STUDIES

Effect of the local wind reduction zone on seed dispersal from a single shrub element on sparsely vegetated land

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Abstract

Accurate predictions of seed dispersal kernels are crucial for understanding both vegetation communities and landscape dynamics. The influences of many factors, including the physical properties of seeds, the time-averaged wind speed and the wind turbulence, on seed dispersal have been studied. However, the influence of local wind speed reduction around a single shrub element (e.g. a small patch of scrub) on seed dispersal is still not well understood. Here, the spatial distribution of the wind intensity (represented by the wind friction speed $u^*$) around a single shrub element is described, with an emphasis on the variation in the streamwise direction, and assuming that the time-averaged lateral and vertical speeds are equal to zero. The trajectories of the seeds were numerically simulated using a Lagrangian stochastic model that includes the effects of wind turbulence and particle inertia. The patterns of seed deposition with and without the effect of local wind reduction were compared. The variation in seed deposition with changing wind intensity, release height and shrub porosity were also simulated. The simulation results revealed that the local wind reduction increased seed deposition in nearby regions and therefore decreased seed deposition in the regions farther away. Local wind reduction had a greater impact on short-distance dispersal than on long-distance dispersal. Moreover, the dispersal in the circumferential direction decreased once the motion of a seed moving in the streamwise direction was reduced due to the local wind reduction. As the wind intensity and release height increased, the effect of local wind reduction on seed dispersal weakened. Seed dispersal was both wider and farther as the shrub porosity increased. These results may help explain the disagreement between the mechanistic models and the fitting curves in real cases. In addition, the results of this study may improve the currently used mechanistic models by either increasing their flexibility in case studies or by helping explain the variations in the observed distributions.

Keywords: Dispersal kernel; long-distance dispersal; release height; vegetation porosity; wind intensity.

Introduction

Wind-driven seed dispersal is important in both microscale and macroscale ecological systems (e.g. Howe and Smallwood 1982; Nathan et al. 2011; Beckman et al. 2020a). The dynamics of ecosystems can only be reasonably modelled or predicted when accurate information regarding seed dispersal kernels (i.e. the probability distribution functions of the dispersed seeds) is available (Beckman et al. 2020b). Therefore, many studies, including field observations (e.g. Dorp et al. 1996; Bullock and Clarke 2000; Nathan et al. 2002b), theoretical derivations (e.g. Greene and Johnson 1989; Katul et al. 2005) and numerical simulations (e.g. Schippers and Jongejans 2005; Duman et al. 2016), have been conducted to obtain the distribution functions of dispersed seeds.

A variety of functions, such as exponential, power, log-sech, inverse Gaussian and Weibull functions, have been proposed for dispersal kernels based on their specific environmental...
settings (Heydel et al. 2014; Bullock et al. 2017, 2018; Cousens et al. 2018). On the one hand, owing to the complexity of real cases, theoretical derivations cannot always reproduce field observations because many of the parameters have been simplified. On the other hand, field measurements cannot both gather all of the dispersed seeds from the plants and provide sufficient wind information, which suggests that empirical functions are usually case dependent.

Compared to both theoretical derivations and field observations, numerical simulation is a more economical and flexible method of studying the dispersal of seeds by wind in both ideal cases and complicated field cases (Bullock and Clarke 2000; Schippers and Jongejans 2005; Kuparin et al. 2007; Bohrer et al. 2008; Duman et al. 2016). However, the reliability of simulation results depends on having a comprehensive and accurate description of the factors that can affect the dispersal of seeds. Typically, once a seed is released, the influencing factors can be sorted into two types. One type originates from the seed itself. For example, seed size, density and morphology can each affect the aerodynamic drag coefficient and the vertical terminal settling velocity of the seeds (Greene and Quesada 2016). The second type is the driving vector—wind speed. In earlier studies, only the time-averaged wind speed was used to estimate the dispersal kernel (e.g. Greene and Johnson 1989; Nathan et al. 2001). Later, turbulence was found to be crucial to seed wind dispersal, especially for long-distance dispersal (e.g. Katul et al. 2005). The influence of the vegetation density, which is parameterized using either the canopy attenuation coefficient or the leaf area index, has also been included to help describe the wind and turbulence in the presence of multiple plants (Raupach et al. 1991; Kaimal and Finnigan 1994). Thus, seed dispersal kernels can vary with vegetation density (Nathan et al. 2002a). Geographical features such as hills can also affect both wind and turbulence, and consequently seed dispersal (Trakhtenbrot et al. 2014). Recently, it was found that the intermittency of the turbulence dissipation rate increased the long-distance dispersal of seeds in a forest landscape (Duman et al. 2016).

Generally, in previous studies, wind speed has usually been assumed to be only height-dependent, and variation in wind speed in the streamwise direction has rarely been considered. Although the effect of wind reduction on seed dispersal when considering the distance from the edge of the forest to a clearing has been recognized (Greene and Johnson 1995, 1996), the effect of the wind reduction region, which is formed both within and in the lee of a single vegetation element in an open landscape, on seed dispersal has not been studied. For a single taller tree, the local wind reduction may have a limited impact on seed dispersal (Greene and Johnson 1996). Nevertheless, for a single vegetation element with a low height, the effect of the local wind reduction on seed dispersal may be significant because of the low wind speed at a low height in the atmospheric boundary layer. Once a seed is released, it may immediately move into the wind reduction region. Thus, the reduction region could thus dominate the early stage of seed dispersal process, which may be very important for the subsequent trajectories of seeds.

Measurements and simulations (e.g. Leenders et al. 2007; Yang et al. 2016; Liu et al. 2018) have revealed that the lateral and leeward flow around vegetation is affected by the presence of vegetation. In other words, the interaction between the vegetation and air flow changes the spatial distribution of the wind speed not only in the vertical direction but also around the vegetation element as well. Furthermore, the distribution of the wind reduction regions is not only affected by the vegetation height but also affected by the porosity of the vegetation elements (Leenders et al. 2011; Mayaud et al. 2017). The porosity is one parameter that can be used to describe the density level of a single vegetation element, and it is typically represented by the optical porosity (ranging from 0 to 1). A porosity value of 0 indicates a solid element with a strong effect on air flow, while a porosity value of 1 indicates a fully porous structure with no effect on air flow.

Shrubs, which reduce the risk of wind erosion, are an important vegetation type in several places, such as in arid regions and the edges of deserts (Okin 2008; Mayaud et al. 2017). Therefore, it is important to predict the development of a shrub community through seed dispersal. In this study, the influences of the local wind reduction on seed dispersal around a single shrub element were investigated, with emphasis on the local wind reduction in the streamwise direction. The spatial distribution of the local wind reduction and its parameterization are described in detail. All of the seeds were assumed to be released from a point source from a single shrub element standing alone on a surface with a low roughness. In addition to the traditional probability distributions of the deposited seeds in the radial directions, the deviation of the dispersal distance in the circumferential direction (hereafter called ‘circumferential displacement’) was also investigated, because of the heterogeneous variations of the streamwise wind speed reduction in the lateral direction. The variations in the effects of the local wind reduction on seed dispersal were investigated, and the wind intensity, release height and vegetation porosity were taken into account.

Materials and Methods

Owing to the diversity of shrub shapes in nature, for convenience, the shape of a single vegetation element was assumed to be a circular cylinder (Fig. 1A), as per previous studies (Raupach 1992; Okin 2008). The goal of this study was to investigate seed dispersal over a sparsely vegetated land surface, meaning that interactions among neighbouring shrub elements could be ignored (Leenders et al. 2007; Mayaud et al. 2017; Fu et al. 2019). A surface with a low roughness was used, based on the assumption that the ground surface was not very rough and that the height of the ground vegetation cover was small. The origin of the Cartesian coordinate system was fixed at the centre of the circular cylinder base. All of the seeds were assumed to be perfectly spherical.

Wind spatial distribution including local wind speed reduction

In real situations, the air movement around a single vegetation element is very complex due to the coupling responses between the vegetation and air flow (Mayaud and Webb 2017; Kang et al. 2019). Many studies have been conducted on the air around cylindrical elements (e.g. Kawamura et al. 1984; Rostamy et al. 2012; Fu et al. 2019). These studies have found that a local wind reduction region can form in the lee of a circular cylindrical element. The flow patterns (e.g. the vortex structures) in this region are diverse and depend on the boundary thickness, surface roughness, cylinder height and Reynolds number. However, in this study, the average lateral wind speed and average vertical wind speed were assumed to be zero for three reasons. First, the average vertical wind speed in the leeward wind reduction region of a solid circular cylinder with a low
area ratio (frontal area vs. basal area) is low (Rostamy et al. 2012). Second, the vegetation porosity could affect both the vertical and lateral wind speeds (Lv et al. 2014; Taddei et al. 2016; Tang et al. 2019). Third, the seed release point was positioned in the centre of the shrub element, meaning that the effects of both the lateral and vertical winds on the seeds’ trajectories in a wind reduction region could thus be limited. In fact, detailed field measurements of the lateral and vertical wind speeds around a shrub element are rare in comparison to streamwise wind speed measurements. Therefore, this study mainly focuses on the effects of streamwise wind reduction on seed dispersal.

The wind speed at any location over a flat surface could be expressed by Equation (1) (Raupach 1992):

\[
U(x, y, z) = \frac{u_0(x, y, z)}{\kappa} \ln \left( \frac{z}{\delta} \right)
\]

where \(U(x, y, z)\) and \(u_0(x, y, z)\) are the time-averaged streamwise speed and wind friction speed, respectively. The \(x, y\) and \(z\) coordinates correspond to the streamwise, lateral and vertical directions, respectively. \(\kappa\) is the von Karman’s constant and is usually taken as 0.41. In all of the calculations, the aerodynamic surface roughness \(\delta\) was assumed to be constant. The description of the wind speed distribution in this work was divided into two parts in accordance with previous studies (e.g. Raupach 1992; Okin 2008; Leenders et al. 2011), and as shown in Fig. 1. The first part includes vegetation elements and the leeward wind speed reduction region (Fig. 1A). The second part is the remaining region, in which the flow is not disturbed by the vegetation element (or the disturbance is so weak that it could be ignored). For the undisturbed region, the friction speed was set to be equal to the friction speed of the incoming flow, \(u_0\), as was done in previous studies (Bullock and Clarke 2000; Nathan et al. 2002a). The determination of the wind speed in the first part is relatively complicated because the friction speed of the streamwise wind was assumed to be spatially variable.

First, the friction speed at ground level along the streamwise direction should be defined. Triangles, rectangles and half-ellipses have been proposed for the basal shape of the wind reduction region in the lee of plants (Raupach 1992; Okin 2008; Leenders et al. 2011). Recent observations (Leenders et al. 2011; Chen et al. 2012; Mayaud et al. 2017) and simulations (Yang et al. 2016; Sadique et al. 2017) have indicated that the half-ellipse scheme proposed by Leenders et al. (2011) seems to be more reasonable for porosity vegetation elements, as is shown in Fig. 1B. The semi-minor axis of the half-ellipse used here was set to be \(D/2\) (where \(D\) is the diameter of the circular cylinder) (Leenders et al. 2011). The maximum streamwise length \(L_x\) of the wind reduction region (i.e. the semi-major axis) is set as \(7.5H\) (where \(H\) is the height of the circular cylinder) (Leenders et al. 2011).

The half-ellipse scheme suggests that the streamwise wind reduction in the lateral direction is heterogeneous. This indicates that, for a fixed value of \(x\) (i.e. the streamwise location coordinate), the friction speeds at different values of \(y\) over the ground \((z = 0)\) within the wind reduction region are different. For example, Leenders et al. (2011) assumed that the friction speed increases exponentially with increasing the leeward distance from the leeward edge of a shrub element towards the maximum streamwise length in the form of a half-ellipse contour (Fig. 1B). According to another study (Chen et al. 2012), the ground friction speed within a porous shrub element was assumed to decrease linearly from the windward edge of the element to the leeward edge, also in the form of half-ellipse contour (Fig. 1B). Thus, the spatial distribution of the friction speed on the ground \(u(x, y, 0)\) within the wind reduction region was determined through two steps. The first step was using Equations (2a) and (2b) (Leenders et al. 2011; Chen et al. 2012) to find the friction speed at the location where \(x = L_x\), \(L_x\) is the streamwise distance to the origin of the coordinate system along the central line (i.e. along the line \(y = 0\) in plane \(z = 0\); see Supporting Information—Fig. S1). The second step was to assign \(u(x, y, 0)\) to \(u(x, y, 0)\) when \(x\) and \(y\) satisfy the ellipse equation \((\frac{x}{L_x^2})^2 + (\frac{y}{D_y^2})^2 = 1\) (the dotted lines in Fig. 1B). Here, according to Mayaud et al. (2017), \(u_0 = (1.46 \times 0.4076)u_0\), and \(b = 1.05 \times 0 + 0.1627\), where \(u_0\) is the minimum friction speed at the leeward edge of the shrub element, \(0\) is the shrub porosity and \(b\) is the speed recovery rate of a shrub element of height \(H\).

\[
\begin{align*}
\text{if } & D/2 \leq L_x \leq D/2, \\
\text{then } & u_0(L_x, 0, 0) = (u_0 + u_0)/2 - (u_0 - u_0)L_x/D \text{ if } -D/2 \leq L_x \leq D/2, \\
\text{and } & u_0(L_x, 0, 0) = (u_0 - u_0)/2 - \exp(-L_xb)\text{ if } D/2 < L_x \leq L_x \\
\end{align*}
\]

Next, the vertical variation in the friction speed within a wind reduction region was calculated. Previous studies (Rostamy et al. 2012; Lv et al. 2014; Taddei et al. 2016) have suggested that the spatial morphology of the wind reduction region in the lee of a...
single shrub element could be roughly depicted by a quarter of an ellipse (Fig. 1A). Thus, the spatial distribution of the friction speed at height \( z \) (in the \( z \) plane within the wind reduction region) could be expressed by the half-ellipse scheme mentioned above, with a height-dependent half-ellipse \( \left( \frac{L_x}{2} \right)^2 + \left( \frac{L_y}{2} \right)^2 = 1 \) \((0.5D < L_x < L_y)\), where \( L_x \) is the maximum streamwise length of the wind reduction region at height \( z \). Moreover, the continuity of the wind speed at the interface between the wind reduction region and the undisturbed region should be maintained. Here, for simplicity, the value of the friction speed at a location \((x, y, z)\) was assumed to linearly increase from the ground to the interface as the vertical coordinate \( z \) increased (Equation (2c)):

\[
u_0(x, y, z) = \nu_0(x, y, 0) + (\nu_0 - \nu_0(x, y, 0)) / z_{\text{max}} \quad \text{if} \quad 0 \leq z \leq z_{\text{max}} \tag{2c}
\]

where \( z_{\text{max}} \) is the height (i.e. the distance from the ground to the interface) of the wind reduction region at location \((x, y)\). Note that the height of local wind reduction region is limited by shrub height (Fig. 1A), which suggests \( 0 \leq z_{\text{max}} \leq H \).

The influence of the atmospheric turbulence on seed movement was also considered. Thus, the instantaneous wind speed consists of two parts: a time-averaged wind speed and a turbulence fluctuation speed. Therefore, the instantaneous wind speeds in three directions could be written as \( u = U + u' \), \( v = V + v' \) and \( w = W + w' \). The prime represents a speed fluctuation. The streamwise speed \( U \) was determined using Equation (1). Although the time-averaged lateral speed \( V \) and vertical speed \( W \) were assumed to be zero, the effects of speed fluctuations in these two directions on seed movements were still taken into account. Because empirical wind speed and turbulence parameterizations were used and heavy particles are likely to violate the well-mixed conditions by accumulating in turbulence parameterizations were used and heavy particles are likely to violate the well-mixed conditions by accumulating in the flow, the motion of seeds in the atmospheric boundary layer is subject to many forces (Maxey and Riley 1983), for simplicity, only gravity and drag were considered in this study.

In addition, the translational movement of the seeds was calculated while the rotation was ignored, in accordance with the study of Duman et al. (2016). For a seed with an average diameter of \( d_s \), its mass is \( m \) is equal to \( \pi \rho_d d_s^3 / 6 \), where \( \rho_d \) is the seed density. The drag force acting on the seed can be estimated as \( F_{\text{drag}} = \frac{1}{2} \rho_d C_D d_s V_t^2 \), where \( \rho_d \) is the air density, \( C_D \) is the drag coefficient, which is defined as \( C_D = [(3/2 \Re_T)^{1/2} + 1]^{3/2} \) for irregular particles (Cheng 1997), \( \Re_T = \rho_d d_s V_t / \mu \), where \( \mu \) is the dynamic viscosity of air, and \( V_t \) is the speed of the particles relative to the surrounding flow. Thus, the seed's motion in three directions could be calculated using Equation (4) when turbulence is included:

\[
\begin{align*}
\frac{dx_p}{dt} &= F_{\text{drag},x} = \frac{3 \rho_d C_D}{4 \rho_p d_s} \left( \frac{dx_p}{dt} - u \right) \\
\frac{dy_p}{dt} &= F_{\text{drag},y} = -\frac{3 \rho_d C_D}{4 \rho_p d_s} \left( \frac{dy_p}{dt} - v \right) \\
\frac{dz_p}{dt} &= F_{\text{drag},z} = -\frac{3 \rho_d C_D}{4 \rho_p d_s} \left( \frac{dz_p}{dt} - w \right) - g
\end{align*}
\]

where \( x_p, y_p, \) and \( z_p \) represent the locations of the seeds in the horizontal, lateral and vertical directions, respectively, and \( g \) is the gravitational acceleration.

**Table 1.** Some constants used in this work. \( D, H/D, d_s, \rho_s, \rho_d, \mu, g \) and \( z_0 \) are shrub diameter, ratio of shrub height to diameter, seed diameter, seed density, air density, dynamic viscosity of air, gravitational acceleration and aerodynamic surface roughness, respectively.

| \( D \) (m) | \( H/D \) | \( d_s \) (mm) | \( \rho_s \) (kg m\(^{-3}\)) | \( \rho_d \) (kg m\(^{-3}\)) | \( \mu \) (kg m\(^{-1}\) s\(^{-1}\)) | \( g \) (m s\(^{-2}\)) | \( z_0 \) (m) |
|---------|---------|---------|----------------|----------------|----------------|----------------|---------|
| 1      | 0.5\(^a\) | 0.5\(^a\) | 500\(^b\)      | 1.225          | 1.78 \times 10\(^4\) | 9.81           | 0.001\(^c\) |

\(^{a}\)Based on Bullock and Clarke (2000), Leenders et al. (2011) and Mayaud et al. (2017).

\(^{b}\)Based on Bullock and Clarke (2009) and Venable et al. (2008).

\(^{c}\)Based on Raupach et al. (1991).
relative speed between the particle and the flow was adopted to depict the trajectory-crossing effect (Anderson 1987). Thus, the modified Lagrangian time scale \( T_{pz} \) is estimated using Equation (5):

\[
T_{pz} = \frac{T_r}{\sqrt{1 + (\beta V_i / \sigma w)}}
\]

where \( \beta = 1.0 \) (Kok and Renno 2009). Thus, the discrete time step for the trajectory calculation according to the Runge–Kutta method was determined to be \( dt = 0.01 \times T_{pz} \).

The inclusion of the turbulence effect (Equation (3)) leads to variations in the trajectories of seeds with the same initial speed and wind intensity conditions. Therefore, 10 stochastic runs \( 10^6 \) seeds were released in a single run) were performed for each defined calculation condition. Owing to the variable wind speed, all of the results described below are the average values for 10 runs. To obtain the statistical information for seed dispersal kernels, starting at the central location of the shrub element, 100 discrete grids were applied along the streamwise direction. The intervals of the 1st–10th, 11th–20th, 21st–30th, 31st–40th and 41st–50th grids are 0.1H, 0.2H, 0.3H, 0.4H and 0.5H, respectively. The intervals of the remaining grids are 1H.

Then, the distribution function and cumulative probability of the dispersed seeds were calculated and analysed by grid. Two streamwise distances, i.e. the L50 for which the cumulative probability reaches 50 % and the L99 for which the cumulative probability reaches 99 %, were recorded to help with the data analyses. Furthermore, the circumferential displacement \( \Delta c \) and the SD of the circumferential displacement \( \sigma_{dc} \) were calculated as

\[
\Delta c = \left( \sum_{i=1}^{n} |\Delta c_i| \right) / n \quad \text{and} \quad \sigma_{dc} = \sqrt{\frac{1}{n-1} \sum_{i=1}^{n} (\Delta c_i - \bar{\Delta c})^2} / (n - 1)
\]

where \( n \) is the total number of seeds in a grid. To eliminate the high scatter caused by the generation of random numbers in the grids where deposited seeds are very rare, the statistics for both \( \Delta c \) and \( \sigma_{dc} \) started from the grid in which the cumulative probability of the deposited seeds reached 1 %, and ended by the grid in which the cumulative probability reached 99 %. Moreover, to clarify the role of shrub porosity, the L50, L99, maximum \( \Delta c \) and normalized maximum \( \sigma_{dc} \) among all grids were normalized using the values for a shrub porosity \( \theta = 1.0 \) (i.e. without considering the local wind reduction).

The lowest friction speed that could cause seed release was assumed to be 0.2 m s\(^{-1}\) (Schipper and Jongejan 2005). To investigate how wind intensity affects the influence of the local wind reduction on seed dispersal, five sets of uniform wind intensity values \( (u_a = 0.2, 0.3, 0.4, 0.5 \text{ and } 0.6 \text{ m s}^{-1}) \) were used for the incoming air flow. Additionally, five seed release heights \( (H_r = 1.0H, 0.9H, 0.7H, 0.5H \text{ and } 0.3H) \) were used. When the effect of the local wind reduction was not considered, the shrub porosity was equal to 1. The other five values of porosity, which were based on recent field observations, were 0.3, 0.4, 0.5, 0.6 and 0.7 (Mayaud et al. 2017). Under natural conditions, wind intensity is not temporally uniform, but rather it follows the Weibull distribution law. For the hourly-averaged wind speed, the cumulative probability of the friction speed is expressed as

\[
f(u; k, c) = 1 - \exp[-(u / u_a)^k]
\]

where \( k = 2 \) (Seguro and Lambert 2000), and \( c = 2u_a / \sqrt{\pi} \). \( u_a \) is the average friction speed, where the subscript ‘a’ indicates an average value. Here, to compare the seed deposition pattern that includes the local wind reduction with the pattern that does not include it, the Weibull distribution of the wind intensity was used for the incoming air flow, where \( u_a = 0.30 \text{ m s}^{-1} \) with a maximum friction speed cut-off of \( u_a = 0.65 \text{ m s}^{-1} \).

**Verification of the model**

The numerical model was verified using the observed data for heather Calluna vulgaris presented in Table 3 of Bullock and Clarke (2000). According to their work, the size and density of the seeds were determined to be 0.58 mm and 225 kg m\(^{-3}\), respectively, and the average release height \( H_r \) was set as 0.144 m. However, the wind speed at the reference height was not given directly (Katul et al. 2005), and the architecture of the shrub element (e.g. vegetation porosity) was also not clearly described (Bullock and Clarke 2000). Here, a long-time-averaged wind friction speed of \( u_a = 0.10 \text{ m s}^{-1} \) (corresponding to the speed of 3.25 m s\(^{-1}\) at height \( H = 10 \text{ m} \)) following a Weibull distribution law and a vegetation porosity of \( \theta = 0.3 \) were assumed. Because the total number of seeds released was not clear, the relative proportion of the seed gathering was used. The relative proportion at a gathering location is the number of seeds at gathering location versus the total number of seeds at all of the gathering locations. The simulated results for the settings described above and the observed data are shown in Fig. 2. The simulated results are in good agreement in nearby regions but do not agree well at greater distance (no seeds were collected at the leeward distance > 3 m in the simulated results). This disagreement is likely mainly caused by the uncertainties in the source distribution of the seeds (related to the effective release height) and the wind information details (particularly for high wind speeds). Therefore, the numerical model is capable of capturing the main features of the observed field data and can produce reasonable outcomes.

**Results**

**General influences of the local wind reduction on seed dispersal**

Based on the comparison of the distribution pattern of the deposited seeds that considers the effect of the local wind reduction zone and the distribution pattern that does not consider the effect of the local wind reduction zone, the
local wind reduction does affect the dispersal of seeds (Fig. 3). For the figure, the average friction speed ($u_a$) is 0.30 m s$^{-1}$, the release height ($H_r$) is half the shrub height and the shrub porosity ($\theta$) is 0.5. The L50 (0.85 m) obtained for the case in which the local wind reduction is considered is reduced by 32% lower than that (1.25 m) obtained for the case in which the local wind reduction is not considered. Similarly, the L99 is 29% (5.625 m) lower when the local wind reduction is considered than when it is not considered (7.375 m). The results show that the inclusion of the local wind reduction does not change the distribution pattern of the deposited seeds. However, it does increase the probability of seeds being deposited in the nearby region, and thus, it decreases the probability of seeds being deposited in regions farther away. Moreover, the average circumferential displacement $\bar{d}_C$ (Fig. 3C) and the SD of the circumferential displacement $\sigma_{dc}$ (Fig. 3D) linearly increase as the streamwise distance increases both with and without considering the effect of the local wind reduction. However, in comparison to the case in which the local wind reduction is considered, seeds are dispersed farther away in the case in which the local wind reduction zone is not considered, which suggests that they could be dispersed over a wider area. Based on the comparison of the case that considers the local wind reduction and the case that does not consider it, the simulated data reveal that an ~25% decrease occurs at the maximum $\bar{d}_C$ (0.21 m vs. 0.28 m), and an ~27% decrease occurs at the maximum $\sigma_{dc}$ (0.16 m vs. 0.22 m) under the current wind intensity. These results suggest that not considering the local wind reduction could lead to the overestimation of seed dispersal in the circumferential direction.

**The impacts of wind intensity**

As expected, increasing the wind speed led to an increase in the probability that seeds were deposited at distances farther from the vegetation element [see Supporting Information—Fig. S3A and B], both with and without considering local wind reduction. Here, a uniform wind intensity (represented by $u_a$) was used rather than natural wind conditions. The change in the wind speed did not alter the linear responses of either $\bar{d}_C$ or $\sigma_{dc}$ to the streamwise distance [see Supporting Information—Fig. S3C and D]. The collected characteristic distances (L50 and L99) are presented in Table 2. The maximum values of both $\bar{d}_C$ and $\sigma_{dc}$, which were captured at the location where the

![Figure 3](https://academic.oup.com/aobpla/article/13/4/plab025/6279781)
cumulative probability reached 99 %, are presented in Table 3. The L50, L99, maximum $\overline{dD}$ and maximum $\sigma_{dc}$ all monotonously increased with increasing wind intensity. The variations in L50, L99, the maximum $\overline{dD}$ and the maximum $\sigma_{dc}$ with increasing wind intensity were fitted using the least square method (in the software Origin 8.0; May and Stevenson 2009).

The results indicate that L50, L99, the maximum $\overline{dD}$ and the maximum $\sigma_{dc}$ increase exponentially with increasing wind intensity ($R^2 > 0.99$ for all cases), both with and without considering the local wind reduction. The curve for L50 is $L_{50} = A_{50} \exp(k_{50}u) - 1$. The fitting constants are $A_{50,u} = 0.92$ and $k_{50,u} = 1.94$ for the case in which the local wind reduction is considered (represented by the subscript ‘w’), and the fitting constants are $A_{50,u} = 2.45$ and $k_{50,u} = 1.21$ for the case in which the local wind reduction is not considered (represented by the subscript ‘nw’). The curve for L99 is $L_{99} = A_{99} \exp(k_{99}u) - 1$. The fitting constants are $A_{99,u} = 0.57$, $k_{99,u} = 5.31$, $A_{99,u} = 0.80$ and $k_{99,u} = 5.10$. The curve for the maximum $\overline{dD}$ is $\overline{dD} = A_{\overline{dD}} \exp(k_{\overline{dD}}u) - 1$. The fitting constants are $A_{\overline{dD},u} = 0.05$, $k_{\overline{dD},u} = 3.69$, $A_{\overline{dD},u} = 0.06$ and $k_{\overline{dD},u} = 3.73$. The curve for the maximum $\sigma_{dc}$ is $\sigma_{dc} = A_{\sigma_{dc}} \exp(k_{\sigma_{dc}}u) - 1$. The fitting constants are $A_{\sigma_{dc},u} = 0.04$, $k_{\sigma_{dc},u} = 3.63$, $A_{\sigma_{dc},u} = 0.05$ and $k_{\sigma_{dc},u} = 5.59$. The rates of increase (i.e. $k$-values) for L99, the maximum $\overline{dD}$ and the maximum $\sigma_{dc}$ for the case in which the local wind reduction is considered are slightly different than those for the case in which the local wind reduction is not considered. However, the rate of increase of L50 for the case in which the local wind reduction is considered is −1.6 times that for the case in which the local wind reduction is not considered. Based on the fitting curves described above, the ratio (RL50) of the L50 considering the local wind reduction versus the L50 not considering it gradually increases from 0.64 to 0.76 as the friction speed $u$ increases from 0.2 to 0.6 m s$^{-1}$.

### The impacts of the release height

The simulation data reveal that decreasing the release height resulted in more seeds being deposited in the nearby region both with and without considering local wind reduction [see Supporting Information—Fig. S4A and B]. The change in the release height did not alter the linear responses of either $\overline{dD}$ or $\sigma_{dc}$ to the streamwise distance [see Supporting Information—Fig. S4C and D]. The characteristics distances (L50 and L99) are presented in Table 4, and the maximum $\overline{dD}$ and the maximum $\sigma_{dc}$ are presented in Table 5. It was determined that L50, L99, the maximum $\overline{dD}$ and the maximum $\sigma_{dc}$ increase with increasing release height. Further curve fittings suggest that they all linearly increase with release height. The curve for L50 is $L_{50} = B_{50} + B_{50}H/H$; and the fitting constants are $B_{50,u} = -0.99$, $l_{50,u} = 5.16$, $B_{50,w} = -0.18$ and $l_{50,w} = 4.49$. The curve for L99 is $L_{99} = B_{99} + B_{99}H/H$; and the fitting constants are $B_{99,u} = -3.81$, $l_{99,u} = 23.25$, $B_{99,w} = -0.63$ and $l_{99,w} = 20.34$. The curve for the maximum $\overline{dD}$ is $\overline{dD} = B_{\overline{dD}} + l_{\overline{dD}}H/H$; and the fitting constants are $B_{\overline{dD},u} = -0.08$, $l_{\overline{dD},u} = 0.71$, $B_{\overline{dD},w} = 0.02$ and $l_{\overline{dD},w} = 0.62$. The curve for the maximum $\sigma_{dc}$ is $\sigma_{dc} = B_{\sigma_{dc}} + l_{\sigma_{dc}}H/H$; and the fitting constants are $B_{\sigma_{dc},u} = -0.06$, $l_{\sigma_{dc},u} = 0.54$, $B_{\sigma_{dc},w} = -0.02$ and $l_{\sigma_{dc},w} = 0.47$. Similar to wind intensity, L50 exhibits the highest sensitivity to the change in the release height (referring to the values of $l$) compared to the other three quantities (i.e. L99, the maximum $\overline{dD}$ and the maximum $\sigma_{dc}$).}

### Table 2. Variations of the characteristic distances (L50 and L99) in seed dispersal from a single shrub element with wind intensity (represented by $u$). The table headings ‘with’ or ‘without’ indicates that simulations were conducted with or without considering the effect of the local wind reduction. $H = 0.5$ m, $H = 0.5H$ and $\theta = 0.5$.

| $u$ (m s$^{-1}$) | L50 (m) | L99 (m) |
|----------------|---------|---------|
|                | With    | Without | With    | Without |
| 0.2            | 0.475   | 0.650   | 1.00    | 1.350   |
| 0.3            | 0.750   | 1.050   | 2.175   | 2.775   |
| 0.4            | 1.050   | 1.575   | 4.200   | 5.25    |
| 0.5            | 1.500   | 2.025   | 7.50    | 9.50    |
| 0.6            | 2.025   | 2.625   | 13.25   | 16.25   |

### Table 3. Variations of the maximum circumferential displacement (\(dD\)) and the SD of the circumferential displacement (\(\sigma_{dc}\)) in seed dispersal with wind intensity ($u$). ‘With’ or ‘without’ indicates that simulations were conducted with or without considering the effect of the local wind reduction. $H = 0.5$ m, $H = 0.5H$ and $\theta = 0.5$.

| $u$ (m s$^{-1}$) | Max $\overline{dD}$ (m) | Max $\sigma_{dc}$ (m) |
|----------------|-------------------------|-----------------------|
|                | With    | Without | With    | Without |
| 0.2            | 0.054   | 0.065   | 0.042   | 0.050   |
| 0.3            | 0.102   | 0.125   | 0.078   | 0.096   |
| 0.4            | 0.169   | 0.210   | 0.129   | 0.161   |
| 0.5            | 0.266   | 0.326   | 0.203   | 0.250   |
| 0.6            | 0.406   | 0.501   | 0.315   | 0.382   |

### Table 4. Variation of the characteristic distances (L50 and L99) in seed dispersal with release height ($H$). ‘With’ or ‘without’ indicates that simulations were conducted with or without considering the effect of the local wind reduction. $H = 0.5$ m, $u = 0.5$ m s$^{-1}$ and $\theta = 0.5$.

| $H/H$ | L50 (m) | L99 (m) |
|-------|---------|---------|
|       | With    | Without | With    | Without |
| 1.0   | 4.200   | 4.300   | 19.750  | 19.750  |
| 0.9   | 3.700   | 3.900   | 17.000  | 17.875  |
| 0.7   | 2.550   | 2.925   | 12.250  | 13.250  |
| 0.5   | 1.500   | 2.025   | 7.500   | 9.500   |
| 0.3   | 0.650   | 1.200   | 3.500   | 5.625   |

### The impacts of the shrub porosity

Generally, the normalized L50 (NL50), normalized L99 (NL99), normalized maximum $\overline{dD}$ and normalized maximum $\sigma_{dc}$ all increase as the shrub porosity increases (Fig. 4), which suggests that more seeds are deposited at farther distances from the vegetation element, and the dispersal in the circumferential direction is enhanced. The details of the variations in the cumulative probability, probability density, average circumferential displacement and SD of the circumferential displacement with the streamwise distance are shown in Supporting Information—Fig. S5. Additionally, the NL50s were smaller than the NL99s before the shrub porosity reached 1.0 (Fig. 4A), which also implies that the local wind reduction has a greater effect on short-distance dispersal than on long-distance dispersal.
The curve fittings suggest that the cumulative probabilities of the different shrub porosities could be expressed as a logistic function ($R^2 > 0.98$; see Supporting Information—Fig. S6), that is, Equation (6):

$$y = A_2 + (A_1 - A_2)/(1 + (x/x_0)^p)$$  \hspace{1cm} (6)

where the initial value is $A_1 = 0$; the final value is $A_2 = 1.0$; $x_0$ is the location at which the cumulative probability reaches 50% (the same as the L50 defined above); and $p$ is the power that describes the shape variation of the fitting curve.

The key fitting parameters, $x_0$ and $p$, of the different shrub porosities are presented in Table 6. The fitting of $x_0$ is in excellent agreement with the collected L50 from the simulation data [see Supporting Information—Fig. S7]. The power values of $p$ decrease slightly at first and then increase as the shrub porosity increases, reflecting the main variation of the shape of the cumulative probability curve. The data analysis (Fig. 5A) reveals that $x_0$ increases exponentially as the shrub porosity increases: $x_0 = 2.69 - 2.39 \exp(-1.41 \theta)$ ($R^2 > 0.99$). Furthermore, a distance-weighted streamwise wind intensity, $u_{wc} = \int_0^\infty u_w(x,0,0)dx/u_{x}$, is proposed for the local wind reduction region. The variation in $u_{wc}$ with shrub porosity (insert in Fig. 5B) is similar to that of $x_0$ (Fig. 5A). However, $x_0$ increases linearly as the shrub porosity increases: $x_0 = 6.84u_{wc} - 1.33$ ($R^2 > 0.98$). This suggests that the effect of shrub porosity on short-distance dispersal may be reflected by its role in altering the distance-weighted wind intensity within local wind reduction region.

### Discussion

In this study, the wind dispersal of seeds released from a point source above an open landscape that is sparsely populated with shrubs was simulated by parameterizing the spatial distribution of the wind speed around a single shrub element (mainly considering the local wind reduction both within and in the lee of the shrub element) based on previous field observations (Leenders et al. 2011; Mayaud et al. 2017). The main findings obtained from the simulation are discussed below. These results increase our understanding of the reasons for the disagreement between theoretical studies and field observations and help to determine possible directions for future studies.

Although the effect of wind reduction within forests on seed dispersal has been studied (Nathan et al. 2002b, 2011), local wind reduction has not been considered when modelling the dispersal of seeds in an open landscape (Bullock and Clarke 2000; Nathan et al. 2002a), for example, seed dispersal from a shrub element in a sparsely vegetated area. However, the simulated results obtained in this study reveal that local wind reduction has a significant effect on seed dispersal in the streamwise and circumferential directions (Fig. 3), which suggests that the effect of local wind reduction should not be ignored. It should be noted that the size of the wind reduction zone is finite. Thus, the effect of local wind reduction on seed dispersal is limited, particularly for seeds that could quickly escape the wind reduction zone and have a high potential for long-distance dispersal. Therefore, local wind reduction is likely to exert a greater impact on short-distance dispersal than on long-distance dispersal.

These finding may be crucial for predicting shrub succession, which plays an important role in hindering erosion and reducing sediment transport (Leenders et al. 2007; Okin 2008; Leenders et al. 2011) in degraded and desert areas. In these areas, shrub reproduction is likely to depend on the amount of seeds in the soil seed bank because the germination of seeds and the survival of seedlings are difficult because of the extremely poor conditions in these environments (Clauss and Venable 2000).

![Figure 4](https://academic.oup.com/aobpla/article-abstract/13/4/plab025/6279781/13441_agak20527981)  

**Figure 4.** The normalized characteristic distances NL50 and NL99 (A); and the normalized maximum circumferential displacement ($\bar{\sigma}_{dc}$) and the SD of the circumferential displacement ($\sigma_{dc}$) (B) versus shrub porosity ($\theta$). $H = 0.5 \text{ m}$, $H = 0.5H$ and $u_0 = 0.5 \text{ m s}^{-1}$.  

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**Table 5.** Variation in the maximum circumferential displacement ($\bar{\sigma}_{dc}$) and the SD of the circumferential displacement ($\sigma_{dc}$) in seed dispersal with release height ($H$). ‘With’ or ‘without’ indicates that simulations were conducted with or without considering the effect of the local wind reduction. $H = 0.5 \text{ m}$, $u_0 = 0.5 \text{ m s}^{-1}$ and $\theta = 0.5$.

| $H/H$ | Max $\bar{\sigma}_{dc}$ (m) | Max $\sigma_{dc}$ (m) |
|-------|--------------------------|----------------------|
|       | With | Without | With | Without |
| 1.0   | 0.648 | 0.643 | 0.498 | 0.489 |
| 0.9   | 0.538 | 0.586 | 0.410 | 0.445 |
| 0.7   | 0.423 | 0.434 | 0.314 | 0.335 |
| 0.5   | 0.266 | 0.326 | 0.203 | 0.250 |
| 0.3   | 0.140 | 0.213 | 0.108 | 0.162 |
Therefore, short-distance dispersal (or seed deposition near the source region), which usually has a high probability density, is more ecologically meaningful for variations in local vegetation patterns than long-distance dispersal, which has a very low probability density, in these areas (Venable et al. 2008). However, the effect of local wind reduction on long-distance dispersal should not be overlooked.

In areas where suitable seed germination conditions exist, the long-distance dispersal of seeds is still crucial for the expansion and invasion of vegetation (Jongejans et al. 2008). A small difference in predicting the probability of long-distance dispersal may lead to a large mistake in the estimation of the change of species over time, such as in the case of responses to global climate change (Bullock et al. 2012; Corlett and Westcott 2013). Thus, previous studies that did not consider local wind reduction in open landscape cases (Bullock and Clarke 2000; Nathan et al. 2002a) may have underestimated the deposition of seeds in nearby regions and thereby have overestimated the probability of long-distance dispersal.

Typically, seeds are dispersed both wider and farther away as the shrub porosity increases (Figs 4 and 5). Changes in shrub porosity could remarkably alter the dispersal kernels under a given wind intensity. Because of the diversity of vegetation structures, the vegetation porosity differs among species, and it could also vary with time due to seasonal and growth stage changes. Therefore, field observed dispersal kernels in different locations could be diverse even if the wind intensities are almost identical (Nathan et al. 2000). Consequently, empirical fitting curves cannot be applied to other dispersal conditions (Bullock et al. 2017). Thus, it is

Figure 5. The parameters $x_0$ and $p$ versus shrub porosity ($\theta$) (A) and the parameter $x_0$ versus the distance-weighted wind intensity ($u_r^*$) (B). $H = 0.5$ m, $H_r = 0.5$ and $u_* = 0.5$ m s$^{-1}$.
worth including porosity into the distribution function of dispersed seeds.

The simulated results reveal that the cumulative probability of the dispersed seeds along the streamwise direction could be expressed well by a logistic function [see Supporting Information—Fig. S6A]. There are two main reasons why the commonly used log-normal probability density function was not employed in this study. First, the characteristic distance L50 is more optimally predicted using a logistic function as opposed to a log-normal probability density function [see Supporting Information—Figs S6 and S7]. The curve fitting using a log-normal function was less accurate in terms of the predictions in both the streamwise location and the value of the peak probability density [see Supporting Information—Fig. S6C and D]. Second, compared to the probability density function, the cumulative probability function is only streamwise distance-dependent and is independent of the size of the collecting grids.

The distance-weighted wind intensity, \( u_{w*} \), in which shrub porosity is included, was introduced to describe the \( x_c \) where the cumulative probability reaches 50 % (Fig. S5). The success of this introduction should be based on the fact that the majority of seeds were always deposited within the wind reduction zone under current simulation settings. However, such an attempt is still empirical, and the theoretical derivation based on physical and mathematical rules may obtain not only quantitative but also general results. Although the simulated data under the current specific settings support the selection of a logistic function, the logistic function sometimes performs poorly in locations where the cumulative probability is <10 %. Disagreement between the fitting curves and the original data is a common problem in data analyses (both field and simulation data) (Bullock et al. 2017, 2018; Cousens et al. 2018). Therefore, it would be beneficial to find a reliable method, e.g. a density function, cumulative function (Brown and Mayer 1988; Schippers and Jongejans 2005) or survival function (McNair et al. 2012) to describe the dispersal kernels in the field or for simulation data analysis of long-distance dispersal.

In this study, all of the above results and discussion mentioned above are for a single shrub element, and they were obtained by employing the spatial distribution of the wind speed constructed based on existing measurements (Mayaud et al. 2017). These measurements may capture the main features of the average wind speed around the shrub element, but the designed spatial grids used for the measurement are too large to confirm the exact shape or the boundary of the wind reduction region. There is also a lack of measurements of the wind variation within the shrub element (Mayaud et al. 2017). The height of the vegetation is another important factor affecting the local wind reduction region (Okin 2008; Leenders et al. 2011; Mayaud et al. 2017). Its effects on the description of the local wind reduction and seed dispersal require further investigation. Generally, the description of the wind speed around a single shrub element is empirical and simple. Additional studies would be valuable if they considered both the vertical and lateral wind speeds within the local wind reduction region. This requires not only studies in which ideally rigid vegetation models (both solid and porous) (e.g. Krajnović 2011; Rostamy et al. 2012; Lv et al. 2014; Taddei et al. 2016; Fu et al. 2019) are used, but also studies in which real and flexible vegetation (e.g. Walter et al. 2012; Mäiri et al. 2017; Kang et al. 2019) are used.

The shape changes and dynamic responses of vegetation to the incoming air flow may alter the vertical and lateral wind speeds and thus affects seed dispersal. Additionally, the effect of local wind reduction in cases with multiple vegetation elements is not yet clear. Large eddy simulation may be a good choice (Bohrer et al. 2008; Dupont and Brunet 2008; Pan et al. 2015) for dense vegetation cases; however, the huge computational costs arising from the grid precision, computation domain, and coupling dynamics of the air flow and vegetation are still obstacles that prevent us from obtaining reliable wind speed and turbulence values around vegetation, accurate vegetation dynamics data and subsequently, accurate information regarding the dispersal of seeds.

Finally, the effect of local wind reduction is not limited to shrub vegetation, and it may also apply to other low vegetation. For instance, it may be conditionally suitable for low trees with large crowns in an open landscape. However, the basic physical model of a tree is typically different from that of a shrub (Liu et al. 2018). Studies of the parameterization of the wind reduction region in the lee of a tree should initially focus on the differences in the geometric shape and height of the tree compared to that of a shrub, followed by the subsequent application of this method to other vegetation types.

**Supporting Information**

The following additional information is available in the online version of this article—

**Figure S1.** The distribution of surface friction velocity \( (u_w) \) along streamwise direction.

**Figure S2.** The definition of the circumferential displacement \( (dc) \) in circumferential direction.

**Figure S3.** The variation of the effect of local wind reduction on seed dispersal with the change of wind intensity.

**Figure S4.** The variation of the effect of local wind reduction on seed dispersal with the change of release height.

**Figure S5.** The distributions of deposited seeds with the change of the porosity of a single shrub element.

**Figure S6.** Curve fittings for cumulative probability and probability density of deposited seeds with the change of the porosity of a single shrub element.

**Figure S7.** Comparison of \( x_c \) obtained by fitting curves with L50 obtained by original simulated data.

**Raw data excel file.** Raw data in Figs 2–5.

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**Conflict of Interest**

None declared.

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**Data Availability**

The supplementary materials and raw data are available as Supporting Information.
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