

DISPERSAL SPECIAL FEATURE

Non-random seed abscission, long-distance wind dispersal and plant migration rates

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Summary

1. In plants, long-distance dispersal (LDD) is a widespread phenomenon of great importance, especially in spatial dynamics such as in metapopulations, invasions and migration. Much has become known about the mechanisms underlying LDD by wind, but selective release mechanisms have received little attention. Recent papers call for particular effort in clarification of the seed release stage of the dispersal process, which is our aim here.

2. We studied non-random seed release at a range of spatial scales, from the individual plant to species' spatial dynamics. We did this by combining wind tunnel experiments, field trap data and simulation and analytical models, using two common wind-dispersed heathland plants (*Calluna vulgaris* and *Erica cinerea*) as study species.

3. In both species, seed release from the plant increases with increasing wind velocity. There is a minimum release threshold, above which the probability of seed release increases with increasing wind velocity. The drag caused by the wind is the motive force for seed release.

4. Simulations of seed dispersal with non-random seed release match measured dispersal kernels better, especially in the tails, than 'conventional' simulations with random seed release. Seed release during gusts gives the most realistic kernel. This result matches previous findings that seeds are released primarily at the start of gusts and during turbulent wind flow.

5. Dispersal kernels assuming non-random seed release had large impacts on analytically modelled population migration rates. Wavespeeds assuming seed release during gusts were, on average, more than double those assuming random seed release. Increases in wavespeeds under different seed release assumptions were due mostly to increases in the tail of the dispersal kernel.

6. *Synthesis.* This study shows how the small-scale process of a seed being released from the plant could affect the large-scale spatial dynamics of plant species in landscapes. The mechanism of non-random seed release, i.e., seed release during gusts, is an important mechanism for attaining LDD by wind. As such, non-random seed release influences landscape-scale species dynamics such as invasions and migration.

Key-words: dispersal model, long-distance dispersal, migration, non-random seed abscission, non-random seed release, seed dispersal, seed shadow, wavespeed model, wind dispersal

Introduction

In sessile organisms such as plants, propagules that disperse over long-distances contribute disproportionately to the spatial dynamics of species, as these propagules have the potential to reach sites that are separated from the source populations by great distances or an uninhabitable matrix. As such,

long-distance dispersal (LDD) of propagules is crucial in metapopulations and other forms of spatial dynamics (Hanski 1998; Nathan & Muller-Landau 2000; Freckleton & Watkinson 2002; Higgins & Cain 2002; Soons *et al.* 2005), invasion biology (Clark *et al.* 2001; Caswell *et al.* 2003) and migration, for example, in response to climate change (Clark 1998; Higgins & Richardson 1999). Overall, LDD is 'a widespread phenomenon of great importance' (Nathan 2006), although its importance has mainly been demonstrated

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theoretically using models (studies cited above) as LDD is extremely difficult to measure (Bullock & Clarke 2000; Nathan *et al.* 2003). Recent progress in modelling and measuring LDD has been mostly in quantifying LDD by wind (Kuparinen 2006). This is because wind is a very common and physically relatively well-characterized dispersal vector, and therefore easier to study than the other main dispersal vectors, for example water, animals and humans.

Detailed data on LDD by wind have been collected for seed dispersal distances up to 80 and 100 m (Bullock & Clarke 2000; Tackenberg 2003) and models have been developed to study the mechanisms that cause LDD by wind (Andersen 1991; Greene & Johnson 1995; Nathan *et al.* 2002; Tackenberg 2003; Soons *et al.* 2004a; Katul *et al.* 2005) and to study the effects of the environment on LDD (Soons *et al.* 2004b; Bohrer *et al.* 2008; Pouden *et al.* 2008; Schurr *et al.* 2008). These data and model studies show that several mechanisms increase numbers of seeds that are dispersed over long-distances by wind. First, plants can increase LDD by producing more and lighter seeds and releasing seeds higher above the ground. Lighter seeds and seeds released at greater heights have longer flight times and hence longer time intervals during which they are transported by the wind. Second, LDD is increased under conditions of high wind speeds and strong updrafts. Updrafts are caused by shear stress or thermals and cause seeds to be lifted up, again increasing their flight time. Most studies agree that windy conditions, which combine high wind speeds and high turbulence, cause the greatest increase in LDD (Andersen 1991; Greene & Johnson 1995; Horn *et al.* 2001; Nathan *et al.* 2002; Soons *et al.* 2004a).

If plants release seeds selectively during windy conditions, this mechanism would increase LDD further. Such non-random seed release, in that a threshold wind speed may be needed to detach a seed from the parent and/or detachment probability may increase with wind speed, has been found in three species of *Asteraceae* (Greene 2005; Skarpaas *et al.* 2006). A modelling study by Schippers and Jongejans (2005) showed that introducing an arbitrary threshold wind speed for seed release increased seed dispersal distances. These studies suggest that selective seed release under windy conditions is an additional important mechanism for LDD by wind.

However, the hypothesized link between non-random seed release, increased dispersal distances and the subsequent consequences for large-scale species dynamics has not been tested fully. Recent review papers have called for particular research effort on the quantification and modelling of the seed release stage of the dispersal process (Kuparinen 2006; Nathan 2006), which is our aim here. In this paper we test the following sequence of hypotheses using a combination of field data, wind tunnel experiments and modelling: (i) Seed release probability increases at higher wind speeds; (ii) Non-random release leads to increased seed dispersal distances; (iii) Field data showing fat-tailed dispersal kernels can be explained better by models which incorporate non-random release; and (iv) Increased dispersal distances caused by non-random release lead to significantly higher rates of migration. Using this combination of approaches we can link the small-scale

process of a seed detaching from the plant to the spatial dynamics of plant species in landscapes, and assess whether non-random seed release really is an important mechanism for LDD by wind.

Methods

We selected two heather species, *Calluna vulgaris* and *Erica cinerea*, for our study. Both species have tiny seeds which are dispersed by wind (see The studied species). Data quantifying the seed dispersal distributions of these species up to 80 m are available from field studies and show distribution tails that indicate LDD by wind (Bullock & Clarke 2000), making these species ideally suited for our study. To test our four hypotheses, we started by investigating the relationship between seed release and horizontal wind velocity in *Calluna* and *Erica* in wind tunnel experiments. We then simulated seed dispersal kernels for different possible relationships between seed release and horizontal wind velocity to quantify effects on dispersal distances. We compared the results of these simulations to the measured dispersal distributions available from the field studies to assess the accuracy of the simulated relationships. Finally, we modelled species migration rates based on the simulated seed dispersal kernels to quantify the significance of the differences for population spread.

THE STUDIED SPECIES

Calluna vulgaris (L.) Hull and *Erica cinerea* L. are dwarf shrubs. They are dominant species in the oceanic heathlands of north-west Europe, where they reach maximum heights of 1.25 m (*Calluna*) and 0.8 m (*Erica*; Gimingham 1960; Bannister 1965). In this low, open vegetation, wind is an important dispersal agent. Both species have tiny seeds (maximum diameter of *Calluna* seeds 0.58 mm, *Erica* seeds 0.85 mm; Bullock & Clarke 2000) which are dispersed by wind (Gimingham 1960; Bouman *et al.* 2000), as expected from the small seed sizes (Hughes *et al.* 1994). In both species the seeds are borne in capsules which open gradually as they dry out and seed shedding occurs simply by the seed falling from the open capsule. In *Calluna*, especially, Gimingham (1960) already noted that seeds appear to be shed from the capsules particularly during windy conditions. Fallen capsules containing a few unshed seeds may also be blown by wind over the ground (Gimingham 1960) or through the air (Bullock & Clarke 2000). *Calluna* and *Erica* plants produce very large quantities of seeds, with large plants producing tens of thousands (*Erica*; Bannister 1965) to hundreds of thousands (*Calluna*; Gimingham 1960) seeds per year.

Data quantifying the seed dispersal distributions of these species are available from a field study (Bullock & Clarke 2000). The seed dispersal distributions were measured in a seed trapping experiment. Large *Calluna* and *Erica* plants were transplanted to isolated sites in grasslands with very short vegetation. The plants were surrounded by seed traps at a range of distances, with the nearest traps at the edge of the plants and the furthest traps at 80 m distance. Seed traps were placed in linear transects in four wind directions (NW, NE, SW and SE) and were emptied twice during the seed dispersal season. Seeds and seed capsules in the seed traps were counted. Bullock and Clarke (2000) found that the vast majority of seeds fell within 1 m of the plant, but that a small number of *Calluna* and *Erica* seeds can disperse to distances up to 80 m. In the present study these data are compared with simulated seed distributions.

Calluna and *Erica* plants are long-lived, with individual life spans up to at least 30 and 19 years, respectively (Gimingham 1960;

Bannister 1965). Effective reproduction is mainly by seed (Gimingham 1960; Bannister 1965). For the modelling of migration rates the demography of the species was studied in detail, as described under Modelling of migration rates.

WIND TUNNEL EXPERIMENTS

To test whether seed release probability increases at higher wind speeds we carried out seed release experiments in a closed-circuit wind tunnel at Vrins Luchtonderzoek, Wageningen, the Netherlands (Oosterhuis & Vrins 2001). Heather plants were placed in the experimental section of the wind tunnel, in front of an impaction plate and an obstacle seed trap (see Appendix S1 in Supplementary Material). The impaction plate was sprayed with a sticky substance to trap seeds. An impaction plate with small strip-width (2 mm) was used, because *Calluna* seeds are so light and small that they do not impact on wider strips. The impaction plate trapped only *Calluna* seeds. The obstacle seed trap was a 0.05-m high bar stretching across the wind tunnel at floor height. Dispersed seeds were trapped in the sheltered area on the wind tunnel floor in front of the obstacle trap. The wind tunnel floor was covered by white filter paper to enhance seed trapping and seed visibility. Both *Calluna* and *Erica* seeds were trapped by the obstacle seed trap. Velocity of the air-flow was measured at approximately average plant height (0.10 m) close to the plant (see Appendix S1 Supplementary Material).

We used nine *Calluna* and nine *Erica* pot-grown plants with ripe seeds for the experiments. The plants were placed in the wind tunnel for the first time 1, 2 or 3 weeks after transportation to the wind tunnel site. After that, the plants were replaced in the wind tunnel at 1, 2 or 3 weeks intervals to test for changes in the release process over time. Three plants of each species were used for each time interval. During each wind tunnel experiment one plant was placed in the wind tunnel and the wind velocity was gradually increased from zero. Numbers of trapped seeds were counted for wind velocity intervals of 0.0–2.0, 2.0–4.0, 4.0–6.0, 6.0–8.0 and 8.0–10.0 m s⁻¹ at 0.10 m height. In addition the wind velocity at which the first seed was released was noted. At the end of all experiments the loose seeds that still remained on the plants were counted (seeds were removed from the plants by holding the flower heads upside down and tapping them gently). Films of the release experiments are presented in Supplementary Appendix S1.

SIMULATION OF SEED DISPERSAL KERNELS

To test if non-random seed release leads to increased seed dispersal distances, we used a mechanistic seed dispersal model to simulate seed dispersal kernels for four different seed release mechanisms: (i) random seed release, (ii) seed release above a minimal horizontal wind velocity (threshold velocity), (iii) seed release as a function of horizontal wind velocity, and (iv) seed release during gusts only. In all four scenarios we used the wind velocity distribution as measured during the field dispersal experiment (Bullock & Clarke 2000) as distribution of available wind speeds, modified in different ways depending on the release mechanism simulated. During the field dispersal experiment, wind velocities were measured by a Munro cup anemometer connected to a digital logger, recording hourly averages of horizontal wind velocity and direction (plus the velocity and direction of the maximum gust in each hour, the maximum gust being the highest wind velocity in any one minute period during each hour). For the random seed release simulations we used the wind velocity distribution as measured during the field dispersal experiment as model wind velocity input. For the threshold velocity

simulations we used the same wind velocity distribution as input, but set the minimum velocity at which a seed was released during the wind tunnel experiments as threshold velocity for seed release. For the release as a function of wind velocity simulations we did the same, but instead of setting a threshold we used a sigmoid function to relate the probability of seed release to the horizontal wind velocity. This function was fitted to wind tunnel data. For the simulation of seed dispersal in gusts, we assumed that seeds are released only during the maximum gust within each hour and used the gust data described above as wind velocity input.

We used the Markov chain synthetic turbulence generation model (STG model) developed by Nathan *et al.* (2002) and tested by Soons *et al.* (2004a,b) as simulation model. This mechanistic model predicts LDD in a realistic way (Nathan *et al.* 2002; Soons *et al.* 2004a,b) and might therefore be more successful in simulating dispersal of *Calluna* and *Erica* seeds than previously tested models (Bullock & Clarke 2000). The STG model is a trajectory model and simulates the dispersal trajectories of individual seeds in three-dimensional space based on the gravitational force pulling the seeds downwards and the air resistance force moving the seeds horizontally and vertically with the wind flow (including wind turbulence). Wind turbulence is simulated to retain the spatial and temporal coherence of eddies, which is crucial in predicting realistic LDD of seeds (Nathan *et al.* 2002; Soons *et al.* 2004a). A detailed description of the model used can be found in Soons *et al.* (2004a). The model input parameters seed terminal velocity, seed release height and vegetation height and LAI were determined from seed measurements and field data. The remaining model input, the distribution of mean horizontal wind velocities, was selected as described above. As the model simulates wind turbulence in a stochastic way we simulated 50 000 seed dispersal trajectories for each release mechanism.

COMPARISON OF SIMULATED TO MEASURED SEED DISPERSAL KERNELS

To test if field data showing fat-tailed dispersal kernels can be explained better by models which incorporate non-random release, we compared the results of the simulations to the dispersal distances measured during the field seed trapping experiments. For this we simulated seed traps in the same sampling design as used in the field experiments: four 80 m long transects in the NW, NE, SW and SE directions for each species. We compared simulated to measured seed trap densities per transect and species using Kolmogorov–Smirnov *Z* values for independent samples to compare the overall shapes of the kernels. Because few data lie in the tails, *K*–*S* or other statistics give little information about the fit of the modelled data to the observed tail (e.g. Bullock & Clarke 2000; Skarpaas *et al.* 2004), so these data were analysed graphically.

MODELLING OF MIGRATION RATES

To assess whether increased dispersal distances caused by non-random release lead to significantly higher rates of spread we used a model to quantify migration rates. We used the analytical wavespeed model of Neubert and Caswell (2000) that combines matrix models describing population growth with integrodifference equations describing dispersal. This represents a population spreading from a starting location in discrete time steps and so is a general, if simplified, approach to modelling the expansion of a population into unoccupied habitat (Buckley *et al.* 2005; Le Corff & Horvitz 2005; Garnier & Lecomte 2006). Population density at location *x* at time *t* + 1 is described by

$$\mathbf{n}(x, t+1) = \int_{-\infty}^{\infty} [\mathbf{K}(x-y) \cdot \mathbf{B}_n] \mathbf{n}(y, t) dy. \quad (\text{eqn 1})$$

\mathbf{B}_n is a stage-structured population projection matrix which describes density-dependent population growth at location y . This is an advance on earlier approaches which represented populations as unstructured, which is unrealistic for most plants and led to the implicit assumption that plants in sessile stages would disperse in the same way as, for example, seeds. $\mathbf{K}(x-y)$ is a matrix of dispersal kernels which describe the set of probabilities of the relocation from y to x of individuals undergoing each demographic transition. Complex dispersal kernels can be included because dispersal is described through a probability density function, with the simplifying assumption that dispersal from y to x depends only on the relative locations of the two points. Under this model a population forms a wave of constant shape which advances at constant speed and this asymptotic wavespeed c^* can be derived analytically.

This approach requires a stage-structured population projection matrix \mathbf{A} ($= \mathbf{B}_0$) which summarizes demography at low density and a matrix $\mathbf{M}(s)$ summarising the dispersal kernel for each life-history transition in terms of a moment generating function. Matrix models with 16 stages for *Calluna* and 14 stages for *Erica* (seeds in the soil, seedlings and 14 or 12 adult stages) were constructed from demographic data gathered at two sites near to the dispersal experiment site, which were acid grasslands undergoing colonization by the two heather species (J.M. Bullock, unpubl. data). These gave population growth rates (the maximum eigenvalue λ) of 2.62 for *Calluna* and 2.15 for *Erica* ($\lambda = 1$ indicates a stable population). We derived the moment generating function of each dispersal kernel using the empirical estimation approach shown by Caswell *et al.* (2003). For the simulated kernels we took the 5×10^4 (N) simulated dispersal distances r_1, \dots, r_N and used the equation

$$m_{ij}(s) = \frac{1}{N} \sum_i \cosh(sr_i) \quad (\text{eqn 2})$$

to calculate each entry for the matrix $\mathbf{M}(s)$ in which seed dispersal takes place (for non-dispersing transitions $m_{ij}(s) = 1$). The parameter s describes the shape of the wave (Caswell *et al.* 2003).

We modelled migration rates for each simulated dispersal kernel. This was done to allow examination of the consequences of the different seed release assumptions, rather than to provide an accurate estimation of true migration rates of each species. The kernel for each direction was assumed to represent unidirectional dispersal in one-dimension (see Lewis *et al.* 2006).

Results

WIND TUNNEL EXPERIMENTS

No seed release was observed at horizontal wind velocities below 2.8 m s^{-1} (*Calluna*) and 2.1 m s^{-1} (*Erica*). The average release thresholds in all trials were $4.3 \pm 0.82 \text{ m s}^{-1}$ (*Calluna*) and $5.7 \pm 2.2 \text{ m s}^{-1}$ (*Erica*). In both species the release thresholds followed a normal distribution, but in *Calluna* the range was narrower than in *Erica* (Table 1).

There was no relationship between release threshold and number of weeks since plant transport or previous wind tunnel trial in either species (linear regression; $R^2 = 0.07$, $P = 0.30$ for *Calluna*; $R^2 < 0.01$, $P = 0.82$ for *Erica*). This indicates that the seed release threshold changes slowly, if at all, over time.

In both species there was a clear relationship between seed release and horizontal wind velocity (Table 1). If drag caused by the wind is the motive force for seed release it is expected that the probability of seed release is related to the square of the wind velocity (P (release) related to U^2 ; Greene 2005). We tested this by linear regression of the log of release probability against the log of the horizontal wind velocity ($^{10}\log P$ (release) = b $^{10}\log(U) + ^{10}\log a$; zero release probabilities excluded). When considering only the seeds that were released, our results show that the probability of release was indeed related to the square of the wind velocity ($b \approx 2$; Table 1). No other parameters (such as week since plant transport or previous

Table 1. The wind tunnel experiments demonstrate that seed release is related to the horizontal wind velocity. A minimal horizontal wind velocity is required for seed release. Above this threshold velocity seed release (for released seeds) increases with the square of the horizontal wind velocity. For all wind velocities and all (total) seeds, seed release follows a sigmoid function of horizontal wind velocity

Species	Seed release thresholds			
<i>Calluna</i>	Average release threshold: $4.3 \pm 0.82 \text{ m s}^{-1}$ Range: 2.8–5.3 m s^{-1}			
<i>Erica</i>	Average release threshold: $5.7 \pm 2.2 \text{ m s}^{-1}$ Range: 2.1–9.2 m s^{-1}			
Relationships between seed release and wind velocity				
Released seeds only; release function $a U^b$				
	Linear regression (variables $^{10}\log$ -transformed)	a	b	95% confidence interval of b
<i>Calluna</i>	$R^2 = 0.70$ ($P < 0.001$)	1 (NS)	1.9 ± 0.17 ($P < 0.001$)	1.5–2.2
<i>Erica</i>	$R^2 = 0.61$ ($P < 0.001$)	1 (NS)	1.9 ± 0.23 ($P < 0.001$)	1.4–2.4
Released seeds as percentage of total seeds; release function $c U^d/(k^d + U^d)$				
	Nonlinear regression	c	d	k
<i>Calluna</i>	$R^2 = 0.26$	95.0	2.59	24.9
<i>Erica</i>	$R^2 = 0.21$	3.10	3.16	18.1

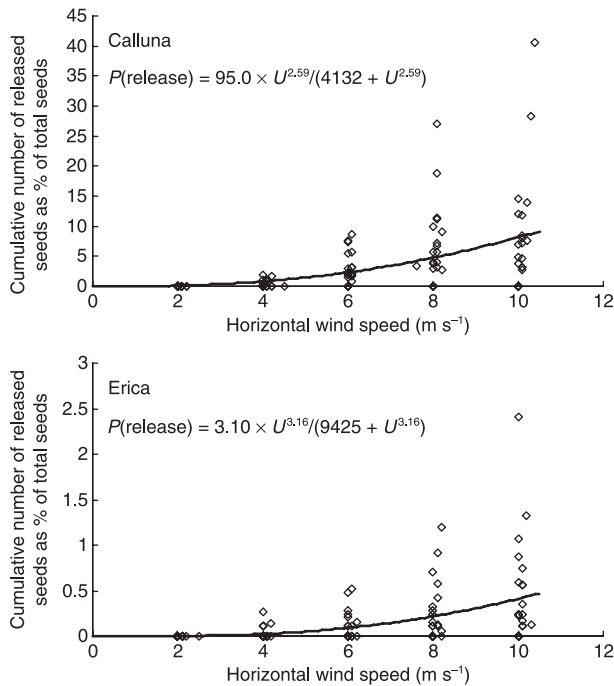


Fig. 1. Seed release increases with horizontal wind velocity, as shown by cumulative release probabilities (diamonds) from wind tunnel experiments. Sigmoid functions (lines) are from Table 1.

wind tunnel trial, or number of seeds left on the plant) were significantly related to seed release.

To describe the general relationship of seed release to wind velocity we included all loose seeds on the plants (i.e. all seeds that were released and all seeds that fell off the plant when it was shaken gently upside down after the wind tunnel experiments). We related released seeds as a cumulative percentage of total seeds to horizontal wind velocity using nonlinear regression ($P(\text{release}) = c U^d / (k^d + U^d)$). The resulting equations for *Calluna* and *Erica* are presented in Table 1 and plotted in Fig. 1, together with the wind tunnel data.

SIMULATED SEED DISPERSAL KERNELS

For the simulation of seed dispersal kernels with random seed release we used the wind velocity distribution measured during the Bullock and Clarke (2000) field experiments as wind velocity input. For simulation of dispersal kernels with a release threshold we used 2.8 m s^{-1} at seed release height as threshold in *Calluna* and 2.1 m s^{-1} in *Erica*. These are conservative values as many plants had higher release thresholds in our wind tunnel experiment. For simulation of dispersal kernels with a relationship between seed release probability and horizontal wind velocity we used the relationships from Fig. 1. For the simulation of dispersal kernels for gusts we used the gust velocity distribution measured during the Bullock and Clarke (2000) field experiments.

These simulations show that non-random seed release increases dispersal distances. Figure 2 shows the simulated

Table 2. A comparison of the simulated dispersal distributions to the dispersal distributions measured in field experiments shows that the gust model is most realistic. The lower the Z statistic, the smaller the difference between the simulated kernel and the measured kernel. All Z statistics are not significant ($P > 0.05$)

Species	Transect	Kolmogorov–Smirnov Z statistics for the full dispersal kernels			
		Random	Threshold	Sigmoid	Gust
<i>Calluna</i>	NW	1.07	1.07	1.07	0.88
	NE	0.88	0.71	0.71	0.53
	SW	0.53	0.71	0.53	0.35
	SE	0.53	0.53	0.53	0.53
<i>Erica</i>	NW	0.53	0.53	0.53	0.35
	NE	0.53	0.35	0.35	0.35
	SW	0.71	0.71	0.71	0.35
	SE	0.18	0.53	0.35	0.35

dispersal distance distributions (kernels) for the *Calluna* NE transect, which is a representative example for the other transects. A seed release threshold velocity and a relationship between seed release probability and wind velocity both shift the mode of the dispersal kernel to the right and increase the length and fatness of the tail. Seed release during gusts does not affect the location of the mode but increases the length and fatness of the tail more than the other mechanisms of non-random seed release.

The same can be seen in Fig. 3, which compares the simulated seed traps (data from the model simulations) to the measured seed traps (data from the field measurements) for each transect and species. This shows that non-random seed release improves the fit of the tails of simulated dispersal kernels to measured tails, although the measured tail is always fatter than under any simulations. The fit is best for seed release during gusts (Fig. 3, Table 2). The distributions for seed release during gusts have the best-fitting tails and the mode at the right location, whereas the distributions for a seed release threshold velocity and a relationship between seed release probability and wind velocity both shift the mode of simulated dispersal kernels away from the measured mode. Especially for the threshold velocity this shift is unrealistic in comparison to measured data. This result is found in both species.

MODELLED MIGRATION RATES

Similar patterns in the modelled wavespeeds c^* were seen in both species and all directions (Table 3). Non-random seed release always increased c^* , and the assumption of seed release during gusts always gave the highest c^* values: on average more than double those under random release. Dispersal distributions for a threshold velocity and for a sigmoidal relationship between wind velocity and release gave similar c^* values, but the higher value was usually under the threshold assumption. These variations in c^* among the seed release assumptions were driven more by differences in the tails of the simulated dispersal distributions than by differences

Table 3. Modelled migration rates using the simulated dispersal kernels are highest for seed release during gusts. The SW threshold kernels were not used as all seeds fell within the first trapping distance

Species	Transect	Modelled migration rate (c^*) myr^{-1}			
		Random	Threshold	Sigmoid	Gust
<i>Calluna</i>	NW	0.509	0.710	0.544	0.984
	NE	1.063	1.408	1.259	2.107
	SW	0.043	–	0.045	0.175
	SE	0.476	0.758	0.588	0.965
<i>Erica</i>	NW	0.211	0.324	0.267	0.396
	NE	0.425	0.588	0.663	1.139
	SW	0.022	–	0.023	0.082
	SE	0.207	0.361	0.303	0.416

in the average dispersal distances: the 99th percentile dispersal distance explained substantially more of the variation in c^* (R^2 from linear regression) for both *Calluna* and *Erica* (0.989 and 0.983, respectively) than did the mean distances (0.659 and 0.740).

The causes of differences between modelled wavespeeds can be studied using the decomposition analysis approach described by Caswell *et al.* (2003; see also Jongejans *et al.* 2008). An initial contrast can be made between the contributions of differences in demography and dispersal. Here, the analysis is simplified because all *Calluna* wavespeeds were calculated using the same demographic matrix (ditto *Erica*). So, the difference between two *Calluna* (or *Erica*) c^* values $c^{*(1)}$ and $c^{*(2)}$ is

$$c^{*(2)} - c^{*(1)} \approx \sum (r_{[h]}^{(2)} - r_{[h]}^{(1)}) \frac{\partial c^*}{\partial r_{[h]}} \Big|_{(r_1 + r_2)/2} \quad (\text{eqn 3})$$

whereby the 5×10^4 simulated dispersal distances are described in terms of order statistics and arranged such that the first is the minimum distance and the last the maximum. So $(r_{[h]}^{(2)} - r_{[h]}^{(1)})$ is the population difference in the h th order statistic of the dispersal distances and $(\partial c^* / \partial r_{[h]})$ is the sensitivity of c^* to this statistic, where c^* is calculated using the mean of the two dispersal kernels.

We illustrate our general findings here with comparisons among the models for the *Calluna* NE simulations. Comparison of the two scenarios with the smallest and largest wavespeeds – random release vs. release during gusts – gave similar results to comparison of the scenarios with the intermediate wavespeeds – threshold vs. sigmoidal relationship (Fig. 4). Virtually all of the differences in c^* were due to differences in the distances traveled by the furthest dispersers: the furthest 1% of distances accounted for 88% and 79%, respectively, of the differences between non-random release and release during gusts and between threshold and sigmoidal relationship.

Discussion

The results show that both *Calluna* and *Erica* have seed release thresholds. A minimum wind velocity is required to release seeds from the parent plants. There is not just a threshold, however, but the probability of seed release from the plants also increases with increasing wind velocity above the threshold.

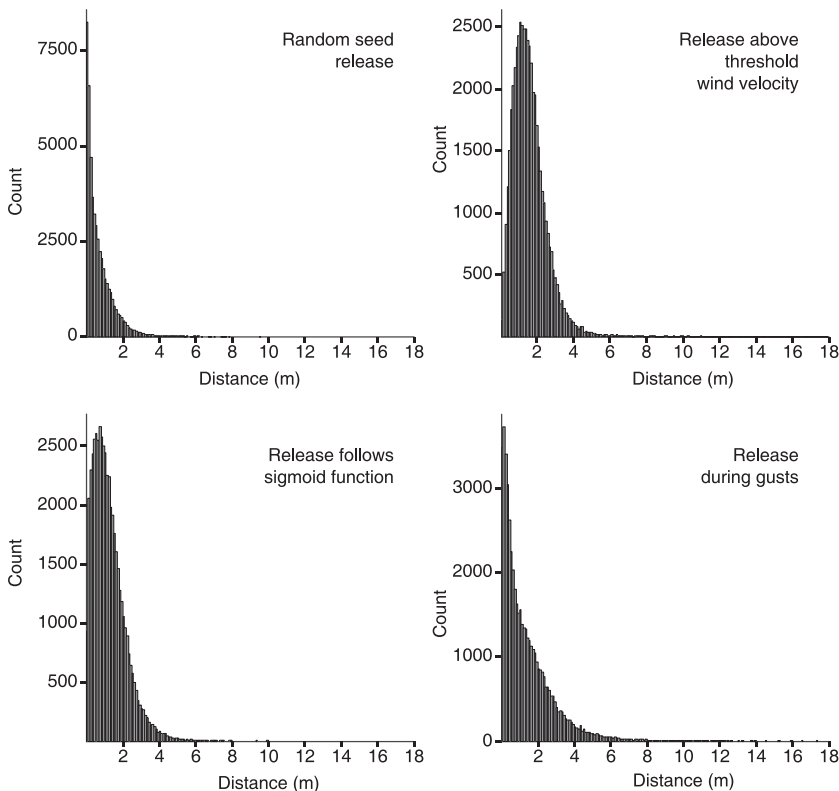


Fig. 2. Histograms of simulated dispersal distances show that non-random seed release increases dispersal distances. A seed release threshold velocity and a relationship between seed release probability and wind velocity both shift the mode of the dispersal kernel as well as increase the tail. Seed release during gusts does not affect the location of the mode but increases the tail more than the other mechanisms of non-random seed release. All histograms for *Calluna* NE transect.

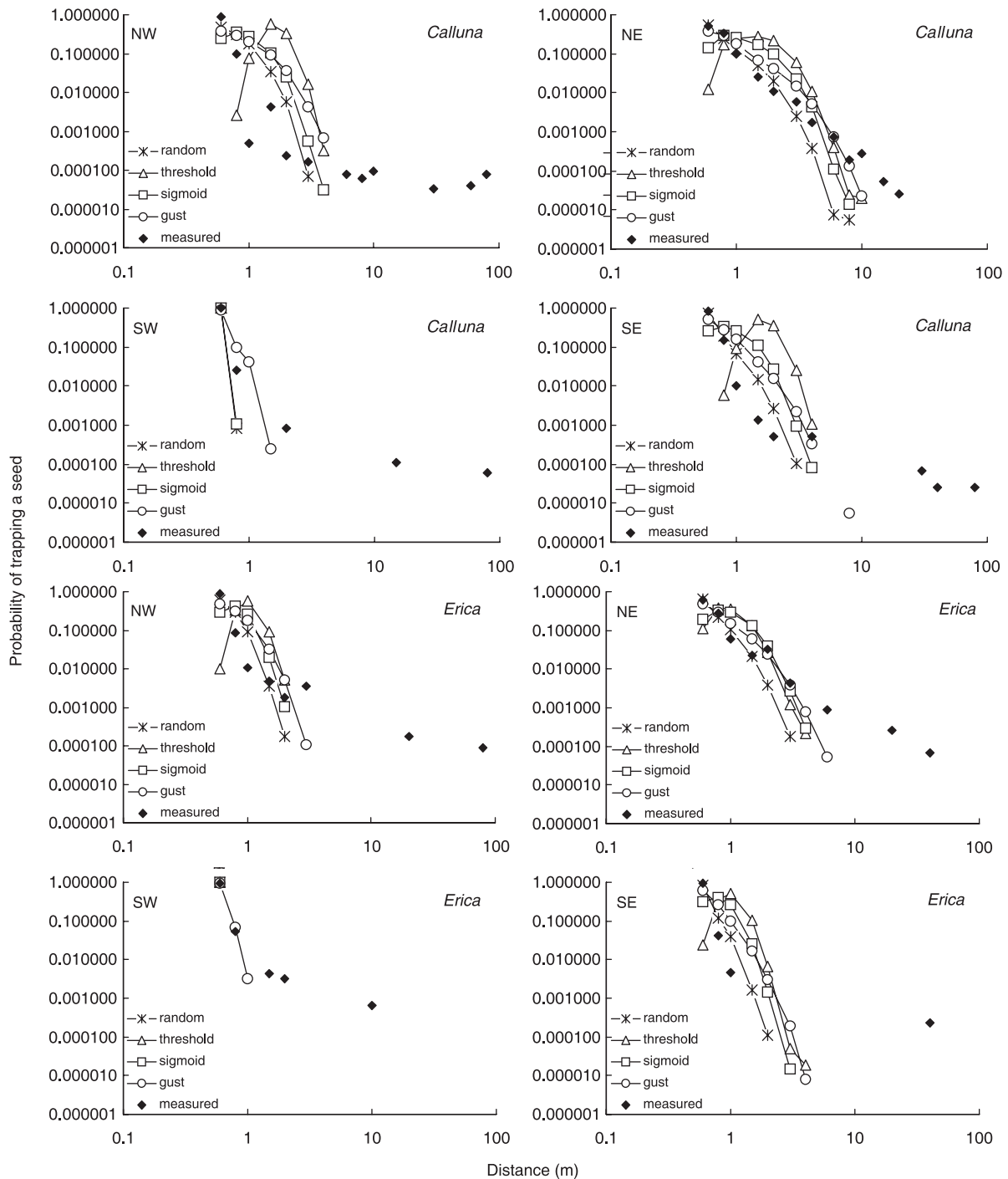


Fig. 3. Simulation of non-random seed release improves the fit of simulated tails of dispersal kernels to measured tails. The fit is best for seed release during gusts. Simulation of a seed release threshold velocity and a relationship between seed release probability and wind velocity both shift the mode of simulated dispersal kernels. Especially for the threshold velocity this shift is unrealistic in comparison to measured data. Zero values are not plotted.

These results support our first hypothesis, that seed release probability increases at higher wind speeds. This was also found in dandelions and five wind-dispersed tropical species by Greene (2005) and Greene *et al.* (2008) and in two thistle species by Skarpaas *et al.* (2006). Greene demonstrated that the drag force caused by the wind was the motive force for

seed release in dandelions, and our study confirms this mechanism for heather species. This suggests a general rule for wind dispersal of all types of seeds. While thistles and dandelions have similar, plumed, seeds which are held in an open inflorescence, heathers have simple seeds with no appendages which are held in a semi-closed capsule.

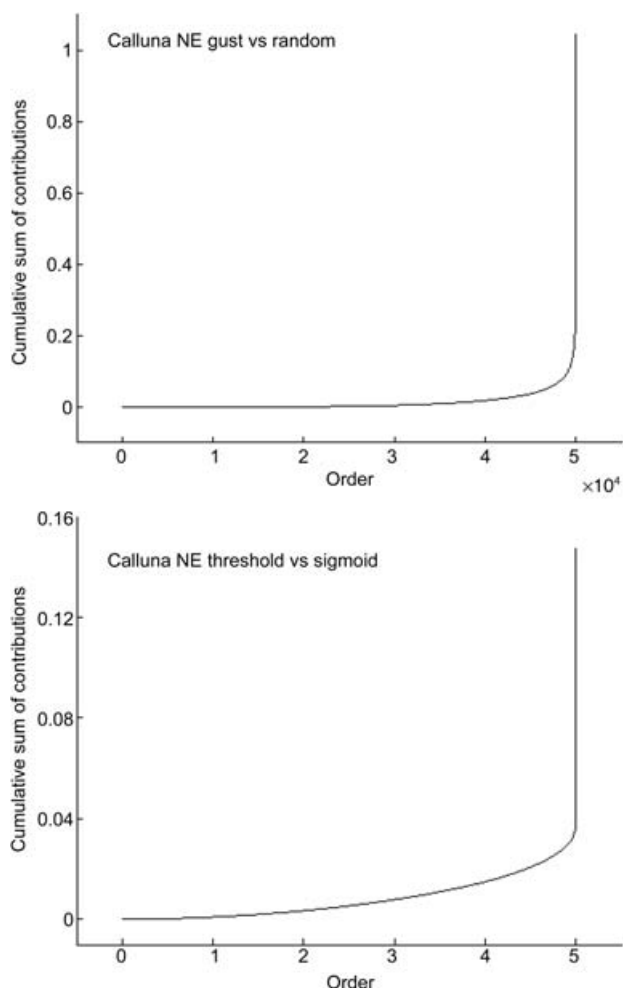


Fig. 4. Decomposition analysis showing the contributions of differences in dispersal order statistics (minimum to maximum dispersal distances from left to right) to the difference in c^* values. Here we analyse c^* values modelled using dispersal distances simulated under alternative seed release criteria for *Calluna* NE. The cumulative sums of the contributions are shown to illustrate the low contribution of the lower order statistics.

Simulations with the mechanistic dispersal model show that, as expected from our second hypothesis, non-random release leads to increased seed dispersal distances. A seed release threshold velocity and a relationship between seed release probability and wind velocity both change the mode and the tail of the dispersal kernel: they shift the mode of the dispersal kernel to the right and increase the length and fatness of the tail. Seed release during gusts does not affect the location of the mode, but increases the length and fatness of the tail more than the other mechanisms of non-random seed release. Schippers and Jongejans (2005) also found that, in comparison to simulation of random seed release, simulation of a seed release threshold shifts the dispersal kernel to the right. Our results however show that this shift does indeed increase dispersal distances, but in a less realistic way than seed release during gusts. When comparing the simulated dispersal kernels to measured dispersal kernels, the dispersal kernel for seed dispersal during gusts matches the measured kernels better

than dispersal kernels for a release threshold velocity or a relationship between seed release probability and wind velocity. This indicates that in reality, seeds are likely to be primarily released during gusts.

Our finding that seed release is likely to occur primarily during gusts agrees with the qualitative description of the seed release process in dandelions made by Greene (2005), that seed release almost always occurs at the start of a gust, and with the early observation by Gimingham (1960) that *Calluna* seeds appear to be shed from their capsules particularly during windy conditions. It also agrees with the results of studies on thistles by Skarpaas *et al.* (2006) and Jongejans *et al.* (2007), which indicate that seed release is more likely to occur under turbulent conditions. These results imply that in many wind-dispersed species selective seed release may occur especially in highly turbulent, windy, conditions, which are the conditions that favour LDD by wind (Andersen 1991; Greene & Johnson 1995; Horn *et al.* 2001; Nathan *et al.* 2002; Soons *et al.* 2004a).

The model with seed release during gusts explained a large part of the measured dispersal kernels, supporting our third hypothesis that field data showing fat-tailed dispersal kernels can be explained better by models which incorporate non-random release. However, certainly not all of the fatness measured in the tails was explained by the models. This may be because the underlying simulation model underestimates dispersal distances, but this is not the most likely explanation. The Markov Chain STG model has been shown to predict LDD in a realistic way in previous studies (Nathan *et al.* 2002; Soons *et al.* 2004a,b). A more likely explanation is that other processes, which are not included in the model, play a role in the field: for instance, secondary transport of seeds along the vegetation or the ground surface (Schurr *et al.* 2005). In the field the total dispersal kernel of the species was measured, which is in more cases than not the result of a combination of dispersal mechanisms (Nathan 2006). Inclusion of secondary transport is likely to enhance dispersal distances simulated by the model, but is beyond the scope of the present study.

Our fourth hypothesis, that increased dispersal distances caused by non-random release lead to significantly higher rates of invasion, was also supported. For all species \times direction combinations the modelled migration rates were higher under non-random seed release. While the particular assumptions for non-random seed release changed the simulated dispersal kernels in terms of both the mode and the length of the tail, it was the latter which had by far the greatest effect on the migration rates. So, seed release during gusts, which changed the tail but not the mode, led to a doubling (on average) of the migration rates. The other two assumptions had less of an impact because they led to shifts in the mode and only small increases in the tail. The overwhelming importance of the dispersal tail compared to other dispersal statistics in causing changes to plant dynamics is often seen, not only in simple migration models such as that used here (Kot *et al.* 1996; Caswell *et al.* 2003), but also in more complex simulation models of invasions (Higgins & Richardson 1999) and metapopulations (Bohrer *et al.* 2005).

In addition to our finding that non-random seed release during gusts increases seed dispersal distances and invasion rates, it is important to note that selective seed release during gusts may also affect the direction of seed dispersal and invasion if stronger winds have a dominant direction, such as is the case in coastal or mountainous terrain (Greene *et al.* 2008). The ecological effects of non-random seed release during gusts may thus be greater yet than found in this study.

Our study shows that the small-scale process of a seed detaching from a plant could affect the large-scale spatial dynamics of plant species in landscapes. Our results demonstrate that non-random seed release in the field is most likely to consist of seed release primarily during gusts, and that this process is an important mechanism for LDD by wind. The finding that non-random seed release is caused by seed release during gusts again supports the idea that for LDD it is not the average conditions (such as average wind speed), but rather the occasional deviation from average conditions (gusts, turbulence) that matter most (Nathan 2006). The idea that non-random seed release plays an important role in increasing the probability of LDD has now been demonstrated for typically wind dispersed species from the *Asteraceae* (Greene 2005; Skarpaas 2006) and *Ericaceae* (this study). It is likely to be a general mechanism, which should be taken into account in further wind dispersal studies. Future studies on the capacity for LDD in plant species should include non-random seed release and not focus on seed terminal velocity and release height alone.

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Supplementary material

The following supplementary material is available for this article:

Appendix S1 Set-up of the wind tunnel experiments.

This material is available as part of the online article from:
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