Seed dispersal by wind: towards a conceptual framework of seed abscission and its contribution to long-distance dispersal

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Summary

1. Diaspore abscission determines many aspects of seed dispersal by wind. While there is yet no complete mechanistic framework for understanding abscission by wind, empirical studies to date have suggested that abscission generally (i) occurs above some threshold wind speed and (ii) depends on the drag force generated by the wind.

2. We revisit these findings and formulate two alternative hypotheses for abscission mechanisms based on a simple model of a forced harmonic oscillator: large diaspore displacement [through a maximum deflection threshold, (MDT)] and material fatigue [through a maximum cumulative stress threshold (MCST)]. We use simulations of abscission events based on these hypotheses and experiments on diaspore abscission of three Patagonian grasses and a cosmopolitan herb to test the performance of two abscission functions differing in whether they have a threshold wind speed for abscission. We also quantify the effects of non-random diaspore abscission on dispersal distances using a well-tested model for seed dispersal by wind.

3. Both the MDT and MCST hypotheses appear realistic and indicate that while the instantaneous wind speed determines abscission, the history of wind speeds experienced prior to the detachment from the plant also plays a role.

4. An evaluation of abscission functions against simulated and experimental abscission data shows that while the presence of a threshold wind speed in theory appears unrealistic, in practice a threshold may appear to exist in high-wind-speed environments where all diaspores are blown off the plant before the abscission layer can develop sufficiently to break during lower wind speeds.

5. Under non-random diaspore abscission, high-wind-speed events during otherwise calm periods increase long-distance dispersal (LDD), thereby decreasing differences in dispersal distances between low- and high-wind-speed environments.

6. *Synthesis.* We formulated two realistic mechanisms of diaspore abscission by applying concepts from materials science: large diaspore displacement and material fatigue. These reveal that the ambient wind speed 'history' experienced by a diaspore plays an important role in the timing of abscission and in the distance travelled, without any thresholds, and that the effect of the diaspore–wind interaction on LDD varies between environments with different wind speed regimes.

Key-words: anemochory, coupled Eulerian–Lagrangian closure (CELC) model, diaspore abscission, dispersal, drag, seed oscillation, seed release, seed vibration, stress–strain relationship, wind dispersal

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Introduction

It has recently become clear that, for wind-dispersed plants, the abscission (or release) of diaspores is not merely the first step in dispersal. Instead, diaspore abscission is a crucial determinant of many aspects of subsequent plant movement (Greene, Quesada & Calogeropoulos 2008; Soons & Bullock 2008; Wright *et al.* 2008; Nathan *et al.* 2011). More specifically, the environmental conditions during the final stage of fruit and seed maturation and release can significantly affect dispersal distances (Kuparinen 2006; Nathan 2006; Soons & Bullock 2008), directionality (Greene, Quesada & Calogeropoulos 2008; Wright *et al.* 2008; Savage *et al.* 2010) and the probability of reaching favourable site conditions for germination (Nathan *et al.* 2000; Cousens, Dytham & Law 2008).

The timing of the abscission of diaspores (that either contain, or are equivalent to, seeds) is in the first instance controlled by phenology, which is in turn influenced by degree day sums and day length (Cleland *et al.* 2007). For wind-dispersed plant species, once the phenological stage permitting seed release has been reached, the timing of abscission on a diurnal basis will be governed by a number of short-term exogenous and endogenous factors. Almost invariably among angiosperm species, daytime (or prolonged) low relative humidity speeds the drying of the vascular bundle that connects the diaspore to the plant and, for some species (e.g. many Bombacaceae or Asclepiadaceae), expansion of the drag-producing fibres (Greene & Johnson 1992; Roberts *et al.* 2000; Greene & Quesada 2005; Greene, Quesada & Calogeropoulos 2008). In some cases (e.g. many Asteraceae), high relative humidity can physically prevent diaspore abscission, even under wind turbulent conditions, by hindering the opening of the involucres (Greene 2005) or promoting the closing of the drag-producing fibres (Skarpaas, Auhl & Shea 2006; Jongejans *et al.* 2007; Marchetto *et al.* 2012). The increasing brittleness in the vascular bundle sets the stage for abscission. Subsequently, wind gusts produce a fluctuating drag force that fractures the now brittle vascular tissue still connecting the diaspore to the plant (Greene & Quesada 2011) and abscission soon follows. Wind gusts are more frequent and more intense during high-wind-speed conditions, but may also occur under otherwise calm conditions. Gusts are associated with strong turbulent events whose energy spectrum is active across a wide range of frequencies and hence can introduce vibration at a resonant frequency that leads to material fatigue and subsequent failure in the brittle vascular bundle tissue. The effect of such a dynamic load (i.e. a force fluctuating in time such as the drag force exerted by the plant organs on the wind) that leads to fatigue and subsequent failure in brittle material may be derived from stress–strain relationships developed in materials science, which can assist in unravelling the mechanics of diaspore abscission (Marchetto *et al.* 2010).

The main conclusion from many diaspore abscission studies thus far is that high wind speed and turbulence promote abscission in plant species from a wide range of taxa (Greene & Johnson 1992; Greene 2005; Skarpaas, Auhl & Shea 2006;

Jongejans *et al.* 2007; Greene, Quesada & Calogeropoulos 2008; Soons & Bullock 2008; Wright *et al.* 2008). Further, low relative humidity and high air temperatures will tend to be correlated diurnally with higher horizontal wind speed and mechanical turbulence and thus favour long-distance dispersal (LDD) (Soons, Nathan & Katul 2004; Soons *et al.* 2004; Greene, Quesada & Calogeropoulos 2008; Savage *et al.* 2012). These covarying environmental conditions promoting abscission suggest that non-random diaspore release (related to weather variables) may be important for LDD (Soons & Bullock 2008; Wright *et al.* 2008; Greene & Quesada 2011; Nathan *et al.* 2011; Savage *et al.* 2012). However, a mechanistic, conceptual framework for the abscission process for wind-dispersed diaspores remains lacking. There is not even a consensual methodology for either quantifying the dependence of the probability of abscission on factors such as wind speed and relative humidity or the incorporation of an abscission function into seed dispersal models.

Almost all models of seed dispersal by wind have, for mathematical convenience or lack of information, implicitly argued that abscission was random with respect to wind speed (Greene & Johnson 1989; Okubo & Levin 1989; Tackenberg 2003; Soons *et al.* 2004; Katul *et al.* 2005). This represents an important drawback in the estimation of dispersal distances, especially LDD (Schippers & Jongejans 2005; Soons & Bullock 2008; Skarpaas, Shea & Jongejans 2011). The few studies incorporating an abscission function into a dispersal model have used a direct relationship between climatic variables (wind speed, humidity) and abscission. For instance, Nathan, Safriel & Noy-Meir (2001), Wright *et al.* (2008) and Savage *et al.* (2012) incorporated the timing of seed release in relation to climatic variables on diurnal and seasonal basis into their dispersal models to account for the effect of seed release on dispersal distances. By contrast, Greene & Johnson (1996) and Soons & Bullock (2008) developed functions where the abscission probability depended solely on drag (and thus on the square of the wind speed) at time-scales of a few seconds.

Alternatively, some studies assumed that seed release was achieved only when a pre-defined threshold wind speed was surpassed. The probability of abscission was treated as a binary function shifting from zero to unity across this threshold (Schippers & Jongejans 2005; Stephenson *et al.* 2007; Bohrer *et al.* 2008; Soons & Bullock 2008); beyond the threshold, abscission was unrelated to wind speed. According to this model, no abscission can occur if the threshold is not attained. These two approaches – threshold wind speed and drag as motive force – have a mechanistic basis and have shown promising results in empirically explaining some diaspore abscission patterns of different species (Greene 2005; Greene, Quesada & Calogeropoulos 2008; Soons & Bullock 2008; Greene & Quesada 2011). Discerning between these two approaches can be difficult because, ignoring wind tunnel studies such as those of Skarpaas, Auhl & Shea (2006), Jongejans *et al.* (2007) and Soons & Bullock (2008), there have been few outdoor studies using a time-scale congruent with the characteristic time of the diaspore abscission process

(one to several seconds). For example, Greene (2005) argued that the 24-h time-scale of abscission observations used by Tackenberg, Poschlod & Kahmen (2003) was misleading as it completely obscured the inverse diurnal relation between wind speed and relative humidity and thus could not detect the strong role of wind speed in abscission. Likewise, Stephenson *et al.* (2007) argued that the lack of fit of their dispersal models, either incorporating a wind threshold or not, to both natural and experimental dispersal data would be a consequence of wind data collected at too low temporal resolution.

Meanwhile, the notion that drag is the only motive force for diaspore abscission begs the question of precisely how the effect of this force is exerted. Previous studies on the anatomy of the abscission zones of several species have demonstrated biochemical changes that result in the disintegration of the middle lamella and the cell wall of specialized cells (Elgersma, Leeuwangh & Wilms 1988). In addition, mechanical stress enhances tissue fracture that leads to the development and propagation of cracks in the abscission zone (Elgersma, Leeuwangh & Wilms 1988; Roberts *et al.* 2000; Thurber, Hepler & Caicedo 2011). Thus, while spontaneous abscission in the absence of any wind (i.e. by gravity alone) is likely to be possible, mechanical forcing provided by wind drag would lead to faster crack propagation and abscission. This suggests that drag plays a central role in the abscission process because perfect sheltering from wind is highly improbable in nature (unless for plants located in very closed canopies or subjected to low-wind-speed regimes with high frequency of extended calms). However, this also casts some doubts on the concept of a wind threshold as a biophysical mechanism for diaspore abscission. Specifically, the determination of wind thresholds may be only a consequence of the experienced wind speed regime, as plants subjected to high speeds would not realistically ever release their diaspores at low, or even zero, wind speeds.

On this basis, mechanistic approaches to diaspore abscission should incorporate the possibility for a nonzero probability of abscission at either zero or low wind speeds. As detailed in the subsequent modelling section, we propose two possibilities for the effect of drag on abscission. First, there may be a threshold for the maximum deflection angle as the wind pushes the diaspore to an acute angle from the vascular bundle. A crack develops and causes abscission in the brittle tissue *immediately* as the deflection exceeds the maximum angle [in a related way, this idea of an all-at-once event may be a useful concept for a taxon such as *Papaver* where the already-abscised seeds need to be released through perforations within the upper part of the dried, hollow fruit; once a threshold angle is reached, the seed is ejected from the fruit (Blattner & Kadereit 1991; Vogel 1994)]. Alternatively, there may be an accumulated stress build-up analogous to 'wear-and-tear' in material fatigue failure (Greene & Johnson 1992). Here, the separation layer in the bundle develops a crack due to the stress exerted by drag. This crack is subsequently propagated and ultimately the cumulative stress leads to abscission (In a sense, the model of Schippers & Jongejans (2005),

where the abscission threshold declines with time, is hinting at the concept of cumulative stress leading to abscission.) Either of these two models represents novel mechanistic approaches to diaspore abscission incorporating the dynamic nature of the drag force originating from the turbulent component of the wind.

Our study has three objectives. First, we expand the two above-mentioned hypotheses into two alternative (but not mutually exclusive) mechanistic models for non-random diaspore abscission. Secondly, we clarify the mechanisms underlying diaspore abscission in relation to fluctuations in ambient wind speed and wind speed history. This clarification is achieved by fitting abscission functions, including and excluding the possibility of the existence of wind thresholds, to both field data with short averaging times and simulated data based on the mechanistic hypotheses for non-random abscission. Finally, we use a wind dispersal model to evaluate the effects of different diaspore abscission functions on seed dispersal distances.

MECHANISTIC MODELS OF DIASPORE ABSCISSION

Given our first objective, we propose two alternative mechanistic models for the effect of wind drag on abscission. We begin by drawing an analogy between the diaspore connected to a vascular bundle subjected to a fluctuating wind and a harmonic oscillator subjected to a random but autocorrelated force f_x. The angular displacement (θ) of the centroid of the diaspore is given by the mass-spring-damper equation [modified from eqn 3 in de Langre (2008)]:

$$\frac{\mathrm{d}^2\theta}{\mathrm{d}t^2} + 2\zeta\omega_n\frac{\mathrm{d}\theta}{\mathrm{d}t} + \omega_n^2\theta = \omega_n^2 f_x(t) \qquad \text{eqn 1}$$

where ζ is a non-dimensional damping coefficient, ω_n is the natural (resonant) frequency of the diaspore and f_x is proportional to the product in the drag force $C_n u^2_A$, with C_n the dimensionless drag coefficient and u_A the ambient wind speed.

Our first mechanistic model, as introduced in the previous section, posits a critical threshold for the deflection angle (θ_c), any deflection being a proxy for the induced stress within the drying vascular bundle. Consideration of eqn (1) shows that in this *maximum deflection threshold* (MDT) model, there is no direct relation between deflection angle and wind speed because of the effect of damping and inertia. Naturally, when $\mathrm{d}^2\theta/\mathrm{d}t^2 = 0$ (no acceleration) and when $\zeta = 0$ (no damping), the deflection becomes proportional to the dimensionless drag force. This means that for a theoretical abscission threshold, in which exceedance of a particular critical wind speed invariably leads to immediate diaspore abscission (Schippers & Jongejans 2005), the unrealistic situation of no inertia and no friction in the system must be assumed. In contrast, the implication of this model is that when all three terms on the left side of eqn (1) are significant, the critical threshold angle can be attained at different instantaneous wind speeds, depending on the recent 'wind history' experienced by the diaspore.

In the second mechanical model, as introduced in the previous section, a cumulative stress in the abscission zone eventually leads to failure. Although the abscission layer might start to develop early during flowering, the stresses experienced by this layer during seed development would be the most significant for diaspore abscission as this period coincides with cell wall thickening and sclerification of the abscission layer, and with the gradual drying of the vascular bundle (Elgersma, Leeuwangh & Wilms 1988; Thurber, Hepler & Caicedo 2011). More specifically, standing as proxy for the internal energy build-up, the cumulative stress (τ) is proportional to the integral:

$$\int_0^t \left(\frac{d\theta}{dt}\right)^2 dt \qquad \text{eqn 2}$$

Abscission occurs when the diaspore has exceeded a critical cumulative threshold, θ_c^2. Notably, this *maximum cumulative stress threshold* model (MCST) mainly accounts for the stresses originated from dynamic loadings of diaspores by wind (e.g. wind gusts, small scale shear turbulence around the infructescence) (Marchetto *et al.* 2010), thus permitting the cumulative effects of a large number of small speeds (and thus small stresses) to play at times an important role in abscission by slowly lengthening an incipient crack.

Summarizing, both the MDT and MCST models, derived from materials science, allow low wind speeds to potentially play a role in diaspore release, although abscission may actually seldom occur at low wind speeds. Indeed, both models permit the history of stresses (via the history of wind speeds) on a diaspore to play a role in explaining the instantaneous or average speed at which it abscised. A detailed description of the MDT and MCST models, as well as their implementation, is provided in Appendix S1 in the Supporting Information.

EMPIRICAL FUNCTIONS OF DIASPORE ABSCISSION

To assess the performance of the two proposed mechanistic models (described above) in reproducing observed patterns of diaspore abscission, two simple functions were fitted to field and simulated abscission data using both (MDT and MCST) mechanistic models. First, we followed Greene & Johnson (1992) and subsequent empirical studies in viewing diaspore abscission solely as a function of drag and endogenous properties. Since drag is proportional to the square of the ambient wind speed (u_A), the abscission probability, p, is given as:

$$p \propto u_A^2 \qquad \text{eqn 3}$$

We term this simple function relating abscission to wind speed the *no threshold* (NT) model.

Our second function is one where, as with previous authors, there is a *simple minimum threshold* (SMT) for the wind speed (u_t), but now, for the first time in the abscission literature, this approach also includes the effect of the magnitude of the wind:

$$\text{either } p = 0 \quad \text{if } u_A \leq u_t$$
$$\text{or } p \propto u_A^2 \quad \text{if } u_A > u_t \qquad \text{eqn 4}$$

Notably, while both the NT and SMT models agree that the magnitude of the wind is crucial, the SMT model possesses the property that in low-wind-speed environments such as deep within a plant canopy, abscission might well never occur.

Materials and methods

Above, we formulated two alternative, mechanistic hypotheses for non-random diaspore abscission (MDT and MCST). Using this abscission framework, we proposed two functions of the effect of wind speed on diaspore abscission (NT and SMT) to fit abscission data. To clarify the mechanisms underlying diaspore abscission in relation to ambient wind speed and wind speed history, we compared the two diaspore abscission functions (NT and SMT) against both field abscission data with short averaging times and simulated abscission data based on the mechanistic hypotheses. Finally, we used a wind dispersal model to evaluate the effects of different diaspore abscission functions on seed dispersal distances.

DATA COLLECTION: STUDY SPECIES

We experimentally quantified diaspore abscission in relation to instantaneous wind speed for four wind-dispersed species. Three of these species were perennial grasses native of the arid Patagonian Monte shrublands, Argentina (42–44° S, 64–68° W): *Poa ligularis* Nees ex Steud., *Nassella tenuis* (Phil.) Bark. and *Pappostipa speciosa* (Trin. & Rupr.) Romasch. (hereafter *Poa*, *Nassella* and *Pappostipa*, respectively). These dominant species in the herbaceous layer (Pazos, Bisigato & Bertiller 2007) differ in diaspore size and morphology and inflorescence morphology (Correa 1978; Pazos & Bertiller 2008) (see also Fig. S1). The length and width of the caryopsis of *Poa* vary between 3.4–5.4 and 0.6–1.2 mm, respectively, and it possesses long sticky hairs at the base. Diaspore weight ranges from 0.40 to 0.58 mg (Table 1). The spikelets, which consist of about 5–10 tightly packed diaspores, are spread along the rachis forming a ~10-cm-long compact spike bearing 80–150 diaspores. The spindle-shaped caryopsis of *Nassella* ranges from 5.4 to 7.6 mm in length and from 0.4 to 0.8 mm in width (Table 1). Diaspores have spikelet stalks [*sensu* Gutterman (1993)] and a hygroscopic 2-geniculate awn 6.5–10.8 mm long. Total diaspore weight (caryopsis + awn) ranges from 1.2 to 3.5 mg. Spikelets are 1-seeded and form sparse panicles about 10–15 cm long bearing 15–40 diaspores. In *Pappostipa,* caryopsis length and width vary between 7.1–16.1 and 0.4–1.4 mm, respectively (Table 1). Diaspores possess a spikelet stalk and a hygroscopic 1-geniculate awn 2.5–7.7 mm long with a plume 5–15 mm in diameter in the column. Diaspore weight ranges from 2.9 to 15.9 mg. Spikelets are 1-seeded and housed in a panicle about 8–10 cm long bearing 10–30 diaspores.

The seed maturation and dispersal period of the three grass species is September to mid-January, the driest seasons of the year (Bertiller, Beeskow & Coronato 1991). The height of the inflorescences of these species is variable and strongly dependent on the livestock grazing pressure. In heavily grazed sites, inflorescences reach < 20 cm height, while in non-grazed, well-conserved sites, inflorescences up to 35–45 cm high can be frequently found (G.E. Pazos, unpublished data). Seed dispersal distances for these three grass species have not previously been reported in the literature, but the spatial patterning of plants and of the soil seed bank suggest that they are short (a few

Table 1. Mean ± SE (CV%) of different diaspore traits of the three grass species. Ranges are provided in the text (see Materials and Methods)

	Poa ligularis	*Nassella tenuis*	*Pappostipa speciosa*
Caryopsis length (mm)	4.49 ± 0.06 (9.6)	6.32 ± 0.08 (8.6)	11.57 ± 0.40 (24.2)
Caryopsis width (mm)	0.93 ± 0.04 (16.2)	0.60 ± 0.01 (14.2)	0.95 ± 0.03 (20.6)
Diaspore weight (mg)	0.480 ± 0.006 (8.8)	2.40 ± 0.07 (20.4)	7.84 ± 0.50 (45.3)
Awn length (mm)	–	8.54 ± 0.21 (13.1)	4.17 ± 0.31 (40.8)

metres) (Pazos & Bertiller 2008). *Nassella* and *Pappostipa* dispersal distances would be limited by plant traits hindering wind dispersal potential (seed terminal velocity exceeds 1.5 m/s and low seed release height) (Tackenberg 2003), while the plants of *Poa*, the species with the higher wind dispersal potential, are mainly located underneath shrub patches where wind speed is strongly reduced (Pazos, Bisigato & Bertiller 2007).

The fourth species was the cosmopolitan herb, *Taraxacum officinale* (hereafter *Taraxacum*). Diaspore abscission of this species was previously studied by Greene (2005), and it was included here to provide an extra data set of abscission at contrasting (low) wind speeds (in comparison with the grasses). This allowed us to evaluate our models for a wider range of species and wind speed conditions. In *Taraxacum*, about a 100 individual flowers (florets) are packed on a radially symmetric disc (capitulum). In turn, the capitulum lies atop a roughly vertical green shoot (scape) 15–35 cm in height, rising from a rosette of leaves near ground level. The scape serves to place the capitulum above the adjacent herbaceous canopy of other species. Individual diaspores (achenes) on the capitulum are each topped with a radially symmetric set of single-celled fibres (collectively, the pappus) that increase the drag during descent (Greene 2005). *Taraxacum* has a very high potential for LDD.

DATA COLLECTION: MEASURING DIASPORE ABSCISSION

Diaspore abscission experiments were performed for the four study species. The set-up for the experiments was selected in each case with the aim of securing a large open space of free wind flow, without interferences by other objects that would massively affect wind flow and make it impossible to generalize the results. Abscission experiments on grass inflorescences were carried out in an open environment (vegetation height about 15 cm) in a vacant lot in the Centro Nacional Patagonico (Puerto Madryn, Argentina) between November and January (austral spring-summer) from 10:00 to 19:00 each day. Wind flow was unobstructed for about 100 m windward from the location of the experiments, and there were no obstructions on the leeward. Complete inflorescences of the three grass species were attached to a horizontal wooden bar at 35 cm height and freely exposed to wind. These conditions approximate those in an open intershrub space of Monte vegetation. Only panicles exhibiting clear clues of seed ripeness were used (*Poa*: clear exposure of the sticky hairs, yellow-coloured spikelets; *Nassella*: light brown-coloured caryopsis, wide glume-pair angles; *Pappostipa*: wide glume-pair angles, exposure of the plume outside the spikelet; in addition, the lack of one or two apical diaspores in the panicles of the three species indicated full ripeness). The number of diaspores released from each inflorescence was observed by eye and recorded at 30-s intervals during 15-min episodes, while the horizontal wind speed was simultaneously recorded at the same height at 1-second intervals using a digital propeller anemometer (TMA40, Amprobe Test Tools, Glottertal, Germany). Wind speed was then averaged over 30-sec intervals to match the abscission time series. Field observations were carried out

until a minimum number of 50 released diaspores for each species were observed over the entire period. Between 10 and 30 inflorescences (8–13 plants) of each species were used in total.

Diaspore abscission data of *Taraxacum* from Greene (2005), who recorded abscission using a Nikon camcorder at a speed of 30 frames per second, were also re-examined. Experiments were performed in Montreal (Quebec) during three different days in May 2004. The *Taraxacum* plants had been transplanted into planter boxes a week earlier and kept in a sheltered spot; these boxes were then placed on trestles 1 m above the ground in a narrow laneway (5 m across; 40 m long) with scapes extending about 10–30 cm above the box edges (this was similar to the height range of capitula above the mown herbaceous vegetation from which the plants had originally been taken: Greene 2005). Diaspore release height ranged from approximately 1.1 to 1.3 m above the ground. These relatively high release heights (compared with natural conditions, where release height rarely exceeds 0.35 m) partly compensated for the low wind speeds experienced in the sheltered laneway. Still, measured wind speeds during the experiments were very low (Fig. 1). Filming occurred for several open capitula freely exposed to the wind. A cup anemometer was placed adjacent to the scapes within the field of view of the camera, and average wind speed was calculated for each 10-second time interval. Four tapes were obtained from these experiments: tape 1 included diaspore abscission from six capitula during 1 h, tapes 2–3 contained diaspore abscission from seven capitula during 2 consecutive hours and tape 4 contained the filming of a single capitulum for 1 h. See Greene (2005) for a more detailed description of the experimental setting up.

For each species, the relative frequency distribution of wind speeds measured by the anemometer (u_A) at each time interval during each experiment was calculated. Likewise, the u_A of the time intervals at which diaspores of the four species released were recorded. This latter subset of u_A represents the wind speeds 'sampled' by the released diaspores (u_S) (Greene 2005). To test for differences between u_A and u_S, both the median and coefficient of variation of u_A and u_S were compared for each species using randomization tests (Manly 1997) and their frequency distributions using the Kolmogorov–Smirnov test (Conover 1999). These analyses were performed in R 2.13.0 (R Development Core Team 2011).

TESTING THE DIFFERENT ABSCISSION FUNCTIONS AGAINST FIELD DATA

To achieve our second objective, the functional relationship between the distribution of u_A and u_S was formulated and tested for a population of released diaspores under different assumptions regarding the mechanism of diaspore release. As u_S is a sample of u_A that depends on the diaspore release mechanism, the relative frequency distributions of u_S and u_A for a given species will be related as follows:

$$f_R(u_S) = f_R(u_A) \times \text{TF}(u_A) \qquad \text{eqn 5}$$

where $f_R(.)$ denotes relative frequency and TF is a species-specific transfer function of wind speed. Transfer functions are used in systems
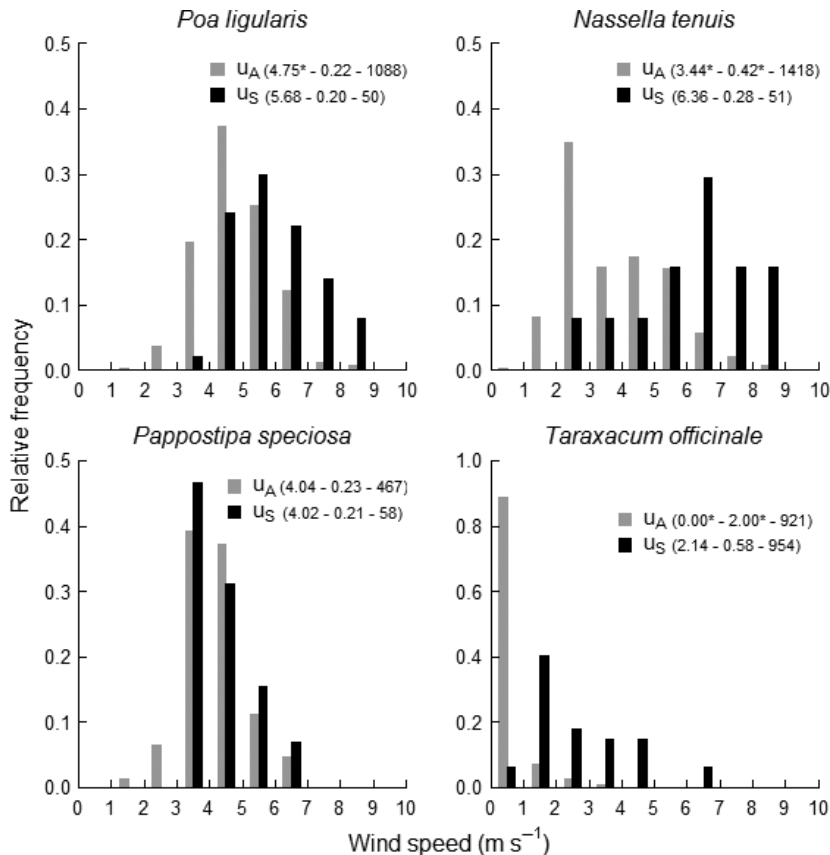
Fig. 1. Relative frequency distribution of the anemometer measured wind speed (u_A) and the wind speeds sampled by the released diaspores (u_S) for the four study species. Numbers in parentheses indicate the median, coefficient of variation and sample size, respectively. Asterisks indicate significant differences ($P < 0.01$) between u_A and u_S for the indicated value. Note the much greater frequency of low wind speeds for *Taraxacum* versus the three grass species.

control theory and stochastic processes when analysing the relationships between probability distribution functions of stationary outputs and inputs of a system (Gardner 1986). Similar methods aimed at obtaining biased wind speed distributions from u_A have been used in previous studies (Greene & Johnson 1996; Skarpaas, Shea & Jongejans 2011). The TF indicates which wind velocities (u_A) are either 'amplified' or 'dissipated' when considering u_S, and its shape reflects important attributes of the diaspore abscission mechanism. Using eqn (5), the TF for the four species was estimated from their corresponding frequency distributions of u_A and u_S. Interval classes of wind speed of 0.5 m s^{-1} and 0.25 m s^{-1} were used for the three grasses and for *Taraxacum*, respectively, to calculate $f_R(.)$. Both the NT and SMT functions (eqns 3 and 4, respectively) were then compared with the experimentally determined TF through linear regression and their relative performance and accuracy evaluated through standard techniques of model selection. Note that random release, typifying almost all published dispersal functions, assumes that the probability of diaspore release is independent of horizontal wind speed. This means that u_S is an unbiased random sample of u_A and the TF will be 1 at any wind speed class (no wind speed is amplified nor dissipated).

(1) No threshold model (NT). This model assumes a power–law relationship between the probability of diaspore release and wind speed. Thus, it would be expected that along the range of wind speeds experienced by the diaspores, the lower speeds are dissipated, while the larger ones are amplified at a positive rate b, as follows:

$$TF = a \times ws^b \qquad \text{eqn 6}$$

where a and b are species-specific parameters and ws represents the midpoints of the wind speed interval classes. The data were log10-transformed (adding 0.01 to avoid zeroes) and the model fitted by standard linear regression:

$$\log(TF + 0.01) = \log(a) + b \times \log(ws) \qquad \text{eqn 7}$$

(2) Simple minimum threshold model (SMT). This mechanism assumes that wind speeds are amplified at a power of b but only once a threshold wind speed, u_t, has been surpassed. We used piecewise regression (Crawley 2007) to fit two different functions over the range of wind speeds, defining u_t as the break parameter. Indeed, we used a plot of the deviance against ws to confirm that the break equalled u_t leads to the best fit (Crawley 2007). In this way, the model results:

$$\begin{aligned} &\text{either } \log(TF+0.01) = \log(0.01) + 0 \times \log(ws) \quad \text{if } ws \le u_t \\ &\text{or } \log(TF+0.01) = \log(a) + b \times \log(ws) \qquad \text{if } ws > u_t \end{aligned} \qquad \text{eqn 8}$$

We only used piecewise regression for those species where the test of the SMT model was justified, that is, where TF = 0 in at least one of the lowest wind speed classes. Models NT and SMT for each species were compared through the coefficient of determination (R^2) and Akaike Information Criterion (AIC). The latter allowed us to assess the improvement in model performance given the addition of a third parameter (u_t) to the function. These analyses were performed in R 2.13.0 (R Development Core Team 2011) following Crawley (2007) and Bolker (2008).

TESTING THE DIFFERENT ABSCISSION FUNCTIONS AGAINST SIMULATED DATA

Model runs with MDT and MCST diaspore abscission mechanisms for different combinations of parameter values were conducted to generate data sets of theoretical diaspore abscission following the two hypotheses for abscission mechanisms (see Appendix S1). Although there are no published damping coefficients for plant parts of the size of diaspores, we set $\zeta = 0.1$ as an order of magnitude estimate based

on previous studies on anther vibration (King & Buchmann 1995, 1996) and woody branches and entire herbaceous plants (de Langre 2008). To explore the effect of the wind speed distribution on diaspore vibration and release, we ran two sets of simulations of MDT and MCST models. For the first set, we used as input the measured anemometer wind speeds (u_A) of *Poa* experiments, while for the second set, we used values from the *Taraxacum* experiment. Both wind data sets strongly differ in median speed and skewness, with *Taraxacum* wind data strongly skewed towards low wind speeds (Fig. 1). For the simulations, we used different combinations of values of the natural vibration frequency (ω_n): 0.01, 0.05 and 0.50, and drag coefficient (C_n): 0.02, 0.20 and 2.0). We took the combination $C_n = 0.02$ and $\omega_n = 0.01$ as the reference case and then changed either of the two parameter values. The drag coefficients span the expected range for diaspore sizes (Greene & Johnson 1990; Vogel 1994). A simulation run was considered acceptable when the number of released diaspores was larger than 60.

For each combination of parameter values and u_A input, u_S was determined at the prescribed failure mode for each released diaspore allowing calculation of the corresponding TF. The NT and SMT functions were then fitted to the computed TF in the same way as with the field data. Again, we only tested the SMT model in those cases where TF = 0 in at least one of the lowest wind speed classes.

EFFECT OF DIASPORE ABSCISSION ON DISPERSAL DISTANCES

To accomplish our final objective, the NT and SMT diaspore release functions were incorporated into a mechanistic model of seed dispersal by wind to evaluate their effect on dispersal distances for *Poa*. The Markov chain Synthetic Turbulence Generation model (STG model) developed by Nathan *et al.* (2002) and Soons *et al.* (2004) was used to estimate dispersal distances. This mechanistic model predicts dispersal distances (including LDD) and has been tested for wind dispersal in forests (Nathan *et al.* 2002) and grasslands (Soons, Nathan & Katul 2004; Soons *et al.* 2004). The STG model is a 3-dimensional coupled Eulerian–Lagrangian trajectory model of individual diaspores, simulating dispersal as a function of the gravitational force acting on the diaspores in the vertical direction and the air resistance force (including wind turbulence) moving the diaspores horizontally and vertically with the wind flow. The modelled wind turbulence retains the spatial and temporal coherence of eddies, which is crucial in realistically predicting uplift and LDD (Nathan *et al.* 2002; Soons *et al.* 2004). We selected the STG model because it can be parameterized and it has been evaluated against real dispersal data in similar landscapes, whereas its extended version (the Atmospheric Stability Correction or ASC model; Soons *et al.* 2004) is limited by lack of surface sensible heat flux data under experimental conditions and as yet remains untested against real dispersal data. It should be emphasized here that the addition of sensible heat flux is accompanied by alterations to the first and second moments of the velocity fluctuations driving the STG model via a so-called stability correction function. This function varies with the stability parameter $-z/L$ that measures the relative importance of buoyant to mechanical production of turbulent kinetic energy, where z is the distance from the ground (or zero-plane displacement) and L is the Obukhov length. Because of the small z and strong winds at the site (resulting in high $-L$), $-z/L$ and the concomitant stability correction functions are likely to be small even when the sensible heat flux is finite. Input parameters to the STG dispersal model are seed terminal velocity, seed release height and wind speed distribution at 10 m height. For the computa-

tion of the flow field, vegetation height and the Leaf Area Index (LAI) must also be provided. To the detailed description of the model in Soons *et al.* (2004), here we simply added the conditional release functions from eqns (3) and (4).

The dispersal of *Poa* for typical open spaces between shrub patches of the Patagonian Monte region was modelled assuming the flow field is high Reynolds number, stationary and planar homogeneous. The model input parameters were determined from field and laboratory measurements and available literature. Mean diaspore terminal velocity, measured on 20 diaspores in an airtight fall tower (dimensions $0.5 \times 0.5 \times 2.0$ m), was 0.995 m s^{-1} (SD = 0.150) (cf. Soons & Heil 2002). Diaspore release height ranged between 0.20 and 0.50 m, measured on 40 well-watered, non-grazed plants. Vegetation height was 0.20 m and corresponded to maximum vegetation height in open intershrub spaces in three typical shrublands of the Patagonian Monte, measured on four 50-m linear transects at each site. Finally, a LAI value of 0.30 m^2 m^{-2} was used in the computation of the flow field, which was derived from Bisigato & Bertiller (1997) and Campanella & Bertiller (2008). We assumed that the slippage Reynolds number defined by the difference between the seed and air velocity is sufficiently small so that the seed and air flow accelerations are identical.

Two different sets of wind speed input data were used, namely a high-speed scenario (reflecting the wind speed distribution of a windy period or location) and a low-speed scenario (reflecting the speed distribution of a relatively calm period or location). For the former, we used the distribution of horizontal wind speeds at 10 m height for the 2009–2010 dispersal season in Puerto Madryn, Argentina (median = 4.55 m s^{-1}, mean = 4.95 m s^{-1}, SD = 2.62), measured by the Meteorological Station of the Oceanography and Meteorology Research Unit, Centro Nacional Patagonico (CONICET), which is located exactly at the site where experimental seed releases were carried out ('high-wind-speed scenario'). For the latter, to provide the model with realistic wind speed data highly skewed towards low values, we generated wind speed data following a lognormal distribution with a mean and standard deviation (of the logarithms) of 0.714 and 0.529, respectively, corresponding to the Estella meteorological station in Navarre, Spain (García *et al.* 1998) ('low-wind-speed scenario'). A total of 10 000 diaspore dispersal trajectories for each wind data set and release function were simulated.

Results

EXPERIMENTAL DIASPORE ABSCISSION DATA: FREQUENCY DISTRIBUTIONS OF U_A AND U_S

The anemometer wind speeds (u_A) measured during the grass experiments ranged from 1 to 8.3 m s^{-1} and were modestly right skewed (Fig. 1). In contrast, the u_A measured in the *Taraxacum* videotapes ranged between 0 and 6.7 m s^{-1} and were highly skewed to the right. The frequency distribution of wind speeds 'sampled' by released diaspores (u_S) was significantly shifted to the right of the distribution of u_A in three of the four species (Fig. 1) (*Poa*: K-S = 0.369, *Nassella*: K-S = 0.570, *Taraxacum*: K-S = 0.824; $P < 0.001$ in all cases). *Pappostipa* was the only species in which u_A and u_S distributions did not significantly differ (K-S = 0.161, $P = 0.140$), although u_S showed a higher mode and a slightly fatter tail than u_A (Fig. 1). The u_S frequency distributions of *Poa*, *Nassella* and *Taraxacum* (tapes 1–3) had significantly

larger median values than did the corresponding u_A, while the shape of the u_S distributions also varied in relation to that of u_A in *Nassella* and *Taraxacum*, as estimated by the coefficient of variation (Fig. 1).

TESTING THE DIFFERENT ABSCISSION FUNCTIONS AGAINST FIELD DATA

The TFs of the four species were strongly biased towards higher speeds (Fig. 2). In the case of the three grass species, wind speeds lower and higher than about 4 m s^{-1} were dissipated and amplified, respectively, while in *Taraxacum,* this transition occurred at about 1 m s^{-1}. For the grass species, the SMT model fitted the data better than the NT model, with highly varying b-parameter values among the three species beyond u_t (Table 2). In the case of *Pappostipa*, the b value for SMT was not significantly different from zero, indicating no relationship between diaspore abscission and wind speed after the threshold was surpassed. In *Poa* and *Nassella*, b values ranged from 3.2 to 5.3. The u_t values slightly varied among the three grass species. The NT and SMT models were equivalent in *Taraxacum*, that is, there was no indication of a measurable threshold in the data (Table 2 and Fig. 2). In this case, the b value was not significantly different from 2. Finally, the u_A for the three grass species tended to be so large (Fig. 1; Table 2) that the speed classes less than the estimated u_t were comprised of only a few observations.

TESTING THE DIFFERENT ABSCISSION FUNCTIONS AGAINST SIMULATED DATA

For *Poa*, the TFs of the simulations of diaspore abscission following the MDT hypothesis and the MCST hypothesis displayed varying shapes, but they nonetheless both resembled those obtained from abscission field data (Fig. 3). For either

MDT or MCST, the SMT function provided a significantly better fit (using AIC with a difference of at least 2.0) than the NT model in eight of 10 cases (Table 3). The only two cases in which the test of the SMT function was unjustified occurred with $C_n = 0.02$, $\omega_n = 0.50$ and $C_n = 2.0$, $\omega_n = 0.01$, both for MCST simulations. As in the case of the abscission field data for grasses, the proportion of u_A measurements lower than u_t was very low in all the simulations (Table 3).

For *Taraxacum*, the TF of almost all the MDT and MCST simulations resembled that of the *Taraxacum* field data (Fig. 4). A wind threshold could not be discerned in eight of 10 comparisons, and thus, the SMT model was unjustified. For one of the other two cases ($C_n = 0.02$, $\omega_n = 0.05$, MDT), the addition of a third parameter (u_t) to the model was not justified. The only case with unambiguous superiority for the SMT model occurred with $C_n = 0.02$ and $\omega_n = 0.50$, under a MDT scenario. The proportion of u_A measurements lower than u_t (when the threshold could be identified) was much larger for these simulations than for those using the *Poa* wind speed distribution (Table 4).

EFFECT OF DIASPORE ABSCISSION ON DISPERSAL DISTANCES

The inclusion of non-random diaspore abscission in the dispersal model led to a 5- and 2.7-fold increase in the median dispersal distances and a 3- and 2-fold increase in the 99.9 percentile, of *Poa* diaspores under 'low-' and 'high-'wind-speed scenarios, respectively (Fig. 5). Both for random and non-random abscission, all calculated percentile dispersal distances were larger for the high than for low-wind-speed scenario, but differences between the two wind speed scenarios were smaller under non-random abscission. The dispersal distances were increased slightly more in the SMT than in the NT model, but this difference was only noticeable at the

Table 2. Parameter estimates of the empirical models fitted to the observed transfer functions of each study species shown in Fig. 2. For SMT, parameter estimates correspond to the increasing function to the right of the threshold wind speed (u_t) estimated by piecewise regression. The last column is the percentage of anemometer wind speeds (u_A) measured in the experiments lower than the corresponding u_t for each species (sample size in parentheses)

	log(a)*	b*	u_t†	P	R^2	AIC‡	$u_A < u_t$
Poa ligularis							
NT§	−3.901 (0.350)	5.303 (0.510)	–	2.3e-07	0.900	16.7	7.7 (1088)
SMT§	−3.756 (0.509)	5.192 (0.658)	3.3	5.2e-08	0.971	**3.33**	
Nassella tenuis							
NT	−2.275 (0.249)	3.389 (0.387)	–	4.7e-07	0.846	24.01	20.9 (1418)
SMT	−2.095 (0.452)	3.234 (0.618)	2.3	1.9e-07	0.937	**13.81**	
Pappostipa speciosa							
NT	−3.210 (0.592)	4.591 (0.987)	–	1.6e-03	0.730	20.34	3.2 (467)
SMT	−0.466 (0.643)	0.743 (0.947)	2.7	1.7e-04	0.958	**5.85**	
Taraxacum officinale							
NT	0.123 (0.116)	2.045 (0.245)	–	8.3e-07	0.833	**21.2**	–
SMT	0.123 (0.116)	2.045 (0.245)	–	8.3e-07	0.833	21.2	

*Standard error indicated in parenthesis.
†u_t: the threshold wind speed in m s^{-1} (eqn 8).
‡AIC: Akaike Information Criterion for each model, with the best model indicated in bold.
§NT and SMT: 'no threshold' (eqn 7) and 'simple minimum threshold' models (eqn 8), respectively.
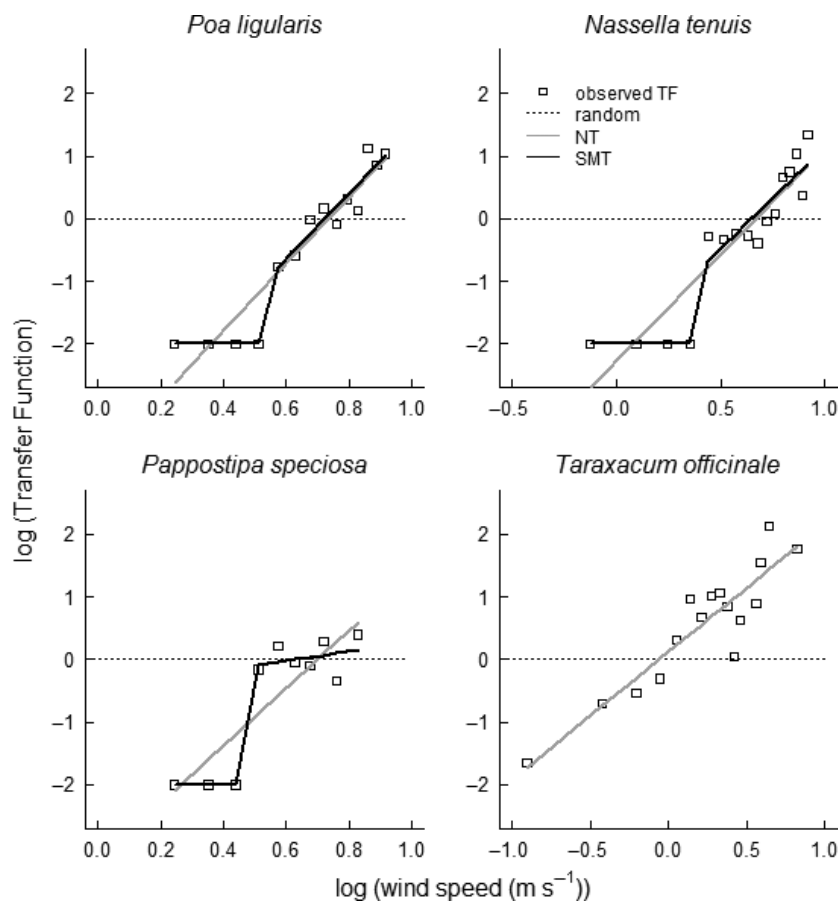
Fig. 2. Observed transfer functions (TFs) as a function of wind speed (in log–log scale) of the four study species. TF values lower or larger than zero indicate that environmental wind speed is dissipated or amplified, respectively, when considering diaspore release. The dashed line indicates the expected TF for random diaspore release (no relationship with wind speed). NT and SMT are the 'no threshold' and 'simple minimum threshold' models, respectively. Model parameter estimates are in Table 2.

highest percentile (the tail of the dispersal kernel) (Fig. 5). Furthermore, the difference between dispersal distances of both models was larger in the low (13% in average across percentiles) than in the high (3% in average) wind speed scenario, though it approached 25% in both scenarios at the 99.9 percentile. The longest dispersal distances ranged from 10.9 to 18.8 m and corresponded to NT and SMT simulations, respectively, for the high-wind-speed scenario. The wind speeds (at 10 m height) experienced by the dispersing diaspores were stronger for non-random than for random abscission under both wind speed scenarios (Fig. 5). In addition, the percentile wind speeds of the SMT were larger than those of NT simulations, with the largest differences for the low-wind-speed scenario (Fig. 5).

Discussion

Based on the principles from materials science, we formulated two alternative, mechanistic hypotheses on the details of the abscission process. Following both hypotheses, we conclude that not only the instantaneous wind speed but also the 'history' of wind speeds during the seed ripening period can play a role in determining the exact moment and wind speed at which a diaspore abscises. Although the importance of wind speed history was speculated on before, we now have a formal framework detailing the possible mechanisms. Our experimental diaspore abscission data support both mechanis-

tic hypotheses and clearly show a bias towards abscission at higher wind speeds, as was found in previous studies (Nathan, Safriel & Noy-Meir 2001; Greene 2005; Greene, Quesada & Calogeropoulos 2008; Soons & Bullock 2008; Wright *et al.* 2008). Each of the four species used in our abscission experiments showed u_S shifted to the right of u_A and Transfer functions amplified higher wind speeds. Hence, our findings confirm that diaspore abscission is non-random and occurs predominantly during the higher wind speeds of the ambient wind speed distribution. Our results also confirm the very short-time-scale of the relationship between the probability of abscission and wind speed and demonstrate that measuring wind speed at time intervals of a few seconds is essential. Finally, we show that non-random diaspore abscission greatly increases dispersal distances, especially LDD, but that the effect of a threshold is relatively small in comparison with the effect of the power relationship between abscission probability and wind speed.

MECHANISMS AND EMPIRICAL FUNCTIONS OF ABSCISSION

The diaspore abscission patterns simulated with the two biomechanical models proposed in this study, MDT and MCST, resembled those observed in the field. This suggests that the two proposed mechanisms, large diaspore displacement and material fatigue, respectively, can both be major determinants
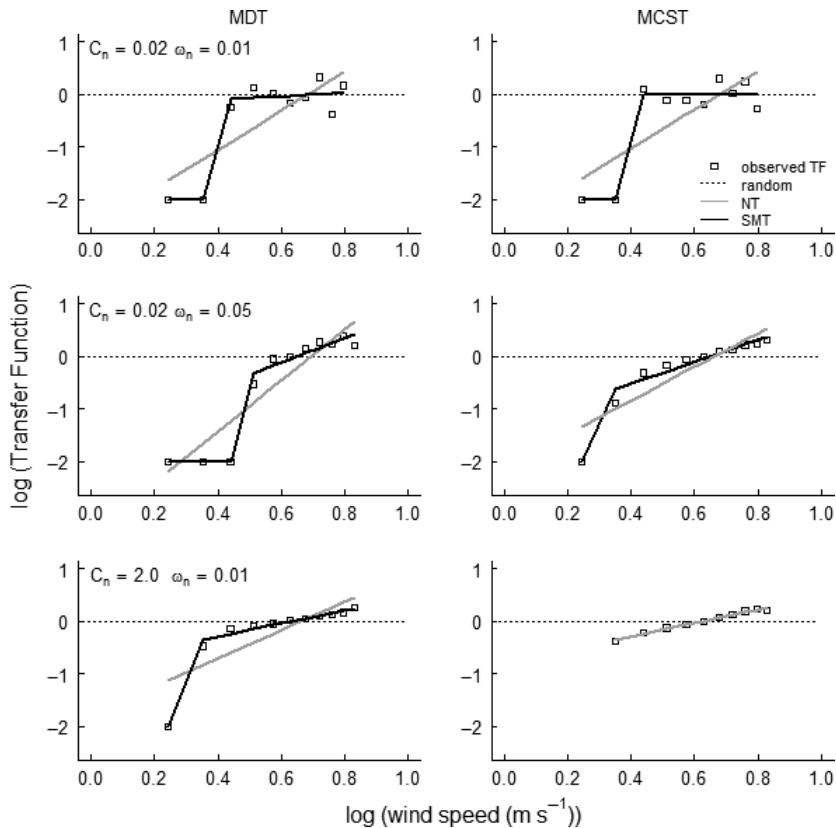
Fig. 3. Transfer functions and fitted NT and SMT models (as in Fig. 2) for selected examples of simulations based on the mass-spring-damper equation (eqn 1) parameterized with the anemometer wind speeds measured in the *Poa* experiments. The damping coefficient was set to 0.1 in all cases. The C_n and ω_n parameters indicated in each case are the simulated dimensionless drag coefficient and the natural oscillation frequency of the diaspore, respectively. For each case, results are shown for both the maximum deflection threshold (MDT) and the maximum cumulative stress threshold (MCST). Parameters estimates of the models are given in Table 3.

of diaspore abscission. The novel feature of these models is that both take into account the effect of the 'history' of wind speeds (though with some conceptual differences), experienced by the diaspores during seed ripening, on the final abscission event. This helps elucidate diaspore abscission, as, in biophysical terms, our models accommodate the effect of all the forces mainly derived from the turbulent component of the wind that contribute to dynamic loading on diaspores (Skarpaas, Auhl & Shea 2006; Jongejans *et al.* 2007; Marchetto *et al.* 2010).

The comparison of the abscission data simulated with both the MDT and MCST models does not allow us to discern which is more realistic. In fact, differences between the patterns of the simulated abscission data are hardly noticeable (Figs 3 and 4) and they were similarly well fit by either of the abscission functions (NT and SMT) (Tables 3 and 4). Discerning between the MDT and MCST models would involve, like the modelling of time to failure of industrial materials, repetitively applying a uniform stress to determine the number of repetitions required to effect failure. Then, one could see whether the results conformed to, for example, the Birnbaum–Saunders life distribution model (Birnbaum & Saunders 1969), which explicitly argues that breakage is due to crack propagation. The immediate conclusion here is, nevertheless, that wind speed history is a key factor that must be considered in diaspore abscission.

In the search for a functional relation between diaspore abscission and ambient wind speed, one theoretical novelty is our consideration of a simple wind threshold in combination

with an abscission proportional to the magnitude of the wind at speeds beyond the threshold; previous authors had not permitted the abscission probability to depend on speed once the threshold was exceeded (e.g. Schippers & Jongejans 2005; Bohrer *et al.* 2008; Soons & Bullock 2008). Comparing the no threshold (NT) model with the SMT model using field data showed that the three grass species were better explained by the latter, with thresholds (u_t) around 3 m s^{-1}. For *Poa* and *Nassella*, the exponent on u for the relationship between wind speed and abscission at $u > u_t$ was significantly larger than the value of 2 expected when the drag force directly releases diaspores (Greene & Johnson 1992; Greene 2005; Greene, Quesada & Calogeropoulos 2008; Soons & Bullock 2008; Greene & Quesada 2011). For the NT model fit, all three grass species also had an exponent significantly larger than 2. By contrast, for *Taraxacum,* the threshold parameter could not be identified and the SMT model was not justified. Further, only *Taraxacum* had an exponent near 2. Hence, there appears to be no universal superiority of the NT model over the SMT model and this indicates that, *in practice*, threshold wind speeds indeed appear to be present (see discussion below). Regarding the quadratic relationship to wind speed, the three grass species contradict the previous literature, while *Taraxacum* supports it; thus, it seems that there cannot be any direct simple relationship between abscission and wind speed directly mediated by drag.

Meanwhile, the exponent on u was not significantly different from 0 for *Pappostipa*. This conforms to the Schippers & Jongejans (2005) model, that is, abscission independent of

Table 3. Parameter estimates of the empirical models fitted to the transfer function of the diaspore release simulations with the mass-spring-damper equation (eqn 1) parameterized with the anemometer wind speeds measured in the *Poa ligularis* experiments (Fig. 3). Statistics and acronyms are as in Table 2. The last column is the percentage of anemometer wind speeds (u_A) lower than the corresponding threshold wind speed (u_t) for each simulation (sample size = 46 600 for all the simulations)

	$\log(a)$	b	u_t	P	R^2	AIC	$u_A < u_t$
(a) Maximum deflection threshold (MDT)							
$C_n = 0.02; \omega_n = 0.01$							
NT	−2.540 (0.608)	3.723 (1.021)	–	6.5e-03	0.624	20.5	1.12
SMT	−0.234 (0.492)	0.333 (0.758)	2.51	3.7e-04	0.944	**5.4**	
$C_n = 0.20; \omega_n = 0.01$							
NT	−1.495 (0.521)	2.289 (0.839)	–	3.6e-03	0.628	19.9	0.21
SMT	−0.245 (0.264)	0.469 (0.409)	2.10	2.7e-05	0.928	**−0.4**	
$C_n = 2.0; \omega_n = 0.01$							
NT	−1.795 (0.402)	2.720 (0.647)	–	2.3e-03	0.662	14.2	0.21
SMT	−0.775 (0.092)	1.235 (0.143)	2.10	6.9e-09	0.991	**−23.5**	
$C_n = 0.02; \omega_n = 0.05$							
NT	−3.374 (0.428)	4.874 (0.690)	–	5.9e-05	0.847	15.6	2.22
SMT	−1.486 (0.321)	2.293 (0.462)	2.75	5.2e-07	0.987	**−7.8**	
$C_n = 0.02; \omega_n = 0.50$							
NT	−3.452 (0.399)	5.008 (0.643)	–	2.7e-05	0.871	14.0	2.22
SMT	−1.861 (0.337)	2.841 (0.485)	2.75	6.7e-07	0.986	**−6.7**	
(b) Maximum cumulative stress threshold (MCST)							
$C_n = 0.02; \omega_n = 0.01$							
NT	−2.483 (0.633)	3.656 (1.063)	–	8.8e-03	0.597	21.3	1.12
SMT	−0.015 (0.437)	0.026 (0.673)	2.51	1.8e-04	0.956	**3.1**	
$C_n = 0.20; \omega_n = 0.01$							
NT	−1.727 (0.421)	2.646 (0.678)	–	3.6e-03	0.628	15.2	0.21
SMT	−0.648 (0.056)	1.075 (0.087)	2.10	1.3e-10	0.997	**−34.4**	
$C_n = 2.0; \omega_n = 0.01$							
NT	−0.790 (0.035)	1.269 (0.055)	–	1.3e-08	0.985	**−40.8**	–
SMT	−0.790 (0.035)	1.269 (0.055)	–	1.3e-08	0.985	−40.8	
$C_n = 0.02; \omega_n = 0.05$							
NT	−2.131 (0.323)	3.224 (0.520)	–	1.6e-04	0.811	9.4	0.21
SMT	−1.363 (0.171)	2.106 (0.265)	2.10	5.6e-07	0.973	**−9.9**	
$C_n = 0.02; \omega_n = 0.50$							
NT	−0.609 (0.043)	0.989 (0.066)	–	3.9e-07	0.966	**−37.1**	–
SMT	−0.609 (0.043)	0.989 (0.066)	–	3.9 e-07	0.966	−37.1	

wind speed above the wind threshold. Notably, some MDT and MCST model simulations under the high-wind-speed scenarios adequately reproduced this diaspore release pattern as well ($C_n = 0.02$; $\omega_n = 0.01$; Table 3). Because of the relation between the drag coefficient, wind speed and the projected area of the diaspore (Greene & Johnson 1990), we speculate that drag-producing structures, like the *Pappostipa*'s plume, strongly enhance the effectiveness of wind in breaking the seed–plant connection. An explicit treatment of diaspore morphology in models of diaspore abscission would shed light on this topic and should be seriously considered in future studies. A good example of this was provided by Bohrer *et al.* (2008), who explored the effect of diaspore morphology on dispersal in heterogeneous canopies by explicitly modelling complex aerodynamic properties of diaspores to estimate the drag coefficient and other specific parameters of their dispersal models.

The results thus far suggest that the grasses and *Taraxacum* are different in their response to wind-induced stress; in particular, perhaps *Taraxacum* has such a low u_t that it was difficult to discern statistically. However, it is worth noting that

the grasses and *Taraxacum* also differ strongly in the wind speed regimes experienced during the data collection, the latter species having experienced much lower speeds. This is a major issue if the exponent on u may vary with mean wind speed because, in sheltered conditions (as in the *Taraxacum* experiments), the drag coefficient may decrease with increasing Reynolds number (Vogel 1994). In this sense, consideration of the simulations of abscission data using the two biomechanical models (MDT and MCST) provide important complementary information to further evaluate the NT and SMT functions. The fits to the simulated data indicated that the relative performance of the NT and SMT functions depended on the wind speed scenario. When a high-magnitude wind speed scenario (typical of the grass data sets) is employed (Table 3), the simulations indicate that the SMT model is the better choice. However, when we used a low-magnitude wind speed (Table 4), it becomes difficult to find low-wind-speed classes with no abscission. In this case, only one of 10 simulations was fit best by the SMT model. We argue that this poor performance by the SMT model is because the 'wind speed environment' experienced by the
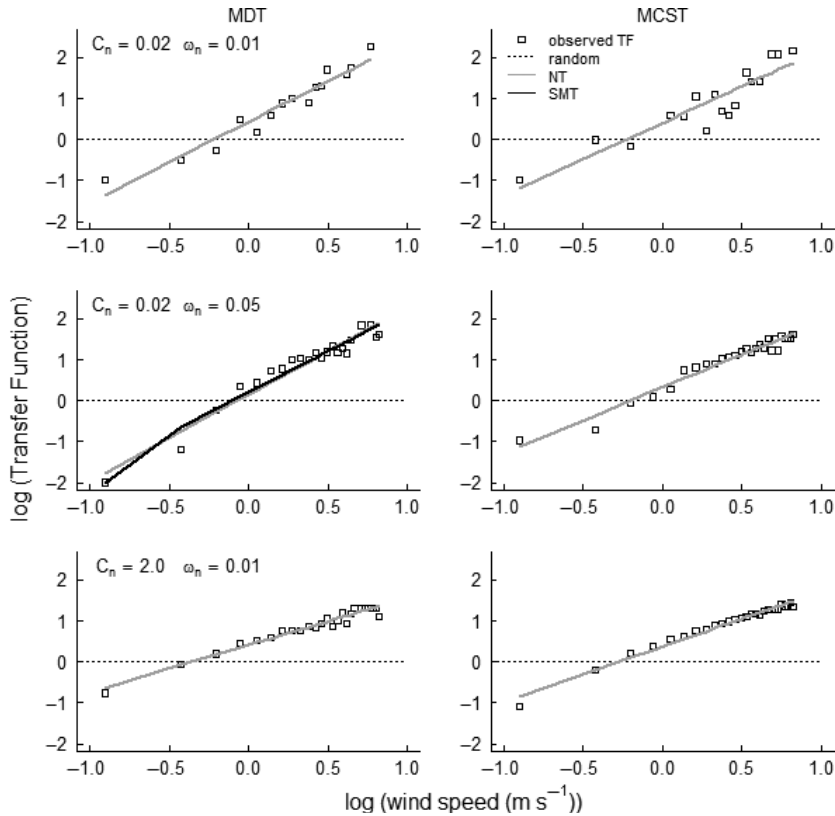
Fig. 4. Transfer functions and fitted NT and SMT models (as in Fig. 2) for the same example simulations based on the mass-spring-damper equation shown in Fig. 3, but parameterized with the anemometer wind speeds measured in the *Taraxacum* experiments. The damping coefficient was set to 0.1 in all cases. Other acronyms here are as in Fig. 3. Parameters estimates of the models are given in Table 4.

simulated diaspores matters. In effect, periods of low wind speeds occurred so rarely in the high-wind-speed environments of the simulations (Table 3) and for the grasses (Fig. 1) that all diaspores are blown off the plant at relatively high wind speeds. Hence, wind classes with zero abscission (the lower wind speeds) occurred and the AIC values warranted a third (threshold) parameter. But while the probability of diaspore abscission at low wind speeds is undoubtedly small, there is no reason to think it is zero. In conclusion, it is likely that the grass abscission results differ from the *Taraxacum* results not because of taxonomy but because of the differing wind speed regimes occurring at the time of the experiments.

Thus, in high-wind-speed environments, there appears to be a threshold wind speed (depending on the wind speed history), while in a low-speed environment, such a threshold cannot be discerned. This explanation is supported by previous studies (e.g. Elgersma, Leeuwangh & Wilms 1988; Greene, Quesada & Calogeropoulos 2008), which show that abscission without a motive force, although quite rarely, could occur. In fact, *Nassella* diaspores are also an example of that; these abscise with no other force than gravity after 2–3 months of sheltering from wind (G.E. Pazos, unpublished data). In nature, this point may very rarely be reached because under normal conditions, diaspores release preferentially at higher wind speeds and presumably none are ever abscised by gravity alone. Based on the biomechanical properties of the abscission zone and the above findings and observations, we propose that *in theory* there exists no distinct abscission wind threshold at any wind speed > 0, but that *in practice* such thresholds appear to exist and are highly dependent on the ambient wind speed environment and history. We showed that the SMT function effectively captures this effect of the ambient wind speed on diaspore abscission data and can easily be incorporated into seed dispersal models to take into account the effect of diaspore abscission on LDD.

Apart from the role of the local abiotic conditions in determining abscission, there may also be species-specific differences in the diaspore abscission patterns between the grasses and *Taraxacum* reflecting perhaps differences in diaspore size and morphology or differences in the development of the abscission zone (Roberts *et al.* 2000; Greene, Quesada & Calogeropoulos 2008; Greene & Quesada 2011; Thurber, Hepler & Caicedo 2011). Indeed, these differences may reflect different selective pressures acting on the species in their environments, especially given that the grass diaspores can also be epizoochorously dispersed by large grazing mammals (Cousens, Dytham & Law 2008; Couvreur *et al.* 2008), while ruderal species like *Taraxacum* may have to invest in relatively costly, drag promoting appendages (besides producing a scape to place the diaspores above the canopy) that enhance not only dispersal distances but also diaspore abscission (by amplifying drag).

EFFECT OF DIASPORE ABSCISSION ON DISPERSAL DISTANCES

How does all this translate to diaspore dispersal? The results of our simulations of seed dispersal of *Poa* under two different wind speed scenarios show that, as might be expected, non-random abscission significantly increases dispersal distances

Table 4. Parameter estimates of the empirical models fitted to the transfer function of the diaspore release simulations based on the mass-spring-damper equation (eqn 1) parameterized using the anemometer wind speeds measured in the *Taraxacum* experiments (Fig. 4). Statistics and acronyms are as in Table 2. The last column is the percentage of anemometer wind speeds (u_A) lower than the corresponding threshold wind speed (u_t) (sample size = 92 000 for all the simulations)

	$\log(a)$	b	u_t	P	R^2	AIC	$u_A < u_t$
(a) Maximum deflection threshold (MDT)							
$C_n = 0.02$; $\omega_n = 0.01$							
NT	0.440 (0.065)	1.978 (0.137)	–	2.3e-09	0.941	**2.3**	–
SMT	0.440 (0.065)	1.978 (0.137)	–	2.3e-09	0.941	2.3	
$C_n = 0.20$; $\omega_n = 0.01$							
NT	0.408 (0.045)	1.317 (0.086)	–	1.6e-12	0.921	**−12.3**	–
SMT	0.408 (0.045)	1.317 (0.086)	–	1.6e-12	0.921	−12.3	
$C_n = 2.0$; $\omega_n = 0.01$							
NT	0.415 (0.026)	1.153 (0.047)	–	2.2e-16	0.963	**−41.5**	–
SMT	0.415 (0.026)	1.153 (0.047)	–	2.2e-16	0.963	−41.5	
$C_n = 0.02$; $\omega_n = 0.05$							
NT	0.154 (0.059)	2.122 (0.112)	–	2.8e-14	0.948	**−0.5**	73.31
SMT	0.217 (0.071)	1.986 (0.141)	0.32	2.4e-13	0.953	−0.9	
$C_n = 0.02$; $\omega_n = 0.50$							
NT	-0.082 (0.116)	2.189 (0.203)	–	6.8e-11	0.823	35.1	75.95
SMT	0.160 (0.152)	1.768 (0.271)	0.39	1.6e-10	0.875	**29.8**	
(b) Maximum cumulative stress threshold (MCST)							
$C_n = 0.02$; $\omega_n = 0.01$							
NT	0.417 (0.102)	1.772 (0.199)	–	2.4e-07	0.840	**17.1**	–
SMT	0.417 (0.102)	1.772 (0.199)	–	2.4e-07	0.840	17.1	
$C_n = 0.20$; $\omega_n = 0.01$							
NT	0.392 (0.032)	1.514 (0.058)	–	2.2e-16	0.969	**−30.7**	–
SMT	0.392 (0.032)	1.514 (0.058)	–	2.2e-16	0.969	−30.7	
$C_n = 2.0$; $\omega_n = 0.01$							
NT	0.379 (0.022)	1.347 (0.038)	–	2.2e-16	0.981	**−55.7**	–
SMT	0.379 (0.022)	1.347 (0.038)	–	2.2e-16	0.981	−55.7	
$C_n = 0.02$; $\omega_n = 0.05$							
NT	0.326 (0.037)	1.603 (0.065)	–	2.2e-16	0.960	**−26.1**	–
SMT	0.326 (0.037)	1.603 (0.065)	–	2.2e-16	0.960	−26.1	
$C_n = 0.02$; $\omega_n = 0.50$							
NT	0.263 (0.071)	1.245 (0.124)	–	2.8e-10	0.802	**8.3**	–
SMT	0.263 (0.071)	1.245 (0.124)	–	2.8e-10	0.802	8.3	

and especially LDD. This has also been found in earlier studies (Greene 2005; Schippers & Jongejans 2005; Soons & Bullock 2008). Novel outcomes from simulations here are that the presence of a threshold wind speed adds to increase dispersal distances, and again especially LDD, further than only the effect of a power relationship between abscission and wind speed. However, the addition is relatively small in comparison with the effect of the power relationship alone. The inclusion of a simple wind threshold in seed dispersal models had different effects on the median and the tail of the dispersal kernels in previous studies, either significantly increasing them (Schippers & Jongejans 2005; Soons & Bullock 2008) or having negligible or non-conclusive effects (Stephenson *et al.* 2007; Bohrer *et al.* 2008). The difference is that here, the threshold was added onto a power relationship and clearly both increase the median and tail of the dispersal kernels.

Perhaps even more importantly, it becomes clear from our results that non-random abscission levels off the differences between low and high-wind-speed scenarios. With random diaspore abscission respective to wind speed, high-wind-speed environments (representative in this case of the windy late-spring dispersal season of the Patagonian Monte, but also for

example of the stormy periods in late autumn in Europe) are conducive to much higher LDD than low-wind-speed environments (representative in this case of the lee sheltered plains of Navarre, Spain (García *et al.* 1998), but also for example of calm periods in European summers). However, when non-random abscission is taken into account, this difference is much reduced. In fact, in a situation where low-wind-speed periods are interspersed with occasional high wind speed, turbulent events (for example a European summer with a few summer storms), that is, an increase in the standard deviation of the lognormal distribution, dispersal distances might even exceed those during a high wind season (see Appendix S2). This effect is caused by most diaspores remaining attached to the plant throughout the calm period, with many diaspores ready, and released, during sudden stormy turbulent intervals. In comparison, diaspores under high-wind-speed and turbulent conditions will continuously be blown off the plant, also at intermediate wind speeds, with less seeds available during stormy events. In this way, adaptations for non-random abscission greatly enhance dispersal distances during both calm and windy periods, and in both calm and generally windy environments. This agrees with Soons & Bullock
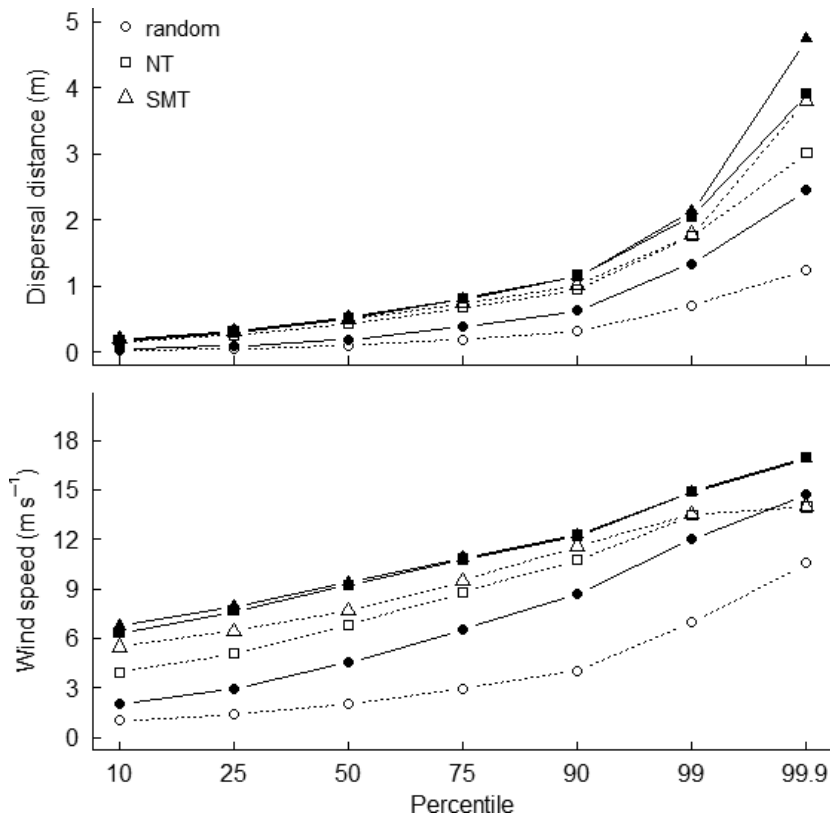
Fig. 5. Percentiles of dispersal distances (top) and experienced wind speeds (bottom) of simulated dispersing diaspores of *Poa ligularis* with the STG model (Soons *et al.* 2004) under two wind speed scenarios: 'low wind speed' (white symbols, dotted lines) is a lognormal distribution with mean and standard deviation (of the logs) of 0.714 and 0.529, respectively; 'high wind speed' (black symbols, solid lines) corresponds to the distribution of horizontal wind speeds at 10 m height for the 2009–2010 dispersal season in Puerto Madryn, Argentina (median = 4.55 m s^{-1}, SD = 2.62). The different lines correspond to the different diaspore abscission functions: random abscission, NT and SMT. Parameter estimates for these latter two models for this species are taken from Table 2. Acronyms are as in Fig. 2.

(2008) who suggested that seed dispersal primarily initiates during gusts, and gusts may even be more important in contributing to LDD than general windy conditions.

In our general framework for seed abscission and dispersal, variations in wind speed play an important role throughout the entire process from pre-abscission mechanisms to diaspore dispersal. These variations are in part caused by turbulence, which may be either mechanically or convectively produced. As such, turbulence plays an important role in both abscission and dispersal. The general condition in most systems will be mechanically produced turbulence, generated by the shear stress of the wind along the ground and vegetation surface, which under high-wind-speed conditions may cause large, autocorrelated deviations from the mean wind speed and can strongly determine abscission and dispersal (for dispersal see Soons *et al.* 2004). Convective turbulence may occur under specific conditions of low wind speeds and high surface heating and may drive abscission and dispersal then (Tackenberg 2003; Soons *et al.* 2004). Our general framework applies to both types of conditions, but as higher wind speeds increase both abscission and dispersal distances, windy conditions with mechanically produced turbulence are likely to play the most important role in the ecology of most species. However, simulations of dispersal using the ASC model (Soons *et al.* 2004) might help unravel the exact contribution of convective turbulence, which may be of interest in some species as for example Greene & Quesada (2011) demonstrated a diaspore abscission bias towards updrafts and against downdrafts in the cosmopolitan weed *Tragopogon dubius* (mediated by a combination of morphological traits and achene orientation).

An interesting comparison with the wind dispersal simulations with the threshold model by Schippers & Jongejans (2005) supports our conclusions. These authors argued that increasing the residence time of the seeds on the plant (via low rate of decay of u_t with time) would increase the probability of encountering fast wind speeds and thus increase LDD. Experimentally, Blattner & Kadereit (1991) earlier discovered that longer residence times also led to a more even spatial dispersal pattern in two *Papaver* species. Our results show that the residence time will be dependent not only on seed ripening but also on the cumulative stress in the abscission zone, which eventually will cause failure and abscission. Hence, as time elapses, the accumulated stress increases (even if produced by an ambient history of low wind speeds) enhancing the chance for abscission. This would mean that in high-wind-speed scenarios, the residence time will be short as the cumulated stress per time unit is high, so diaspores would abscise at medium-to-high wind speeds. In contrast, in low-speed environments, the cumulated stress is lower during calm periods, and although abscission at low wind speeds is possible, the residence time will be (on average) longer, increasing the chance for abscising at high turbulent wind speed events. These processes may in turn be regulated by air humidity at a daily time-scale. High relative humidity may slow down the drying of the vascular bundle and the cells of the abscission layer or cause the closing of the involucres and drag-producing fibres in other species (e.g. Roberts *et al.* 2000; Greene & Quesada 2005; Marchetto *et al.* 2012). Hence, the cumulated stress in the abscission zone would be reduced during these periods, delaying diaspore abscission.

This effect could also be incorporated into seed abscission and dispersal models by integrating other weather data with wind speed to increase the realism regarding the timing of abscission (Nathan *et al.* 2000; Wright *et al.* 2008; Savage *et al.* 2012). For example, diaspore abscission could be conditional not only to wind speed but also to relative humidity through the use of empirical functions estimated in experimental studies (Marchetto *et al.* 2012).

CONCLUDING REMARKS

Our study proposes to apply concepts from materials science to seed dispersal studies and formulates two alternative mechanisms detailing the process of diaspore abscission. Diaspore abscission increases greatly at higher instantaneous wind speeds (and often, but not necessarily, by a quadratic relationship), but is also dependent on ambient wind speed history. Hence, in theory, existence of a threshold wind speed (in addition to a power relationship between abscission and instantaneous wind speed) is unrealistic, but in practice, a lack of calm periods in high-wind-speed environments may result in the appearance of a threshold wind speed, which would then be highly dependent on the exact ambient wind speed history. Non-random diaspore release greatly enhances dispersal distances and LDD, and high-wind-speed events during otherwise calm periods (gusts, summer storms) are likely to contribute most to LDD. Thus, the incorporation of an abscission function like the SMT in seed dispersal models will increase the realism of the estimated dispersal kernels. Apart from these findings, we suggest that future studies may examine the effect of the drag coefficient (C_n) and mass/area of the diaspores, diaspore placement and wind directionality on abscission and further explore the relationship between plant/diaspore traits and abscission in different environments. The framework for interpreting diaspore release is currently unanchored by any appeal to the literature on material strength and failure, and we suggest that progress in this field could be used to further develop our understanding of diaspore abscission by wind.

Acknowledgements

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Figure S1. Photographs of the diaspores of the three grass species.

Appendix S1. Description of the mass-spring-damper model.

Appendix S2. Effects of non-random diaspore abscission on simulated dispersal distances under different wind speed scenarios.