

SEED RAIN PATTERN OF THE INVASIVE WEED *SENECIO INAEQUIDENS* (ASTERACEAE)

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ABSTRACT. — Dispersion capacity of alien invasive plants is a key feature for understanding invasion processes and risks. Here, we present an experimental study focussing on the seed rain pattern of *Senecio inaequidens*, an African plant widespread throughout Europe, under common favourable dispersal conditions. One hundred achenes from two Belgian populations underwent a drop time in still air experiment in order to assess linear correlation between several morphological traits and terminal velocity. Variation in morphological traits was measured for 250 additional achenes per population. The trait best correlated to terminal velocity was the square root of the plume loading. We then used this trait to model terminal velocity using a linear regression (r^2 of 79.7%). With this regression and imposing ecological parameters such as wind speed, turbulences and height of release to be representative of favourable dispersal conditions, we established a Gaussian tilted plume model to predict the seed rain pattern of the species. A wind tunnel experiment consequently permitted to validate the model. Under a wind speed of 5 m s⁻¹ with 2% turbulences along the vertical axis, and height of release of 0.40 m, 99.8 % of achenes were dispersed within 100 meters, with a maximum deposition rate at 5.2 m from the parent plant. Uplifted achenes, not forecasted by the model, represent 6.25% of all achenes.

KEY WORDS. — *Senecio inaequidens*, Gaussian model, invasive plant, plume loading, seed rain pattern.

INTRODUCTION

Biological invasions and seed dispersal are two major topics in plant ecology. As they are considered as the second cause of biodiversity loss worldwide (CRONK & FULLER 1995, PARKER *et al.* 1999), biological invasions have attracted much attention in the last decade (PYSEK *et al.* 2004). Seed dispersal can be regarded as a key

process in the survival and distribution of plant species. Hence, dispersal analysis is important to understand the success of invasive species. Studies on alien species dispersal abilities are of crucial interest to understand plant invasion patterns and dynamics in the field (HARPER 1977, DAUER *et al.* 2006). Although much has been written on the dispersal capacities of invaders, the number of detailed studies of dispersal ability and realized

dispersal patterns is surprisingly low (HIGGINS *et al.* 2001).

The spatial distribution of seeds around their source is called a 'seed shadow' or 'seed rain pattern', a density curve of landing probabilities (WILLSON & TRAVESET 1993, JONGEJANS & SCHIPPERS 1999). Models used to predict seed shadows range from simple phenomenological to complex mechanistic models. Phenomenological models are based on fit to observed data on seed dispersal. Those models generally describe the seed number-distance relationships as leptokurtic (with a higher peak and longer tail than a normal distribution). From the peak outwards, seed densities generally fit a negative exponential curve or sometimes a negative power function (OKUBO & LEVIN 1989, WILLSON & TRAVESET 1993). Although these empirical models are simple and fit some datasets reasonably well, they are only based upon parameters that are not measured or controlled independently, such as wind speed, release height or terminal velocity. Therefore, these models do not allow extrapolation from one situation to another nor do they provide any understanding of the underlying mechanisms. Detailed mechanistic models were developed to predict dispersal of anemochorous plants (OKUBO & LEVIN 1989, GREENE & CALOGEROPOULOS 2002, NATHAN *et al.* 2002, TACKENBERG 2003, SOONS *et al.* 2004). Unlike phenomenological models, these mechanistic models describe the probability distributions of seeds and should be applicable over infinite distances and under any circumstances (BULLOCK & CLARKE 2000). Some of these models have the advantage to take into account the seed uplift, which is supposed to be responsible for very long distance dispersal. Unfortunately, they have to be very accurate to give satisfactory results. Another shortcoming is that validating patterns with real data and obtaining basic input data is complicated (NATHAN *et al.* 2002, TACKENBERG 2003, SOONS *et al.* 2004).

Between phenomenological and mechanistic approaches, Gaussian models represent simple and yet poorly explored seed shadow models. These models generally compute the horizontal and vertical distribution of wind-borne particles under the influence of diffusion and advection.

For particles with non-negligible weight, such as most plant diaspores, the Gaussian tilted plume model is used, which takes gravitational settling into account (e.g., CSANADY 1963). The most important species-specific characteristic used in wind dispersal models is the terminal velocity (V_t), i.e., seed fall velocity in still air. It is relatively easy to measure and has been used as an index of relative dispersal ability among species (SHELDON & BURROWS 1973, MATLACK 1987, SCHULZ *et al.* 1991, ANDERSEN 1992, 1993, KAHRS 1994, ASKEW *et al.* 1997, TACKENBERG *et al.* 2003). Dispersal capability of wind-dispersed propagules, including terminal velocity, can often be successfully predicted from their morphological characteristics (SHELDON & BURROWS 1973, MORSE & SCHMITT 1985, MATLACK 1987, CODY & OVERTON 1996, SOONS & HEIL 2002). Besides the selection of a pertinent, and yet pragmatic model of seed dispersal, the problem of model validation is of crucial importance. Wind tunnels provide repeatable controlled experimental conditions to generate seed shadows and validate seed dispersal models.

Senecio inaequidens DC. is a perennial herbaceous Asteraceae. It was originally distributed in Lesotho and on the South African west coast, on river edges and in stony meadows (ERNST 1998). It was accidentally introduced in Europe in the early 20th century via the wool trade. During several decades it was only found in the vicinity of a few wool-processing areas (GUILLERM *et al.* 1990, ERNST 1998). From 1950 onwards, *S. inaequidens* expanded throughout western, central and southern Europe, and to environments outside the wool industry. By the 1970s, the species was considered as a weed in agricultural areas in France, especially in vineyards (GUILLERM *et al.* 1990), as well as in road ditches and in grazing meadows where it is unpalatable to livestock. By the 1990s, it was also recorded in natural habitats (MICHEZ 1995). *S. inaequidens* has a highly effective production of capitula over a long flowering period (i.e., six months). Tubula and ligula become wind-dispersed achenes, provided with an unbeaked pappus (Fig. 1). Some individuals can produce up to 1500 capitula during a flowering period (MONTY, unpublished

data). Each capitulum bears roughly one hundred achenes (LOPEZ-GARCIA & MAILLET 2005).

With this study we aimed at evaluating the dispersal capacity of the achenes of the invasive *S. inaequidens*, on a hundred-metre scale, using a Gaussian modelling approach. We then tested the model with wind tunnel data. Also, our aim was to test the adequacy of this approach under common favourable dispersal conditions in order to provide the basis for future studies on the factors affecting dispersal of this species.

MATERIAL AND METHODS

ANALYSIS OF MORPHOLOGICAL TRAITS AND DETERMINATION OF A PROXY FOR TERMINAL VELOCITY

To run a Gaussian model, terminal velocity of the particle is the only characteristic needed. However, our approach included a validation test of the selected model in a wind tunnel. In this validation experiment, achenes were captured on a sticking paper and were no longer available for direct terminal velocity measurements. We thus needed to find a proxy for terminal velocity based on morphological traits.

S. inaequidens propagules were collected in December 2004 in two populations located in waste lands in Belgium: Seraing (50°36'9.1"N; 05°29'46.0"E; alt. 120 m; population area 350 m²) and Antwerpen (51°14'37.4"N; 04°23'12.3"E; alt. 2 m; population area 700 m²). In both populations, five capitula were randomly collected on five randomly selected individuals. Capitula were stored at ambient temperature in pierced boxes insuring uniform spread of plume fibres. Terminal settling velocity was measured on two achenes per capitulum: one external (at the periphery of the receptacle) and one internal (near the centre of the receptacle) (50 achenes per population). The achene-pappus unit was dropped down a transparent vertical Plexiglas tube (diameter 139 mm; height 2 m). The Plexiglas tube was connected to the ground with a copper wire to discard static electricity interferences. The descent was timed by an observer with an electronic stopwatch (precision: 0.01 s) along one meter, where terminal velocity was assumed to be reached (SHELDON & BURROWS 1973). Three replicate measurements were made per achene. From the same capitula, five external and five internal additional achenes were randomly picked and measured (250 achenes per population). The following morphological traits were measured on all achenes: (1) total propagule mass

(achene-pappus unit, in mg; precision: 0.1mg); (2) achene mass (without pappus, in mg); (3) pappus mass (mg) calculated as the difference (1)-(2); (4) pappus length (mm; precision: 0.1 mm); (5) pappus radius (radius of the wider circle made by the pappus, in mm); (6) achene length (without pappus, in mm); (7) maximal and (8) minimal achene diameters (without pappus, in mm) (Fig. 1). The following trait combinations were calculated: (9) achene flattening [(8)/(7)]; (10) pappus mass-radius ratio [(3)/(5)]; (11) achene-pappus mass ratio [(1)/(3)]; (12) plume loading. The latter was defined as the ratio of the total propagule mass (1) to the area of the horizontal projection of the wider circle made by the pappus (Fig. 1) (AUGSPURGER & FRANSON 1987, MATLACK 1987). It was preferred to the square root of the seed mass divided by the horizontal projection of the wider circle made by the pappus, which is sometimes used instead (SOONS & HEIL 2002), to allow comparison with a more abundant literature. Both trait combinations were highly correlated anyway ($r = 0.949$).

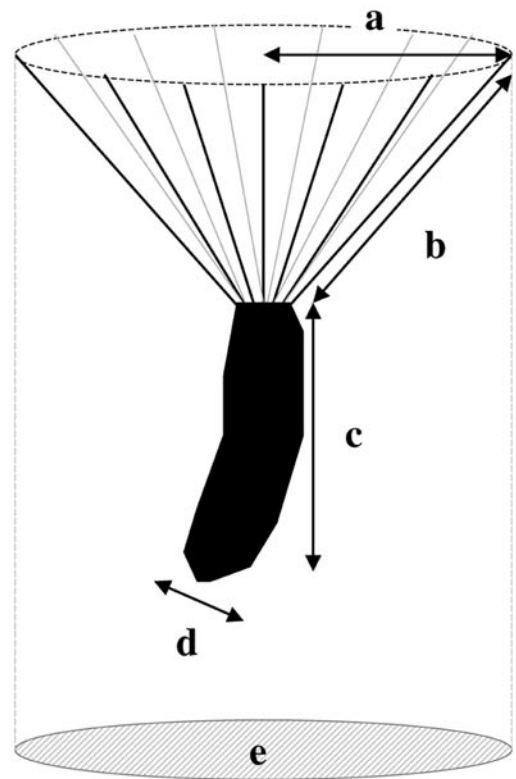


Fig. 1. *S. inaequidens* propagule with (a) pappus radius; (b) pappus length; (c) achene length; (d) one achene diameter and (e) area of the horizontal projection of the wider circle made by the pappus, used to calculate the plume loading.

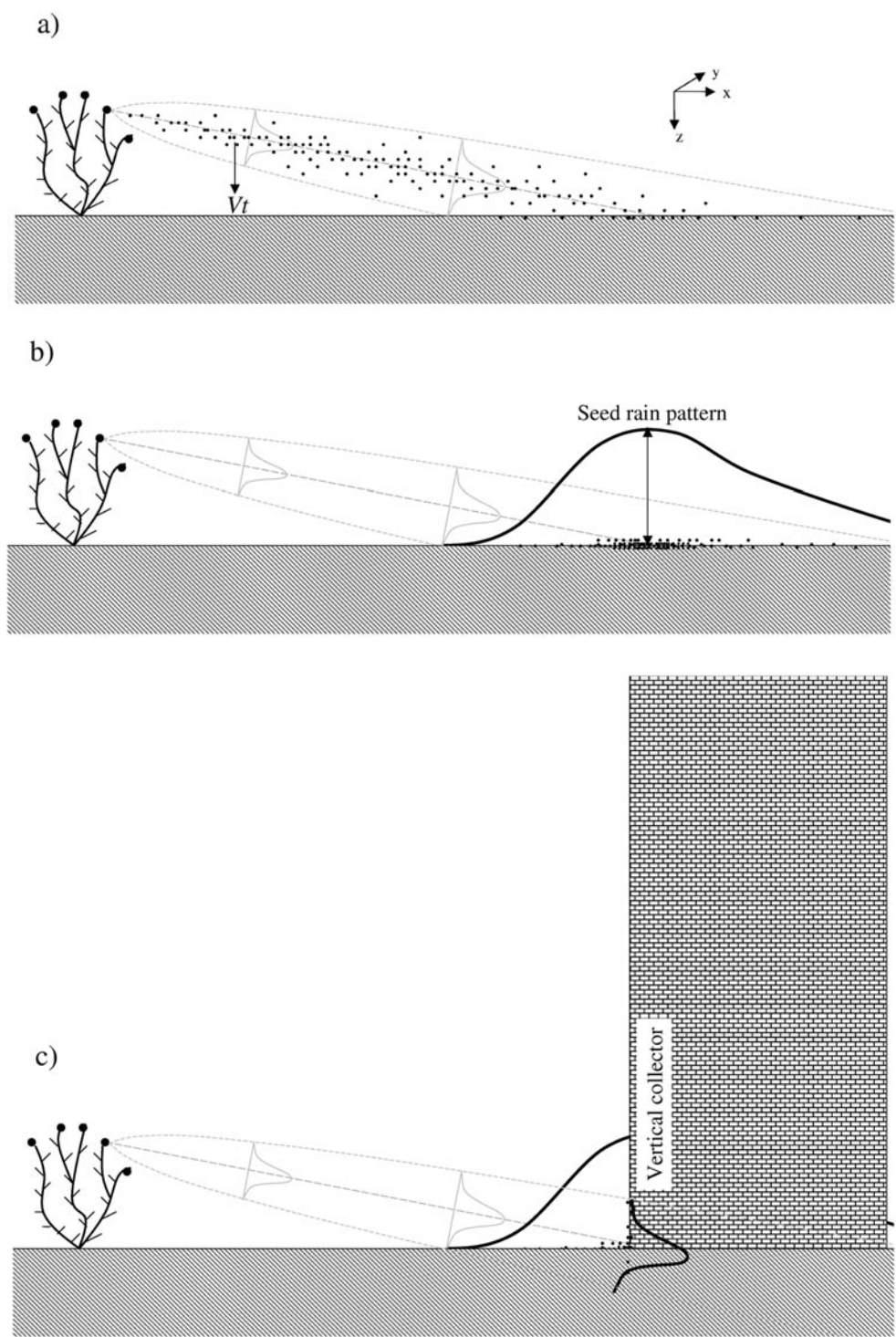


Fig. 2. Schematic representation of (a) tilting plume model dispersion; (b) seed rain pattern and (c) seed rain pattern intercepted horizontally and vertically in the wind tunnel.

Population, individual, capitulum and position (internal/external) differences for those morphological traits were analysed using nested ANOVA on the 500 achenes dataset with position nested within capitulum, capitulum nested within individual and individual nested within population, all of them being random factors. We calculated the linear correlation (Pearson's r) coefficient between morphological traits on the one hand, either directly measured or mathematically transformed (square, square root, logarithm, exponential) and terminal velocity on the other hand, to find the best morphological proxy trait of terminal velocity. In addition, linear regression (with stepwise selection) using least-square estimation was used to model terminal velocity by morphological proxy. All statistical analyses were executed using MINITAB ver. 13.20 (MINITAB Inc., State College, Pennsylvania).

MODELLING SEED RAIN PATTERN

Model construction

A Gaussian tilted plume model was selected with the aim to predict the seed rain pattern of *S. inaequidens* based on terminal velocity estimations. Gaussian models (PASQUILL 1962, HANNA *et al.* 1982) are commonly used to study very light particle dispersal, such as atmospheric pollutants or aircraft spray drift (e.g., STAINIER *et al.* 2006). However, they have also been applied to spore dispersal (GREGORY *et al.* 1961, FITT & MCCARTNEY 1986). With some adaptations they can be used for heavier particle dispersal (OKUBO & LEVIN 1989) where the wind direction is considered as the centre line of the propagule flow. On the perpendicular direction to the wind, the distribution has a Gaussian shape with an increase of amplitude while moving downwind from the source. This is the Gaussian tilted plume model (Fig. 2a), which extends the Gaussian models to cases where particles have a non-negligible settling velocity. A major shortcoming of these models is that they cannot explicitly simulate particle uplift.

In computing the deposition rate for those particles, this model ignores bouncing or resuspension of particles hitting the ground and assumes that deposition due to diffusion is negligible compared to sedimentation. So, the deposition rate on the ground is given by:

$$D = S(x, y, 0)Vt \quad (\text{eq. 1}),$$

where Vt is the terminal deposition velocity. The expression for the concentration of particles at the ground level is (OKUBO & LEVIN 1989):

$$D = Q(x, y) = \frac{nVt}{2\pi u \sigma_y \sigma_z} \exp \left\{ \frac{y^2}{2\sigma_y^2} - \frac{\left(H - Vt \frac{x}{u} \right)^2}{2\sigma_z^2} \right\} \quad (\text{eq. 2}),$$

where n is the number of particles at source, u is the mean wind speed along X direction at height of release H . Generally, $n = n_x$ (the effective number of particle at distance x) and standard deviations σ_y and σ_z depend on x (PASQUILL 1962), but one can simplify by ignoring the decay in n and assuming that n is constant (OKUBO & LEVIN 1989).

Since our main interest is to study how far *S. inaequidens* achenes move downwind, we suppressed the crosswind distribution (along y axis, which is Gaussian) by integrating in that direction (OKUBO & LEVIN 1989). The result, called the crosswind-integrated deposition (CWID), is given by (eq. 3) and represents the seed rain pattern along the X axis.

$$CWID = Q(x) = \frac{nVt}{u\sigma_z \sqrt{2\pi}} \exp \left\{ \frac{-\left(H - Vt \frac{x}{u} \right)^2}{2\sigma_z^2} \right\} \quad (\text{eq. 3})$$

To model the seed rain pattern of *S. inaequidens*, environmental parameters were imposed to mimic favourable and generally encountered dispersal circumstances, with steady winds on a flat open field. Height of release was 0.4 m, similar to the mean capitula height observed in Belgian populations (PIERET, unpublished data). A constant wind speed of 5 m s⁻¹ was selected, corresponding to the minimal wind speed needed to detach all the achenes from the receptacle (PIERET & STAINIER, unpublished data). It represents a frequently encountered wind in open areas over the flowering season in northwestern Europe. For instance, in the Loncée (central Belgium) meteorological station, such a wind was reached (at 0.4 m high) 68 days (31.7%) over the 2005 flowering season (June – December). Turbulences along the Z axis were fixed at 2% of wind speed along the X axis. As it appeared that terminal velocity exhibited a high intraspecific variation among achenes, the model was adapted to take into account this variability within achene populations rather than simply considering the mean observed terminal velocity. In order to be

consistent with the experimental conditions imposed in the wind-tunnel validation, the terminal velocity of achenes was derived from the morphological proxy trait using the linear regression fitted above. The values used by the model are no direct estimations but the centres of proxy trait classes given in Table 1.

Table 1. Plume loading classes (kg m⁻²) considered for terminal velocity estimations from morphological measurements.

Class	Minimum	Maximum
1	0	0.005
2	0.005	0.01
3	0.01	0.015
4	0.015	0.02
5	0.02	0.025
6	0.025	0.03
7	0.03	-

The model was set up using MATLAB ver. 7.1 (MATHWORKS Inc., Natick, Massachusetts). It provided a curve of crosswind-integrated deposition along X axis, i.e., the seed rain pattern of the species in the considered environmental conditions.

Model validation

The model was validated in a controlled dispersal experiment in the low-speed wind tunnel of the Mechanics and Construction Department of the Gembloux Agricultural University. The environmental conditions in the tunnel for validation were imposed to be the nearest to those used for model fitting. The tunnel is a closed loop re-circulating wind tunnel designed around a 1200 mm diameter axial blower driven by a 22 kW electric motor with a variable speed controller. To stabilize turbulence intensity, the wind tunnel has a 1 m long honeycomb of 200 mm edge square tubes with a monoplane windbreak grid upstream and a porous textile sheet downstream. The test section of the wind tunnel is 2 m wide, 2 m high, 6 m long and located 1 meter downstream of the fabric. The blower located at the loop opposite to the test section draws air through the tunnel at the desired velocity within the range 0-6 m s⁻¹. The wind speed and the turbulences are controlled by a triaxial supersonic anemometer (precision: 0.05 m s⁻¹).

Three capitula were collected in Gembloux on December 2004 (50°34'27.1''N; 04°41'15.8''E; alt. 140 m, population area 400 m²) and stored at ambient temperature in pierced boxes. A capitulum

was maintained vertically ahead of the blowing engine on a pedestal at 0.40 m above the ground and hidden by a cylindrical plastic bowl. The ground was covered with a 6-metre-long adhesive paper reaching the end of the test section of the tunnel. The bottom of the test section (at the opposite of the blowing engine) was covered with a vertical collector (textile), which allowed achene fixation. During the experiment, turbulences, defined as the ratio of the standard deviation of the wind speed along the axis considered to the average wind speed along the wind direction (X axis), reached 7% (Y axis), 2% (Z axis) and 3% (X axis). The experiments began when the wind reached 5 m s⁻¹ and remained constant. The bowl was then lifted up so that the achenes could disperse. After measuring their distance from the capitulum on the adhesive paper, or their distance from the floor on the vertical collector, achenes were collected for the same morphological measurements as described above. Besides morphological measurements, aborted or non-aborted aspect was noted for each achene (binary character). Aborted achenes are typically flat and whitish. Data of the three capitula were pooled for analysis. As there were no replications, no direct adjustment test could be statistically conducted.

With the morphological proxy trait of the achenes, along with the regression equation of *Vt* previously described, we defined a prediction interval around this regression with $\alpha = 0.2$. By definition this interval, limited by hyperboles presented in equations (4) and (5), contains 80% of the data of the drop time in still air experiment

$$Vt_{max} = \hat{V}T(x_0) + t_{1-\alpha/2} * \sqrt{\sigma_{VT,x}^2} * \left[(n+1)/n + (x_0 - x)^2 / SCE_x \right] \tag{eq. 4}$$

$$Vt_{min} = \hat{V}T(x_0) + t_{1-\alpha/2} * \sqrt{\sigma_{VT,x}^2} * \left[(n+1)/n + (x_0 - x)^2 / SCE_x \right] \tag{eq. 5}$$

Using these two equations instead of the terminal velocity regression in the constructed model, we produced two crosswind deposition curves, “model min” and “model max”. These curves encompass the seed rain pattern provided by the model in the imposed environmental conditions. If 80% of the real dispersion data in the wind tunnel are situated between equations (4) and (5), henceforth referred to as the 80% interval, the model is considered as valid (Fig. 3).

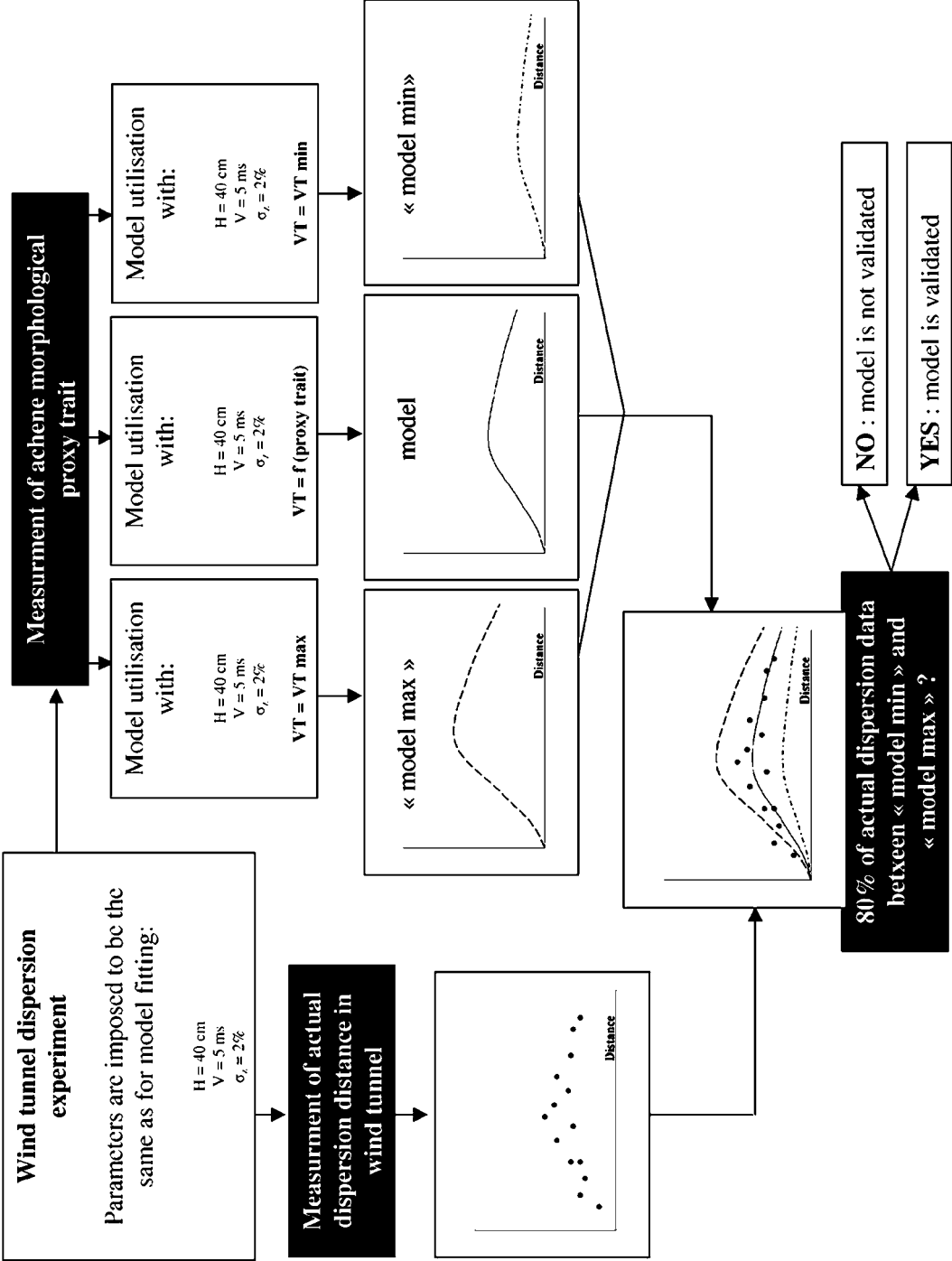


Fig 3. Schematic representation of model validation.

Table 2. Nested ANOVA to investigate the effects of individual, capitulum and propagule position (centre vs. edge) on morphological traits and terminal velocity.

Trait	Individuals (population)				Capitulum (individuals)				Position (capitulum)			
	df	MS	F	P	df	MS	F	P	df	MS	F	P
Total propagule mass (mg)	8, 400	0.0397	3.358	**	40, 400	0.0118	3.886	***	50, 400	0.003	1.921	***
Achene mass (mg)	7, 360	0.03 ^a	3.98	**	36, 360	< 0.01 ^a	3.12	***	45, 360	< 0.01 ^a	1.95	***
Pappus mass (mg)	7, 359	0.002 ^a	6.15	***	36, 359	< 0.01 ^a	1.77	*	45, 359	< 0.01 ^a	1.64	**
Pappus length (mm)	8, 399	9.66 ^a	9.2	***	40, 399	1.05	1.13	n.s.	50, 399	0.9324	6.02	***
Pappus radius (mm)	8, 400	4.926	2.948	*	40, 400	1.6709	1.124	n.s.	50, 400	1.487	6.83	***
Achene length (mm)	8, 400	2.3412	11.69	***	40, 400	0.2003	3.966	***	50, 400	0.0505	5.00	***
Maximal achene diameter (mm)	8, 400	0.0083	3.639	***	40, 400	0.0023	1.199	n.s.	50, 400	0.0019	1.348	n.s.
Minimal achene diameter (mm)	8, 399	0.02 ^a	5.19	***	40, 399	< 0.01 ^a	1.25	n.s.	50, 399	< 0.01 ^a	1.19	n.s.
Achene flattening	8, 399	0.150 ^a	2.74	*	40, 399	0.0548	1.12	n.s.	50, 399	0.0489	0.97	n.s.
Pappus mass-radius ratio (g m ⁻¹)	7, 359	< 0.01 ^a	8.82	***	36, 359	< 0.01 ^a	1.97	*	45, 359	< 0.01 ^a	0.76	n.s.
Achene-pappus mass ratio	7, 359	19102 ^a	0.99	n.s.	36, 359	19362 ^a	0.99	n.s.	45, 359	19468	1.11	n.s.
Plume loading (mg mm ⁻²)	8, 400	< 0.01 ^a	2.319	*	40, 400	< 0.01 ^a	1.099	n.s.	50, 400	< 0.01 ^a	4.554	***
Terminal velocity (m s ⁻¹)	8, 200	2.586	2.336	*	40, 200	1.11	0.74	n.s.	50, 200	1.5	61.98	***

Note. ***. $P < 0.001$; **. $0.001 \leq P < 0.01$; *. $0.01 \leq P < 0.05$; n.s.: not significant; ^a not an exact F-test.

RESULTS

POPULATION, INDIVIDUAL, CAPITULUM AND POSITION EFFECT ON PROPAGULE TRAITS AND TERMINAL VELOCITY

In the drop time in still air experiment, no difference was found between populations for any morphological trait or for terminal velocity (Table 2). A significant part of the variability in morphological traits was explained either by individuals, by capitula and/or by the position of the achene on the receptacle. Individual differences were significant (at 0.05 level) for most traits, showing important intra-population variability. External and internal achenes significantly differed for most traits. These differences were particularly marked for pappus morphology (31.5% and 45.7% of the variance explained by achene position for pappus length and pappus radius, respectively). External achenes had a smaller pappus but a similar mass, and, therefore, a greater plume loading. Terminal velocity differed among individuals and positions. The major part (85.0%) of the variability was explained by the achene position, with lower Vt for central achenes.

MORPHOLOGICAL PROXY TRAITS AND TERMINAL VELOCITY REGRESSION

Terminal velocity values in the drop time in still air experiment ranged from 0.171 to 0.513 m s⁻¹ (mean = 0.309 m s⁻¹; SD = 0.066 m s⁻¹).

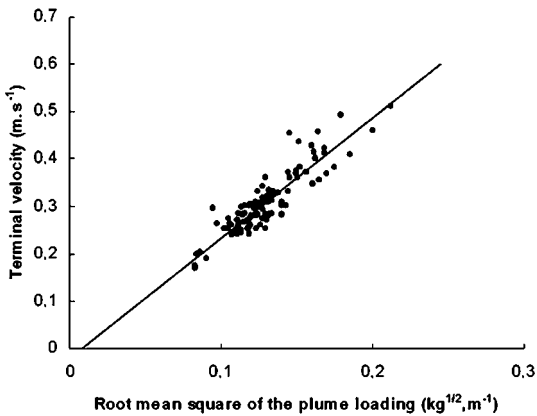
The quantitative morphological trait best correlated with terminal velocity was the square root of plume loading (SRPL) ($r = 0.891$; Table 3). This trait is thus a suitable proxy trait for terminal velocity estimations. Using this proxy trait, terminal velocity regression was fitted as follows:

$$Vt = -0.0192 + 2.53 * SRPL \tag{eq. 6}$$

The coefficient of determination was 0.797. Any additional variable in the model did not increase the coefficient by more than 0.025 so this equation was selected and used in the model to provide terminal velocity values estimated from achene morphology (Fig. 4).

Table 3. Pearson's coefficient of correlation (r), calculated between all morphological traits on the one hand, as measured or mathematically transformed, and terminal velocity on the other hand.

Morphological trait	Mathematical transformation				
	None	Square	Square root	Logarithm	Exponential
Total propagule mass (mg)	0.3012	0.2571	0.3233	0.3433	0.2904
Achene mass (mg)	0.3652	0.3251	0.3837	0.398	0.3571
Pappus mass (mg)	-0.3060	-0.2742	-0.3072	-0.2882	-0.3051
Pappus length (mm)	0.0531	-0.2735	0.0786	0.0829	-0.3648
Pappus radius (mm)	-0.6681	-0.6277	-0.686	-0.7017	-0.567
Achene length (mm)	-0.1961	-0.2013	-0.1929	-0.1893	-0.2051
Maximal achene diameter (mm)	0.0184	0.0149	0.0199	0.0213	0.0166
Minimal achene diameter (mm)	0.0441	0.0387	0.0486	0.0543	0.0424
Achene flattening	0.0276	0.0254	0.0306	0.0351	0.0268
Pappus mass-radius ratio ($\text{kg } 10^{-3} \text{ m}^{-1}$)	0.0855	0.0855	0.0854	0.0842	0.0855
Achene-pappus mass ratio	0.2459	0.0486	0.3695	0.4601	-0.0602
Plume loading (kg m^{-2})	0.8849	0.8325	0.8905	0.8794	0.8842

**Fig. 4.** Model equation for predicting terminal velocity using the square root of the plume loading.

MODEL VALIDATION

Among the 192 dispersed propagules in the three pooled wind-tunnel experiments, 101 (52.6%) fell on the horizontal 6-metre-long collector and 91 (47.4%) on the vertical one. Among the latter, 21 were collected above 0.4 m and cannot be considered for the Gaussian tilted plume model, as the model cannot simulate uplift. The case of those uplifted achenes is treated separately. Fig. 5 shows the horizontal and vertical repartition of the remaining 171 achenes considered in the wind tunnel, along with the modelled curve and the earlier described

80% interval. Horizontally 77.2% and vertically 75.7%, were inside this 80% interval. The model, therefore, does not reach proper validation, but can be considered as reasonably fitting the achene dispersal in the wind tunnel.

SEED RAIN PATTERN

Once the model constructed, the seed rain pattern under the selected environmental conditions was assessed. Fig. 6 shows the curve of the cumulated crosswind-integrated deposition for each plume loading class (Table 1) against the distance from the source (step 0.05 m). On a flat open area, under a 5 m s^{-1} stable wind and for an average height of release, 32.10% of the dispersed achenes are deposited in the nearest 6 m from the mother plant, with a peak at 5.2 m; 63.19% are dispersed within 10 m, and 99.83% within 100 m.

The 21 uplifted achenes (10.94% of all dispersed achenes) were collected from 0.43 to 0.86 m above ground. Nine of them were aborted. Viable uplifted achenes represented 6.25% of all dispersed achenes. They were not significantly different from non-uplifted achenes for achene mass (Mann-Whitney test; $W = 12036$; $P = 0.431$), pappus surface (Mann-Whitney test; $W = 12019$; $P = 0.752$) and plume loading (Mann-Whitney test; $W = 12132$; $P = 0.688$).

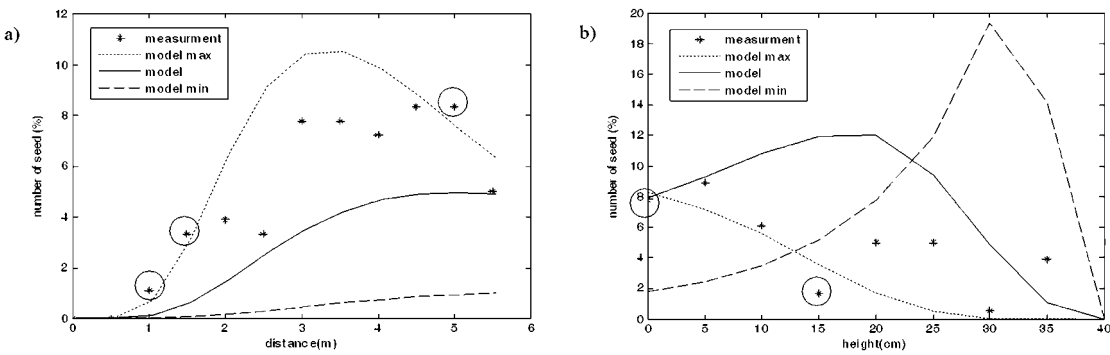


Fig. 5. Horizontal (a) and vertical (b) repartition of the 171 non-uplifted achenes dispersed in the wind tunnel, along with the modelled curve and the 80% interval (“model min” and “model max”). Dots represent the proportion of achenes per 5 cm class along the horizontal and vertical collectors. Circled measurement dots are outside the 80% interval. In the second figure, height is along the horizontal axis whereas it is vertical in the wind tunnel.

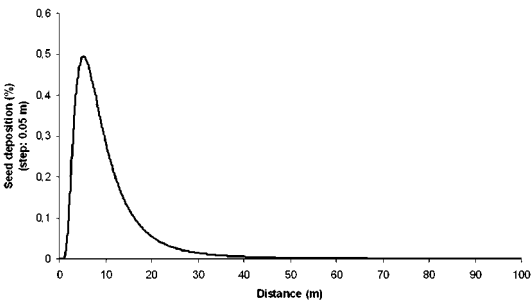


Fig. 6. Seed rain pattern of *S. inaequidens*. The curve is shown for the nearest 100 m from the parent plant. Percentage of deposition was calculated every 0.05 m.

DISCUSSION

The Gaussian tilted plume model provided a seed rain pattern for the environmental conditions that we imposed. It did not reach proper validation at the 80% level, but fitted the data obtained in the wind tunnel reasonably well. The produced pattern corresponds to a simplified situation as compared to field conditions, as several hypotheses were assumed for model fitting (no resuspension of seeds, *n* constant, negligible deposition due to diffusion). The validation experiment was limited to three dispersal events and showed a good agreement between predicted and measured data only for short distances. The seed rain pattern is only efficient under the

environmental conditions considered for model construction: flat area, wind speed around 5 m s⁻¹, low turbulences and release height of 0.40 m. Under these conditions, most achenes deposit in the vicinity of the parent plant: 63.2% within 10 m; 99.8% within 100 m. The maximum deposition rate is reached at 5.2 m. In the field, maximum winds and turbulences can be higher than those considered. Under those conditions the global seed rain pattern may be more spread out and the proportion of uplifted seeds can be higher, especially in the case of gusts. Nevertheless, the wind speed considered is such that most (if not all) achenes are detached from the receptacle. If wind speed increases gradually, most achenes are already dispersed when faster winds occur, even if achene abscission was shown not to be independent of wind speed (GREENE 2005). If wind speed increase is not gradual, gusts may however make the seed rain pattern different. Other aspects, such as topography or surrounding vegetation and shape of the parent plant (NIKLAS 1984) may also impact seed rain pattern in the field, so that the real pattern may dramatically differ from that modelled here. Besides, the invasion pattern of *S. inaequidens* was shown not to be isotropic: the species seems to disperse preferentially along roadsides and railways, which act like corridors along which stronger winds are more often reached (ERNST 1998).

The settling terminal velocities measured for *S. inaequidens* in this study are comparable to those given by ERNST (1998) for populations in the Netherlands. However, they are relatively low compared to other Asteraceae: among 39 species for which terminal velocity values were found in the literature and ranked increasingly, *S. inaequidens* ranked eleventh (SHELDON & BURROWS 1973, MATLACK 1987, SCHULZ *et al.* 1991, ANDERSEN 1992, 1993, KAHRS 1994, ASKEW *et al.* 1997, TACKENBERG *et al.* 2003). This indicates that *S. inaequidens* has a relatively high potential for exploiting favourable wind conditions. As generally reported for Asteraceae, the square root of the plume loading was the best proxy trait for terminal velocity (AUGSPURGER 1986, MATLACK 1987, ANDERSEN 1993, but see SOONS & HEIL 2002). Our assessment of terminal velocity by regression on the square root of the plume loading showed an acceptable precision compared to other studies (MATLACK 1987, ANDERSEN 1993, CODY & OVERTON 1996). As terminal velocity of a wind-dispersed diaspore is a major component of its dispersal ability (GREENE & JOHNSON 1986, MATLACK 1987), our results indicate that *S. inaequidens* achenes with low plume loading have a longer dispersal distance, i.e., light propagule and/or large pappus will be the best characteristics for dispersion.

In the context of plant invasion, estimating the tail of the seed shadow is of particular interest as it can have very important consequences on the colonisation rate of new sites (PORTNOY & WILLSON 1993). Although our model and experimental approach are not explicitly designed to evaluate rare long distance events, some interesting insights may be gained from both the modelled seed shadow and the observed dispersal pattern in the wind tunnel. Our model suggests a capacity for dispersal up to 200 m under favourable and relatively common wind conditions over the flowering season. Measuring seed dispersal capacity beyond tens of metres directly in the field is usually constrained by experimental design. Because of the necessity to keep sampling effort constant over increasing distances, the number of seed traps should be doubled when doubling distances (BULLOCK & CLARKE 2000).

This results in unmanageable experimental designs. We demonstrated that simple mechanistic models, such as the Gaussian plume model, with morphological seed characteristics that are relatively easy to measure such as plume loading, might help to understand the vulnerability of neighbouring unoccupied sites to colonisation from established populations.

In addition to seed included in the tail of the seed shadow, it has long been known that seed uplift is a key mechanism for long distance dispersal (NATHAN *et al.* 2002). In our experiment 6.25% of viable achenes were uplifted. These were not forecasted by the model. Long-distance dispersal may therefore represent up to 6.25% even under wind conditions with low turbulences. In comparison, in a study of another Asteraceae with a high dispersal capacity, *Cirsium vulgare*, KLINKHAMER *et al.* (1988) found that just over 10% of the dispersed seeds were caught by updrafts and were carried out of the study area (more than 32 m). Studying the dispersal of *Crepis praemorsa*, SKARPAAS *et al.* (2004) found that 4% of the seeds were uplifted and carried away from the population. In a recent study on the wind-dispersed invasive *Conyza canadensis* (Asteraceae), DAUER *et al.* (2006) found that seeds regularly dispersed at least 500 m from the source population despite that 99% of seeds were found in the nearest 100 m. As one *S. inaequidens* plant can produce up to 1500 capitula annually (MONTY, unpublished data) bearing roughly 100 achenes each (LOPEZ-GARCIA & MAILLET 2005), the seed rain (total amount of achenes produced per year) of *S. inaequidens* can reach 150 000 achenes plant⁻¹ y⁻¹ under favourable conditions. A single large *S. inaequidens* individual can thus potentially generate more than 9 000 uplifted achenes out of the population (i.e., more than 200 m away from the parent). This value is found for low turbulent conditions in the wind tunnel; hence it may be an underestimation compared to natural conditions. This represents an important colonisation potential, but information on post-dispersal survival is needed to predict long-distance colonisation. Diaspore weight and dispersal structure are linked to separate ecological functions, which may lead to contrasting forms of selection during invasion.

Diaspores with lower plume loadings will be the best disperser for colonisation of new areas, but heavier seeds are more likely to produce large and vigorous seedlings (BLACK 1956, DOLAN 1984), and, therefore, presumably confer an advantage in competition and fitness. According to this, one may expect that seeds with low plume loading and heavier seeds, i.e., larger pappus surface, would be favoured during invasion, thanks to a higher probability to found new populations. Yet, our results do not support this hypothesis because uplifted achenes were not morphologically different from others.

The present study shows how a seed dispersal modelling approach resulted in valuable information about further *S. inaequidens* invasion. The Gaussian tilted plume model might be generalised to other anemochorous alien species if long-distance dispersal is not the major focus, at least if one acknowledges the limitations of the model about seed uplift.

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