Plant canopy may promote seed dispersal by wind

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Seed dispersal has received much research attention. The plant canopy can intercept diaspores, but the effect of the plant canopy (the aboveground portion of a plant consisting of branches and leaves) on dispersal distance has not been explored empirically. To determine the effect of plant canopy on seed dispersal distance, a comparison of diaspores falling through open air and through plant canopy was made in a wind tunnel using three wind speeds and diaspores with various traits. Compared with diaspores falling through open air, the dispersal distance of diaspores falling through plant canopy was decreased or increased, depending on wind speed and diaspore traits. When falling through a plant canopy, dispersal distance of diaspores with thorns or those without appendages was promoted at low wind speed (2 m s−1), while that of diaspores with low wing loading (0.5 mg mm−2) and terminal velocity (2.5 m s−1) was promoted by relatively high (6 m s−1) wind speed. A plant canopy could increase seed dispersal distance, which may be due to the complicated updraft generated by canopy. The effect of maternal plants on seed dispersal regulates the distribution pattern and the species composition of the community.

Seed/diaspore dispersal can influence the spatial pattern and dynamics of a plant species at the population and metapopulation levels1–3, and it is an important research topic6,7. Seeds can be dispersed in multiple ways, and, on average, 10–30% of seeds and up to 70% of the plant species in temperate plant communities are more conducive to wind dispersal8. Any seed will be affected by wind9, which may further affect seed dispersal. Wind dispersal of diaspores occurs in all types of vegetation1, Wind can promote lateral dispersal speed of diaspores, and diaspor dispersal time/distance can be prolonged by strong horizontal wind2,10. The common wind levels in open xerophytic forest are 3–7 of Beaufort scale, occasionally can reach 8 levels, and wind speeds above 8 levels are rare8. Since wind speed and direction are variable, it is difficult to collect data on diaspor dispersal in the field11. Thus, wind tunnels make it possible to conduct controlled experiments on the effects of wind on diaspor dispersal12–15.

Dispersal distance means how far a seed is moved away from the mother plant1, which affects the distribution pattern of seeds10,16,17. The pattern of diaspor dispersal will determine if the new plant becomes established in a habitat where the level of competition is low enough to be favorable for establishment and growth or if there is a high level of competition17. Thus, dispersal of diaspores may increase regional biodiversity18, and it can affect the management of weeds and endangered species19. Research on seed dispersal distance can facilitate an accurate prediction of population dynamics and distribution and improve the theoretical basis for vegetation restoration and biodiversity conservation.

Seeds are often the diaspores that are dispersed9, but the dispersed diaspores of angiosperms can be fruits or fruits plus appendages such as the bracts, perianth or parts of plants, tumbleweeds dispersal through whole plants20–22. The type of diaspor appendages will affect the way of seed dispersal22,23, and the diaspor with hairy or wing will be subjected to greater updraft2, which is more conducive to wind dispersal. Winged diaspores often fall in a rotating manner through the air, and the speed at which the size of the wing decreases is significantly correlated25. Diaspor traits, such as the maximum speed when air resistance exerted on the seed is equal to its pull of gravity during free fall in motionless air (terminal velocity) and the ratio of mass to projected area (wing loading), are important indicators to evaluate seed wind dispersal24.

The assumption in most theoretical studies, especially models on diaspor dispersal distance, is that diaspores are released through open air, and these studies have considered the movement of diaspores from the release point20,26,27. Although Cousens and Rawlinson (2001) considered the shape of the canopy into the seed dispersal model, they did not explore the influence of the morphological properties of the diaspor28. Previous
Surface) were set at 2, 4 and 6 m \( s^{-1} \), and they correspond to categories 3–5 of meteorological wind measures (Mather, 1987). In this study, wind speeds (measured 1 m above the flat sand surface) connected with a Magnesense II Differential Pressure Transmitter (MS2-W102-LCD, Dwyer Instruments, Inc., Indiana, USA) were monitored inside the tunnel with a Pitot tube (160-96, Dwyer Instruments, Inc., Michigan, USA). Wind speed was controlled by a wind tunnel (with a test section 2 m high \( \times \) 2 m wide \( \times \) 20 m long) was used to test our hypothesis, controlled experiments were conducted in a wind tunnel, using 29 species with different diaspore traits.

### Materials and methods

#### Diaspore selection and trait measurements.

To determine the relationship between diaspore traits and dispersal distance of diaspores passing through plant canopy versus through open air at different wind speeds, we selected diaspores of 29 plant species that differ in appendage type, mass, projected area, shape index, wing loading, and terminal velocity (Table 1), differences in traits of the selected species were not restricted by phylogeny, and each diaspore was only considered as a representation of its own morphological attributes. Firstly, diaspores with different types of appendages (samara, wing, thorn, hair and balloon) were selected, and then the gradient of the same appendage diaspores was set according to the quality.

To facilitate seed dispersal investigation, diaspores with samaras, wings, thorns, and without appendage were lightly sprayed with red aerosol paint, while diaspores with hairs were colored using red water-based markers. The dyed diaspores were naturally air-dried and placed in plastic boxes to ensure the integrity of morphological structure. Diaspore traits are measured after dyed and dried.

Twenty intact diaspores of each type were selected the same species for measurements of length, width, and thickness of each diaspore were measured with Vernier caliper (0.01 mm accuracy). Diaspore shape index (Vs) was calculated using an equation we developed from ideas in Thompson et al. (1993).

\[
V_s = \frac{\sum (x_i - \bar{x})^2}{N},
\]

where \( N = 3 \), \( x_1 = \frac{\text{Length}}{\text{Length}} \), \( x_2 = \frac{\text{Width}}{\text{Length}} \), and \( x_3 = \frac{\text{Height}}{\text{Length}} \).

Diaspore mass was determined using an electronic balance (0.0001 g), mass range of 29 diaspores were 1.12–316 mg. The projected area of diaspore was scanned with a digital scanner, and measured with analysis software (Motic Image Plus 2.0, Motic China Group Co., Xiamen, China), and project area range of 29 diaspores were 5–604 mm\(^2\). The wing loading was calculated as seed mass divided by projected area (Thompson et al. 1993) and wing loading range of 29 diaspores were 0.04–2.1 mg mm\(^{-2}\). Terminal velocity was measured with a camera described by Zhou et al. (2020), and terminal velocity range of 29 diaspores were 0.7–40 m s\(^{-1}\) (Table 2).

#### Wind speed control.

A wind tunnel (with a test section 2 m high \( \times \) 2 m wide \( \times \) 20 m long) was used to control wind speed. Wind speed was monitored inside the tunnel with a Pitot tube (160-96, Dwyer Instruments, Inc., Indiana, USA) connected with a Magnesense II Differential Pressure Transmitter (MS2-W102-LCD, Dwyer Instruments Inc., Indiana, USA) (Liang et al. 2020). In this study, wind speeds (measured 1 m above the flat sand surface) were set at 2, 4 and 6 m s\(^{-1}\), and they correspond to categories 3–5 of meteorological wind measurements, which is basically close to the common range of wind speeds under natural conditions (Mather, 1987). The underlying surface is set with a flat fixed sand surface in this experiment.

#### Model plant canopy setting.

A young tree (sapling) of *Ulmus parvifolia* was selected for use as the model canopy because it has a high density of branches and many leaves. Further, this species is relatively easy to transplant and tolerant of high wind speed. Plant height was 1 m (Fig. 1), all leaves were present, and size of canopy was 1.0 m high \( \times \) 1.2 m wide. The model plant selected was only used to explore the effect of canopy on seed dispersal of diaspores.
Effect of wind speed on diaspore dispersal through plant canopy. Five replicates of 20 diaspores of each type were used for each wind speed. The 20 diaspores were released simultaneously from the release device through the plant canopy, when the target wind speed was reached (2, 4 or 6 m s⁻¹). We turned off the wind tunnel after 2 s of diaspore dispersal. The horizontal (dispersal) distance that each of the 20 diaspores was moved from the release point as the center of the canopy, 10 cm below the top of the canopy and 90 cm from the soil surface. A 4 cm diameter stainless steel tube was used as the release device. The release device was inserted into the canopy from the top of the wind tunnel. Diaspores were released from the upper part of the steel tube (which was controlled by a bottom flap to ensure that initial release rate was zero) when the target wind speed was reached. Five replicates of 20 diaspores of each type were used for each wind speed.

### Statistical analysis.

The difference in the dispersal distance of each type of diaspore passing through the canopy versus through open air at different wind speeds was compared. Redundancy analyses (RDA) based on correlation matrices of diaspore dispersal distance and explanatory factors were conducted using Canoco 5.0.
(version 5.0, Microcomputer Power, Ithaca, NY, USA; Tackenberg, 2003). We analyzed the contribution of diaspore mass, projected area, wing loading, terminal velocity, and shape index to dispersal distance and the relationship between the plant's effect on dispersal distance and diaspore traits. Statistical analyses were conducted using IBM SPSS Statistics 22.0 (IBM Corporation 1989, 2013, USA), and plots were drawn by Origin Pro 8.5 (Origin Lab Corporation 1991–2010, USA).

**Results**

**Influence of plant canopy on diaspore dispersal distance at different wind speeds.** Plant canopy either increased or decreased diaspore dispersal distance, depending on diaspore traits and wind speed. Compared with dispersal through open air, dispersal distance of nine diaspore types (1 samara (of 7 tested), 3 thorn (of 5 tested), 4 without an appendage (of 7 tested), and 1 balloon (of 2 tested)) was significantly promoted by the plant canopy at a wind speed of 2 m s\(^{-1}\). Dispersal distance of diaspores with a thorn or those with no appendage was more likely to be promoted by the plant canopy than that of the other kinds of diaspores at a wind speed of 2 m s\(^{-1}\). However, dispersal distance of diaspores with a wing and those with hair was decreased by the plant canopy. The dispersal distance of all types of diaspore passed through the canopy were not significantly increased compared with that of diaspore passed through the open air when the wind speed was 4 m s\(^{-1}\). Dispersal distance of six diaspore types (3 samara (of 7 tested), 1 wing (of 7 tested), 1 hair (of 4 tested), and 1 balloon (of 2 tested)) was significantly increased by the plant canopy at a wind speed of 6 m s\(^{-1}\), and dispersal distance of diaspores with a thorn or those with no appendage was decreased by the plant canopy. At a wind speed of 6 m s\(^{-1}\), dispersal of diaspores with a wing was increased more by the canopy than that of the other kind of diaspores, and dispersal distance for diaspores without an appendage was significantly decreased (Fig. 2).

**Influence of diaspore traits on dispersal distance by wind.** The contribution (percentage) of diaspore traits to dispersal distance increased with wind speed (Table 3). Wing loading and terminal velocity had negatively correlations with diaspore dispersal distance for diaspores released through open air and through the plant canopy at wind speeds of 4 and 6 m s\(^{-1}\), and wing loading was more important than terminal velocity...
for dispersal distance. However, wing loading and terminal velocity did not have a significant effect on diaspore dispersal distance through the plant canopy at a wind speed of 2 m s⁻¹. Neither shape index, projected area nor mass had a significant effect on diaspore dispersal distance either through the plant canopy or through open air at any of the three wind speeds. At a wind speed of 6 m s⁻¹, the plant canopy increased dispersal-distance of diaspores with a small wing loading (≤ 0.5 mg mm⁻²) and terminal velocity (≤ 2.5 m s⁻¹), and samaras had the greatest dispersal distance followed by diaspores with wing, hair, and balloon. The plant canopy decreased dispersal distance of diaspores with high wing loading and high terminal velocity (Fig. 3).

**Table 3.** The relationship between diaspore traits and dispersal through open air and through plant canopy. E, percentage explained by diaspore traits; PA, projected area (mm²); WL, wing loading (mg mm⁻²); TV, terminal velocity (m s⁻¹); SI, shape index; MS, diaspore mass (mg); *0.01 < p < 0.05; ** p < 0.01.

| Dispersal treatment         | Wind speed (m s⁻¹) | E    | WL     | TV     | SI     | PA    | MS    |
|----------------------------|--------------------|------|--------|--------|--------|-------|-------|
| Release through open air   | 2                  | 43.70| 36.0** | 23.50**| 0.90   | < 0.01| 6.00  |
|                            | 4                  | 73.20| 69.20**| 51.80**| 12.10  | 0.04  |       |
|                            | 6                  | 83.50| 73.90**| 46.30**| 4.90   | 17.20*| 0.80  |
| Release through canopy     | 2                  | 17.40| 7.20   | 12.60  | 12.20  | < 0.01| 4.40  |
|                            | 4                  | 57.90| 45.00**| 34.00**| 12.80* | 15.80*| 1.40  |
|                            | 6                  | 70.60| 53.90**| 48.50**| 1.50   | 11.40 | 0.00  |

**Figure 2.** Dispersal distance of diaspores of the 29 species that passed through plant canopy or through open air at three wind speeds. (a–c) wind speed was 2, 4, and 6 m s⁻¹, respectively. * (P < 0.05) and ** (P < 0.01) indicate significant differences between dispersal distance after passing through plant versus open air.
Discussion

Our study indicated that compared to dispersal through open air, diaspores with thorns or without an appendage were more strongly deflected by the canopy at low wind speed, thus their dispersal distance was also more likely to increase. Previous study found that the plant canopy had little effect on interception of diaspores with thorns and without appendages, but it will disperse farther after passing through the canopy at low wind speed. Other diaspores (samara, hair, wing, and balloon) will be more easily intercepted by plant canopy at low wind speed, and thus their dispersal distance was more likely to be decreased. Our study showed that the dispersal distance of samara diaspores were more easily increased by plant canopy at a higher wind speed than dispersal through air (Fig. 2), this may because samara diaspores were subjected to a strong updraft. The effect of wind on seed dispersal distance is complex in nature, resulting in different vertical and horizontal components of air flow including turbulence and complex updrafts potentially increasing wind dispersal within a canopy.

The promotion of dispersal distance of some diaspores falling through the plant canopy (Fig. 3) is contrary to the branch interception of diaspores. Increased dispersal distance may due to induction of an updraft by wind hitting the plant canopy or by change in direction of diaspores that collide with a plant part can change the original dispersal trajectory and increase dispersal distance. Wind conditions can be altered when wind passes through a plant canopy, such as by the generation of an updraft, increasing of vertical wind speed, and reducing of horizontal speed. Low horizontal wind speed will decrease diaspore dispersal distance, but an updraft or vertical wind speed can increase dispersal time, thereby increasing diaspore dispersal distance. Thus, the plant canopy can increase or decrease diaspore dispersal distance compared to diaspores passing through open air at the same wind speed.

Tackenberg et al. found that updrafts are important for long-dispersal of dandelion in an open meadow environment. Our results showed that plant canopy not only promoted the dispersal of hairy diaspores, but also promoted the dispersal of diaspores with samara, wing, and balloon, which might be because of localised updrafts.
and eddies caused by plant canopy. Variety of plant canopy types will cause differences in turbulence, which may further affect the distance of seed wind dispersal. The canopy of branch and leaf density may produce complex updrafts, therefore, we speculate that a dense canopy of branches and leaves is more likely to promote seed wind dispersal, and wind-borne seeds are easier to dispersal over long distances in forests than in deserts, of course, this needs further research to confirm.

Diaspore dispersal distance is strongly correlated with wing loading and terminal velocity. Our study indicated that the dispersal distance of diaspores with small wing loading and terminal velocity can be promoted by the plant canopy at high wind speed but not at a low wind speed (Fig. 3). This is because diaspores with low wing loading and terminal velocity are easily accelerated laterally by the drag of the wind following a collision with a solid object during high wind speed. Diaspores that are dispersed by wind generally have a smaller terminal velocity and wing loading, this means that wind-borne species are distributed more widely in vegetation-covered areas than in open landscapes.

In conclusion, a plant canopy may increase dispersal of diaspores with thorns or those without appendages during low wind speed, and dispersal of diaspores with small wing loading and terminal velocity at high wind speeds. An estimation of the plant canopy effect on diaspore dispersal distance can improve the accuracy of the assessment of dispersal distance of a cohort of diaspores in the real world. Accordingly to our results, we can predict that diaspores with small terminal velocity and wing loading are easier to dispersal long distances under hurricane or storm conditions.

Data availability
The data presented in this study are available on request from the corresponding author.

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Author contributions
Z.L., M.L., Z.W., and X.Q. conceived the idea and designed the methodology; X.Q., Z.X., and Q.Z. collected the data. X.Q. analyzed the data and wrote the first draft of the manuscript. Z.L., W.L., C.B., and J.B. revised several drafts of the manuscript. All authors approved the manuscript for publication.

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Competing interests
The authors declare no competing interests.

Additional information
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