Relationship between seed morphological traits and wind dispersal trajectory

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Abstract

The structure and dynamics of plant populations and communities are largely influenced by seed dispersal. How the wind dispersal trajectory of seeds shifts with differences in seed morphology remains unknown. We used a wind tunnel and video camera to track the dispersal trajectory of seven species of *Calligonum* whose seeds have different kinds of appendages and other morphological traits, using variable wind speeds and release heights to determine the relationship between seed morphological traits and wind dispersal trajectory. Concave-, straight-line-, horizontal-projectile- and projectile-shaped trajectories were found. Dispersal trajectories such as the horizontal projectile (HP) and projectile (P) tended to have a long dispersal distance. Straight line (SL) and concave curve (CC) trajectories tended to have a short dispersal distance. Seeds with bristles and large mass tended to have SL and CC trajectories, those with wings or balloon and small mass tended to have HP and P trajectories. Wind speed tended to have a stronger influence on the dispersal trajectory of light and low-wing-loading seeds, and release height tended to have a stronger influence on the dispersal trajectory of heavy and high-wing-loading seeds. Thus, seed wind dispersal trajectory is not only determined by seed morphological characteristics but also by environmental factors such as wind speed and release height.

Introduction

The structure and dynamics of plant populations and communities in the landscape are largely influenced by dispersal distances of seeds. Distance can be determined by seed dispersal trajectory, which may be influenced by seed traits, release height and wind conditions (wind speed and orientation) (Thomson *et al.* 2011; Savage *et al.* 2014; Zhu *et al.* 2016). Seed traits such as seed mass (Augspurger 1988), terminal velocity (Andersen 1993) and wing loading (Matlack 1992) have profound effects on seed dispersal patterns and distances. Some seed appendages are assumed to facilitate wind dispersal of seeds (Jongejans and Telenius 2001; Nathan *et al.* 2011). Seeds can then be dispersed far away from their mother plants, depending on release height and wind speed, as they all affect seed flying time (Tackenberg 2003), dispersal distance and pattern (vanDorp *et al.* 1996; Thomson *et al.* 2011). However, only a few studies have been conducted on the relationship between release height, seed morphological characteristics, and wind conditions in shaping the wind dispersal trajectory of seeds. Information on the wind dispersal trajectory of seeds and factors influencing the shape of the trajectory is therefore essential to understanding the seed distribution pattern and its effect on population structure and dynamics of plant species (Nathan 2001). Such information is also needed for restoration management in establishing and improving structural and functional connectivity of landscape to ensure possibilities for species dispersal to target sites from neighboring habitat patches (Aavik and Helm 2018).

Calligonum (Polygonaceae) species are the dominant anemochorous shrubs on active

and stabilized sand dunes in deserts of China (Ren *et al.* 2002; Shi *et al.* 2009; Feng *et al.* 2010; Gouja *et al.* 2015). Their dispersal characteristics no doubt vary due to large

inter-specific differences in appendage types and structures (wings, bristles, balloon

and wings+thorns). Considering that the seeds of *Calligonum* species also have a

relatively low inter-specific variation in shape and mass (Ren *et al.* 2002; Ren and Tao

2004; Flora of China Editorial Committee 2006; Abdurahman *et al.* 2012), they could

be ideal for studying the relationship between seed morphology and wind dispersal

trajectory.

The objectives of this study were to answer the following questions: 1) How is the

primary dispersal trajectory of seeds linked to their morphological traits? 2) How is

the relationship between seed primary dispersal and seed morphological traits

regulated by wind speed and release height? Previous research has documented that

seed dispersal modes appear to be associated with morphological traits (Augspurger

1986; Stevenson *et al.* 2015), but wind speed and plant height might be closely related

to dispersal distance (Thomson *et al.* 2011; Zhu *et al.* 2016). Based on these earlier

observations, we propose a hypothesis that the major factors determining seed

dispersal trajectory modes are seed morphological traits rather than wind speed and

release height. Seeds evolved a variety of morphological traits potentially affecting

seed dispersing (Stevenson *et al.* 2015) and, key factors in determining dispersal

trajectory of various seeds might be different. Thus, we test a hypothesis that the key

factors shaping primary dispersal trajectory of seeds are variations in their morphological traits.

Material and Methods

Seed collection

Seeds of *C. arborescens* and *C. mongolicum* were collected in the Ulanbuh Desert (106°09′–107°10′E, 40°09′–40°57′N, 1050 m above sea level) of Inner Mongolia, and those of *C. rubicundum C. aphyllum C. densum C. junceum C. klementzii* in Tazhong (83°40′E, 39°00′N, 1099 m above sea level) of the Taklimakan Desert in Xinjiang, Northwestern China. Four hundred intact seeds were collected for each species from 20 individual plants after seed maturity in July and August 2016. All seeds were air dried and stored in laboratory until experiment began.

Fig 1 here

Measurement of morphological and aerodynamic traits

Twenty intact seeds were randomly selected to measure the dimension, shape index, mass, projected area, wing loading and terminal velocity. Three dimensions (length, width and height) of each seed were measured using a digital caliper (0.01 mm

accuracy) (Zhu *et al.* 2016). Seed mass was determined with an electronic balance

(0.1 mg accuracy). Seeds were scanned and then analyzed by WinSEEDLE (Regent

Instruments Inc., Canada) image analysis system to measure projected areas (PA)

(Zhu *et al.* 2016). The wing loading (WL) was calculated as the ratio of seed mass to

projected area (Matlack 1987; Howlett 1995; Greene and Johnson 1997). The shape

index (I_s), expressed as extent approximate to a sphericity, was calculated with the

equation as following (Thompson *et al.* 1993):

$$I_s = \frac{\sum X_i^2}{n} - \frac{(\sum X_i)^2}{n^2}$$ (Equation 1)

Here n=3, *i*=1, 2 or 3, X_1=length/length, X_2 = width/length and X_3= height/length.

The terminal velocity (TV) was determined by a camera recording method. Each seed,

taken by a pair of tweezers, was released from the top opening of a settling tower (200

cm high). We used a video camera to record the falling process of 20 seeds of each

species at a shooting speed of 50 frames per second (fps). The videos were played

frame by frame using Quick Time Player (Apple Macintosh, version 7.79.80.95,

2016). The falling distance of a seed in each frame (1/50 second) was determined

from readings against a scale in the video. When falling distances were equal in two

consecutive frames, the seed reached its terminal velocity. The vertical falling

distances within 10 frames (0.2 s) were measured by reading the scale. The terminal

velocities were calculated as a ratio of the falling distance to the time (0.2s):

$$V_t = \frac{\textit{Falling distance}}{\textit{Time interval}} = \frac{(P_2 - P_1)}{10 \textit{ Frames}} = 5(P_2 - P_1)$$ (Equation 2)

Here, V_t is the terminal velocity (m s^{-1}); P_1 starting position on the scale; P_2 ending

position on the scale after 10 frames.

Table 1 here

Wind-tunnel experiments

Since wind conditions in nature are very complex, it is almost impossible to trace an

individual seed under natural conditions (Jongejans and Telenius 2001; Jones and

Muller-Landau 2008). Thus, we used a wind tunnel (with test section of 2 m high, 2 m

wide and 21-m-long) for quantifying the primary seed dispersal distance and

distribution pattern (Dauer *et al.* 2006; Zhu *et al.* 2016). The experiment was

conducted in a section of the wind tunnel 10 m away from the fan. A square grid scale

(N) was drawn on the side wall of the wind tunnel (Fig. 2). Markers (M)

corresponding to the square grids were drawn on the opposite wall at the bottom of

the observation window. Marking lines (P) were drawn to facilitate measurement of

the position of fallen seeds. A pitot tube (A), inserted from ceiling of the tunnel, and a

differential pressure transmitter (B, Dwyer Instruments Inc., Indiana, USA),

connected to the pitot tube, were used to monitor the wind speed at 1 m high (Zhu *et*

al. 2016). Seeds were released via a seed releaser (C) inserted through the middle of

the tunnel ceiling. Seeds were put into the top inlet (2 m in length, 6 cm in diameter)

of the releaser. A baffle plate (E), controlled by a wrench (D), was located on the

outlet of the releaser to keep the seed motionless. The seed release height (H) was the distance from the ground to the outlet. Twenty seeds (replications) for each species were released under four different wind speeds (4, 6, 8 and 10 m s^{-1}) and five release heights (0.2, 0.4, 0.6, 0.8 and 1.0 m), resulting in a total release of 2800 seeds. A video camera (G) (GC-P100AC, JVC, Japan) was used to record the dispersal processes using a speed of 50 frames per second (fps) (Fig. 2). The shooting distance was adjusted according to wind speed and release height to obtain an overall view of the seed dispersal processes.

Fig. 2 here

Determination of trajectory and dispersal distance

Videos were analyzed by QuickTime player (Apple Macintosh, version 7.79.80.95, 2016) to determine seed position and dispersal distance. Since video captured by camera is a 3-dimensional scene, coordinate transformation should be conducted to obtain projected coordinates on the square grids scale based on perspective principle (Fig. 3). Every frame of a video was printed on a paper, then two marking lines GH and JK were drawn on the paper intersecting at the point V, i.e., the vanishing point according to the perspective principle. Line HK was an intersection line of the side wall and the ground. Point A was the position of the falling seed in the picture. A vertical line was drawn from point A intersecting with the central line LM at point B.

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Point C was an intersection between line BV and HK. A vertical line was drawn from

point C intersecting with the line AV at point P_i. The P_i (x_i, y_i) was the projected

coordinates on the scale (Fig. 3). By the same method, successive projected

coordinates of every video frame were obtained. A projected trajectory of each seed

was drawn from the release point P_o (x_o, y_o) to the falling point P_t (x_t, 0) on paper. The

dispersal distance DP_t was (x_t–x_o) cm, where the x_t, and x_o were the abscissa of P_t and

P_o, respectively (Fig. 3).

Fig. 3 here

Data analysis

Redundancy analyses (RDA) was conducted by using Canoco 5.0 (version 5.0,

Microcomputer Power, Ithaca, NY, USA) (Tackenberg 2003) to assess the explanatory

power of wind speed (WS), appendage structure (AS), shape index (SI), seed mass

(SM), wing loading (WL), terminal velocity (TV) and release height (RH) to the

trajectory modes of the seven *Calligonum* species. Since types of appendage

structures and trajectory modes are not scaled attributes, we defined four variables for

the occurrence of appendage structures, AS_1, AS_2, AS_3 and AS_4, with the property that

AS_i=1 if the appendage structure was wings, bristles, a balloon or wings +thorns,

otherwise AS_i=0. Further, we defined *n* variables for the occurrence of trajectory

modes as TM_1, TM_2, TM_3 and TM_4 … TM_n. Each explanatory power was tested to

assess the contribution of two environmental (wind speed and release height) and five

morphological factors (seed mass, terminal velocity, wing loading, shape index and

seed appendages) to the variation in dispersal trajectory shifts by using forward-

selection procedures.

Hierarchical clustering analysis was used to classify the dispersal distance of the

seven species. A dendrogram was drawn by Ward's method (Ward 1963; Murtagh and

Legendre 2014) after transforming values of dispersal distance into standardized Z

scores. The hierarchical clustering analysis and dendrogram plot of seed dispersal

distance, curve estimation of trajectory mode, and descriptive statistics were analysed

using PASW Statistics Software version 18.0 (IBM Corp., Armonk, New York, USA).

Box plot, curve fit and scatter plot were drawn using SigmaPlot version 10.0 (Systat

Software, Inc., USA).

Results

Trajectory modes of seven *Calligonum* species under different release heights and

wind speeds

Projected coordinates of 2800 trajectories (five release heights × four wind speeds ×

seven species × 20 replications) were determined under different release heights and

wind speeds. Trajectories were classified into four modes, i.e., concave curve (CC),

straight line (SL), horizontal projectile (HP) and projectile (P), according to seed

launching angle (Fig. 4).

Fig. 4 here

The CC, fitted by exponential decay functions ($y=ae^{-bx}$), had the largest launching angle between horizontal and launching direction (Fig. 4). The SL, fitted by linear functions ($y=y_0+ax$), had a smaller included angle than that of CC. The HP, fitted by quadratic functions ($y=y_0+ax+bx^2$), had the smallest launching angle (approximate to 0). The P, fitted by cubic functions ($y=y_0+ax+bx^2+cx^3$), had a launching angle above the horizontal direction (Fig. 4).

Occurrence probability of 4 trajectory modes under 4 wind speeds and 5 release heights

Four modes of trajectory shifted with a probability of occurrence under each wind speed and release height. With an increase in wind speed, the CC mode showed random occurrence probability, ranging from 17.0%-32.0% (Fig. 5 A). The SL mode had a decreased probability, ranging from 31.6% to 18.3% (Fig. 5 B). The HP and P modes showed increased probability, from 1.1% to 47.1% and from 2.3% to 50.6%, respectively. The accumulative probability of the HP and P modes was more than 80%, when the wind speed was above 8 m s^{-1} (Fig. 5 C and D).

Fig. 5 here

With increase in release height, the CC mode significantly decreased in occurrence probability, from 68.5% to 0, occurred mainly within 20-40 cm (Fig. 5 E). The occurrence probability of the SL mode fluctuated slightly, from 17.4% to 22.6% (Fig. 5 F). The HP and P modes showed increasing tendency from 9.6%-34.9% and 4.7%-31.7%, respectively. Accumulative occurrence probability of the HP and P modes was above 75% when the release height was from 60 cm to 100 cm (Fig. 5 G and H).

Relationship between seed dispersal distance and trajectory mode

For CC, SL, HP and P, the average dispersal distance was 43.7 cm, 48.8 cm, 134.0 cm and 208.3 cm, respectively, at 20 cm release height; 42.5 cm, 92.4 cm, 206.6 cm, and 235.5 cm, respectively, at 40 cm release height; 79.3 cm, 118.1 cm, 242.3 cm, 306.1 cm, respectively, at 60 cm release height; 120.4 cm, 155.6 cm, 296.9 cm and 412.6 cm, respectively, at 80 cm release height; 149.7 cm, 173.8 cm, 327.0 cm, 464.6 cm, respectively, at 100 cm release height, . Totally, the average of dispersal distance for CC, SL, HP, and P was 48.2 cm, 121.1 cm, 269.8 cm and 357.7 cm, respectively, at 20-100 cm release height. (Fig. 6).

Fig. 6 here

Clustering of dispersal distance

The seven species could be classified into three groups according to dispersal distance (Fig. 7). Group I included *C. arborescens*, *C. densum*, and *C. klementzii*, with bristles, large mass and high terminal velocity (Table 2). Mean dispersal distance for Group I was 124.3 cm ± 84.3 cm (mean ± SD), ranging from 10 cm to 395 cm (median 104.5 cm). Group II included *C. mongolicum* and *C. rubicundum* with bristles and wings+thorns, respectively. *C. mongolicum* had small mass and terminal velocity, while *C. rubicundum* had large mass and terminal velocity (Table 1). Mean dispersal distance of Group II was 151.7 cm ±108.8 cm, ranging from 6 cm to 650 cm (median 124.0 cm). Group III included *C. aphyllum* and *C. junceum* with small mass and terminal velocity. *C. aphyllum* had wings and *C. junceum* had a membranous balloon. Mean dispersal distance of Group III was 181.0 cm ±120.8 cm, ranging from 18 cm to 750 cm (median 150.0 cm).

Fig. 7 here

Relationship between proportion of trajectory modes and dispersal distance

Calligonum arborescens, *C. densum* and *C. klementzii* had short dispersal distances with modes of CC (>10%) and SL (>75%) modes, which accounted for more than 90% of total trajectories, on the other hand, HP (<7.5%) and P (not found in the three

species) modes were less than 10% (group I). *Calligonum mongolicum* and *C. rubicundum* had medium dispersal distances with CC and SL modes, which accounted for 58-85% of total trajectories, and the HP and P modes for 13.8%-41% (group II). In group III, *C. aphyllum* and *C. junceum* had long dispersal distance with CC and SL modes making up < 65% of the total trajectories, and the HP and P modes accounting for >35% of the total trajectories (Table 2).

Relationship between wind speed, release height, seed morphological traits, and trajectory modes

The terminal velocity (TV), wings (AS$_1$), balloon (AS$_3$), release height (RH) and shape index (SI) were positively linked with HP (TM$_3$) and P (TM$_4$) modes, but negatively linked with the CC (TM$_1$) and SL (TM$_2$) modes. Seed mass (SM), TV, bristles (AS$_2$), wings+thorns (AS$_4$) and wing loading (WL) were negatively linked with HP (TM$_3$) and TM$_4$, and positively linked with TM$_1$ and TM$_2$ (Fig. 8 A).

Fig. 8 here

For all seven species, wind speed (WS) had the most explanatory power, explaining 9.2% (*p*=0.002) of variation in trajectory modes, followed by SM, explaining 6.1% of the variation. The combination of other factors explained 6.3% of the variation (Table 3). The explanatory power on the trajectory modes (TM) in descending order was

WS, SM, RH, TV, AS$_4$, SI and WL (Table 3).

Table 3 here

In Group I, RH, TV, WS and SM were the significant explanatory variables (p=0.002), explaining 16.0% of the variation in trajectory modes (Table 3). RH was positively linked with TM$_2$, but TM$_3$ was negatively linked with TM$_1$. TV was positively linked with TM$_1$ but negatively linked with TM$_2$. WS was positively linked with TM$_3$ but negatively linked with TM$_2$. SM was positively linked with TM$_2$ but negatively linked with TM$_3$ (Fig. 8 B). RH was the most significant factor explaining 13.4% (p=0.002) of the variation, while TV, WS and SM only explained 2.5% of the variation (Table 3).

In Group II, WS, SI and RH were the significant explanatory variables (p=0.002), explained 32.4% of the variation in trajectory mode (Table 3). WS and RH were positively linked with TM$_3$ and TM$_4$ but negatively linked with TM$_1$ and TM$_2$. SI was positively linked with TM$_1$ and TM$_2$ but negatively linked with TM$_3$ and TM$_4$ (Fig. 8 C). WS was the key factor, explained 20.5% of the variation, followed by SI and RH, which explained 12.1% of the variation (Table 3).

In Group III, the significant explanatory variables (p=0.002) were WS, RH and SI, explained 23.3% of the TM variation (Table 3). WS and RH were positively linked with TM$_3$ and TM$_4$ but negatively linked with TM$_1$ and TM$_2$. SI was positively linked

with TM$_2$ but negatively linked with TM$_1$, TM$_3$ and TM$_4$ (Fig. 8 D). WS was the key

factor, explaining 20.3% of the variation in trajectory modes, while RH and SI only

explained 3.0% (Table 3).

Discussion

Relationship between seed morphological traits and the wind dispersal trajectory

Seed morphological traits are deemed to be an evolutionary adaptation to wind

dispersal (Horn *et al.* 2001; Jongejans and Telenius 2001; Zhu *et al.* 2016). Our results

showed that seed morphological traits, particularly seed mass and appendage structure

determined the majority of trajectory modes of primary wind dispersal (Table 2 & 3;

Fig. 8). Our study demonstrated that, despite having the same appendage structures,

C. arborescens had a lower proportion of HP and P than *C. mongolicum* (Table 1, 2),

likely because small seeds disperse better than large ones. Seeds with large mass are

poorly accelerated and dispersed by wind (Augspurger and Franson 1987; Greene and

Johnson 1993; Thomson *et al.* 2011), since they have limited lateral movement but a

quick rate of descent (Matlack 1987, 1992; Greene and Johnson 1993). Appendages

on wind-dispersed seeds are designed for slowing the descent rate by lowering wing

loading or increasing the roughness of seed surface and the chance of exposure to

wind (Augspurger 1986; Andersen 1993; Nathan *et al.* 2011). Our study showed that

seeds with wings or a balloon (*C. aphyllum* and *C. junceum*) had a higher proportion

of HP and P than those with bristles (*C. arborescens C. densum C. klementzii and C.*

mongolicum), indicating that winged- and ballooned-seeds are more effectively

dispersed by wind than bristled-seeds. Indeed, field observations revealed that *C.*

junceum and *C. mongolicum* have a wider geographical distribution than *C.*

arborescens and *C. rubicundum* (Feng *et al.* 2008; Fan *et al.* 2018), which could be

related to the aforementioned traits.

Relationship between wind speed, release height and trajectory modes

Contrary to our hypothesis, our results showed that wind speed is the key factor

determining the shape of seed dispersal trajectories and greatly affects the probability

of occurrence of trajectory modes (Fig. 5, Table 3). Wind could be an important factor

in determining seed dispersal behavior (Soons *et al.* 2004; Zhu *et al.* 2016), likely for

two reasons. Firstly, seed dispersal by wind is largely affected by not only horizontal

wind but also turbulent fluctuations in vertical updrafts (Greene and Quesada 2011).

The horizontal wind promotes lateral dispersal speed of seeds (Horn *et al.* 2001;

Travis *et al.* 2010). Vertical updrafts are generated by a shearing action of the

horizontal wind (Greene and Johnson 1995; Levine and Murrell 2003; Soons *et al.*

2004) and fluctuations of the updrafts with increasing horizontal wind speed (Greene

2005). Secondly, the horizontal wind and fluctuations of updrafts can change the drag

force exerted on the seed in flight (Nathan *et al.* 2011), further retarding or increasing

the horizontal and vertical speeds of seeds. As a result, dispersal trajectory shapes and

probability of occurrence of trajectory modes are largely influenced by wind speed.

Our results implied that seeds with a high air-drag structure (e.g. *C. aphyllum* and *C.*

junceum) are likely to be dispersed longer distances, than those with a low air-drag

structure since the appendage on the former can have greater dragging force at a given

wind speed. Thus, seeds with an appendage can get a higher proportion of trajectories

like HP and P, even if the species have the same plant height as one with seeds that

lack appendage.

Our results also showed that release height is an important factor affecting seed

dispersal trajectory shapes and occurrence probability of trajectory modes (Fig. 5,

Table 3). Previous studies showed that release height is positively correlated with

dispersal distance due to changes in seed falling time (Thomson *et al.* 2011; Savage *et*

al. 2014). Tall plant species (e.g. *C. arborescens*, 2-4 m high) are likely to have a

longer primary dispersal distance than short species (e.g. *C. klementzii*, 0.5-0.9 m

high) because a longer time is needed from a tall plant than from a short plant. In

addition, a longer fall time offers more opportunities to change seed dispersal

trajectory and trajectory shapes due to the horizontal wind and vertical updrafts

exerting force on the seed (Nathan *et al.* 2011).

Release height tended to have the strongest explanatory power on seeds with bristles,

while wind speed tended to have the strongest explanatory power on seeds with wings

(Table 3). One possible reason is that wind exerts a lower drag force on seeds with

bristles than on those with wings. Thus, release height tended to have a larger effect

on trajectory modes of seeds with bristles than on those with wings. On the contrary,

wind speed tended to have a larger effect on trajectory modes of seeds with wings

than on those with bristles (Table 3). Therefore, our hypothesis that the key factors

shaping primary dispersal trajectories of seeds are variations in their morphological

traits is supported.

Relationship between seed dispersal distance and trajectory modes

Our findings showed that the HP and P tended to have a long dispersal distance, likely

because the launching angle of HP and P modes are closer to 45 degrees than in the

CC and SL modes. As we know, an object travels the farthest when it is launched at an

angle of 45 degrees. High wind speeds could also contribute to the phenomenon since

the HP and P mostly occurred after the wind speed reached 8 m s^{-1} (Fig. 5). As

previously reported, high wind speed is positively correlated to seed dispersal distance

(Horn *et al.* 2001; Soons *et al.* 2004; Zhu *et al.* 2016). In contrast, CC and SL tended

to have a short dispersal distance (Fig. 6), possibly because the launching angles of

the CC and SL are negative (Fig. 4). Therefore, the seeds with trajectories shaped like

a CC and SL tend to have a shorter dispersal distance than those shaped like a HP and

P. This suggests that species with a high proportion of trajectory shapes like HP and P

appear to be better dispersers than those with a high proportion of trajectory shapes

like CC and SL, gaining long primary dispersal distance in windy conditions. In many cases, this trait enables some species to extend their geographical distribution (Nathan 2001; Nathan *et al.* 2008; Soons and Bullock 2008; Gillespie *et al.* 2012). In contrast, species that have trajectory shapes like CC and SL appear to be poorly dispersed by wind. However, these species may have secondary dispersal adaptation by, for example, rolling on the soil surface.

In summary, due to having high proportion of trajectories like HP and P, those species with light, winged- and ballooned-seeds can disperse far away from their mother plants in high wind velocity and plant height, which can promote quickly invading new habitats and spreading plant population. However, those species with heavy, bristled- or wing+thorned -seeds with a high proportion of trajectories like CC and SL can disperse only a short distance despite of high wind speed and plant height, which is not favorable for spreading the plant population.

To conclude, seed morphological traits determine the proportion of trajectory modes of primary wind dispersal. Seeds with bristles and large mass tend to have SL and CC dispersal trajectories and those with wings and small mass or membranous balloon and small mass tend to have HP and P dispersal trajectories. Wind speed is the key factor determining seed dispersal trajectory shapes and greatly affects the probability of the occurrence of trajectory modes. Wind speed tends to have a stronger influence on the dispersal trajectory of light and low-wing-loading seeds than on those with heavy and high-wing-loading seeds, while release height tends to have a stronger

influence on the dispersal trajectory of heavy and high-wing-loading seeds than on those with light and low-wing-loading seeds. Seeds having HP and P trajectories tended to have long dispersal distance, however, those having SL and CC trajectories tended to have short dispersal distance. Our study indicated that seed wind dispersal trajectory is not only determined by seed morphological characteristics but also by the environmental factors such as wind speed and release height.

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Figure legends:

Fig. 1 Side and top view of seeds of seven species of *Calligonum.* (A) *C. aphyllum;* (B) *C. arborescens;* (C) *C. densum;* (D) *C. junceum;* (E) *C. klementzii;* (F) *C. mongolicum;* (G) *C. rubicundum.*

Fig. 2 Diagram of wind tunnel for recording seed trajectory and dispersal distance in wind tunnel. A: a pitot tube; B: differential pressure transmitter; C: a seed releaser; Z: detailed structure of the releaser; D: a release controller with a wrench; E: a baffle plate controlled by the wrench; F: a seed released from the releaser; H: release height; G: a camera; M: a marker; L: the centre line of the tunnel ground; N: square grids scale; P: a marking line.

Fig. 3 Diagram of factors involved in determing coordinate transformation of seed position from a 3-dimensional scene into a 2-dimensional surface based on perspective principle. NHKQ: square grids scale on the wall of wind tunnel; HGJK: ground of wind tunnel; HK and GH: intersection lines of the side wall and the ground; LM: the centre line of the ground; GH and JK: two marking lines; V: vanishing point, extended lines of GH, JK and their parallel lines intersected at the point; O: seeds release point; A: any point in seed dispersal trajectory; F: seed fall point; E and B: projected point of O and A on the ground; D $(x_o, 0)$, C $(x_i, 0)$ and P_t $(x_t, 0)$: intersection points of VE, VB and VF with HK; P_o (x_o, y_o), P_i (x_i, y_i) and P_t $(x_t, 0)$:

projected points of point O, A and F on the scale; R: a marker.

Fig. 4 Four trajectory modes of primary seed wind dispersal of seven *Calligonum* species under different release heights and the wind speed. Here, CC: Concave curve; SL: Straight line; HP: Horizontal projectile; P: Projectile.

Fig. 5 Probability of the occurrence of 4 trajectory modes under four wind speeds and five release heights. The left panels (A~D) show probability of the occurrence of four trajectory modes under four wind speeds. The right panels (E~H) show probability of the occurrence of four trajectory modes under five release heights.

Fig. 6 Relationship between trajectory modes and primary dispersal distance at release heights of 20cm, 40cm, 60cm, 80 cm, 100 cm and 20-100 cm. Here, CC: Concave curve; SL: Straight line; HP: Horizontal projectile; P: Projectile, Total: total dispersal trajectory modes.

Fig. 7 The clustering of primary dispersal distance of seven *Calligonum* species using hierarchical method (D1) *C. aphyllum;* (D2) *C. arborescens;* (D3) *C. densum;* (D4) *C. junceum;* (D5) *C. klementzii;* (D6) *C. mongolicum;* (D7) *C. rubicundum.*

Fig. 8 Relationship between wind speed, release height, seed morphological traits,

and shifts of trajectory mode of (A) seven species (in total); (B) three species in group

one; (C) two species in group two; (D) two species in group three. TM: trajectory

mode; TM_1: concave curve (CC), TM_2: straight line (SL); TM_3: horizontal projectile

(HP); TM_4: projectile (P); SM: seed mass (mg); TV: terminal velocity (m/s); WL:

wing loading (mg/cm^2); SI: shape index; RH: release height (cm); WS: wind speed

(m/s); AS: appendage structure; AS_1: wings; AS_2: bristles; AS_3: membranous balloon;

AS_4: wings+thorns. Explanatory factors are indicated by red lines with hollow arrows.

Trajectory modes are showed by blue lines with solid arrows.
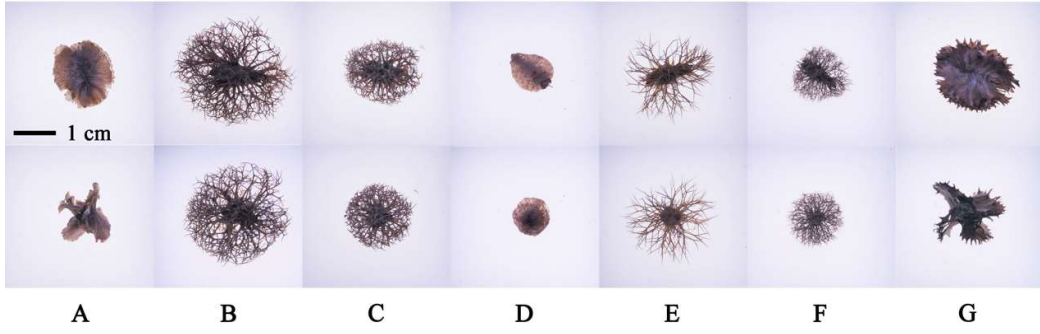
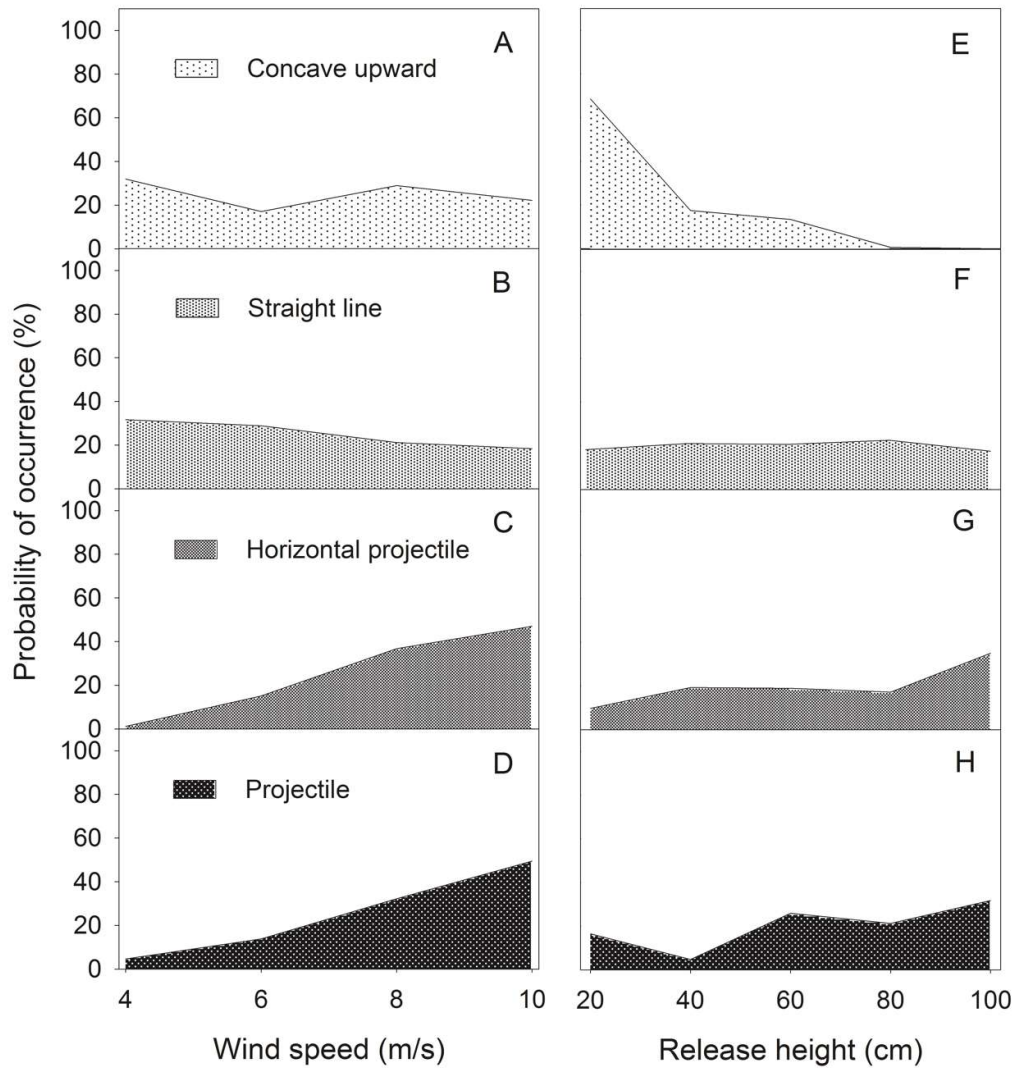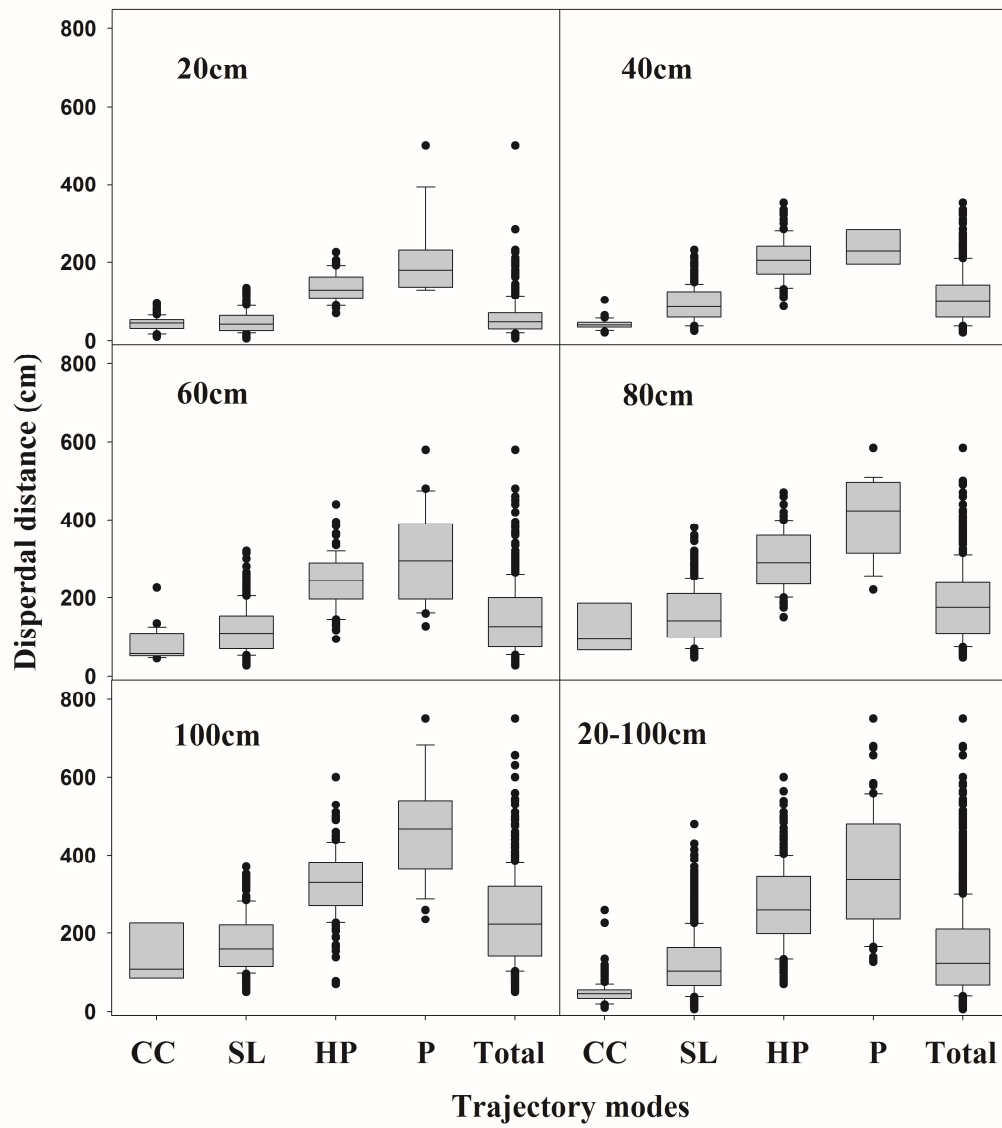Figure 1
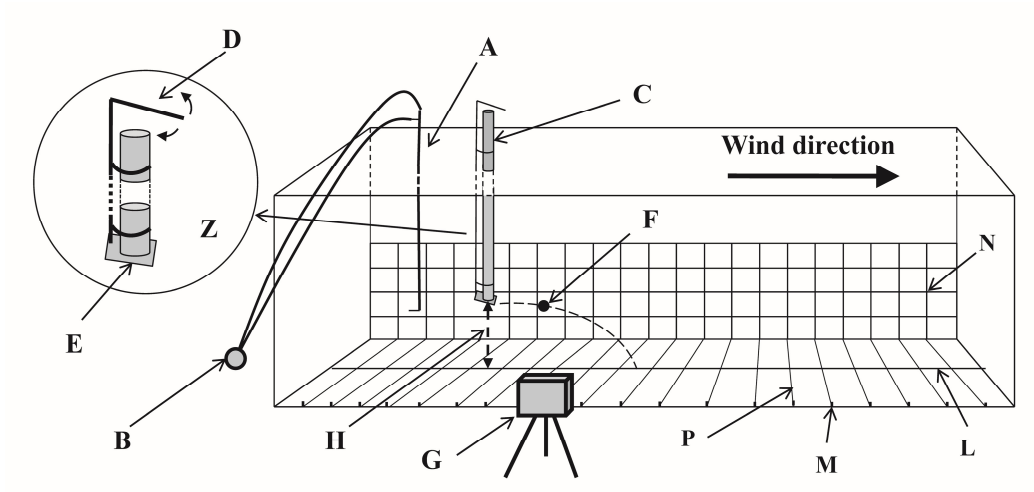
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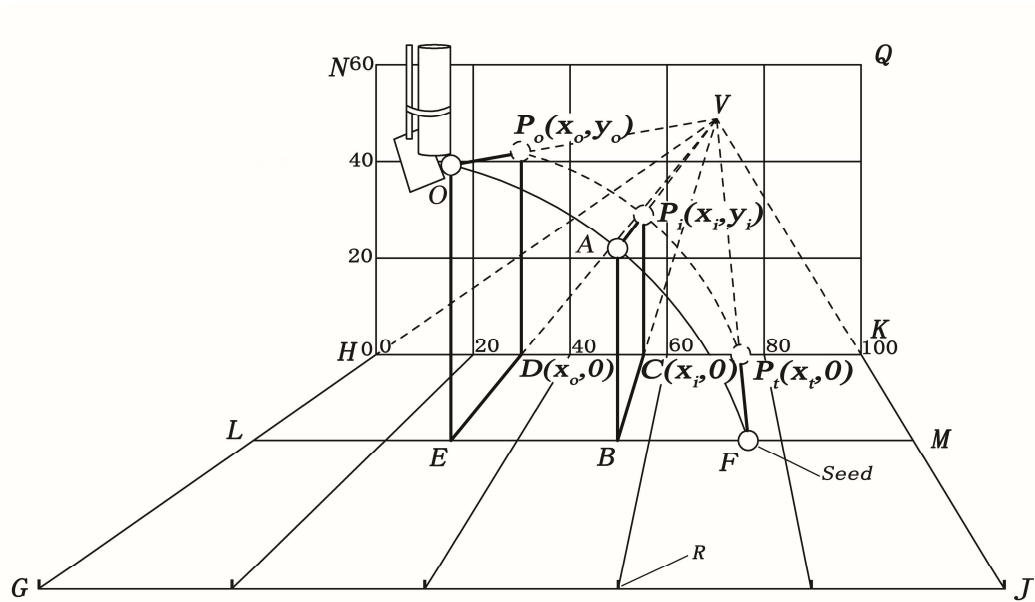
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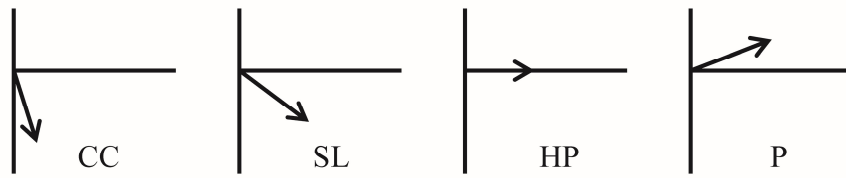
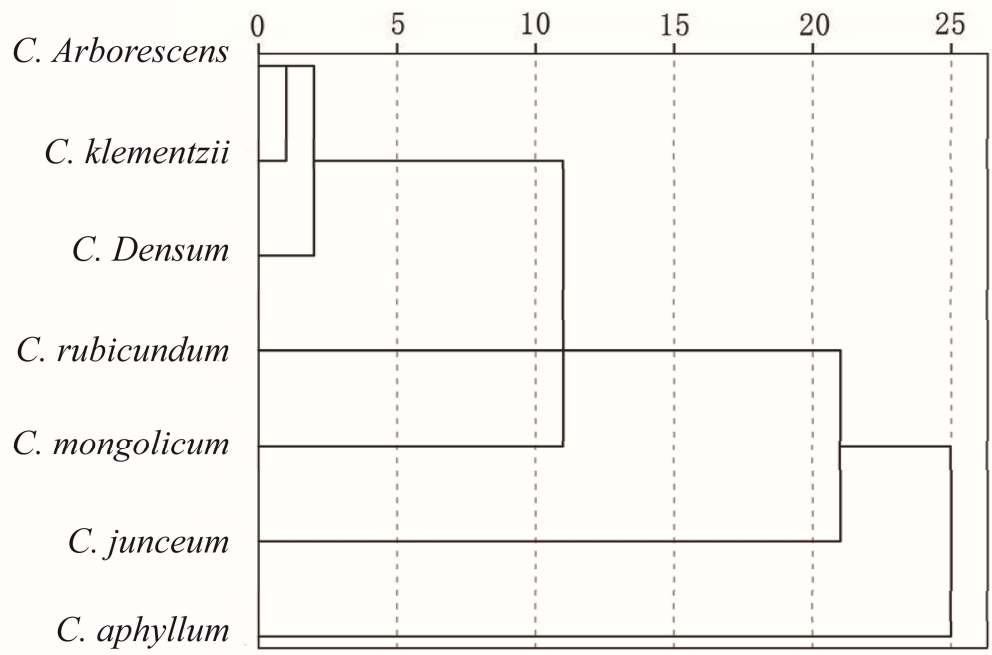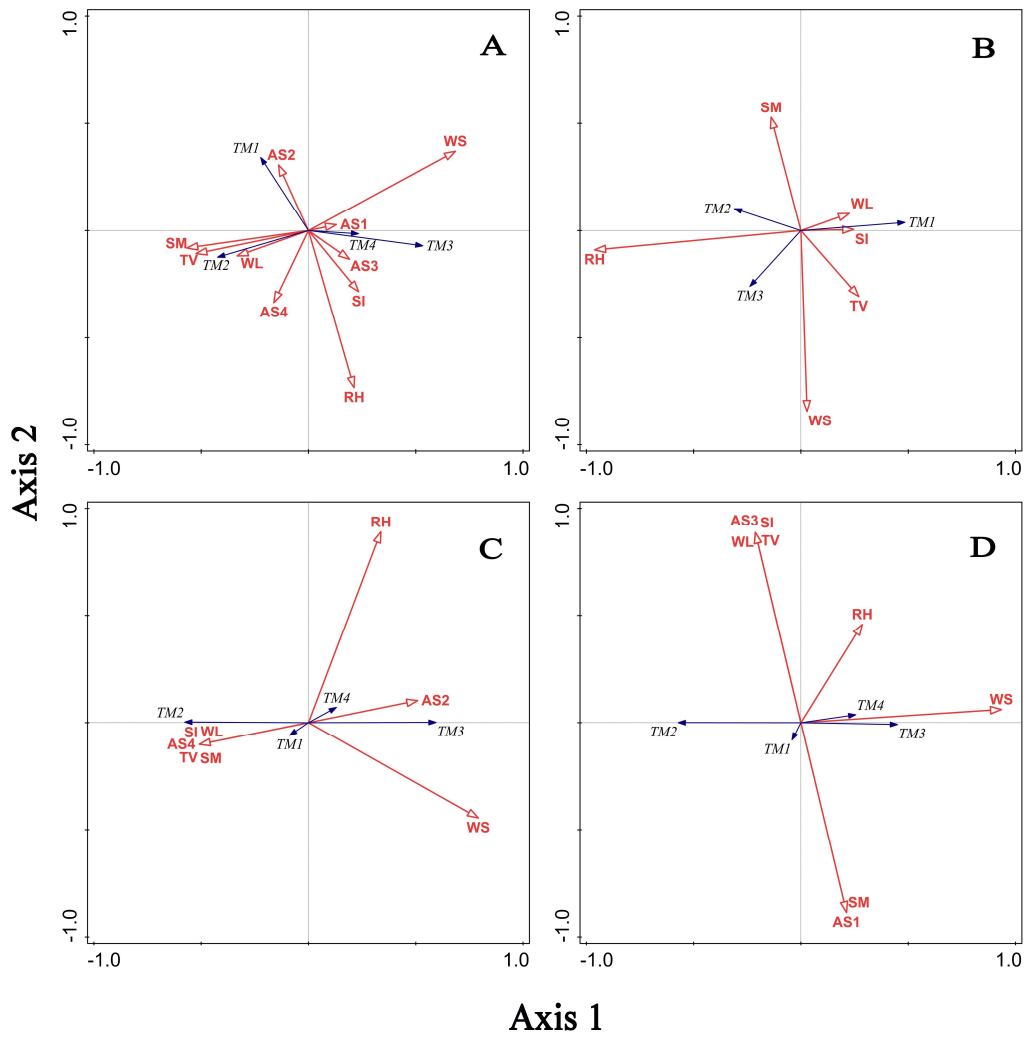Launching angle of four trajectory modes
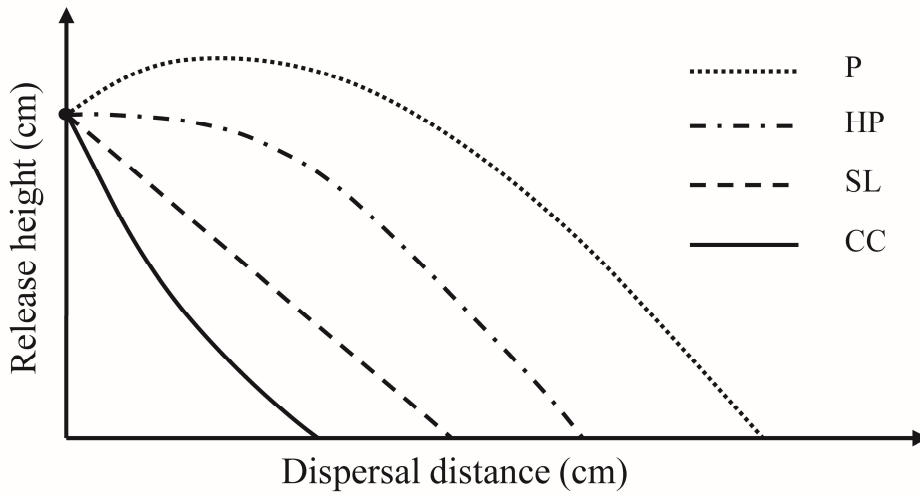
Figure 4

Figure 5

Figure 6

Figure 7

Figure 8