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Costs and benefits of non-random seed release for long-distance dispersal in wind-dispersed plant species

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Oikos
127: 1330–1343, 2018
doi: 10.1111/oik.04430

Subject Editor: Calvin Dytham
Editor-in-Chief: Dries Bonte
Accepted 8 March 2018

The dispersal ability of plants is a major factor driving ecological responses to global change. In wind-dispersed plant species, non-random seed release in relation to wind speeds has been identified as a major determinant of dispersal distances. However, little information is available about the costs and benefits of non-random abscission and the consequences of timing for dispersal distances.

We asked: 1) to what extent is non-random abscission able to promote long-distance dispersal and what is the effect of potentially increased pre-dispersal risk costs? 2) Which meteorological factors and respective timescales are important for maximizing dispersal? These questions were addressed by combining a mechanistic modelling approach and field data collection for herbaceous wind-dispersed species.

Model optimization with a dynamic dispersal approach using measured hourly wind speed showed that plants can increase long-distance dispersal by developing a hard wind speed threshold below which no seeds are released. At the same time, increased risk costs limit the possibilities for dispersal distance gain and reduce the optimum level of the wind speed threshold, in our case (under representative Dutch meteorological conditions) to a threshold of 5–6 m s^{-1}. The frequency and predictability (auto-correlation in time) of pre-dispersal seed-loss had a major impact on optimal non-random abscission functions and resulting dispersal distances.

We observed a similar, but more gradual, bias towards higher wind speeds in six out of seven wind-dispersed species under natural conditions. This confirmed that non-random abscission exists in many species and that, under local Dutch meteorological conditions, abscission was biased towards winds exceeding 5–6 m s^{-1}.

We conclude that timing of seed release can vastly enhance dispersal distances in wind-dispersed species, but increased risk costs may greatly limit the benefits of selecting wind conditions for long-distance dispersal, leading to moderate seed abscission thresholds, depending on local meteorological conditions and disturbances.

Keywords: long-distance dispersal, risk costs, seed abscission

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Introduction

Seed dispersal in plants enables gene flow between existing populations and colonization of new habitat sites, and is therefore fundamental to species survival in a changing world (Howe and Smallwood 1982, Levin et al. 2003, Renton et al. 2012). To predict plant species survival and potential range shifts in response to global changes, we need to be able to estimate species dispersal distances across a wide range of environmental conditions (Brooker et al. 2007). Wind is a common dispersal vectors of plant seeds (Van der Pijl 1982, Willson et al. 1990) and for this vector mechanistic models have been developed to estimate dispersal kernels from species-specific plant traits (Nathan et al. 2011). However, even advanced mechanistic wind dispersal models that have been compared to measurements tend to underestimate the tail of measured dispersal kernels (Soons et al. 2004a, Katul et al. 2005, Soons and Bullock 2008). This is problematic, as the tail is of disproportionate importance since it contains long-distance dispersal (LDD) events. It is conjectured that non-random seed release during specific meteorological conditions significantly enhances dispersal distance and is partly responsible for this underestimation (Greene 2005, Skarpaas and Shea 2007, Bohrer et al. 2008, Soons and Bullock 2008, Greene and Quesada 2011, Maurer et al. 2013, Pazos et al. 2013).

Several studies have shown a direct relation between meteorological variables (such as wind speed, turbulence and humidity) and seed release (hereafter termed 'abscission'; with this term we cover all detachments of seeds – including potentially attached structures, such as dispersal enhancing wings or plumes, or other plant parts – from their parent plant). Most studies focused on wind speed and they established a rapid or exponential increase of abscission probability with increasing wind speed (Greene 2005, Skarpaas et al. 2006, Jongejans et al. 2007, Soons and Bullock 2008, Greene and Quesada 2011, Pazos et al. 2013). This is an intuitive result, as the motive force for breaking the connection between a seed and its parent plant is drag, which is proportional to the square of wind speed (Greene 2005, Pazos et al. 2013). At the same time, abscission during stronger wind speeds increases dispersal distances (Soons et al. 2004a, b, Schippers and Jongejans 2005, Soons 2006, Soons and Bullock 2008, Pazos et al. 2013, Savage et al. 2014), which may result in selective pressures on non-random abscission mechanisms with a bias towards high wind speeds in plant species for which LDD is beneficial. While we acknowledge that not all plants optimize their dispersal by maximizing LDD specifically and many species exist for which LDD may be disadvantageous (Gilman et al. 2010, North et al. 2011, Soliveres et al. 2014), non-random abscission has been shown a potentially effective way to increase the tail of the dispersal kernel.

Turbulence and updrafts due to mechanical shear or convection also promote LDD (Nathan et al. 2002, 2011, Tackenberg 2003, Soons et al. 2004a, Wright et al. 2008, Maurer et al. 2013, Savage et al. 2014) and some plants have been found to release more seeds during turbulent conditions or updrafts (Skarpaas et al. 2006, Greene and Quesada 2011, Borger et al. 2012, Maurer et al. 2013). Furthermore, solar radiation, temperature and humidity may affect seed ripening processes and the drying of the tissue between seed (and potentially associated structures) and parent plant (Greene et al. 2008, Marchetto et al. 2012). Radiation, temperature and humidity are correlated with convective updrafts (Stull 1988) and could also act as a trigger for abscission during periods of convective conditions. However, the relative importance of convective updrafts for LDD in comparison to that of mean horizontal wind speed varies strongly between plant species (Tackenberg 2003, Soons et al. 2004a, Maurer et al. 2013).

The timing of abscission in relation to local meteorological conditions is thus likely to play an important role in determining dispersal distances in wind-dispersed plant species. However, a comprehensive mechanistic understanding of which traits determine abscission timing, and how these traits interact with the environment, remains lacking. Abscission is an instantaneous process that occurs when a drag force exceeding a certain threshold breaks the connecting tissue between seed and plant (Greene and Quesada 2011, Pazos et al. 2013, Thompson and Katul 2013). This threshold, therefore, is a strong determinant of the meteorological conditions during dispersal. The threshold may be dynamic in time through processes of material fatigue (Pazos et al. 2013, Thompson and Katul 2013), drying (Borger et al. 2012, Marchetto et al. 2012) and processes at the cell level such as degradation of an abscission layer (Liljegren et al. 2000, Thurber et al. 2011), which act on timescales ranging from minutes (material fatigue and drying) to days (drying and plant-regulated processes) (Savage et al. 2014). Phenology determines the flowering and fruiting periods of plants at monthly, seasonal, to yearly timescales (Chuine 2010). As meteorology fluctuates across a range of timescales, from turbulence (millisecond-second), to diurnal variation (hour), synoptic weather systems (day), and seasonal variation (month; Stull 1988), selective pressures may be acting at a range of timescales in order to optimize the dispersal kernel by non-random abscission.

Non-random abscission also comes with risk costs (Bonte et al. 2012). In many regions around the world, mean wind-speed variability is approximated by strongly right-skewed distributions (Supplementary material Appendix 1 Fig. A8) and high wind speeds remain rarities (Stull 1988). Hence, a high abscission threshold would result in a potentially long seed exposure time, entailing an increased risk of pre-dispersal seed loss by e.g. damage or predation (Moles et al. 2003, Bonte et al. 2012). The effects of these risks can play an important role in shaping non-random abscission patterns and, hence, dispersal kernels.

Here, we examine how different mechanisms operating at a wide range of timescales shape non-random abscission and, hence, dispersal kernels. We conducted a modelling and a field study to answer the following questions: 1) to what extent is non-random abscission able to promote LDD?

2) What is the effect of potentially increased risk costs on non-random abscission strategies and dispersal kernels? 3) Which meteorological factors and respective timescales are important for maximizing LDD? The combined modelling and field study allowed the exploration of the theoretical effects of different abscission strategies on LDD. These different abscission strategies are then compared to actual abscission strategies for seven wind-dispersed herbaceous plant species under natural conditions.

Material and methods

We used a mechanistic modelling framework to evaluate the extent to which abscission timing is able to promote LDD and how increased risk costs affect abscission strategies and dispersal kernels. As a second step, we used this framework to examine timing mechanisms across timescales and quantify the consequences for LDD. Finally, we carried out a field study to determine to what degree non-random abscission mechanisms exist in selected wind-dispersed plant species and to evaluate whether the mechanistic model-based predictions regarding abscission timing are plausible.

Model description

In our modelling framework, we combined a mechanistic dispersal model with an abscission submodel (a schematic overview of the modelling framework is provided in the Supplementary material Appendix 1 Fig. A1). We used the coupled Eulerian–Lagrangian closure model (CELC; Katul and Albertson 1998, Nathan et al. 2002, 2011, Soons et al. 2004a, b) as the seed dispersal model to compute dispersal kernels for a range of wind speeds and plant species and used these kernels as input for the abscission submodel. CELC, relative to large Eddy simulation models, offers a computationally cheap approach to quantify seed dispersal kernels as function of prescribed atmospheric profiles of wind and turbulent statistics (Nathan et al. 2002, 2011, Soons et al. 2004a, b). CELC randomly generates auto-correlated time series of turbulence velocity fluctuations around a profile of mean wind speed within and above vegetated canopies, which can be used to model entire dispersal trajectories of seeds. Additional details and settings are provided in the Supplementary material Appendix 1.

By simulating the trajectories of 50 000 seeds, we estimated the dispersal kernel for a plant species at a given wind speed. We repeated this procedure for 20 wind speeds (ranging from 1 to 20 m s^{-1} at a reference altitude of 10 m) and for the seven plant species that were observed in the field study. Note that wind speed typically increases with altitude and the actual wind speeds experienced by the seeds are typically lower than the reference wind speed at 10 m altitude. An overview of the plant species and the required model parameters (1) seed release height and (2) terminal fall velocity of the seed, is given in Table 1. For parameterisation of the canopy profile, we assumed a homogeneous field with a maximum vegetation height of 1 m and a leaf area index (LAI) profile similar to a fen-meadow characterized in Fliervoet (1984) (Supplementary material Appendix 1 Fig. A2). For each species, we used the resulting dispersal kernels K_u (20 in total, belonging to mean hourly wind speeds of 1 to 20 m s^{-1}) as input for the abscission submodel.

The abscission submodel simulates a seed dispersal kernel (K_y) for an individual plant (represented by a combination of seed terminal velocity and seed release height) for a full calendar year. The yearly dispersal kernel is calculated as a cumulative sum of all the hourly seed dispersal distances distributions (D_t), divided by the total seeds produced over the entire year;

$$K_y = \left(\sum P_t\right)^{-1} \sum D_t \quad (1)$$

where P_t is the number of seeds produced at time step t (one time step equals one hour). In the main simulations the plant produces an equal number of seeds every hour throughout the year. We also performed tests with variable seed production, which are presented in the Supplementary material Appendix 1 Fig. A6. Each hour, the probability of abscission, pA_t, is calculated as a function of wind speed (Eq. 4). The released seeds disperse according to the dispersal kernel (K_u, from the CELC model). The hourly distribution of seed dispersal distances (D_t) is then calculated as;

$$D_t = K_u\left(S_t + P_t\right) pA_t \quad (2)$$

where S_t is the number of seeds on the plant at time step t and pA_t is the probability of seed abscission at time step t.

For each hour, the remaining seeds from the end of the previous hour are available for dispersal:

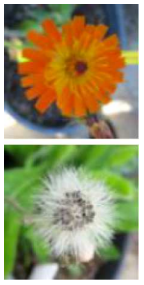
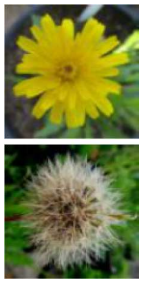
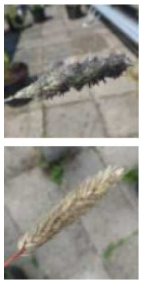
$$S_t = \left(S_{t-1} + P_{t-1}\right)\left(1 - pA_{t-1}\right) \quad (3)$$

At any specific instant in time, an individual seed requires a drag force exceeding a threshold to break its connection to the plant. This threshold can vary between seeds on an infructurescence. We assume that a sigmoid function is a reasonable descriptor of abscission when exploring full infructurescences instead of individual seeds (Thompson and Katul 2013). The logistic function of the hourly mean wind speed (u_t) is intuitive as the midpoint and the slope of the curve can be defined with parameter α (slope, s m^{-1}) and β (midpoint, m s^{-1});

$$pA_t\left(u_t\right) = \left(1 + e^{-\alpha\left(u_t - \beta\right)}\right)^{-1} \quad (4)$$

u_t (in m s^{-1}) used here to characterize the flow is the measured value at 10 m altitude. By varying the α and β parameters in parallel model runs, we examined the effects of non-random abscission relative to wind speed on a yearly dispersal kernel.

Table 1. Overview of the species observed during the field study and their most important characteristics. Individuals were collected from wild plant breeders or dug out from nearby fields (in situ). Species characteristics are based on the LEDA traitbase (Kleyer et al. 2008).

	Cirsium arvense	*Sonchus asper*	*Hieracium aurantiacum*	*Tussilago farfara*	*Taraxacum officinale*	*Leontodon hispidus*	*Alopecrus pratensis*
Location	De Uithof, Utrecht	De Uithof, Utrecht	De Heliant, Wapserveen	De Uithof, Utrecht	De Uithof, Utrecht	De Heliant, Wapserveen	De Uithof, Utrecht
Method	In situ	In situ	Breeder	In situ	In situ	Breeder	In situ
Number of sites	6	3	1	3	8	1	8
Collection dates	16-19 May 2014	16 May 2014	23 May 2014	17-22 April 2014	24-25 April 2014	23 May 2014	1 May 2014
Observation period	20 June - 25 August	26 May - 19 July	10 June - 3 October	23 April - 23 May	28 April - 9 May	26 May - 3 October	7 May - 25 July
Seed terminal velocity in m s^{-1}	0.3	0.6	0.3	0.2	0.6	0.9	2.2
Seed release height in m	0.75	0.75	0.35	0.17	0.35	0.4	0.6
Number of seeds per inflorescence	200	198	50	313	155	77	100
Number of plants	25	7	24	25	23	34	30
Number of inflorescences	96	329	278	56	64	312	172
Number of observation	1368	876	2633	1087	873	6427	16481
Flower							

To simulate realistic meteorological scenarios, measured time series of hourly wind speed, precipitation, temperature and relative humidity from the KNMI (Royal Netherland Meteorological Institute) station in De Bilt (<www.knmi.nl/nederland-nu/klimatologie/uurgegevens>) were used as model input in the abscission submodel. To explore potential effects of variation in humidity, we also performed model runs using vapour pressure deficit (VPD) as predictor for non-random abscission probability (Supplementary material Appendix 1 Fig. A6). VPD was estimated from temperature and relative humidity measurements from the same KNMI time series (Tetens 1930). We selected a period of 32 years from the year 1962 to 1993. A 30 year period is deemed sufficiently long to represent normal climatic variation and during this particular period wind speed measurements were taken using a uniform method at 10 m altitude. All our simulation results refer to measured wind speeds at a reference height of 10 m. The CELC resolves actual wind speed at the height of seed release, but to facilitate comparisons we present wind speeds at reference height.

Simulations

Aim 1. Non-random abscission

We examined the effects of different abscission functions on LDD in the yearly dispersal kernel (K_y) by running the model for 10 × 10 combinations of the slope (α) and midpoint (β) parameters of the sigmoid abscission function (Eq. 4). In these parameter combinations, the slope parameter ranged from very steep to smooth; $\alpha = 4 / i$ where $i = 1, 2, \ldots, 10$. The midpoint of the sigmoid function on the x-axis (hourly mean wind speed) ranged from 1 to 10; $\beta = j$ where $j = 1, 2, \ldots, 10$. We compared the effects of these non-random abscission functions by comparing the distances of the 99th percentiles of the resulting dispersal kernels K_y.

We then examined the effect of potentially increased pre-dispersal risk costs on the effects of different shapes of the abscission function on yearly LDD, by adding a general disturbance event that eliminates all seeds that are attached on the plant. For a simple and quantifiable scenario, we used a rain event as a proxy for a general disturbance. In some wind-dispersed species (such as *Sonchus* and *Cirsium* species), rain events indeed destroy the disc-shaped configuration of the pappi, whereas other species have adaptations to avoid such damage (e.g. *Taraxacum* and *Tragopogon* species), by closing their pappi or infructurescences at increasing air humidity, re-opening them again after the rain event. For simplicity, we assumed elimination of all exposed seeds across all species (seeds neither disperse nor germinate and are considered lost). We included the fraction of seed loss in the calculation of each yearly 99th percentile dispersal distance.

We then tested the robustness of the above results to variation in meteorological conditions by repeating the simulations for the meteorological time series sampled over the 32 different years.

Finally, we explored how far the effect of abscission and the optimal shape of the sigmoid abscission function for LDD vary between species. To achieve this, we quantified the dependence of the midpoint parameter β and resulting dispersal kernels on species characteristics, by running the model for 100 combinations of seed release height ($H = 0.2, 0.4, \ldots, 2.0$) and terminal velocity of the seed ($v_t = 0.2, 0.4, \ldots, 2.0$). We kept α constant at the highest value ($\alpha = 4$) as this was the optimal parameter setting resulting from all previous simulations.

Aim 2. Potential risks

To determine how different pre-dispersal mortality risks shape the abscission strategies and dispersal kernels, we explored the effects of five disturbance scenarios: 1) rain as a disturbance (described above), 2) no disturbance, 3) constant probability of disturbance for each time step set at a probability of 0.05, 4) constant probability of 0.22, and 5) constant probability of 0.33. The frequency of rain events was 0.22 in the KNMI data, however, in contrast to disturbance scenario 3, 4 and 5, rain is typically auto-correlated over time. Comparison of scenario 1 and 4 thus facilitates the comparison between an auto-correlated and a constant risk over time, with equal magnitude, while scenario 3 and 5 represent lowered and increased risks. We ran scenario 1 for all seven study species (Table 1) and the other scenarios for *Hieracium aurantiacum* and *Leontodon hispidus*, since the differences between species were qualitatively similar (Fig. 2).

Aim 3. Timing mechanisms across different timescales

To evaluate how plant physiological processes acting at different timescales may determine abscission timing and LDD, we modelled the effects of abscission timing across timescales (second – hour – day – season – year).

Second. Abscission timing is dependent on the turbulent fluctuations, happening at (milli)second timescale, around hourly mean wind speeds, which together determine the instantaneous wind speed that may break the seed-plant connection. In CELC, acceleration is generated by a deterministic drift term that varies with the flow statistics and randomly from a normal distribution with a standard deviation that is correlated with mean wind speed at a given hour. By setting a wind speed threshold of three standard deviations above the mean wind speed we examined the effect of dispersal only during turbulent gusts. We performed this exercise for hourly wind speeds of 2, 4, 6 and 8 m s^{-1} and compared dispersal kernels from abscission during gusts with dispersal kernels from normal random seed abscission. Note that in this case, only the mechanistic dispersal model CELC is used (Supplementary material Appendix 1 Fig. A1).

Hour. We examined the effects of non-random abscission at hourly timescales on dispersal kernels by optimizing the non-random abscission function (Eq. 4) as discussed in the sections above (Simulations 1. Non-random abscission).

Day. Non-random seed ripening and exposure may be traits that influence dispersal on daily timescales, either by selecting beneficial dispersal conditions or lower probabilities of disturbance. In the model we experimented with variable seed production based on VPD. A high VDP represents dry

conditions which may decrease the probability of a rain disturbance. We tested two strategies: 1) seeds are only exposed when VPD exceeds 1500 Pa and 2) seeds are only exposed when VPD crosses a threshold of 1000 Pa.

Season. Phenology determines in which season(s) plants disperse. Here, we assessed whether seasonality in meteorology has an effect on optimal seed abscission functions and dispersal distances by running the model for three-month periods (seasons) instead of a full year and thereby changed the meteorological input data of the model. For this, we divided the year into four seasons; winter (Dec, Jan and Feb), spring (Mar, Apr and May), summer (Jun, Jul and Aug) and autumn (Sep, Oct and Nov).

Year. To test how inter-annual variability in meteorological time series affects optimal seed abscission functions, and thereby may determine if non-random abscission strategies are evolutionarily stable, we ran the model for 32 years separately (1962–1993) and compared the optima across the years.

Field study

We examined abscission under field conditions for seven wind-dispersed plant species native to northwestern Europe: *Cirsium arvense, Hieracium aurantiacum, Leontodon hispidus, Sonchus asper, Taraxacum officinale* and *Tussilago farfara* (Asteraceae) and *Alopecurus pratensis* (Poaceae) (Table 1). The seeds of the Asteraceae species all have plume-like structures (pappi), to reduce the terminal velocity of the seeds. The Poaceae species has seeds surrounded by glumes with long, feathery hairs that also reduce terminal velocity of the seed. We aimed to collect around 30 individuals from each species pre-flowering from at least five different fields in the surroundings of Utrecht, the Netherlands. However, as some species were not abundant and difficult to recognize in pre-flowering stage, some species were collected from fewer fields or from wild plant breeders. We potted the plants in the botanical gardens at Utrecht University. The pots were placed outdoors in a part of the botanical garden exposed to natural meteorological conditions, except for that they were watered during periods of little rainfall.

During an entire growing season, we examined the timing of budding, flowering, seed exposure and seed abscission. Each day between 9:00 am and 16:00 pm (GMT+1), the percentage of seeds on each produced infructurescence was scored visually every hour. By dividing the decline of seeds per hourly interval by the total number of seeds at the beginning of the hour, we determined the probability of abscission per observed hour. These data were merged with hourly meteorological records from the KNMI station at De Bilt, which is located at ~1 km from the experimental setup. The meteorological station as well as our setup in the botanical gardens was located in a field with no major wind obstructions in the near surroundings (< 50 m distance). However, some bushes and an open greenhouse were located within 20 m from our setup, which may have caused local deviations from the measured wind conditions at KNMI. We used hourly mean wind speed as predictor variable. During the field study, hourly mean wind speed was recorded at 20 m altitude (note that the input data for the model was recorded at 10 m; the altitude of the wind sensor changed to 20 m after 1993). Although abscission is an instantaneous process dependent on wind-induced drag that fluctuates at very fine timescales (ms to s), hourly mean wind speed was significantly correlated to the maximum wind gust per hour ($R = 0.94$, $p < 0.005$, Supplementary material Appendix 1 Fig. A3) and we used this as an approximation.

We estimated the shape of the abscission function for each plant species by non-linear least squares fitting procedures with a sigmoid function through the data. With four non-fixed parameters, this function retained the flexibility to select a linear or exponential shape (besides a sigmoid). In addition, we applied generalized linear models to quantify the effect of wind, VPD and timing mechanisms at longer (than hourly) timescales; for example a decreasing seed release threshold (time since opening) and non-random seed release depending on time of day. We used a logit-link function because of the binomial structure of the abscission probability data. All analyses were performed in Matlab R2014b.

Data deposition

Data available from the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.14g26j8> (Treep et al. 2018).

Results

Model results

Aim 1. Non-random abscission

Our model runs confirmed that non-random abscission with bias towards high wind speeds increases LDD. In the absence of any risk, the optimal (simulated) non-random abscission strategies resulted in a major increase in LDD across the entire tail of the dispersal kernel in comparison to random abscission (Fig. 1a–b). At the 99th percentile dispersal distance (1 percent of the seeds exceed this distance), this increase was by a factor 20–40 for the two presented species. However, because some seeds were not released at the end of the simulation period (as the high wind speed threshold was not exceeded after the production of these seeds) this came with the cost of seed loss. When considering the simple case of risk of seed loss by rain events only, model calculations showed that non-random abscission increases LDD as expressed by 99th percentile distances only by a factor of 1.13–1.49 (range across all seven species; Fig. 2a–g). This increase extends across the entire tail of the dispersal kernel (Fig. 1c–d), although, in line with the 99th percentile, the increase was much smaller than for the scenarios without any disturbance (Fig. 1a–b).

In all species and all scenarios, the longest dispersal distances were reached at abscission strategies with a steep sigmoid function (slope parameter $\alpha = 4$), which more closely resembles a 'hard-threshold' function than a sigmoid

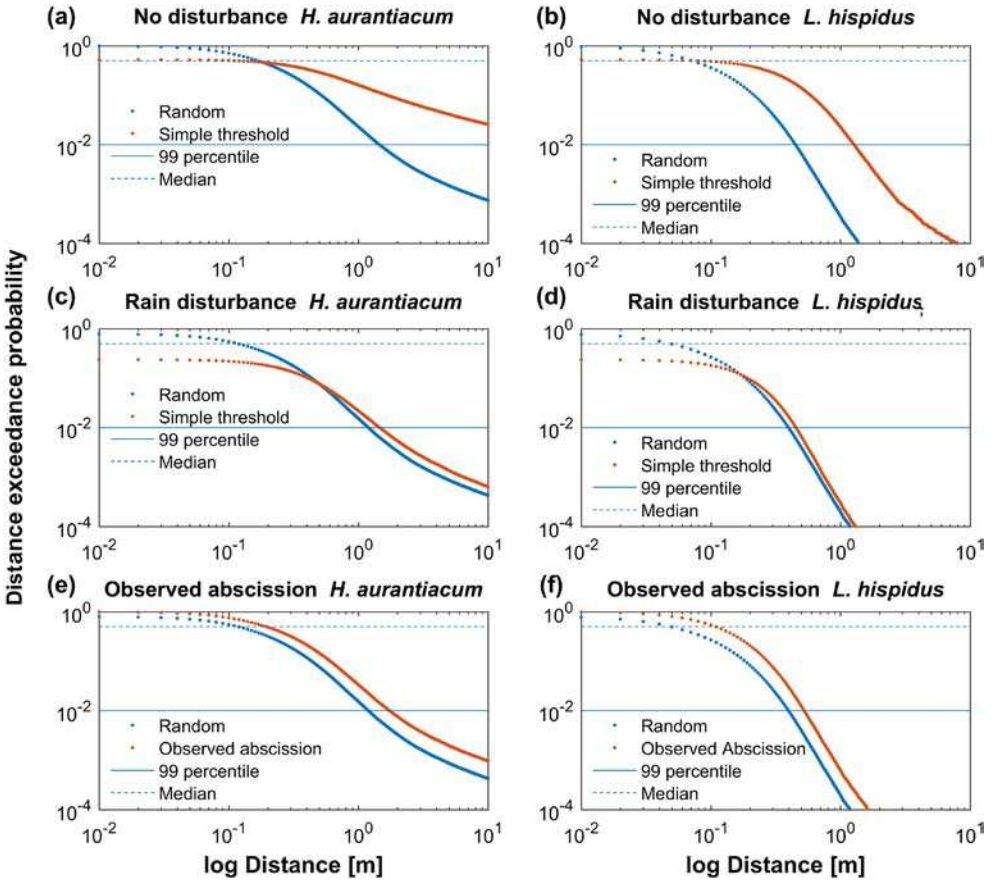


Figure 1. Consequences of abscission strategies for plant dispersal kernels, for *H. aurantiacum* (left panels) and *L. hispidus* (right panels). Top row: dispersal kernels (distance exceedance probabilities) for random seed abscission and for the optimal non-random abscission strategy with no risk included. Middle row: dispersal kernels for random seed abscission and for the optimal non-random abscission strategy with a realistic rain-disturbance scenario. Bottom row: dispersal kernels for random seed abscission and for the abscission function fitted to the field data.

(Fig. 2, 3). The location of this threshold (midpoint parameter β) is very similar across species, but differs between disturbance scenarios. In the rain disturbance scenario, the longest dispersal distances were reached at a threshold wind speed of 5–6 m s^{-1} (midpoint parameter β = 5–6). Higher thresholds resulted in less LDD as simply more seeds were lost to rain disturbances (Fig. 2h).

Despite the similarities in abscission strategies for maximizing LDD between the species, there also existed several small but consistent differences. In all cases, the slope parameter remained maximal, but the optimal threshold wind speed increased with species' seed terminal velocity and seed release height (Supplementary material Appendix 1 Fig. A4a). Parameter β ranged from 5 to 6 m s^{-1} within our study species, to potentially $>$ 7 m s^{-1} in species with high seed release height and relatively heavy seeds. Heavier seeds are more dependent on high wind speeds to achieve LDD. The optimal threshold also increased with species' seed release height (Supplementary material Appendix 1 Fig. A4a), as wind speeds increase logarithmically with height above the ground surface (at least for near-neutral conditions) and taller species benefit more from the higher wind speeds. However, according to our model calculations, plant species with very low seed terminal velocity (0.2 m s^{-1}) benefitted the most from non-random abscission (Supplementary material Appendix 1 Fig. A4b), as their seeds have the greatest probabilities of being uplifted and transported over long distances under high mean wind speed, high turbulence conditions.

Aim 2. Potential risks

The effect of potential risks on non-random abscission strategies and dispersal kernels was large. When no disturbances resulting in seed loss are considered, the optimal abscission function for LDD resembled a threshold function (very steep slope, α = 4) but the threshold wind speed was very high, at 12 m s^{-1} (Fig. 3a–b). The resulting dispersal kernels of *Hieracium aurantiacum* and *Leontodon hispidus* had fatter tails and an increased 99th percentile dispersal distance by a factor 40 and 20 respectively, compared to reference kernels for random abscission (Fig. 1a–b). Interestingly, given the meteorological time series used, the threshold did not increase beyond 12 m s^{-1}; even without any risk costs there appeared to be a limit to the value of this threshold, determined by the local wind speed frequency distribution.

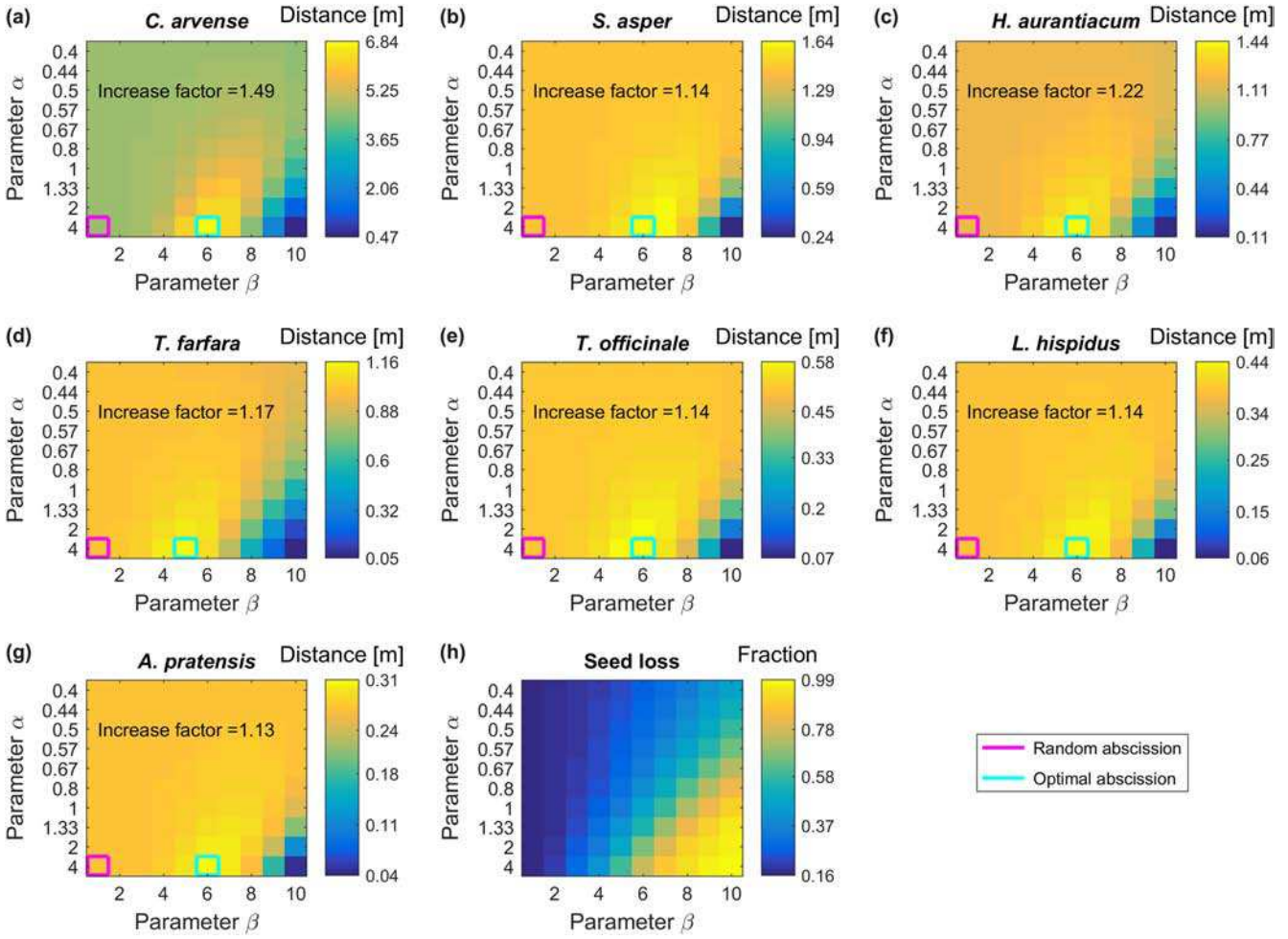


Figure 2. (a–g) Plant species' 99th percentile dispersal distances as a function of the slope (α) and midpoint (β) parameters of the abscission function (Eq. 4). Presented dispersal distances are 32-year means. The lower-left cell in each panel represents the dispersal distance for random abscission (α = 4 and β = 1). (h) Seed loss as a function of the slope and midpoint parameter of the abscission function.

In contrast, addition of a potential risk in the form of a disturbance resulting in seed loss yielded much lower wind speed threshold values. Inclusion of a realistic disturbance in the form of actual rain events resulted in parameters as discussed above (Fig. 2a–g), with threshold values of 5–6 m s^{-1}. When comparing the latter scenario to scenarios with disturbances that are not auto-correlated over time, it became clear that a probability of disturbance of 0.05 yielded very similar results (Fig. 3d–e): although the probability of actual rain disturbance is 0.22, the auto-correlation and regularity of actual rain events resulted in an impact of a similar magnitude to random disturbance with a probability of 0.05. Increasing levels of random disturbances to 0.22 (the equivalent of rain but now random) and 0.33 resulted in much reduced threshold wind speeds, around 2 m s^{-1} (Fig. 3g–h, j–k). Under such conditions, hardly any benefit can be obtained from non-random seed abscission in terms of increasing the 99th percentile dispersal distance.

Aim 3. Timing mechanisms across different timescales

The model results presented above clearly show the importance of mean horizontal wind speeds and short, hourly timescales in determining abscission and its consequences for LDD. Across species, the abscission threshold of individual seeds above wind speeds of ca 5–6 m s^{-1} resulted in most LDD.

At shorter timescales, abscission during turbulent gusts increased median dispersal distances but hardly affected the tail of the dispersal kernels (Supplementary material Appendix 1 Fig. A5). A plausible explanation is that if the conditions achieve sufficient seed uplifting and subsequent LDD, the influence of the instantaneous turbulent gust at takeoff becomes less relevant for long distance dispersing seeds. The tail of the kernel appeared mainly sensitive to the 'background' mean wind speed, i.e. the hourly means used in the remaining model studies.

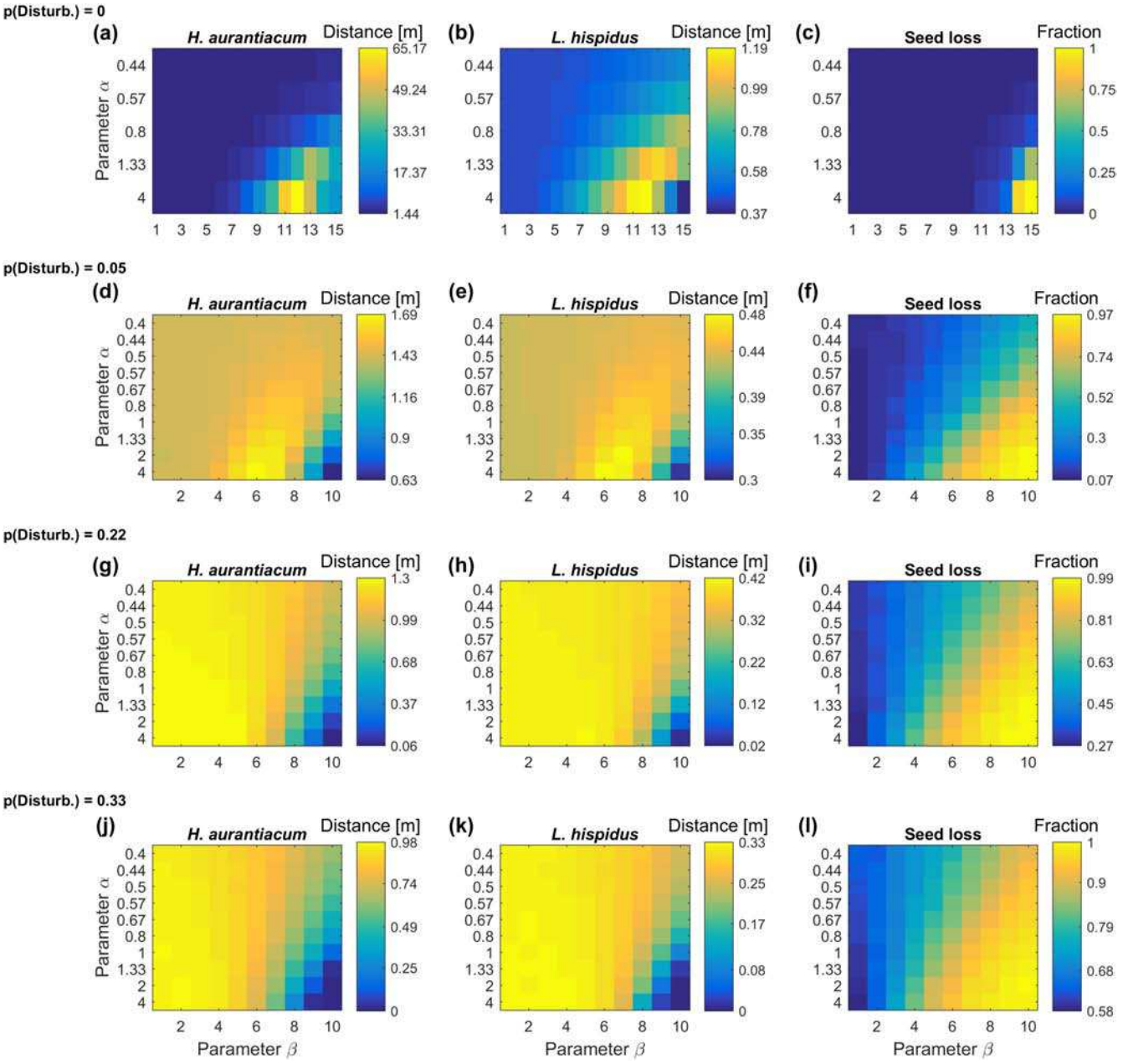


Figure 3. Plant species' 99th percentile dispersal distances and seed mortality as a function of the slope (α) and midpoint (β) parameters of the abscission function (Eq. 4), for different potential risk scenarios: No disturbance (a–c), random disturbance with probability 0.05 (d–f), random disturbance with probability 0.22 (probability equal to rain disturbance in Fig. 2, but without temporal auto-correlation; panels g–i) and random disturbance with probability 0.33 (j–l). Each disturbance event is assumed to result in loss of the exposed seeds. Presented dispersal distances are 32-year means. The lower-left cell in each panel represents the dispersal distance for random abscission ($\alpha = 4$ and $\beta = 1$).

On diurnal timescales, we found no evidence supporting an effect of abscission in relation to VPD on LDD (Supplementary material Appendix 1 Fig. A6), most likely because high wind speeds occur less often during high VPD conditions in the meteorological dataset considered.

At longer timescales, there existed significant differences between seasons. During winter and, particularly, spring the release threshold (optimal midpoint parameter β, given that α was maximal) of the non-random abscission function was significantly higher than during summer and autumn, suggesting that during winter and spring in the Netherlands non-random abscission may result in more LDD than during summer and autumn (Fig. 4). At even longer timescales, across the years, the variation in optimal abscission strategies for LDD was no larger than the seasonal variation (Fig. 4, Supplementary material Appendix 1 A7), suggesting that

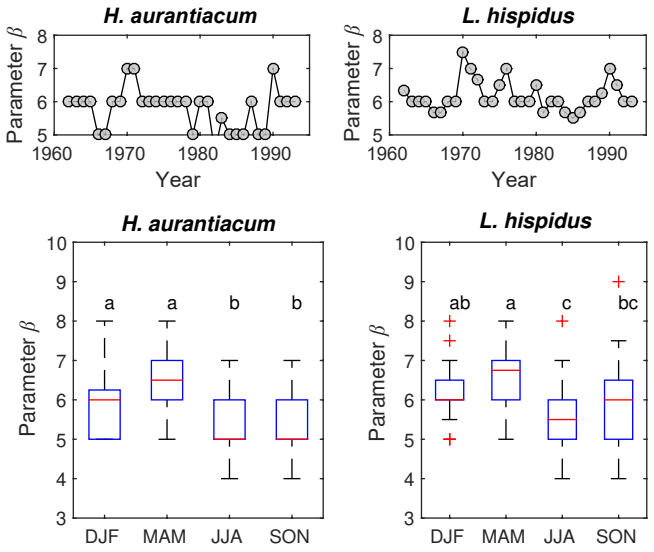


Figure 4. Variation in optimal midpoint parameter (β) values for LDD over a period of 32 years (upper panels) and across the four seasons (lower panels) for *H. aurantiacum* and *L. hispidus*. Differences between seasons were evaluated with a Kruskal–Wallis test for *H. aurantiacum* (χ^2 (3, n = 128) = 29.66, $p < 0.005$) and *L. hispidus* (χ^2 (3, n = 128) = 22.02, $p < 0.005$) and a post hoc Bonferroni test for pairwise differences (marked with a, b and c in the lower panels).

climatic stability was sufficient for non-random abscission strategies to evolve and be effective over multiple generations.

Field study results

In the Asteraceae species, seeds typically dispersed within a few days of first exposure to wind (Table 2). In *Soncus asper* 95% of the seeds of an infructurescence dispersed within 1.55 hours. In *Cirsium arvense* and *H. aurantiacum* this happened within 24 h, and in *Tussilago farfara*, *Taraxacum officinale* and *L. hispidus* in around 2 days. In *Alopecurus pratensis* (Poaceae) it generally took much longer (> 10 days) before seeds dispersed and none of the infructurescences released all seeds.

Table 2. Species overview of mean seed exposure time until 95% of the seeds was released. For this analysis only infructurescenses were used that released at least 95% of their seeds. No statistics could be calculated for *A. pratensis* since none of the infructurescences of this species released 95% of their seeds.

	Mean exposure time (h)	Standard deviation	Number of infructurescences
Cirsium arvense	15.21	39.00	14
Sonchus asper	1.55	0.79	168
Hieracium aurantiacum	17.26	26.55	113
Tussilago farfara	36.17	33.83	6
Taraxacum officinale	49.40	81.55	5
Leontodon hispidus	48.04	45.37	88
Alopecurus pratensis	>10 days		

The field data showed a very clear bias of abscission towards high winds in all species except *T. farfara* (Fig. 5). A sigmoid abscission function provided a good fit to the abscission measurements in *A. pratensis*, *H. aurantiacum*, *S. asper* and *T. officinale*. In *C. arvense* and *L. hispidus* the shape of the abscission function only shows an exponential increase without the characteristic levelling off of a sigmoid function. In contrast to the theoretical abscission functions, the measured functions have a maximum abscission probability lower than 1. In reality the seeds within an infructurescence span a range of ripeness stages with many seeds not fully ripe or being sheltered behind neighbouring seeds at the moment of our observations. We calculated the potential consequences of the observed abscission functions in our model to show how the observed non-random abscission increases the tail of the dispersal kernel (Fig. 1e–f).

As a result of the non-random abscission, the frequency distributions of wind speeds sampled by dispersing seeds were shifted to the right compared to the background wind speed distribution in *C. arvense, H. aurantiacum, L. hispidus and S. asper* (Fig. 5). In these species, the positive bias of seed abscission started at wind speeds of 5–6 m s^{-1}, except for *T. officinale* where it was lower (4 m s^{-1}) and *A. pratensis* where it was higher (7 m s^{-1}; Fig. 5). These wind speeds are similar to the optimal model threshold, although the model predicted a sharp threshold rather than the gradual relation observed in the field. In *T. farfara*, no clear abscission pattern was found.

Abscission was not only non-random in relation to hourly mean wind speed, but also on longer timescales; more seeds dispersed during midday ((12–)13–14 o'clock) compared to morning and late afternoon across the Asteraceae species (but not in *A. pratensis*; Fig. A8). In the two species for which most data were available, *H. aurantiacum* and *L. hispidus*, the predictor variables wind speed, time since opening, time of day and VPD all significantly contributed to explaining abscission probability (Supplementary material Appendix 1 Table A1), together explaining 25 and 10%, respectively, of the variation in abscission. These percentages are considerable given the variation induced by the coarse method of visually scoring abscission. These analyses show that on longer timescales, more seeds dispersed when it was warmer.

Discussion

Our model showed that under the climatic conditions for De Bilt, central Netherlands, non-random abscission with a per-seed threshold wind speed of around 5–6 m s^{-1} provides an optimal strategy promoting LDD by wind, with maximal gain in dispersal distances *versus* minimal loss of seeds to natural (rain) disturbances. Strikingly, this threshold was much lower than would be expected when potential risk costs are not considered (the 'no disturbance scenarios', which resulted in threshold wind speeds of around 12 m s^{-1}). Also, the threshold was much higher than would be expected when potential risks would be much higher than purely from rain (or a similar disturbance of equal size, like a random

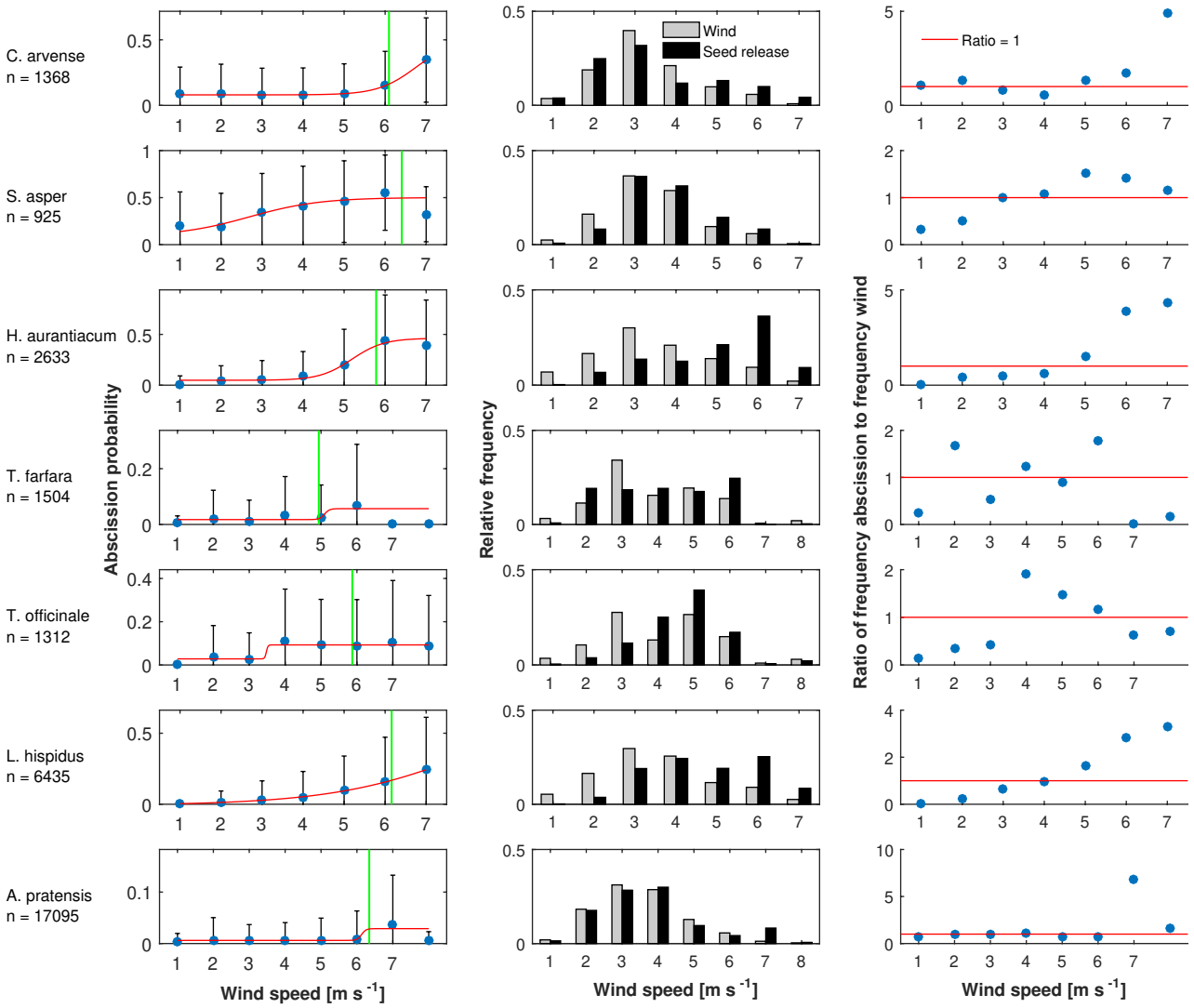


Figure 5. Left column: mean abscission probabilities (blue dots, ± SD), measured hourly throughout an entire growing season, as a function of hourly mean wind speed measured at 20 m altitude at KNMI station De Bilt. The red lines are fitted sigmoid functions. The green lines indicate the optimal value of parameter β from the model simulations (scenario with auto-correlated rain disturbance). Middle column: relative frequencies of mean wind speed (grey bars) and seed release (black bars) measured hourly throughout an entire growing season. Right column panels: ratios of the relative frequency of seed abscission to relative frequency of occurrence, per wind speed (blue dots). The red lines represent a ratio of one; ratios higher than one indicate seed abscission biased towards the respective wind speeds. 'n' is the number of observations.

disturbance occurring with a probability of 0.22, which resulted in threshold wind speeds < 3 m s^{-1}). The field study data showed that in reality, for central Netherlands meteorological conditions, non-random abscission occurs in six out of the seven studied wind-dispersed plant species, at wind speeds above ca 5–6 m s^{-1}. The field study also clarified that abscission on a per-infructurescence basis is less like a threshold (and more like a sigmoid) than the simulated abscission on a per-seed basis.

To what extent is non-random abscission able to promote LDD?

Non-random abscission with a per-seed threshold wind speed of 5–6 m s^{-1} enhances LDD, as shown in this study (increase of 99th percentile distance by a factor of 1.13–1.49). Earlier studies already showed that increases in abscission with wind speed or updrafts may increase LDD by a factor of 1.2 (Savage et al. 2014), 1.3–2.6 (Soons and Bullock 2008) or even 2–3 (Maurer et al. 2013, Pazos et al. 2013).

In previous studies, as well as in our field data, a more exponential or sigmoid-shaped abscission function in relation to wind speed was found than the steep threshold-like function in our modelling study (Greene 2005, Skarpaas et al. 2006, Jongejans et al. 2007, Soons and Bullock 2008, Greene and Quesada 2011, Pazos et al. 2013). This is likely caused by natural variation in 'ripeness' of the seeds and/or material fatigue in the tissue connecting seed to plant, resulting in a combined exponential- or sigmoid-shaped function of many different thresholds for the entire infructurescence (the typical

unit of measurement in seed abscission studies; (Pazos et al. 2013, Thompson and Katul 2013). This combined function may serve as a safe bet-hedging strategy to limit the risk of losing all seeds through a major disturbance or a lack of wind. In contrast, maximizing LDD is achieved by a single and constant hard-threshold wind speed for abscission according to the model. This strategy allows the midpoint/threshold wind speed to be higher and closer to the minimum caused by seed loss at even higher wind speeds (Fig. 2).

What is the effect of potentially increased risks on non-random abscission strategies and dispersal kernels?

Non-random abscission reduces the probability of dispersal during low wind speeds and therefore causes seeds to remain attached to the plant longer during low wind speed conditions. This strategy comes at increased risk costs (Bonte et al. 2012). Potential risks include seed predation and damage of the seeds or pappi by rain or other weather extremes (Jongejans et al. 2007, Bonte et al. 2012). Both risks have a stochastic nature, but when the frequency of such events remains constant on evolutionary timescales, plants may evolve non-random abscission strategies that increase LDD while minimizing seed loss. We found clear optima of the slope and the midpoint which are quite stable over a 32-year period. Such stability may indicate that plant species have time to evolve non-random seed abscission mechanisms over multiple generations.

We have assumed that rain destroys all seeds, which may be a crude assumption. For some wind-dispersed species, rain makes the pappi of different seeds stick together, as in *Sonchus asper* among our study species, but other species have mechanisms that cause the pappus to close and wait for reopening until all water has disappeared (Casseau et al. 2015). Our computed optimal wind speed thresholds were highly similar to the measured bias in wind speeds sampled by released seeds in the field study which indicates the presence of a disturbance with similar magnitude. However, we cannot tell whether this was because the assumption of rain events being fatal was realistic, or whether another fatal disturbance, with a lower probability of around 0.05 but uncorrelated over time (i.e. probability of seeds being predated) was limiting the threshold to around 5–6 m s^{-1}. Another option is that pre-dispersal risk costs are much lower than our model results suggest and selection may favour reducing seed loss over maximizing LDD. Furthermore, shorter dispersal distances may even be favoured e.g. in patchy and relatively stable habitats (Cody and Overton 1996).

For all species, the frequency of disturbance has a major impact on optimal seed abscission functions; under increasingly high disturbance regimes plants are better off dispersing seeds as soon as possible.

Which meteorological factors and respective timescales are important for maximizing LDD?

A summary of our findings across timescales is conceptualized in Fig. 6. Abscission is an instantaneous process and occurs when a threshold force is exceeded. Wind gusts play an important role in producing this drag as instantaneous wind speed is composed of mean wind and a turbulent fluctuation around this mean. However, mean wind speed is also a major determinant in shaping the seed trajectories of seeds that travel longer than a few seconds and LDD may therefore be more sensitive to mean wind speed than turbulent gusts at takeoff. On short timescales, for a mechanistic modelling approach, one may need to incorporate dynamic material strength that determines the seed release threshold and may change over time (Borger et al. 2012) due to processes at the cell level (Liljegren et al. 2000) or material fatigue due to drying and or wear-and-tear (Thompson and Katul 2013). Ripening and exposing seeds during periods of low disturbance, for example dry and windy periods, could result in a better exploitation of a non-random abscission strategy. However, we found no evidence of variable seed production

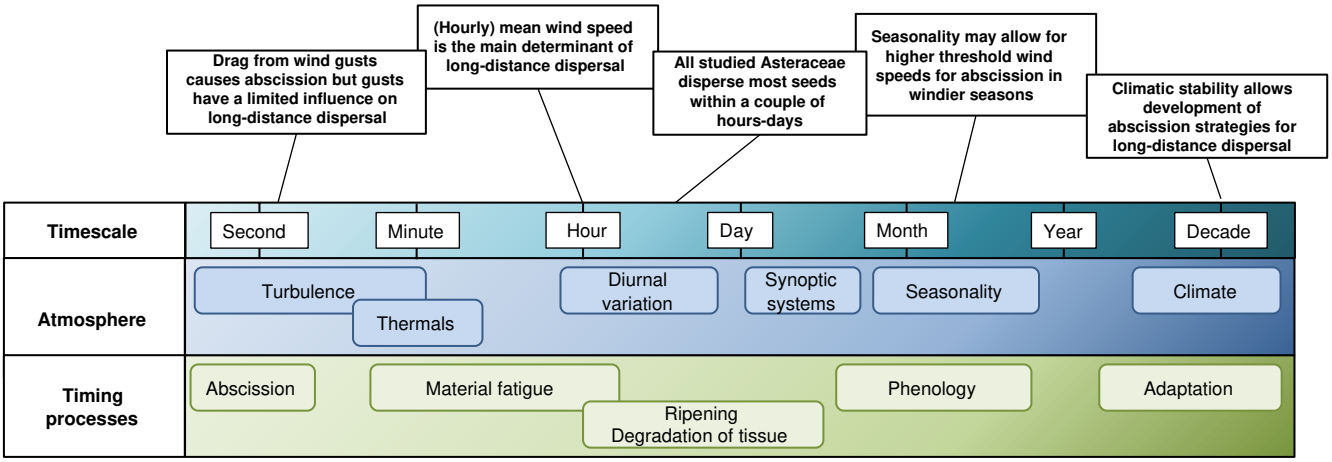


Figure 6. Timescales of the relevant biotic and abiotic factors relevant for the timing of abscission and a summary of the most important results across these timescales.

based on vapour pressure deficit increasing LDD or reducing seed mortality.

On longer timescales, variation over the years was small but variation across the seasons resulted in significant differences in modelled optimal release thresholds, with optimal thresholds being higher in winter and spring. This is caused by more frequent strong winds in winter and spring (Supplementary material Appendix Fig. A9). Interestingly, the only species in our study that produces ripe seeds in spring, *Tussilago farfara*, did not show such a higher release threshold - in fact it was the only species not exhibiting any relation between abscission probability and mean wind speed. However, this species had the fewest infructurescenses (n = 56) of the species in the study, and whether the data on this species are representative of spring-dispersing species we cannot tell.

Conclusions and implications

Based on our results and the existing literature, we conclude that most species aiming to maximize seed dispersal distances by wind have some form of non-random abscission mechanism. Non-random abscission has the potential to increase LDD by wind and may help close the gap between modelled and measured frequencies of LDD events in the tail of the dispersal kernels. However, non-random abscission comes at a cost. Exploring both costs and benefits of non-random abscission over an entire growing season using realistic meteorological data shows that, under realistic risk costs (such as rain), potential positive effects of non-random abscission are much smaller than when such risks are ignored. Inclusion of the costs of non-random abscission will contribute to more realistic estimates of seed dispersal distances and predictions of seed dispersal under global change. Mechanistic dispersal models with non-random abscission functions will improve predictions of range shifts, invasion or colonization processes.

Acknowledgements – *Funding* – This study was supported by an NWO-ALW Vidi grant to MBS. GK acknowledges support from the US National Science Foundation (NSF-EAR-1344703, NSF-AGS-1644382).

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Supplementary material (available online as Appendix oik-04430 at <www.oikosjournal.org/appendix/oik-04430>). Appendix 1.