Effects of seed morphology and orientation on secondary seed dispersal by wind

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Abstract

Aims
Understanding how diaspor (hereafter “seed”) morphology and orientation affect secondary seed dispersal by wind is important to link seed dispersal and post-dispersal processes, such as seed lodging, predation and germination. This study aims to describe the effects of seed morphology and orientation on secondary seed dispersal by wind via mechanistic modelling.

Methods
We extend the mechanistic model of Schurr et al. (2005) in order to describe how secondary seed dispersal by wind is affected by wind conditions, ground surface, seed morphology and orientation. The model simulates the initial landing orientations, dispersal distances and stopping orientations of individual seeds. To parameterise the model, we measured orientation-specific vertical seed projection and seed lift-off velocity (the wind speed at which a seed starts moving on the ground) of the asymmetric seeds of heterocarpous Zygophyllum xanthoxylon, and determined orientation-specific model parameters that depend on properties of seeds and/or the environment. To validate the model, we conducted wind-channel experiments in which we released seeds of Z. xanthoxylon onto a sand-coated tar paper, and recorded the initial landing orientations, dispersal distances and stopping orientations of the seeds.

Important findings
The extended model could precisely predict secondary dispersal distance, and explain up to 99% of variation in the observed proportions of seeds which stopped in various orientations. The model predicts that secondary dispersal distance increases with wind speed and decreases
with aerodynamic roughness length, and that there might be a positive correlation between dispersal distance and germination success.

**Keywords:** *Zygophyllum xanthoxyllon* (Zygophyllaceae), heterodiaspory, mechanistic modelling, phase II dispersal, seed orientation, tumbleweed, winged seed
INTRODUCTION

Seed dispersal, movement of diasporas (plant dispersal units, hereafter simply “seeds”) away from their sessile parent plant (Nathan and Muller-Landau 2000), plays fundamental roles in plant population and community dynamics (Cousens et al. 2008, Levin et al. 2003). Thus, understanding dispersal mechanisms is of critical ecological and evolutionary significance (Clobert et al. 2012). Seed dispersal by wind, one of the most important dispersal mechanisms (Nathan et al. 2011, Willson et al. 1990), consists of primary dispersal (seed movement through the air) and secondary dispersal (all subsequent movement across the ground before the seeds are permanently entrapped) (Schurr et al. 2005, Zhu et al. 2019). Secondary seed dispersal by wind is an important dispersal mechanism in a variety of open habitats (Chambers and MacMahon 1994, der Weduwen and Tuxton 2019) such as deserts (Reichman 1984; Zhu et al. 2019), temperate grasslands (van Tooren 1988), coastal and post-fire landscapes (Schurr et al. 2005), seashore meadows (Redbo-Torstensson and Telenius 1995), snow covered areas (Greene and Johnson 1997; Matlack 1989), as well as in urban areas and on roads (Kowarik and von der Lippe 2011; von der Lippe et al. 2013). Secondary dispersal distance strongly depends on seed morphology which affects seed lift-off velocity (Chambers and MacMahon 1994; Chambers et al. 1991; Johnson and Fryer 1992) and the mode of seed motion across the ground, e.g. turning, sliding or spinning. In nature, most seeds are non-spherical and asymmetric (Burrows 1986), and the asymmetry inevitably causes variation in seed orientations during secondary dispersal. Variation in seed orientation directly changes the angle of attack (the angle between the length of a seed and the wind direction) (Johnson and Fryer 1992), vertical seed projection (hereafter seed height) and the planform area of a seed exposed to airflow (Schurr et al. 2005), which in turn immediately affect seed lift-off velocity and the mode of motion. Therefore, in order to better understand the mechanisms of secondary dispersal and predict secondary dispersal distance, it is
essential to know the effects of seed morphology and orientation on secondary dispersal of asymmetric seeds. So far, however, how seed morphology and orientation quantitatively affect secondary seed dispersal by wind has not been reported yet.

At the same time, as the immediate consequence of secondary dispersal, seed orientation over the ground surface strongly affects subsequent processes, such as seed anchorage (Peart 1984), water uptake (Sheldon 1974), seed germination (Bosy and Aarssen 1995), seedling recruitment, plant distribution and community dynamics (Peart 1984). Therefore, to disentangle the effects of seed dispersal and other demographic processes as well as the environment on population and community dynamics, it is indispensable to know not only dispersal distance but also stopping orientation of seeds. However, seed orientation has not been incorporated into previous mechanistic models for secondary seed dispersal.

Mechanisms for secondary seed dispersal by wind have been well elucidated in the literature (Greene and Johnson 1997; Johnson and Fryer 1992; Schurr et al. 2005). According to the laws of mechanics, when a horizontal airflow is acting on a stationary seed over the ground (Fig. 1), the forces exerted on the seed are gravity, static friction with the ground surface, and lift and drag caused by the airflow. The stationary seed will start to move when the drag force overcomes the initial static friction force

$$0.5 \rho A C_D \overrightarrow{V}^2 \geq \mu_s (mg - 0.5 \rho A C_L \overrightarrow{V}^2) \quad \text{eqn1}$$

where \( \rho \) is air density, \( A \) is the area of the seed exposed to airflow, \( C_D \) is the coefficient of drag, \( \overrightarrow{V} \) is the wind velocity averaged over the seed height, \( \mu_s \) is the coefficient of static friction, \( m \) is seed mass, \( g \) is gravitational acceleration, and \( C_L \) is the coefficient of lift. The condition for starting motion of a stationary seed is

$$\overrightarrow{V} \geq \overrightarrow{U}_{lIFT} \quad \text{eqn2}$$

$$\overrightarrow{U}_{lIFT} = \sqrt{\frac{2mg}{\rho A (C_L + C_D \mu_s)}} \quad \text{eqn3}$$
where $\bar{U}_{lff}$ is seed lift-off velocity, which is the threshold wind velocity averaged over the seed height to move the stationary seed.

It is challenging to quantify the effects of seed morphology and seed orientation on secondary seed dispersal by wind for several reasons. First, the coefficients of drag and lift depend on an object’s shape and Reynolds number which also depends on the object’s shape (Loth 2008; Tran-Cong et al. 2004; Zastawny et al. 2012). Thus, variation in seed morphology directly affects seed lift-off velocity by changing the coefficients of drag and lift (Johnson and Fryer 1992). Second, variation in seed orientation also affects seed lift-off velocity by changing both seed height and seed area that is exposed to airflow (Fig. 1) (Schurr et al. 2005). Variation in seed area changes ‘effective’ wing loading, the ratio of seed mass to seed area (Norberg 1973), which strongly affects seed lift-off velocity (Greene and Johnson 1990; Johnson and Fryer 1992). Variation in seed height changes the wind interception parameter, defined as a dimensionless ratio between the wind velocity averaged over the seed height ($\bar{V}$) and the wind velocity at a reference height ($\bar{U}_{ref}$) (Schurr et al. 2005), determining the wind speed that a seed experiences (Fig. 1). Third, the coefficients of drag, lift, static friction and kinetic friction are difficult to formulate and can only be measured empirically (Johnson and Fryer 1992). However, due to small seed size and asymmetric seed morphology which causes these coefficients to constantly change with seed orientation, conducting experiments to precisely measure the coefficients is technically challenging. Since these mechanical and technical challenges have not been adequately addressed in previous studies on secondary seed dispersal (Johnson and Fryer 1992; Schurr et al. 2005; Thompson and Katul 2009), the effects of seed morphology and orientation on secondary seed dispersal have not been fully understood.

*Zygophyllum xanthoxylon* (Bunge) Maxim. (*Zygophyllaceae*) is ideal for studying the effects of seed morphology and orientation on secondary seed dispersal by wind. The species
is heterocarpous: single individuals can have as many as five distinct winged seed morphologies which differ in wing number and the angles between neighbouring wings, with two seed morphologies being asymmetric (Zhu et al. 2016; Zhu et al. 2019). Accordingly, at least 12 distinguishable seed orientations exist during secondary dispersal in Z. xanthoxylon (Fig. 1).

In this study, we aim to extend the model of Schurr et al. (2005) in order to describe the effects of seed morphology and orientation on secondary seed dispersal by wind. In particular, we want to include three properties of the system that were considered before: (1) kinetic friction is less than static friction; (2) seed height and hence lift-off velocity of the seeds varies with seed orientation; (3) seed orientation changes during secondary seed dispersal, and the new orientation is important for further movement. We postulate that a mechanistic model incorporating these properties of the system not only yields better predictions of secondary dispersal distance, but also accurately predicts the frequency of different stopping orientations in asymmetric seeds.

MATERIALS AND METHODS

Model description

The model is an extension of Schurr et al. (2005) and simulates any seed individually. The model of Schurr et al. (2005) compares the wind speed at the seed height $\vec{V}$ with the seed lift-off velocity $\vec{U}_{lift}$ and determines whether a seed starts to move (equations 1 and 2). When it does, the seed moves at this particular wind speed $\vec{V}$. The extended model further considers three new mechanisms: First, kinetic friction determines seed stopping velocity. After the stationary seed starts to move, $\mu_s$ in equation 3 becomes the coefficient of kinetic friction, $\mu_K$, and the mobile seed will keep moving as long as the drag exceeds kinetic friction. The condition for maintaining the motion of the mobile seed is
\[ \vec{V} > \overline{U_{\text{stop}}} \quad \text{eqn4} \]

\[ \overline{U_{\text{stop}}} = \sqrt{\frac{2mg}{\rho A \left( c_{L,\text{D}} \frac{c_D}{\mu_k} \right)}} \quad \text{eqn5} \]

where \( \overline{U_{\text{stop}}} \) is seed stopping velocity, which is the threshold wind velocity averaged over the seed height to maintain seed motion. From equations 3 and 5 the ratio between \( \overline{U_{\text{stop}}} \) and \( \overline{U_{\text{lift}}} \), denoted as \( \zeta \), is

\[ \zeta = \frac{c_{L,\text{D}} \frac{c_D}{\mu_k}}{c_{L,\text{D}} \frac{c_D}{\mu_k}} \quad \text{eqn6} \]

Since kinetic friction is typically smaller than static friction (\( \mu_k < \mu_s \)) (Rabinowicz 1951), the value of \( \zeta \) is smaller than one.

The two other novel aspects of this model are related to the fact that in the case of non-spherical seeds, seed orientation is expected to affect the initiation, termination and perpetuation of seed movement. Seed orientation determines model parameters seed height, \( \overline{U_{\text{lift}}} \), \( \overline{U_{\text{stop}}} \), and \( \zeta \). A seed can have different starting orientations drawn from an empirical distribution. A starting orientation directly determines seed height, which in turn determines wind speed at seed height \( \vec{V} \), \( \overline{U_{\text{lift}}} \), and \( \overline{U_{\text{stop}}} \) that are orientation-specific. The model then compares \( \vec{V} \) with \( \overline{U_{\text{lift}}} \) to determine if the seed starts to move. When it does, the seed moves at the speed of \( \vec{V} \). The model also compares \( \vec{V} \) with \( \overline{U_{\text{stop}}} \) to determine if the mobile seed stops moving. If the seed stops, the current orientation is its stopping orientation and the distance moved is its dispersal distance.

Seed orientation changes in each time step \( \Delta t \) (0.1 s). After \( \Delta t \), the seed has reached a certain location in the wind field characterized by a lower value of \( \vec{V} \), \( \overline{U_{\text{stop}}} \), and \( \vec{V} \) again depend on seed orientation which is newly drawn from the above-mentioned distribution. If the seed moves on, the comparison is repeated every \( \Delta t \). The extended model can thus
determine whether a stationary seed starts moving or not and whether a mobile seed keeps or stops moving, dependent on the wind speed the seed experiences. We apply the model for a situation of a wind field with a linearly decreasing wind speed based on the measurement of wind speed in a wind channel (see below), so that a seed possibly starts moving and eventually stops moving when reaching a distance where wind speed has become too low.

**Model parameterization**

A wind tunnel (at Experimental Center of Desert Forestry, Chinese Academy of Forestry, test section: 2 m (W) × 2 m (H) × 2 m (L)) was used to determine specific wind profiles for three different ground surfaces (sand, loam, gravel). Wind speed was measured with a Magnesense II Differential Pressure Transmitter (MS2-W102-LCD, Dwyer Instruments Inc., Indiana, USA) and a Pitot tube (160-96, Dwyer Instruments Inc., Indiana, USA), at heights from 0 to 0.2 m (30 measured values). We used a non-linear mixed effects model (R package nlme (Pinheiro et al. 2018) fixed effects: height, random effect: wind speed at reference height 1 m), to fit a logarithmic wind profile to measured values, as follows

\[ u = \frac{u_*}{k} \ln \frac{z-d}{z_0} \]  

**eqn7**

where \( u_* = (\tau/\rho)^{1/2} \) is the friction velocity, where \( \tau \) is the shearing stress, the horizontal force per unit ground area, and \( \rho \) is air density; \( \kappa \) is von Kármán’s constant (0.41); \( d \) is zero-plane displacement distance; and \( z_0 \) is aerodynamic roughness length (Monteith and Unsworth 2013).

Fitting of the wind profile yielded aerodynamic roughness length \( z_0 \) (the theoretical height below which the wind speed becomes zero, i.e. it describes the roughness of the surface) (Monteith and Unsworth 2013). This value is needed to calculate the wind interception parameter \( p \) (defined by Schurr et al. (2005)) as the ratio of the averaged wind
speed over the seed height and any wind speed measured at a reference height $z_{ref}$, $\overline{U_{ref}}$) as follows

$$p = \begin{cases} \frac{(h-d)(\ln(h-d) - \ln z_0 - 1) + z_0}{h(\ln z_{ref} - d) - \ln z_0} & \text{if } h > z_0 + d, \\ 0 & \text{if } h \leq z_0 + d. \end{cases} \text{ eqn8}$$

where $h$ is the seed height.

The wind speed at a characteristic height for the seed, i.e. the wind velocity acting on the seed, is described as follows

$$\overline{V} = p\overline{U_{ref}} \text{ eqn9}$$

For any seed (orientation), $\overline{U_{lifft}}$ was measured following the methodology of Johnson and Fryer (1992). We placed 10 seeds in any orientation and increased wind speed at a reference height of 1 m, $\overline{U_{ref}}$, from 0 m/s at a minimum increment 0.0025 m/s and recorded the threshold velocity when each seed started moving. This was repeated six times, yielding 60 values for each seed orientation. $\overline{U_{lifft}}$ was calculated following Schurr et al. (2005) as

$$\overline{U_{lifft}} = p\overline{U_{ref}} \text{ eqn10}$$

Based on these data, we fitted orientation-specific log-normal distributions of $\overline{U_{lifft}}$, which were later used in model simulations (Table 1). To account for the fact that some seeds did not move we included NA’s in these models.

To determine the distribution of the initial landing orientations, we released 40 different seeds three times each from the height of two meters and recorded the orientations. For orientations with the same probability of landing (when considering wind direction, see Fig. 1), the number of occurrences were divided equally between the two orientations. This was the case for orientations 2 and 3 of T-type, and 1 and 4, 3 and 5 as well as 2 and 6 of $\lambda$-type (Fig. 1). Seed height was measured with an electronic calliper for 40 different seeds in each possible orientation (Table 1).
Experimental model validation

A wind channel was used to obtain data on seed dispersal distance and stopping orientation for model fitting and model validation. The channel was located at the University of Hohenheim, Germany, and consisted of a fan creating wind speed of 3.4 m/s at 0.023 m height 0.1 m downwind from the fan, and had a test section of 0.4 m (W) × 0.4 m (H) × 4.2 m (L). The difference between the wind channel and the above-mentioned wind tunnel is that the wind channel consists of only two lateral walls, with no ceiling. The ground in the test section was covered with sand-coated tar paper (average grain size c. 433 μm). The airflow in the test section was streamlined using iron tubes (diameter of 6 cm, length of 20 cm) to minimize turbulence. Wind speed at different distances downwind was measured with a WIND BEE-Anemometer (Kat. Nr. 42.6003, TFA Dostmann GmbH & Co. KG, Wertheim, Germany). Analysis of these measurements showed that the created wind field can be described almost exactly by an exponential decay of wind speed at a reference height of 0.023 m ($\overline{U}_{ref}$) with distance $d$ from the exit of the iron tubes (the start of the test section). Specifically, the equation

$$|\overline{U}_{ref}| = e^{-0.16d+1.23} \quad \text{eqn11}$$

explains of 99% of the variance in measured $\overline{U}_{ref}$.

In each experimental run, we firstly released 10 individually-marked seeds from a height of 1 m in still air and recorded the landing orientation of each seed. We then moved the seeds to the front of the iron tubes at a lateral distance of 0.1 m, while keeping the orientation of each seed unchanged. Subsequently, we switched on the fan, and the seeds were blown away. After all seeds had stopped, we then recorded the dispersal distance and stopping orientation of each seed.
To quantify the wind profile in the wind channel, we measured horizontal wind velocities at different heights, with the fan running at 3.4 m/s, 3.1 m/s and 2.5 m/s (at a reference height of 0.023 m). The resulting aerodynamic roughness length $z_0$ (equation 7) was 0.038 mm and thus very similar to the roughness length of the sand surface in the wind tunnel (0.04 mm).

**Estimation of parameter $\zeta$ and its relationship with seed parameters**

Considering that the ratio of $\vec{U}_{stop}$ and $\vec{U}_{lift}$, i.e. the parameter $\zeta$, has not been accounted for in previous studies, that it is difficult to measure directly, and that calculation via equation 6 is challenging (other parameters are even harder to measure), we decided to fit $\zeta$ by comparing model output to observations from the wind channel experiment. This experiment can be fully described by the model, because wind speed is known at any location in the wind field (equation 11). To fit $\zeta$, we first obtained the maximum likelihood estimate for $\zeta$ by calculating a likelihood function considering dispersal distance and stopping orientation, and then used the R function optim (R Core Team (2018)) to fit a one-dimensional $\zeta$ for all seed orientations of each seed type, and the R function GenSA (Xiang et al. (2013)) to fit a three- or six-dimensional $\zeta$ for each seed orientation of T- or $\lambda$-type seeds during the course of simulations.

The parameter $\zeta$ is obviously crucial for the process of secondary seed dispersal, but its estimation from dispersal data requires intensive computation. Therefore, after we have estimated $\zeta$, we tested the relationship between the estimated $\zeta$ and $\vec{U}_{lift}$ as well as seed height of each seed orientation, to possibly provide an alternative way of estimating $\zeta$ with these easily measurable seed traits. For this we used a linear model including the interaction between the predictor variables and quadratic terms.
Simulation scheme and model performance assessment

We simulated $10^4$ seeds for various model versions from simple, the model of Schurr et al. (2005), to more complex versions considering $\zeta$, i.e. lower kinetic than static friction, and seed orientation explicitly or implicitly (Table 2).

Implicitly including orientation ($O_i$) means drawing $\vec{U}_{lift}$ from the joint empirical distribution which includes the different $\vec{U}_{lift}$ values for all orientations. Therefore, the probability of different orientations is implicitly considered, but not explicitly specified. Explicitly including orientation ($O_e$) means that in every time step $\Delta t$ (0.1 s) first the orientation is drawn from the empirical distribution, and then $\vec{U}_{lift}$ is drawn from the orientation-specific empirical distribution. This explicit modelling of orientation allows us to predict not only dispersal distance, but also the distribution of seed stopping orientations, which is important for post-dispersal processes such as seed germination and seedling establishment. Considering $\zeta$ (i.e. the ratio of $\vec{U}_{stop}$ and $\vec{U}_{lift}$) in one dimension ($K_{1D}$) means that only one $\zeta$ value is fitted for all orientations; in the three or six dimensional case ($K_{3/6D}$) $\zeta$ is fitted individually for each of the three (T-type) or six ($\lambda$-type) orientations the seed can have during the simulation.

Model performance was assessed by simulating $10^4$ seeds, using the maximum likelihood estimate for $\zeta$, and comparing dispersal distances, as well as stopping orientations, to the observations in the wind channel experiment. Stopping orientation could, of course, only be used for model versions explicitly accounting for seed orientation ($O_e$). For dispersal distance we quantified model performance using root-mean-square error (RMSE), for multivariate distribution of stopping orientations by the generalized coefficient of determination (adjusted $R^2$, (Nagelkerke, 1991)).
Case study

To test the applicability of our extended model version (MOeK_{3/6D}) to predict dispersal distance and stopping orientation of T- and λ-type seeds, respectively over sand, loam and gravel surfaces, using real wind data with a high temporal resolution of 0.1 second (CSAT3A, Campbell Scientific, Utah, USA). From these 3-D sonic anemometer data, we used only the two horizontal axes and assume the wind to be spatially homogeneous while varying temporally, which means that a resting seed can start to move again, when wind speed changes over time. To cover the range of wind speed during the dispersal season, we chose to use data from June to November 2017 in the Ulan buh Desert (106.150°–107.167°E, 40.150°–40.950°N) and simulated seed dispersal of 10^4 seeds for three particular days, namely the day with the lowest daily mean wind speed (18 October, 1.4 m/s, measured at z_{ref} of 2 m), a day with average daily mean wind speed (29 September, 2.7 m/s) and the day with the highest daily mean wind speed (02 June, 6.1 m/s).

RESULTS

Predicted vs observed dispersal distance

For T-type seeds, MO_{K1D} (considering seed orientation implicitly and ζ in one dimension), MO_{K1D} (considering seed orientation explicitly and ζ in one dimension), and MO_{K3D} (considering seed orientation explicitly and ζ in three dimensions) closely predicted both the median (2.58 m, 2.59 m, and 2.76 m for prediction vs 2.54 m for observation, respectively; median test, P > 0.05) and the distribution of the observed dispersal distance (Fig. 2a, Fig. 3, Supplementary Material Figure S1). Predicted dispersal distance from MO_{K1D}, MO_{K1D}, and MO_{K3D} was 82%, 75%, and 68% more accurate than that from M_0(S05), respectively.
For λ-type seeds, both MO_{eK1D} and MO_{eK6D} (considering seed orientation explicitly and ζ in six dimensions) closely predicted the median (0.93 m and 1.35 m vs 1.32 m, respectively; median test, P > 0.05), but only MO_{eK6D} also closely predicted the distribution of the observed dispersal distance (Fig. 2b, Fig. 4, Supplementary Material Figure S2). Predicted dispersal distance from MO_{eK1D} and MO_{eK6D} was 82% and 90% more accurate than that from M_0(S05), respectively.

Models other than the aforementioned ones all significantly underpredicted both the median (median test, p < 0.001) and the interquartile range of the observed dispersal distance (Fig. 2, Fig. 3, Fig. 4).

**Predicted vs observed stopping orientation**

For T-type seeds, MO_{e} (considering seed orientation explicitly), MO_{eK1D}, and MO_{eK3D} predicted 95%, 79%, and 97% of variation in observed proportions of stopping orientation, respectively (Fig. 5a). For λ-type seeds, MO_{e}, MO_{eK1D}, and MO_{eK6D} predicted 97%, 79%, and 99% of variation in observed proportions of stopping orientation, respectively (Fig. 5b).

**Estimation of ζ and its relationship with seed traits**

For T-type seeds, the estimated values of one-dimensional ζ (an overall ratio between \( \bar{U}_{stop} \) and \( \bar{U}_{lift} \) for all orientations) for MK_{1D}, MO_{iK1D}, and MO_{eK1D} were 0.91, 0.45, and 0.49, respectively; the estimated value of three-dimensional ζ (a ratio value between \( \bar{U}_{stop} \) and \( \bar{U}_{lift} \) for each seed orientation) for MO_{eK3D} was (0.54, 0.39, 0.57). For λ-type seeds, the estimated values of one-dimensional ζ for MK_{1D}, MO_{iK1D}, and MO_{eK1D} were 0.99, 0.21, and 0.15, respectively; the estimated value of six-dimensional ζ for MO_{eK6D} was (0.65, 0.08, 0.44, 0.21, 0.06, 0.64).
The linear model that contained $\vec{U}_{lift}$ and seed height as well as their interaction explained less than half of the variation in $\zeta$ ($R^2 = 0.44$; $F_{3,29} = 7.64$, $P < 0.001$). There was a significant interaction between $\vec{U}_{lift}$ and linear term of seed height ($F_{1,27} = 4.61$, $P = 0.040$). However, the effect of the interaction was small (partial $R^2 = 0.09$), and variation in $\zeta$ was mainly explained by the effect of $\vec{U}_{lift}$ (partial $R^2 = 0.34$). There was a negative correlation between $\zeta$ and $\vec{U}_{lift}$ (Pearson's product moment correlation coefficient $r=-0.56$, $P<0.001$).

**Case study**

Predicted dispersal distance depended on a three-way interaction among seed type, surface type and daily mean wind speed ($F_{4,179928} = 13953$, $P < 0.001$). For both seed types, dispersal distance increased with daily mean wind speed (Fig. 6). For T-type seeds, dispersal distance decreased with surface roughness when the daily mean wind speed was the same (Fig. 6a, b and c). For $\lambda$-type seeds, this was only the case on the least windy day (Fig. 6f), on the other two days, however, seed dispersal distance increased with surface roughness (Fig. 6d and e). In the same dispersal environment (same surface and daily mean wind speed), T-type seeds dispersed further than $\lambda$-type seeds (median test, $P < 0.001$).

The proportion of seeds which stopped in orientations in which seed lift-velocity was high (i.e. orientation 2 for T-type and orientations 2 and 4 for $\lambda$-type seeds, see Fig. 1) increased with daily mean wind speed and decreased with surface roughness (Fig. 7). That is, over smooth surfaces or on the windier days, more seeds stop in orientations in which it is harder for them to start moving afterwards; over rough surfaces or on the less windy days, more seeds stop in orientations in which it is easier for them to start moving afterwards.
DISCUSSION

Since the first mechanistic model for secondary seed dispersal by wind, $M_0(S05)$ in this study, was developed and validated in the field (Schurr et al. 2005), it has seldom been explicitly tested or applied in other contexts. In this study, with the heterocarpous *Zygophyllum xanthoxylon* which has a complex seed dispersal system, we have verified the power of mechanistic modelling and further extended its domain for secondary seed dispersal. The extended models $M_{o1}^K_{1D}$ and $M_{o2}^K_{3/6D}$ contain all the essence of $M_0(S05)$, but they also incorporate the extra components for seed movement across the ground: kinetic friction is less than static friction, and seed height and hence seed lift-off velocity explicitly varies with seed orientation. Consequently, the extended models are able to predict both dispersal distance and seed stopping orientation. While both $M_{o1}^K_{1D}$ and $M_{o2}^K_{3/6D}$ accurately predict seed dispersal distance, $M_{o2}^K_{3/6D}$ predicts seed stopping orientation better than does $M_{o1}^K_{1D}$. $M_{o1}^K_{1D}$ is, however, simpler since it requires only one estimated parameter, whereas $M_{o2}^K_{3/6D}$ requires three or six. Therefore, one can choose model versions based on one's interest: if one is interested in dispersal distance only, $M_{o1}^K_{1D}$ may be sufficient; if in both dispersal distance and seed stopping orientation, $M_{o2}^K_{3/6D}$ is better.

Significance of $\zeta$

Compared with $M_0(S05)$, the key to the improved performance of $M_{o2}^K_{3/6D}$ is both the inclusion of $\zeta$ and the explicit consideration of seed orientation. Considering seed orientation enables us to track variation in seed orientation during the process of seed dispersal; including $\zeta$ enables us to accurately predict seed dispersal distance. Notably, variation in $\zeta$ impacts predicted seed dispersal distance dramatically. Take T-type seeds of *Z. xanthoxylon* for example, $M_{o1}^K_{1D}$ with the $\zeta$ value of 0.49 predicts a median dispersal distance almost 10-fold further than does $M_{o2}^K$ or $M_{o1}^K$. Hence, if we only consider seed orientation, either
explicitly or implicitly, without including $\zeta$ (i.e., by indiscriminately implying that its value is 1), we may largely underestimate secondary dispersal distance. Especially, including $\zeta$ may be more influential regarding seeds with complex morphology like $\lambda$-type seeds, for they correspond to an even smaller $\zeta$ than do T-type seeds.

Although it is essential to include $\zeta$ in the model, whether or not to include a multidimensional $\zeta$ may depend on complexity of seed morphology. When it comes to $\lambda$-type seeds, it seems necessary to explicitly include a multidimensional $\zeta$ for various seed orientations. Indeed, $\text{MO}_6K_{6D}$ performs much better regarding both dispersal distance and seed stopping orientation than $\text{MO}_6K_{1D}$. In contrast, for seeds which have comparatively simple morphologies, it seems sufficient to include a one-dimensional $\zeta$. Take T-type seeds, which are more symmetric and globular than $\lambda$-type seeds, no greater improvement is gained by using $\text{MO}_6K_{3D}$ than by using $\text{MO}_6K_{1D}$ to predict dispersal distance. This finding — simple models are sufficient for simple seeds — agrees with Schurr et al. (2005) who used $\text{MO}_0(S05)$, a specific case of $\text{MK}_{1D}$ in which the value of $\zeta$ is 1, to predict proportions of seeds dispersed over a distance of 25 m in Proteaceae, and the model performed well. In this study, however, $\text{MO}_0(S05)$ largely overpredicted seed dispersal distance. The difference in performance of $\text{MO}_0(S05)$ is most likely due to differentiated appendages, sizes and morphologies of seeds used in the two studies. Schurr et al. (2005) used plumed seeds, parachute seeds and winged seeds of various Proteaceae species. Although we also use winged seeds, they are larger, more complex and asymmetric than seeds of those Proteaceae species.

Since different seed morphologies correspond to different values of $\zeta$, seed morphology may in turn play an important role in secondary seed dispersal by affecting the value of $\zeta$. Therefore, one possible way to quantify the effects of seed morphology on wind seed dispersal is to compare morphology-specific $\zeta$ values among seed morphologies. For example, in a particular environment, if two seed morphologies have similar lift-off velocity,
the one with smaller $\zeta$ value will have greater secondary dispersal potential because it is easier for it to maintain movement once it starts moving.

Despite the challenge to further formulate $\zeta$ or directly measure its value, we have demonstrated that one could estimate its value with wind-tunnel experiments and maximum likelihood method. Additionally, the physical nature of $\zeta$ determines that its value merely ranges from 0 to 1, which largely reduces the extensiveness of computation. This knowledge about $\zeta$ thus provides guidance for future study on experimental design and model parameterisation: in wind-tunnel experiments, one can determine seed lift-off velocity and validate model prediction simultaneously, by additionally recording dispersal distance and seed stopping orientation.

**Effects of seed morphology and orientation on processes beyond dispersal**

Seed morphology and orientation play important roles in processes besides dispersal (Harper et al. 1965; Peart et al. 1987; Peart 1979, 1981, 1984; Sheldon 1974). For example, seed morphology and stopping orientation strongly affect seed germination and seedling survival (Peart 1979, 1981, 1984), even in the absence of any variation in substrate (Bosy and Aarssen 1995). This is because stopping orientation affects conditions of the microhabitat where the seed is finally entrapped, such as light condition, temperature, water availability, pathogen density, and predator activity, which in turn influence the probability for seed consumption by granivores, attack by pathogens, or germination; for seedling survival, infection from fungi, grazing, or predation; for juvenile browsing by herbivores, death due to stress, or growth to be a reproductive adult (Chambers and MacMahon 1994; Schupp 2007). Therefore, seed stopping orientations may play an important role in determining the suitability of a site for recruitment and thus dispersal effectiveness (Schupp et al. 2010).
There is a growing consensus that intraspecific variation in seed dispersal has consequences for plant demography, community evolution and global change (Snell et al. 2019). Among all the traits causing intraspecific variation in seed dispersal, seed morphology plays a crucial role (Andersen 1993; Augspurger 1986; Sheldon and Burrows 1973). This study shows that even in an identical dispersal environment (e.g. same daily mean wind speed and ground surface), different seed morphologies give rise to different distributions of dispersal distance and stopping orientation. In a previous study, we found that seed morphology determines primary dispersal distance, secondary dispersal potential, as well as the relationship between primary and secondary seed dispersal by wind (Zhu et al. 2019). Our previous finding is verified in this study from a mechanistic perspective: seed morphology plays an important role in secondary wind dispersal, because it determines seed landing orientation which in turn influences further seed movement. Our findings in both studies suggest that heterocarpous species, i.e. plants producing more than one type of seeds, might fine-tune their adaptation to spatial-temporal variation in the environment by varying not only dispersal distance but also stopping orientation of their seeds, via adjusting the proportion of seeds with different morphology. This adjustment was found in dimorphic seeds (Brandel 2007; Cheptou et al. 2008), and it will be interesting to test whether the seed dispersal system of the heterocarpous Z. xanthoxylon shows similar adaptive responses.

Limitations and future study

Three assumptions in the model could be relaxed. First, we assume that a moving seed changes its orientation every Δt, whereas in reality the interval probably varies with wind velocity, ground surface, seed morphology and the motion of the seed (e.g. velocity and orientation). Future study could test how the interval is affected by these factors and how variation in the interval in turn affects model prediction. Second, we assume that the
probability for a moving seed to change its orientation is independent of its current orientation and moving velocity, ground surface and wind velocity. However, in the field conditions variation in seed orientation is perhaps more complicated and is possibly affected by all the aforementioned factors. Studying how these factors determine variation in seed orientation is especially relevant when predicting secondary wind dispersal in more heterogeneous environments. Third, we assume that the ground surface is homogeneous. Thus, the simulated results in this study should not be interpreted as implementation of the model in the field conditions, although we used real wind data and aerodynamic roughness length of ground surfaces. Future study could explicitly incorporate heterogeneity of the ground surface into the model.

Despite the limitations, the most complex model (MO$_K 3/6D$) has considerable potential for being implemented in various contexts, for being incorporated into other mechanistic models, and for being further extended to better understand the mechanisms for secondary seed dispersal by wind. For example, the model can be used to predict secondary seed dispersal in a wide range of open environments where wind plays important roles (Chambers and MacMahon 1994), and the model may predict dispersal distance of asymmetric seeds, which have complex morphologies, more accurately than do the previous models. Moreover, in combination with mechanistic models for primary seed dispersal by wind (Nathan et al. 2011), MO$_K 3/6D$ enables us to mechanistically predict total dispersal distance by wind which consists of both primary dispersal distance through the air and secondary dispersal distance across the ground, which play different roles in various contexts. For example, in arid and semi-arid environment where many plants are of short stature and where the ground surface is often exposed, secondary dispersal may be very important for many species and in the ‘climax’ community for these habitats (Schurr et al. 2005; Thompson and Katul 2009; Zhu et al. 2019). Predicting both primary and secondary wind dispersal thus allows to quantify the
relationship between different dispersal mechanisms (Zhu et al. 2016; Zhu et al. 2019) and total dispersal kernels (Nathan 2007).

Although the model is flexible for predicting dispersal of seeds with complex morphologies and various orientations, estimation of the value of morphology- or orientation-specific $\zeta$ requires extensive computation. Thus, it is helpful to establish a statistical relationship between $\zeta$ and seed traits which are often easily available across a broad spectrum of seed morphologies. Such a relationship will save time for parameter estimation from ecologists, conservationists and governmental experts who require seed dispersal distance but may be unspecialised in mechanistic modelling, making wide implementation of the model easier. With limited data, our analyses show that $\vec{U}_{lft}$ and seed height explain nearly half of variation in $\zeta$, and there is a significant negative relationship between $\vec{U}_{lft}$ and $\zeta$, that is, the greater the $\vec{U}_{lft}$ the smaller the $\zeta$ value. Since variation in $\zeta$ influences model prediction dramatically, it may be essential to include $\zeta$ in the model when predicting secondary wind dispersal of seed morphologies with high lift-off velocity.

We thus call for more studies on different species with complex seed morphologies to test this model in various contexts. We speculate that wide application of the model in combination with other mechanistic models for primary seed dispersal by wind will lead to more comprehensive understanding of wind dispersal and allow to mechanistically link seed dispersal with other ecological processes.

Conclusions

Using mechanistic modelling and wind-tunnel experiments with asymmetric winged seeds in heterocarpous $Z. xanthoxylon$, we have demonstrated that seed orientation and kinetic friction between moving seeds and the ground surface play critical roles in the distributions of secondary dispersal distance and seed stopping orientation. Therefore, when
predicting secondary wind dispersal of asymmetric seeds, it may be essential to consider effects of seed orientation and kinetic friction on seed movement.

The extended models not only provide a tool to predict dispersal distance and seed stopping orientation in secondary seed dispersal by wind, but also help to understand links between seed dispersal and post-dispersal processes such as seed predation and germination. A better understanding of dispersal mechanisms can help to investigate dispersal processes, represent dispersal patterns, elucidate the consequences of dispersal for population and community dynamics, and explain dispersal evolution (Chambers and MacMahon 1994; Levin et al. 2003).
Funding

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Acknowledgements

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References


Table 1: Seed traits of asymmetric seed morphologies of *Zygophyllum xanthoxylon*. The table gives means and standard deviations of seed height (vertical projection) in different seed orientations. Lognormal distributions of seed lift-off velocity ($\vec{U}_{lft}$) on different surfaces are characterized by the log-scale mean and standard deviation.

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<th>seed morphology</th>
<th>seed orientation</th>
<th>seed height (mm)</th>
<th>$\vec{U}_{lft}$</th>
<th>gravel mean</th>
<th>gravel sd</th>
<th>loam mean</th>
<th>loam sd</th>
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<th>sand sd</th>
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<td>0.14</td>
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**Table 2:** Model versions in this study regarding model complexity and output

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<th>Output</th>
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**Figure legends**

**Figure 1:** Movement across the ground between a perfect sphere (indicated by the solid ball) and an asymmetric seed (indicated by T). The sphere’s vertical projection / height (h or h’) that is exposed to airflow does not change, but the seed’s does change with orientation. \( \vec{V} \): wind velocity averaged over seed height. \( Z_{ref} \): reference height. \( \vec{U}_{ref} \): Wind velocity at \( Z_{ref} \). The insert shows the five seed morphologies and 12 seed orientations during secondary dispersal by wind in *Zygophyllum xanthoxylon*. Symmetric seeds of (a) disc type, (b) Y-type and (c) four-winged type have one orientation. Asymmetric seeds of (d) T-type and (e) \( \lambda \)-type have three and six orientations, respectively. Scale bar indicates a length of 1 cm.

**Figure 2:** Comparison of distributions of observed dispersal distance with predicted dispersal distance by different model versions for (a) T-type and (b) \( \lambda \)-type seeds. Centre lines show the medians; box limits indicate the 25\(^{th}\) and 75\(^{th}\) percentiles as determined by R software; whiskers extend 1.5 times the interquartile range from the 25\(^{th}\) and 75\(^{th}\) percentiles, outliers are represented by open circles: \( n = 640 \) sample points for observation, and \( n = 10^4 \) for model predictions.

**Figure 3:** Comparison of observed dispersal distance with those predicted by different model versions for T-type seeds.

**Figure 4:** Comparison of observed dispersal distance with those predicted by different model versions for \( \lambda \)-type seeds.

**Figure 5:** Comparison of distribution of observed proportions of stopping orientation with those predicted by Moe, MOeK1D, and MOeK3/6D for (a) T-type and (b) \( \lambda \)-type seeds. Bars show mean ± SD.
**Figure 6:** Comparison of dispersal distance predicted by MO$_3$K$_{3D}$ for T-type seeds (top row) and that by MO$_6$K$_{6D}$ for λ-type seeds (bottom row).

**Figure 7:** Comparison of distributions of seed stopping orientation predicted by MO$_3$K$_{3D}$ for T-type seeds and MO$_6$K$_{6D}$ for λ-type seeds.
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