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RESEARCH ARTICLE

Diaspore burial during wind dispersal depends on particle size of the underlying substrate

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Abstract
Purpose Burial of diaspores has significant influence on diaspore fate, seedling recruitment and population dynamics. Some studies indicated that wind speed determines burial, neglecting the effect of matrix. Burial during wind dispersal basically occurs at the matrix surface. However, little is known about how substrate, wind speed and diaspore attributes interact to determine burial.
Methods Four pure substrates with a wide span of particle sizes (from 89.10 μm to 25000 μm) were selected to investigate how the particle size affects burial. Since the real substrates in nature are mainly mixtures of these substrates in different proportions, seven mixtures were also designed to represent some real filed matrices (farmland, riparian, desert and Gobi). Diaspores from 28 species with various length, width, height, mass, shape index, projected area, terminal velocity and wing loading were selected for the burial experiments simulating by a wind tunnel.
Results Substrate but not diaspore attributes or wind speed, contributed the most to burial during wind dispersal. Burial was poorest when placed on a matrix of intermediate-sized particles (200-600 μm) at a high wind speed. With increased matrix particle size, increased wind speed changed from promoting to inhibiting burial. Effects of diaspore attributes on burial were only significant on a substrate with large particle size at all wind speeds or a substrate with small particle size at high wind speeds.
Conclusion Our most important finding is that diaspores are most difficult to be buried by wind if they are dispersal onto a substrate with intermediate-sized particles.

Keywords Diaspore morphology · Underlying matrix · Seed bank · Wind tunnel

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Introduction

Seed dispersal is an important aspect in the life history of plants (Nathan and Muller-Landau 2000; Levin et al. 2003) and includes multiple processes. For many species, burial in soil reduces exposure of diaspores to harsh physical conditions and/or predators on the soil surface (Chambers and MacMahon 1994; Fenner and Thompson 2005), and most burial happens during secondary dispersal not primary diaspore dispersal (Hulme 1998; Nathan et al. 2008; der Weduwen and Ruxton 2019). Burial can have significant consequences on diaspore fate, seedling recruitment and population dynamics (Aavik and Helm 2018; Tellier 2019). Thus, information on burial during secondary diaspore dispersal can help us understand the dynamics of target species at restoration sites, i.e. have diaspores been buried or removed to some other site (Helsen et al. 2015; Aavik and Helm 2018; Wang et al. 2020). Although burial ensures that diaspores will be retained at the site, how the underlying substrate, wind speed and diaspore attributes interact to determine burial is not well understood by ecologists.

The size of particles on the ground surface in relation to near-surface wind speed could determine if diaspores are trapped by wind-generated particle motion or by gaps between particles (Revilla et al. 2004; Burmeier et al. 2010; Ma et al. 2020; Zhou et al. 2020). Thus, we hypothesized that the underlying surface substrate is the most important factor determining diaspore burial during secondary wind dispersal. Field investigations have shown that a ground surface with gaps is more likely to intercept diaspores and increase the formation of seed banks than one without gaps (Johnson and Fryer 1992; Burmeier et al. 2010). The amount of substrate flow /movement of particles determines if the substrate covers diaspores during dispersal (Mulhearn and Finnigan 1978; Raupach et al. 1980). A field experiment in a disturbed alpine ecosystem in Montana (USA) revealed that the number of diaspores trapped by soil particles increased with an increase in particle size up to a threshold (1–2 mm or 2–4 mm, depending on species), after which no diaspores were trapped (Chambers et al. 1991). We hypothesized that this conclusion is still applicable when the range of matrix particle size is enlarged. Despite a few information in the effect of particle size on diaspore burial for single type substrate in particular regions or substrate with large particles in gravel borrow site (Chambers et al. 1991), understanding of the relationship between underlying substrate with different particle size and diaspore burial is still weak.

Studies reported that wind speed is more influential than diaspore attributes in moderating dispersal events such as diaspore burial (Nathan et al. 2002; Soons et al. 2004; Damschen et al. 2014; Liang et al. 2019). At present, it is better to pay attention to the quantitative relationship between wind and diaspore burial (Savage et al. 2014; Pinceel et al. 2016; der Weduwen and Ruxton 2019). However, due to the limitation of experimental methods, field observations make it difficult to meet the demands for a quantitative description of diaspore burial. Lack of information impedes predicting diaspore fate in windy environments and selecting vegetation restoration approaches for degraded habitats. Thus, systematic and empirical studies on how wind speed and characteristics of the underlying substrate determine diaspore should be taken into consideration.

Diaspore attributes can cause differences in motion modes and velocity of diaspore movement during wind dispersal, leading to differences in diaspore burial (Thompson et al. 1993; Egawa and Tsuyuzaki 2013; Thomson et al. 2018). Although some studies have found that mass, shape and other physical or geometric attributes of diaspores can be used to predict the possibility of burial, the conclusions are contradictory (Fenner and Thompson 2005; Liang et al. 2019). Without considering wind speed, Funes et al. (1999) showed that small and spherical diaspores were more likely to be buried on montane grasslands than long and flat diaspores. A contrasting result from a diaspore burial simulation study using eight wind speeds on sand dunes showed that burial was more likely to occur for small or flat elongated diaspores than for large or spherical ones (Liang et al. 2019). The opposite conclusions were concluded because of selection of different substrates and wind condition, so that we speculate the difference between the two studies may be the result of different substrates and wind speeds. However, current studies have paid little attention to how the substrate, diaspore properties and wind speed interact to determine the diaspore burial.

In this study, we asked two questions: 1) which factor is the most important factor in determining diaspore burial? 2) how the substrate, diaspore properties and wind speed interact to determine diaspore burial?

To answer those questions, we examined the importance of biotic and abiotic factors and their interactions on diaspore burial during wind dispersal. The experiments were conducted in a wind tunnel using 11 substrates with different particle sizes, eight wind speeds and eight attributes of the diaspores of 28 species. Specifically, we tested three hypotheses. 1) The underlying surface substrate is the most important factor determining diaspore burial during secondary wind dispersal. 2) More diaspores become buried in substrates with a large particle size than in those with a small particle size. 3) The effect of diaspore attributes and wind speed in determining burial is modified by particle size of the substrate.

Method and materials

Wind tunnel

Experiments were conducted in a wind tunnel at the Experimental Center of Desert Forestry. The wind tunnel consists of three sections: a power section, an air laminating and filtering section that stabilizes the air flow and a detachable experimental section (Fig. 1a). The wind tunnel was 20 m long (experimental section) with a cross Sect. 2 m wide and 2 m high. The operational wind speed can be continuously adjusted between 0 and 18 m•s^{-1}. Due to the large size, this wind tunnel can meet the physical similarity conditions such as geometric similarity, kinematic similarity and dynamic similarity during diaspore motion (Liu et al. 2015), and it has been used to study movement of diaspores on the soil surface and on varied surface configurations (Zhou et al. 2019, 2020).

Selection of the underlying surface substrate

The basic substrates were collected in nature from April 2019 to August 2021 in batches: loam from farmland, aeolian sand from a desert sand dune, river sand from a riparian area and gravel from Gobi desert (Fig. 1b). Loam was collected from the Ulanbuhe irrigation area of Inner Mongolia Province of China (107º35' E, 40º3' N), aeolian sand from the Ulanbuhe desert area (106.35º35' E, 40º17' N), river sand from the riparian zone of the Yongding river in the Haihe River Basin of Hebei Province of China (114º28' E, 38º16' N) and Gobi gravel from the Gobi region at the foot of Wolf Mountain in the Yin mountains of Inner Mongolia Province of China (117º41' E, 41º28' N). For farmland loam, aeolian sand river sand and gravel substrate material to a depth of 30 cm was collected. The area of each sample is 4 m^2. Ten samples were selected using the checkerboard approach on each substrate. To eliminate the influence of moisture on the experiments, the substrates were spread in a thin layer and naturally air-dried, and then all non-substrate materials (plants, gravel) were removed using a sieve (mesh size of 5 mm). Gobi gravel with a diameter of approximately 2.5 cm were selected by hand.

Particle size of the underlying surface substrate

Eleven types of ground surfaces (substrates) including natural loam, aeolian sand, river sand, gravel, and seven mixtures thereof were designed. Natural substrates, included 100% loam (L), 100% aeolian sand (A), 100% river sand (R), 100% gravel (G), Mixtures (like aeolian sand (50%) + gravel (50%) (AG), loam (50%) + gravel (50%) (LG), river sand (80%) + gravel (20%) (RG1), river sand (50%) + gravel (50%) (RG2), river sand (20%) + gravel (80%) (RG3), loam (50%) + aeolian sand (50%) (LA), loam (33%) + aeolian sand (33%) + gravel (33%) (LAG)) were uniformly mixed in a certain volume ratio and air-dried. Particle size of loam, aeolian sand and soil samples were measured using the Particle Size Analyzer (Eye-Tech-combo) and the size of gravel were measured with a Vernier caliper. The particle size of each mixtures was calculated as weighted average particle size (Fig. 1b). All of those substrates laid 20 cm thick in the experimental section of wind tunnel.

Diaspore selection and measurement

Diaspores with different morphological properties from 28 species were used in this study, forming quantitative gradients of mass (M), length (L), width (W), height (H), projected area (PA), shape index (SI), wing loading (WL) and terminal velocity (TV) (Fig. 2). Five plants of each species were haphazardly selected in the natural community, and 10 mature and intact diaspores of each plant were randomly collected. To avoid loss of diaspore, at least fifty diaspores of each species were collected and dried naturally under dry and ventilated environment in the laboratory for the measurement of diaspore attributes

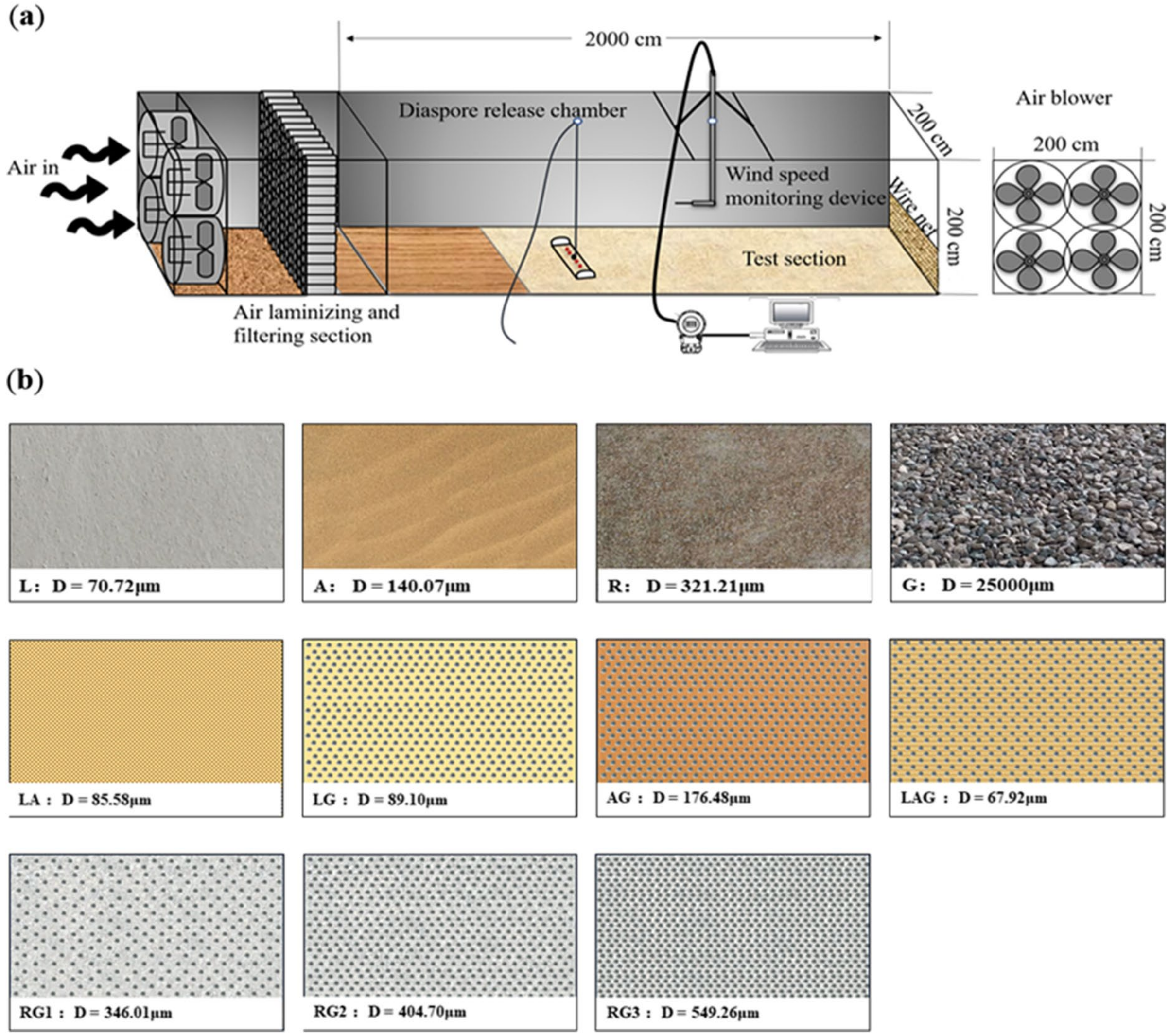

Fig. 1 Diagram illustrating measurement of diaspore burial using a wind tunnel. Schematic diagram of wind tunnel with supporting monitoring equipment (**a**). Eleven types of substrates used in this study (**b**). The basic substrate types are only loam (L), aeolian sand (A), river sand (R) or gravel (G). The seven mixed matrix types are: in Loam (50%) + Aeolian sand (50%) (LA), Loam (50%) + Gravel (50%) (LG), Aeolian sand (50%) + Gravel (50%) (AG), River sand (80%) + Gravel (20%) (RG1), River sand (50%) + Gravel (50%) (RG2), River sand (20%) + Gravel (80%) (RG3) and Loam (33%) + Aeolian sand (33%) + Gravel (33%) (LAG). D is the weighted average particle sizes of each substrate

and diaspore burial percentage. Those dried diaspores were colored with water-based markers (hairs) and red aerosol paint (wings, thorns and diaspores without appendage) to aid in finding buried diaspores.

Twenty individual diaspores of each species were selected for measuring diaspore attributes. Diaspore attributes, including diaspore mass, length, width, height, projected area, terminal velocity, wing loading and shape index, were selected to certain the determinants of diaspore burial, since they frequently have been used for predicting diaspore dispersal by wind (Casseau et al. 2015; Liang et al. 2020; Qin et al. 2022). The diaspore attributes were measured and calculated as in Liu et al. (2021). A mass range of 1.12–231.46 mg, a projected area range of 3.453–448.758mm^2, a wing loading range of 0.018–2.890 mg·mm^{-2}, a terminal velocity range

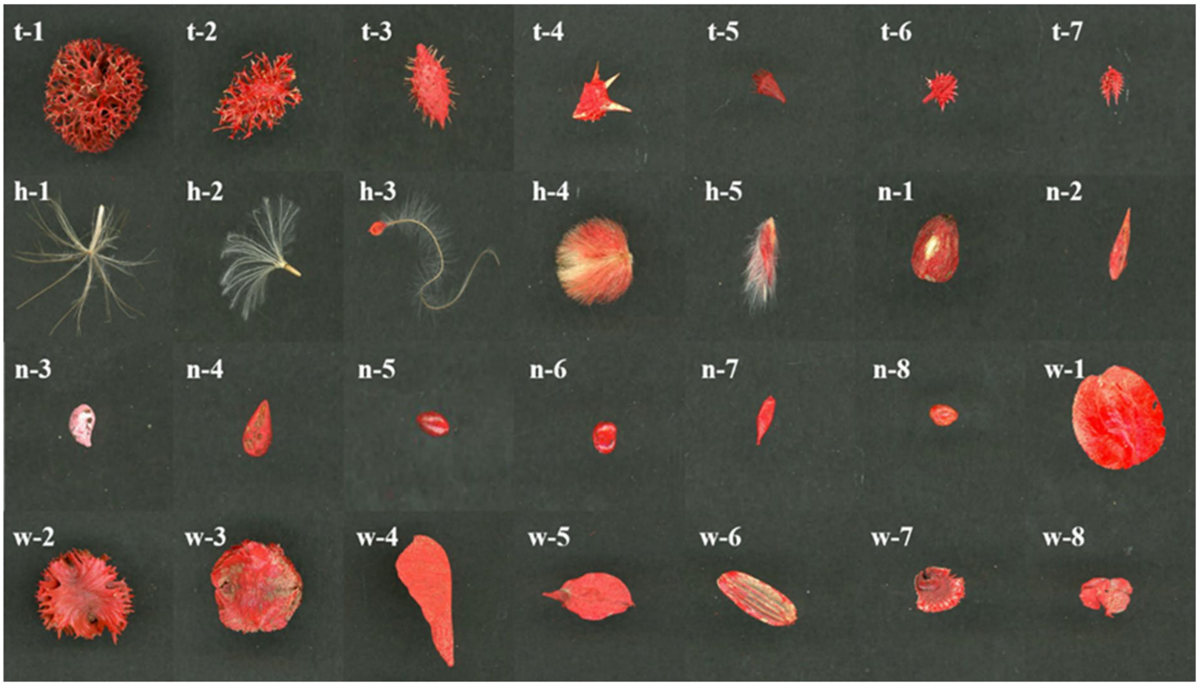

Fig. 2 Diaspores of the 28 studies species. (t-1) *Calligonum arborescens*; (t-2) *Calligonum alaschanicum*; (t-3) *Xanthium strumarium*; (t-4) *Tribulus terrestri*; (t-5) *Agrimonia pilosa*; (t-6) *Lappula intermedia*; (t-7) *Tragus berteronianus*; (h-1) *Scorzonera divaricata*; (h-2) *Saussurea japonica*; (h-3) *Clematis intricata*; (h-4) *Reaumuria trigyna*; (h-5) *Clematis fruticosa*; (n-1) *Tournefortia sibirica*; (n-2) *Leymus racemosus*; (n-3) *Platycladus orientalis*; (n-4) *Nitraria tangutorum*; (n-5) *Panicum bisulcatum*; (n-6) *Euonymus maackii*; (n-7) *Carex lehmannii*; (n-8) *Thermopsis lanceolata*; (w-1) *Sarcozygium xanthoxylon*; (w-2) *Calligonum rubicundum*; (w-3) *Calligonum leucocladum*; (w-4) *Acer negundo*; (w-5) *Ulmus pumila*; (w-6) *Ferula bungeana*; (w-7) *Althaea rosea*; (w-8) *Haloxylon ammodendron*

of 0.585–4.802 m·s^{-1}, a shape index range of 0.001–0.204, a length range of 3.150–34.230 mm, a width length range of 1.814–25.633 mm, a height range of 0.417–25.345 mm.

Wind speed design and control

We modelled the wind velocity in our experiments based on common natural settings and used in our experiments., wind speeds of 3, 4.3, 5.6, 6.9, 8.2, 9.5, 10.8 and 12.1 m·s^{-1} (measured at 1 m above the ground) corresponding to the Beaufort wind scale from level 2 to 6 (Mather 1987). Wind speed was set by adjusting the transducer of the wind tunnel and monitored with a pitot tube (160–96, Dwyer Instruments, Inc., IN, USA) connected to a Magnesense II Differential Pressure Transmitter (MS2-W102-LCD, Dwyer Instruments, Inc.) inside the tunnel. The pitot tube was inserted through the wind tunnel via the pitot hole and was 1 m above the underlying surface and 8 m away from the power section (Fig. 1a).

Measurement of the percentage of diaspore burial

Diaspore burial is the underground distribution of diaspores. In this study we described diaspores covered by matrix to be diaspore burial according to the definition of Liang et al. (2019). Wind tunnel experiment were conducted from April 2019 to August 2021. Ten diaspores of each species were released from 10 cm above the sand surface near the starting point of the test section of the wind tunnel, making diaspores randomly lay on the surface. After landing, diaspores were covered with a specially designed iron cover to prevent movement before the wind speed reached the desired level. When the wind reached a target speed (3, 4.3, 5.6, 6.9, 8.2, 9.5, 10.8 and 12.1 m·s^{-1}), the iron cover was pulled up to expose diaspores to the wind. Five seconds later, transducer of the wind tunnel was turned off. We then used the shovels and brushes to retrieve the diaspores buried within the entire test section. Each trial for each wind speed was replicated five times.

Data analysis

Mixed-effect models were conducted to analyze the effect of substrate type, wind speed and diaspore attributes (M, SI, TV, WL, PA, L, W, H) on diaspore burial. The fixed-effect term of the model was substrate, wind speed or a certain diaspore attribute, and the random-effect term was species. Models were fitted using restricted maximum likelihood estimate (MLE) via R package lme4 (De Boeck et al. 2011). The significance of fixed-effect term was accessed using likelihood ratio tests of the null model without matrix against the full model with matrix (Zuur et al. 2009). One-way ANOVA was conducted to analyze changes in probability of diaspore burial in each substrate with a different particle size. Regression analysis was used to analyze the relationship between diaspore burial and wind speed on each substrate. And then the interaction between substrate and wind speed on diaspore burial was determined by comparing the slopes of regressions. Linear mixed model analysis was also conducted to test the interaction effect of wing loading, wind speed and diaspore attributes on burial percentage. The relationship between diaspore attributes and the probability was accessed by correlation analysis. And then polynomial regression analysis was used to evaluate diaspore burial corresponding to explanatory factors (diaspore mass, projected areas, shape index, wing loading, terminal velocity, length, width, height) on each type of substrate during each wind speed.

Results

Contribution of wind speed, diaspore attributes and underlying substrate to diaspore burial

Characteristics of the underlying substrate, wind speed and diaspore attributes all had a significant effect on the probability of diaspore burial ($F = 500.5$; $p < 0.05$). All factors combined explained 79.6% of the total variation in the percentage of diaspores that was buried. Underlying matrix was the most important factor determining the probability of burial and explained 77.2% of the variation. Wind speed and diaspore attributes explained 0.8% and 4% of the total variation, respectively. Of eight diaspore attributes, terminal velocity was the most important, and it explained 1.0% of the total variance (Table 1).

Percentage of diaspore burial in relation to the particle size of underlying substrate

There was significant variability in diaspore burial percentage on underlying substrates with different particle sizes ($F = 828.5$; $P < 0.05$). In total, mean diaspore burial percentage increased from 0% on the R, RG1, RG2 and RG3 substrate types (particle size of 200–600 μm) to 91.27% on the G substrates (particle size over 600 μm). Diaspores were not buried on substrates R, RG1, RG2 and RG3 with particle size of 200–400 and 400–600 μm. The percentages of diaspore burial on LAG, L, LA, LG, A, AG substrates (particle size less than 200 μm) were less than 10% (Fig. 3a). When accounting for wind speed, mean diaspore burial percentage on substrates R, RG1, RG2 and RG3 (particle size of 200–600 μm) was still lower than that on substrates LAG, L, LA, LG, A, AG and G under each wind speed (Fig. 3b).

Table 1 Explanations and contributions of impact factors to the total variation in diaspore burial percentage

Factors	Traits	R^2	F	P
Wind	Wind speed	0.008	20.86	< 0.05
Diaspore attributes	Mass	0.000	0.301	0.583
	Projected area	0.004	11.09	< 0.05
	Shape index	0.000	0.261	0.609
	Wing loading	0.005	11.88	< 0.05
	Terminal velocity	0.010	23.79	< 0.05
	Length	0.007	17.07	< 0.05
	Width	0.007	16.37	< 0.05
	Height	0.007	17.2	< 0.05
Matrix	Particle size	0.7716	828.5	< 0.05
Total		0.7955	500.5	< 0.05

Significant at the level of $p < 0.05$

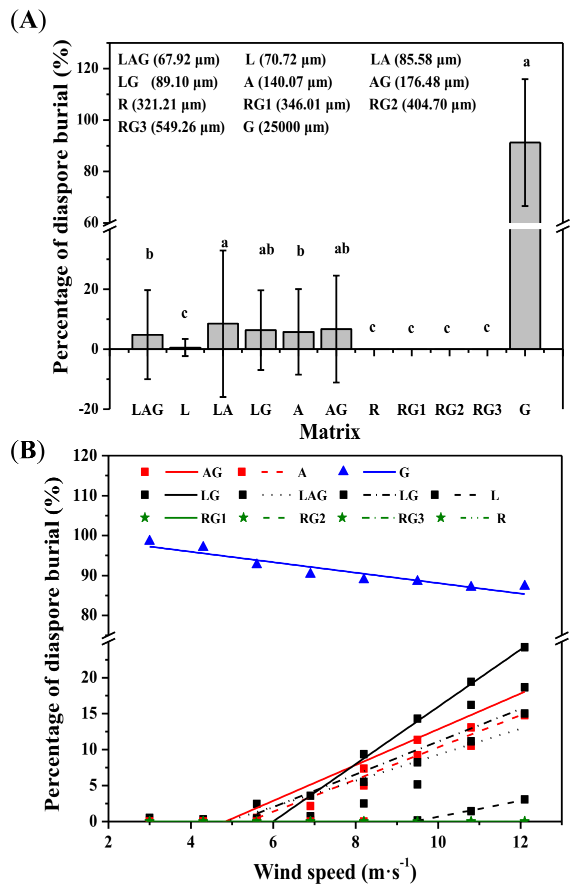

Fig. 3 Comparison of diaspore burial percentage on 11 underlying substrates. In the box plot (**a**), Different letters indicate significance differences between the type of the substrate ($p<0.05$). Vertical bars represent the standard error of the means. In the linear regression diagram between diaspore burial percentage and wind speed on each substrate (**b**), black represents a substrate with particle size of 0–100 μm, red a substrate with particle size of 100–200 μm, green a substrate with particle size of 200–400 μm, blue a substrate with particle size over 600 μm. The regression equations are as follows: $y_{AG}=-12.024+2.484x$ ($R^2=0.755$), $y_A=-12.018+2.653x$ ($R^2=0.921$), $y_G=101.149–1.308x$ ($R^2=0.872$), $y_{LG}=-11.643+2.275x$ ($R^2=0.862$), $y_{LAG}=-8.813+1.811x$ ($R^2=0.692$), $y_{LG}=-11.643+2.275x$ ($R^2=0.862$), $y_L=-10.617+1.126x$ ($R^2=0.990$), $y_{RG1}=0$, $y_{RG2}=0$, $y_{RG3}=0$, $y_G=0$

Interaction of wind speed and substrate particle size on diaspore burial

Wind speed and particle size of the substrate had an interactive effect on diaspore burial percentage ($F=20.86$; $p<0.05$). For substrates LAG, L, LA, LG, A, and AG (particle size less than 200 μm), the percentage of diaspore burial increased with wind speed when the threshold of wind speed was reached. The regression slope indicated that a onefold increase in wind speed was approximately associated with a twofold decrease in diaspore burial percentage except for substrate L. For substrates R, RG1, RG2 and RG3 (particle size of 200–600 μm), the percentage of diaspore burial was 0% and did not vary with wind speed. For substrate G with particle size over 600 μm, the percentage of diaspore burial decreased with wind speed. The regression slope indicated that a onefold increase in wind speed was associated with a 1.3-fold decrease in diaspore burial percentage (Fig. 3b).

Interaction of wind speed, diaspore attributes and substrate particle size on diaspore burial

Diaspore attributes, wind speed and particle size of the substrate had an interactive effect on diaspore burial ($F=4.913$; $p<0.05$). Of eight diaspore attributes, wing loading and terminal velocity were positively correlated with the percentage of diaspore burial. Diaspore length, width height and projected area, were negatively correlated with the percentage of diaspore burial. Diaspore mass and shape index were not significantly correlated (Table 1). For substrate LAG, wind speed was more important than diaspore attributes (Table 2). When wind speed was ≥ 10.8 m/s, the effect of diaspore traits on burial began to be significant: for substrate L wind speed was ≥ 12.1 m/s; LA, ≥ 8.2 m/s; LG and G, 5.6 m/s; AG, ≥ 12.1 m/s (Fig. 4a-f). Thus, diaspore attributes did not affect burial at low wind speeds, and wing loading was the most important determinant of diaspore burial at high wind speeds when the particle sizes were very small. As particle size increased, terminal velocity was the most important determinant of diaspore burial at high wind speeds. For substrates R, RG1, RG2, and RG3, neither wind speed nor diaspore attributes had a relationship with burial (Table 2, Fig. 4g-j). For substrate G, diaspore attributes were more important than wind speed. When wind speed was ≥ 5.6 m/s, most diaspore attributes (L, W, H, PA, WL, TV) influenced diaspore burial, and terminal velocity was the most important diaspore attribute in determining burial at each wind speed (Fig. 4k).

Table 2 Correlation between impact factors and diaspore burial probability on each substrate

Matrix	WS	M	PA	SI	WL	TV	L	W	H
AG	.364**	-.065	-.162*	-.003	.170*	.198**	-.177**	-.196**	-.161*
L	.274**	-.054	-.117	.007	.161*	.162*	-.156*	-.161*	-.131
LA	.356**	-.106	-.216**	-.064	.318**	.291**	-.282**	-.245**	-.187**
LG	.424**	-.095	-.156*	.106	.018	.113	-.138*	-.197**	-.210**
A	.373**	-.073	-.120	.118	.099	.169*	-.080	-.132*	-.193**
AG	.416**	-.037	-.115	.152*	.059	.139*	-.122	-.164*	-.200**
R	0	.000	0	.000	0	0	0	0	0
RG1	0	.000	0	.000	0	0	0	0	0
RG2	0	.000	0	.000	0	0	0	0	0
RG3	0	.000	0	.000	0	0	0	0	0
G	-.158*	.127	-.308**	-.037	.354**	.585**	-.464**	-.375**	-.415**

*: significant at the level of $0.01 < p < 0.05$, **: significant at the level of $p < 0.01$

WS: wind speed ($m \cdot s^{-1}$), M: diaspore mass (mg), PA: projected area (mm^2), SI: shape index, WL: wing loading ($mg \cdot mm^{-2}$), TV: terminal velocity ($m \cdot s^{-1}$), L: diaspore length (mm), W: diaspore width (mm), H: diaspore height (mm)

Discussion

Relative importance of underlying substrate, diaspore attributes and wind speed on diaspore burial

The size of particles of the underlying surface (substrate) plays the most important role in diaspore burial during secondary wind dispersal (Table 1). This was surprising, because wind speed, not underlying substrate, has previously been considered to be the major factor determining diaspore burial during wind dispersal (Liang et al. 2019). The result may be explained that underlying matrix may affect diaspore burial not only by direct tarp but also indirect regulation of near-surface wind speed. Once the diaspores were trapped by underlying matrix, wind speed and diaspore morphology may have little influence on diaspore burial. Thus, the underlying substrate is better than diaspore attributes and wind speed for predicting diaspore burial and thus which substrate potentially would allow the diaspores to form a seed bank.

Influence of underlying substrate on diaspore burial

We found that diaspores on substrates with medium-sized particles are not easily buried by wind (Fig. 3a). Therefore, our hypothesis that more diaspores are buried by substrates with large rather than small particles is partially supported. This may be due to the relative movement between diaspores and underlying substrate particle. When the movement of the diaspores is faster than that of the medium particles, the matrix particles will fail to cover the diaspores and make them buried.

Diaspore burial percentage on substrates R, RG1, RG2, and RG3 was lower than that on substrate G (Fig. 3a, b), suggesting that diaspores are more likely to be buried by substrates with a large particle size than those with a medium particle size. This relationship was also found by Chambers et al. (1991) who used five substrates with particle sizes ranging from 0.5 mm to 16 mm. However, diaspore burial percentage on substrates LAG, L, LA, A, AS, LG, and AG in our study was higher than that on substrates R, RG1, RG2, and RG3 (Fig. 3a, b), indicating that diaspores are less likely to be buried in substrates with a medium particle size than those with a small particle size. This may be because the movement of small particle move faster than medium particles, making it easier for the small particle to cover diaspores than the medium particles. To date, no study has suggested how a substrate with a particle size less than 0.5 mm affects diaspore burial. Therefore, we conclude that diaspores are most difficult to bury in a substrate with medium-sized particles. These findings help support the general perception that a seed bank is not easily formed on substrates with a medium particle size during diaspore dispersal by wind.

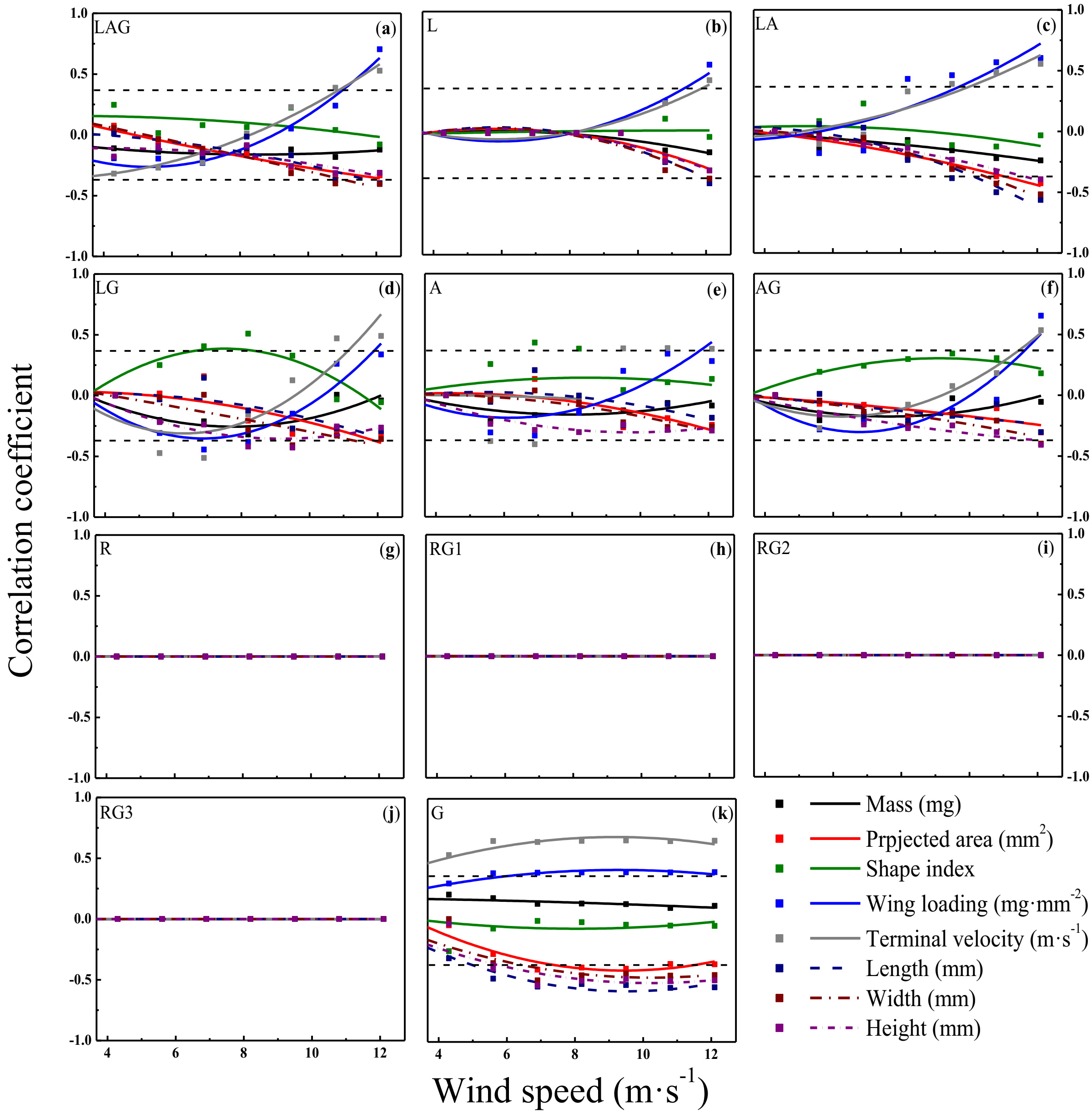

Fig. 4 Correlation coefficient between diaspore attributes (including diaspore mass, projected area, shape index, wing loading, terminal velocity, length, width and height) and burial probability various with different wind speed within each substrate: (**a**) LAG, (**b**) L, (**c**) LA, (**d**) LG, (**e**) A, (**f**) AG, (**g**) R, (**h**) RG1, (**i**) RG2, (**j**) RG3, (**k**) G. Black dashed lines are significant lines. Points outside the horizontal line indicate that the attributes of diaspores have a significant effect on burial. The area between the two lines has no correlation between diaspore attributes and seed burial

Relationships between diaspore burial and wind speed within underlying substrate

Wind speed plays a more important role in diaspore burial on substrates with a small particle size than on those with a large particle size (Table 2), and there was a positive relationship between diaspore burial percentage and wind speed on substrates with small particle size when wind speed reached the threshold at which diaspores are buried (Fig. 3b). Our findings could be attributed to the fact that small soil particles are more easily moved than the diaspores as wind speed increases (Tegen and Lacis 1996; Bo et al. 2013), which will cause burial of the diaspores. However, overall, more diaspores were buried at high than at low wind speed, thus we can predict the burial of diaspores more accurately by knowing the wind speed on a certain type of substrate.

There was a strong negative correlation between wind speed and diaspore burial when diaspores dispersed on substrates with large particle size (Fig. 3b). Substrates with large particle size have many cracks that can trap diaspores (Johnson and Fryer 1992; Burmeier et al. 2010), and the diaspores are more likely to take off from the substrate as wind speed increases, escaping these cracks. Thus, on a substrate with large particles, we must consider the role of wind speed in diaspore burial.

Interaction of underlying substrate, diaspore attributes and wind speed in determining diaspore burial during wind dispersal

Determination of the parameters that can reasonably characterize the capacity of diaspores to become buried during dispersal by wind is an important focus of dispersal biology (Funes et al. 1999; Casseau et al. 2015; Saatkamp et al. 2019). We found no relationship between diaspore attributes and burial on substrates with a medium particle size (Fig. 4g-j), which conflicts with the suggestion that diaspore attributes were a good predictor of diaspore persistence in a dryland riparian ecosystem (Stromberg et al. 2008). This difference may be due to our decision to air-dry substrates to remove the effect of moisture in our study. Moisture of soil could increase diaspore retention by promoting diaspores to secrete mucus or bending its appendage (Chambers et al. 1991). Meanwhile, diaspore retention can increase the chance of seed bank formation, providing the possibility for germination and colonization (Helsen et al. 2015). The effect of moisture on diaspore burial is a very interesting topic and could be studied further. Effects of diaspore attributes on burial were only significant on a substrate with a large particle size at all wind speeds or at high wind speeds on a substrate with small particle size. Thus, the substrate is important in determining if diaspores are buried by the wind, and diaspore attributes can be ignored when predicting diaspore burial on a substrate with medium particle size.

A seed bank was more likely to be formed for small diaspores with poorly flight ability than for large diaspores with strong flight ability (Fig. 4). This may be a trade-off between dispersal and colonization strategies. Species with strong flight ability are predicted to have reduced diaspore retention because their offspring can dispersal to wider space, access to more resources, and hence establish in relatively adverse environments. Liang et al. (2019) reported that diaspore attributes had an effect on burial at a high wind speed in sand dune systems, which supports our conclusion. Shape and mass may be important factors determining diaspore movement (Stromberg et al. 2008; Casseau et al. 2015; Planchuelo et al. 2016), Presumably, elongated diaspores are more likely to be buried on the ground than spherical ones (Liang et al. 2019), but our results showed that only on substrates LG and A during medium wind speed was there a significant positive correlation between diaspore shape (shape index) and burial. Diaspore mass had no effect on burial under any condition (Fig. 4d, e). Liang et al.'s use of rugged terrain of a sand dune as the underlying surface configuration may have led to a contorted estimation of the contribution of diaspore attributes to burial.

Terminal velocity and wing loading may be important parameters for predicting the capacity of diaspore burial, since they are linked to diaspore movement. Johnson and Fryer (1992) showed that the square root of wing loading was associated with terminal velocity, and both wing loading and terminal velocity have a negative relationship with the flight ability of diaspores (Fauli et al. 2019). Here, we focused on the importance of wing loading and terminal velocity in determining diaspore burial and confirmed that wing loading or terminal velocity were the crucial parameters influencing burial on substrate with small or large particle size during high wind speed (Fig. 4). This result provides theoretical support for the establishment of a model for diaspore burial during wind dispersal and for evaluation of the capacity of diaspores to enter the soil.

Diaspore size determined by length, width and height are crucial factors in determining burial (Funes et al. 1999; Pinceel et al. 2016). Some studies suggested that small diaspores are easier to bury than large ones (Fenner and Thompson 2005; Liang et al.

2019). Indeed, our results show that diaspore size (L, W, or H) had a significant impact on burial by substrate types that promote burial (Table. 2). Thus, diaspore size should be taken into consideration in predicting the burial of diaspores.

Conclusions

Our study using 11 flat substrate types with different particle sizes and 28 species with various diaspore attributes enhances our understanding of diaspore burial by wind. Our study illustrates how the underlying substrate, wind speed and diaspore attributes can interact to determine if diaspores become buried in the field. Our data shows that diaspore burial is most closely correlated with substrate particle size instead of wind speed and diaspore attributes. And diaspores are least likely to be buried by wind if they are released on a substrate that has intermediate-sized particles. The results from our study highlight the importance of particle size of the underlying surface matrix on diaspore burial during diaspore secondary dispersal by winds, which is helpful to predict, model and regulate seed availability. And it suggests that we can modify the substrate and select adaptive species to accelerate diaspore burial by wind and thus help facilitate restoration of degraded areas.

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Author contributions ZL, LZ, WL and ML conceived the ideas and designed the study. LZ, LT, ZX, QZ and CB collected the data. LZ analyzed the data and led the writing of the first draft of the manuscript. ZL, and CCB revised several drafts of the manuscript. All authors gave final approval for publication.

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Data availability The data that support the findings of this study are available from the corresponding author upon reasonable request.

Declarations

Conflicts of interest The authors have no conflicts to declare.

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