock                                              [s]
c   TOP        = maximum height during a flight                                 [m]
c   USTAR      = friction velocity                                              [m s-1]
c   VT         = terminal velocity of seed                                      [m s-1]
c   VX         = horizontal velocity of seed                                    [m s-1]
c   VZ         = vertical velocity of seed                                      [m s-1]
c   WXH        = measured windspeed at height H                                 [m s-1]
c   X          = seed position in horizontal direction                          [m]
c   XINI       = initial seed position in horizontal direction                  [m]
c   Z          = seed position in vertical direction                            [m]
c   ZINI       = initial seed position in vertical direction                    [m]
c   ZV         = vegetation height                                              [m]
c   Z0         = roughness length                                               [m]

c declaration of variables

      REAL D,DELT,FINTIM,H,KARMAN,NUL,PLAF,PRINTER
      REAL PRTIME,S,TIME,TOP,USTAR,WXH,Z0
      REAL*8 AX,AZ,GRAV,K,VT,VX,WX,VZ,X,Z
      REAL SEED(100)
      INTEGER ACCEL,IDUM,I,J,PROF,SEEDS,SIM
      CHARACTER*12 FILENAME
```

```
c read instruction file

          OPEN (UNIT=10,FILE='SEEDTRIP.INS',STATUS='OLD')
             READ(10,*) ACCEL
             READ(10,*) DELT
             READ(10,*) FILENAME
             READ(10,*) FINTIM
             READ(10,*) GRAV
             READ(10,*) H
             READ(10,*) KARMAN
             READ(10,*) PLAF
             READ(10,*) PRINTER
             READ(10,*) PROF
             READ(10,*) SEEDS
             READ(10,*) SIM
             READ(10,*) WXH
             READ(10,*) XINI
             READ(10,*) ZINI
             READ(10,*) ZV
          CLOSE (UNIT=10)

c read (negative !) terminal velocity values

          OPEN (UNIT=10,FILE=FILENAME,STATUS='OLD')
             DO I=1,SEEDS
                READ(10,*) SEED(I)
             END DO
          CLOSE (UNIT=10)

c read seed for random number generator

          OPEN (UNIT=10,FILE='IDUM.DAT', STATUS='OLD')
             READ (10,*) IDUM
          CLOSE (UNIT=10)

c open output file
          OPEN (UNIT=11,FILE='SEEDTRIP.OUT', STATUS='NEW')

c definition initial values
          NUL=0.
          AZ=0.
          VZ=0.
          AX=0.
          VX=0.
          X=XINI
          Z=ZINI
          D=10**(0.9793*LOG(ZV)-0.1536)
          Z0=10**(0.997*LOG(ZV)-0.883)
          USTAR=KARMAN*WXH/(LOG10((H-D)/Z0))
          IF (SIM.EQ.1) THEN
             WRITE (11,'(8A11)') 'TIME','WX','AX','VX','X','AZ','VZ','Z'
             WRITE (11,'(8F11.4)') TIME,WX,AX,VX,X,AZ,VZ,Z
          ELSE
             WRITE (11,'(7A11)') 'NUMERO','X','Z','TIME','VT','MAX','K'
          END IF
```

```
c number of seeds loop

          DO J=1,SEEDS
            VT=SEED(J)

c number of simulations per seed loop
            DO I=1,SIM
              TIME=0.
              PRTIME=0.
              AX=0.
              AZ=0.
              VX=0.
              VZ=0.
              X=XINI
              Z=ZINI
              TOP=ZINI
              K=-GRAV/(VT**2)

c simulation loop

              DO WHILE (TIME.LE.FINTIM .AND. Z.GT.0.)

c known and general windprofiles at height Z

                IF (PROF.EQ.2) THEN
                  WX=2.2329+.51947*LOG10(Z)
                ELSE IF (PROF.EQ.3) THEN
                  WX=3.8922+1.0329*LOG10(Z)
                ELSE IF (PROF.EQ.65) THEN
                  WX=7.3047+.99086*LOG10(Z)
                ELSE
                  S=MAX(.15,(Z-D)/Z0)
                  WX=MAX(0.,((USTAR/KARMAN)*LOG10(S)))
                END IF

c time steps
                TIME=TIME+DELT
                PRTIME=PRTIME+DELT

c calculation of velocity without or with acceleration

                IF (ACCEL.EQ.0) THEN
                  VX=WX
                  VZ=VT
                ELSE
                  AX=K*(WX-VX)*(VZ**2.+(WX-VX )**2.)**0.5
                  VX=VX+AX*DELT

                  AZ=GRAV+K* (VZ)* (VZ**2.+(WX-VX )**2.)**0.5
                  VZ=VZ+AZ*DELT
                ENDIF
```

```
c calculation of position with Gaussian perturbation

            X=X+VX*DELT
            GAUSS=((2*KARMAN*USTAR*Z*DELT)**.5)*GASDEV(IDUM)
            Z=Z+VZ*DELT+GAUSS

c maximum height (of windtunnel)

            IF (PLAF.GT.NUL.AND.Z.GT.PLAF) THEN
              Z=PLAF
            END IF
            TOP=MAX(Z,TOP)

c simulation output

            IF (PRTIME.GE.PRINTER.AND.SIM.EQ.1) THEN
              WRITE (11,'(8F11.4)') TIME,WX,AX,VX,X,AZ,VZ,Z
              PRTIME=0.0
            END IF

c end simulation loop

          END DO

          IF (SIM.GT.1) WRITE (11,'(I11,6F11.4)') I,X,Z,TIME,VT,TOP,K

c end individual seed loop

        END DO

c end all seed loops

      END DO

c close output file

      CLOSE (UNIT=11)

c save new seed for random number generator

      OPEN (UNIT=11,FILE='IDUM.DAT', STATUS='UNKNOWN')
        IDUM=INT(10000*(RAN1(IDUM)))
        WRITE (11,*) IDUM,' :'
      CLOSE (UNIT=11)

      END

c Gaussian deviates function (Press et al., 1986, page 203)

      FUNCTION GASDEV(IDUM)
      REAL FAC,GASDEV,GSET,R,V1,V2
      INTEGER ISET
      DATA ISET /0/
      IF (ISET.EQ.0) THEN
1       V1=2.*RAN1(IDUM)-1.
```

```
      V2=2.*RAN1(IDUM)-1.
      R=V1**2+V2**2
      IF (R.GE.1.) GO TO 1
      FAC=SQRT(-2.*LOG(R)/R)
      GSET=V1*FAC
      GASDEV=V2*FAC
      ISET=1
   ELSE
      GASDEV=GSET
      ISET=0
   ENDIF
   RETURN
   END
```

c random number generator function (Press et al., 1986, page 196)

```
   FUNCTION RAN1(IDUM)
   REAL RAN1,RM1,RM2
   INTEGER IA1,IA2,IA3,IC1,IC2,IC3,IDUM,IFF,IX1,IX2,IX3,J,M1,M2,M3
   DIMENSION R(97)
   PARAMETER (M1=259200,IA1=7141,IC1=54773,RM1=1./M1)
   PARAMETER (M2=134456,IA2=8121,IC2=28411,RM2=1./M2)
   PARAMETER (M3=243000,IA3=4561,IC3=51349)
   DATA IFF /0/
   IF (IDUM.LT.0.OR.IFF.EQ.0) THEN
      IFF=1
      IX1=MOD(IC1-IDUM,M1)
      IX1=MOD(IA1*IX1+IC1,M1)
      IX2=MOD(IX1,M2)
      IX1=MOD(IA1*IX1+IC1,M1)
      IX3=MOD(IX1,M3)
      DO 11 J=1,97
         IX1=MOD(IA1*IX1+IC1,M1)
         IX2=MOD(IA2*IX2+IC2,M2)
         R(J)=(FLOAT(IX1)+FLOAT(IX2)*RM2)*RM1
11       CONTINUE
      IDUM=1
   ENDIF
   IX1=MOD(IA1*IX1+IC1,M1)
   IX2=MOD(IA2*IX2+IC2,M2)
   IX3=MOD(IA3*IX3+IC3,M3)
   J=1+(97*IX3)/M3
   IF (J.GT.97.OR.J.LT.1) PAUSE
   RAN1=R(J)
   R(J)=(FLOAT(IX1)+FLOAT(IX2)*RM2)*RM1
   RETURN
   END
```

Instruction file SEEDTRIP.INS as used for the simulations shown in figure 2:

0	ACCEL	acceleration option (1 = yes, 0 = no)
0.001	DELT	timestep
'VT.DAT'	FILENAME	name of file with terminal velocity data
10.	FINTIM	time at which the simulation is stopped anyway
9.81	GRAV	gravitation acceleration
10.	H	height at which wind speed is measured
0.41	KARMAN	von Karman constant
0.	PLAF	height of the windtunnel (0. means no upper limitation)
0.01	PRINTER	time interval between outputs
0	PROF	known wind profile (2, 3 or 65, otherwise general wind profile)
1	SEEDS	number of different terminal velocity values in input file
3	SIM	number of simulations per terminal velocity value
20.	WXH	measured windspeed at height H
0.	XINI	initial seed position in horizontal direction
1.	ZINI	initial seed position in vertical direction
0.5	ZV	vegetation height

Terminal velocity input file VT.DAT as used for the simulations shown in figure 2:

-1.

Example of the random number file IDUM.DAT:

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Appendix 2, Vt-values

Terminal velocity values measured with the dropping method in the fall tower.

Anthoxanthum odoratum	Campanula rotundifolia	Centaurea jacaea	Chenopodium album	Daucus carota
1.023	1.245	3.324	1.548	1.379
1.252	1.341	3.559	2.209	1.599
1.336	1.388	3.801	2.221	1.632
1.346	1.423	3.942	2.225	1.651
1.384	1.425	3.945	2.272	1.683
1.538	1.425	3.951	2.392	1.755
1.541	1.432	3.951	2.455	1.795
1.743	1.500	4.026	2.515	1.807
1.745	1.500	4.059	2.526	1.873
1.768	1.515	4.070	2.593	1.894
1.790	1.537	4.120	2.666	1.909
1.815	1.541	4.201	2.830	1.963
1.933	1.559	4.201	2.903	1.995
2.012	1.583	4.243	3.007	2.047
2.170	1.606	4.391	3.009	2.081
2.300	1.693	4.398	3.059	2.086
2.327	1.710	4.497	3.090	2.266
2.572	1.720	4.524	3.307	2.572
2.577	1.729	4.669	3.434	2.724
2.994	1.777	4.792	3.898	3.411

Terminal velocity values measured with the floating method in the vertical windtunnel.

Anthoxanthum odoratum	Centaurea jacaea	Chenopodium album	Crepis capillaris	Daucus carota
0.894	2.272	1.399	0.200	0.863
0.957	2.493	1.557	0.231	0.873
0.978	2.525	1.746	0.252	0.936
1.063	2.546	1.831	0.252	1.178
1.084	2.799	2.146	0.252	1.231
1.084	2.809	2.178	0.263	1.262
1.199	2.820	2.230	0.274	1.294
1.368	2.830	2.262	0.274	1.452
1.378	3.009	2.325	0.284	1.515
1.420	3.051	2.336	0.305	1.568
1.441	3.083	2.336	0.305	1.568
1.441	3.104	2.336	0.316	1.578
1.652	3.177	2.346	0.326	1.599
1.673	3.272	2.430	0.337	1.620
1.683	3.293	2.493	0.337	1.641
1.767	3.293	2.546	0.379	1.694
1.831	3.314	2.609	0.673	1.820
1.873	3.356	2.630	0.821	1.862
1.873	3.398	2.662	0.873	2.094
1.904	3.440	2.714	0.926	2.609

Terminal velocity values measured with the dropping method in the fall tower.

Festuca ovina	Galium mollugo	Hieracium pilosella	Holcus lanatus	Leontodon autumnalis
0.799	2.187	0.363	0.627	0.429
0.824	2.879	0.528	0.629	0.809
0.995	2.956	0.615	0.668	0.845
1.028	3.030	0.631	0.693	0.958
1.172	3.330	0.687	0.703	0.987
1.206	3.359	0.783	0.718	1.001
1.335	3.514	0.789	0.722	1.003
1.454	3.573	0.916	0.723	1.053
1.480	3.605	0.949	0.741	1.068
1.679	3.689	0.979	0.741	1.077
1.808	3.698	1.065	0.796	1.197
1.814	3.698	1.072	0.822	1.228
1.888	3.887	1.106	0.841	1.275
1.955	3.892	1.129	0.847	1.289
1.975	3.899	1.173	0.852	1.423
1.998	4.103	1.178	0.882	1.625
2.030	4.166	1.252	0.912	1.806
2.038	4.251	1.283	0.917	1.943
2.184	4.267	1.300	0.934	2.470
2.659	4.317	1.808	2.018	3.199

Terminal velocity values measured with the floating method in the vertical windtunnel.

Festuca ovina	Galium mollugo	Hieracium pilosella	Holcus lanatus	Hypochaeris radicata	Leontodon autumnalis
1.157	2.462	0.221	0.537	0.284	0.621
1.168	2.462	0.231	0.579	0.295	0.652
1.273	2.609	0.252	0.600	0.326	0.663
1.431	2.620	0.358	0.621	0.358	0.694
1.547	2.683	0.421	0.631	0.358	0.789
1.578	2.735	0.494	0.652	0.368	0.821
1.715	2.746	0.505	0.663	0.368	0.905
1.789	2.777	0.537	0.673	0.379	0.915
1.810	2.777	0.610	0.673	0.389	0.936
1.810	2.841	0.642	0.768	0.442	0.947
1.841	2.914	0.663	0.800	0.452	0.999
1.883	2.925	0.736	0.821	0.452	1.010
1.883	2.946	0.747	0.831	0.484	1.021
1.925	2.988	0.768	0.842	0.526	1.031
1.957	2.988	0.800	0.873	0.579	1.073
1.957	3.093	0.884	0.873	0.642	1.073
1.967	3.440	0.905	0.947	0.747	1.136
2.041	3.451	0.968	1.010	0.757	1.347
2.073	3.461	0.989	1.231	0.779	1.368
2.115	3.808	1.010	1.515	0.863	1.904

Terminal velocity values measured with the dropping method in the fall tower.					
Leucanthemum vulgare	Linaria vulgaris	Picris hieracioides	Plantago lanceolata	Poa annua	Rumex obtusifolius
1.841	0.473	0.266	1.441	1.810	1.705
1.875	0.674	0.319	2.253	1.820	2.217
2.166	0.703	0.344	2.739	1.921	2.250
2.210	0.776	0.387	2.783	1.963	2.276
2.244	0.780	0.405	2.848	1.989	2.332
2.279	0.816	0.536	3.035	2.014	2.458
2.457	0.865	0.575	3.156	2.029	2.514
2.522	0.865	0.578	3.209	2.205	2.601
2.614	0.913	0.658	3.276	2.257	2.612
2.638	0.954	0.755	3.389	2.275	2.650
2.724	0.971	0.847	3.446	2.358	2.733
2.797	0.988	0.908	3.536	2.359	2.741
2.831	0.998	0.959	3.593	2.421	2.884
2.883	1.000	1.010	3.700	2.476	2.924
2.883	1.004	1.061	3.850	2.628	2.938
2.954	1.085	1.160	3.912	2.757	3.006
3.055	1.089	1.236	4.013	2.777	3.153
3.074	1.134	1.283	4.228	2.786	3.324
3.157	1.184	1.549	4.846	2.916	3.442
3.258	1.188	1.793	4.947	2.953	3.574

Terminal velocity values measured with the floating method in the vertical windtunnel.					
Leucanthemum vulgare	Linaria vulgaris	Picris hieracioides	Plantago lanceolata	Poa annua	Rumex obtusifolius
1.725	0.631	0.263	1.462	1.589	1.862
1.873	0.652	0.274	2.009	1.620	1.883
1.925	0.726	0.284	2.146	1.746	1.946
2.125	0.747	0.284	2.178	1.852	2.125
2.178	0.757	0.284	2.230	1.862	2.136
2.188	0.810	0.305	2.388	1.873	2.157
2.315	0.821	0.337	2.483	2.062	2.188
2.325	0.842	0.484	2.588	2.104	2.199
2.367	0.873	0.505	2.620	2.115	2.209
2.378	0.873	0.526	2.641	2.115	2.209
2.399	0.884	0.589	2.704	2.125	2.209
2.399	0.884	0.600	2.714	2.125	2.241
2.430	0.894	0.600	2.725	2.146	2.272
2.451	0.894	0.621	2.756	2.304	2.315
2.472	0.905	0.810	2.988	2.346	2.367
2.504	0.926	0.831	3.146	2.472	2.388
2.504	0.926	0.873	3.156	2.483	2.420
2.514	0.936	0.926	3.251	2.578	2.462
2.567	1.010	1.021	3.966	2.767	2.483
2.683	1.021	1.189	4.019	2.914	2.535

Terminal velocity values measured with the dropping method in the fall tower.		
Silene latifolia ssp. alba	Tanacetum vulgare	Taraxacum officinale
3.300	0.672	0.357
3.544	0.735	0.360
3.708	0.798	0.373
3.780	0.836	0.380
3.895	0.858	0.393
4.147	0.859	0.394
4.281	0.869	0.397
4.381	0.877	0.402
4.409	0.883	0.414
4.409	0.888	0.416
4.445	0.895	0.418
4.456	1.033	0.431
4.464	1.037	0.434
4.536	1.038	0.453
4.655	1.052	0.467
4.732	1.132	0.471
4.776	1.139	0.481
4.962	1.285	0.489
4.999	1.780	0.493
5.038	2.064	0.538

Terminal velocity values measured with the floating method in the vertical windtunnel.		
Silene latifolia ssp. alba	Tanacetum vulgare	Taraxacum officinale
2.967	0.642	0.126
3.072	0.642	0.242
3.114	0.652	0.252
3.156	0.779	0.263
3.219	0.884	0.263
3.304	0.884	0.295
3.314	0.894	0.295
3.356	0.915	0.316
3.430	0.936	0.326
3.461	0.936	0.337
3.535	0.936	0.337
3.545	0.947	0.337
3.567	0.989	0.337
3.588	1.021	0.347
3.588	1.021	0.347
3.598	1.052	0.358
3.598	1.063	0.368
3.609	1.157	0.389
3.703	1.168	0.400
3.840	1.336	0.452