1 **How do wind speed, release height, seed morphology interact to**
2 **determine seed dispersal trajectory of *Calligonum* (Polygonaceae)**
3 **species**
4 **Wind speed, release height, seed morphology determine seed**
5 **dispersal trajectory**

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26 **Abstract**

27 How seed dispersal trajectory shifts with abiotic and biotic factors and what is the
 28 relationship between seed dispersal distance and dispersal trajectory are remain
 29 unclear. We used wind tunnel and video camera to track the seed dispersal trajectory
 30 of 7 *Calligonum* species with different appendages under the different wind speeds
 31 and the release heights. Dispersal trajectories and distances were determined by video
 32 analysis and spatial coordinate transformation. Based on perspective principle, 4
 33 modes of trajectories were determined. Wind speed, seed mass and release height
 34 were the key factors determining seed dispersal trajectory modes. Release height and
 35 wind speed tended to have the strongest explanatory power on seeds with bristles and
 36 wings, respectively. Different trajectory modes lead to different dispersal distance,
 37 while the same dispersal distance can be the result of different trajectory modes. The
 38 proportion of species' trajectory modes formed its trajectory spectrum. Wind speed
 39 tends to have strong influence on light and low-wind-loading seeds, release height
 40 tends to have that on heavy and high-wind-loading seeds. Species with high
 41 proportion of horizontal projectile and projectile have high dispersal capacity, vice
 42 versa. Therefore, trajectory spectrum of a species reveals its primary dispersal
 43 strategies and evolutionary consequences.

44 **Keywords:** dispersal distance, dispersal pattern, morphological traits, primary
 45 dispersal, trajectory mode, video recording methods, wind tunnel

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54 1. Introduction

55 Exploring the reason why different diaspores have different dispersal distances has
56 been a major challenge for ecologists (Maurer *et al.*, 2013; Nathan, 2001; Tackenberg
57 *et al.*, 2003; Thomson *et al.*, 2011). Seed moving trajectory may explain seed primary
58 dispersal distance (Dauer *et al.*, 2006; Jongejans and Telenius, 2001). Determining
59 seed dispersal trajectory and its relevant factors is essential to clarify the mechanisms
60 underlying the structure and dynamics of plant population and community (Nathan,
61 2001).

62 Seed dispersal trajectory may be influenced by wind conditions (wind speed and
63 orientation), release height and seed traits such as seed weight, appendage, wind
64 loading and terminal velocity (Savage *et al.*, 2014; Thomson *et al.*, 2011; Zhu *et al.*,
65 2016). Horizontal wind can disperse seeds far away from their mother plants
66 (Augspurger, 1986; Soons *et al.*, 2004; vanDorp *et al.*, 1996). Convective updrafts are
67 proposed to promote dispersal distance (Heydel *et al.*, 2014; Nathan *et al.*, 2002;
68 Soons *et al.*, 2004) and change seed dispersal trajectory. So, it is important to quantify
69 the relationship between seed dispersal trajectory and wind conditions.

70 Release height is considered as an important plant trait affecting seed flying time
71 (Tackenberg, 2003), which is closely related to seed primary dispersal distance and
72 pattern (Thomson *et al.*, 2011; vanDorp *et al.*, 1996). Seed traits such as seed mass
73 (Augspurger, 1988), terminal velocity (Andersen, 1993) and wind loading (Matlack,
74 1992) have profound effects on seed dispersal pattern and distance. Seed
75 morphological characters are evolved due to the selection on dispersal ability
76 (Andersen, 1993; Nathan, 2001). Particular seed appendages are generally assumed to
77 help wind-dispersed seeds travel further since they decrease terminal velocity and
78 wind loading but increase the roughness of seed surface (Jongejans and Telenius,
79 2001; Nathan *et al.*, 2011). However, up to date few studies have been conducted on
80 the relationship among release height, seed morphological character, and seed moving
81 trajectory.

82 In reality, wind conditions are so complicated that it is almost insurmountable to
83 measure (Jones and Muller-Landau, 2008; Jongejans and Telenius, 2001). The wind
84 tunnel, manufacturing controllable wind conditions, is necessary for quantifying the
85 primary seed dispersal distance and distribution pattern (Dauer *et al.*, 2006; Zhu *et al.*,
86 2016). It can also be used to determine the dispersal trajectory if special facilities and
87 techniques could be applied.

88 In this study, wind tunnel and video camera were used to track the seed dispersal
89 trajectory of 7 *Calligonum* (*Polygonaceae*) species with different appendages (wings,
90 bristles, membranous-saccate and wings+thorns) under the wind speed of 4, 6, 8 and
91 10 m s⁻¹ and the release height of 0.2, 0.4, 0.6, 0.8 and 1.0 m. Dispersal trajectories
92 were determined by video analysis and coordinate transformation. Redundancy
93 analyses (RDA) was used to explore the relationship between seed moving trajectory
94 and wind speed, release height and seed morphological traits. The objectives of this
95 study were to answer the following questions: 1) how did seed dispersal trajectory
96 shift with wind speed, release height and seed morphological traits? 2) what is the
97 relationship between seed primary dispersal distance and its dispersal trajectory? We
98 especially tested the hypothesis: 1) in descending order, the key factors determining
99 seed dispersal trajectory modes are wind speed, seed morphological traits and release
100 height; 2) key factors shaping primary dispersal trajectory are different for seeds with
101 various morphological traits: wind speed is the key factor for the seed with wings,
102 while terminal velocity is the key factor for the seed with bristles; 3) the same
103 dispersal distance may be the results of different trajectories; the straight-line-shaped
104 trajectory tend to show a short dispersal distance, but the curve-shaped trajectory tend
105 to show long dispersal distance.

106 **2. Materials and Methods**

107 **2.1 Seed collection**

108 Seeds of 7 *Calligonum* species (Fig. 1) were collected in Ulanbuh Desert
109 (106°09'–107°10'E, 40°09'–40°57'N, 1050 m above sea level) in Inner Mongolia and

110 Tazhong (83°40'E, 39°00'N, 1099 m above sea level) of Taklimakan Desert Xinjiang,
111 Northwestern China. Four hundred intact seeds were collected for each species from
112 20 individual plants after seed maturity in natural populations in July and August,
113 2016. All seeds were air dried and stored in laboratory until experiment.

114 **2.2 Measurement of morphological and aerodynamic traits**

115 Twenty intact seeds were randomly selected to measure the dimension, shape index,
116 mass, projected area, wing loading and terminal velocity. Three dimensions (length,
117 width and height) of each seed were measured using digital caliper (0.01 mm
118 accuracy) (Zhu *et al.*, 2016). Seed mass was determined by electronic balance (0.1 mg
119 accuracy). Seeds were scanned and then analyzed by WinSEEDLE (Regent
120 Instruments Inc., Canada) image analysis system to measure projected areas (PA)
121 (Zhu *et al.*, 2016). The wing loading (WL) was calculated as the ratio of seed mass to
122 projected area (Greene and Johnson, 1997; Howlett, 1995; Matlack, 1987). The shape
123 index (SI) was calculated following Thompson *et al.* (1993). The terminal velocity
124 (TV) was determined using an apparatus described by Zotz *et al.* (2016) (Table 1).

125 **2.3 Wind-tunnel experiments**

126 A wind tunnel was used to measure the primary dispersal distance and trajectory of
127 *Calligonum* seeds (Zhu *et al.*, 2016). A square grids scale (N) was drawn on the wind
128 tunnel side wall (Fig. 2). Markers (M) corresponding to the square grids were drawn
129 on the opposite wall at the bottom of observation window. Marking lines (P) were
130 drawn in order to measure the position of falling seed. A pitot tube (A) suspended
131 from the ceiling and a differential pressure transmitter (B, Dwyer Instruments Inc.,
132 Indiana, USA) were used to monitor the wind speed at the test section. Wind speed
133 was measured at the height of 1 m above the ground. Seeds were released via a seed
134 releaser (C) inserted through the middle of the tunnel ceiling. Seeds were put into the
135 top inlet (2 m in length, 6 cm in diameter) of the releaser. A baffle plate (E), controlled
136 by a wrench (D), was covered on the outlet of the releaser in order to keep the seed
137 motionless. The seed release height (H) was the distance from the ground to the outlet.

Twenty treatments in total were designed including four 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). Twenty seeds (replications) for each species were tested for each treatment. In total, 2800 seeds were released during the wind tunnel experiment. A video camera (G) (GC-P100AC, JVC, Japan) was used to record the dispersal processes using the speed of 50 frames per second (fps) (Fig. 2). The shooting distance was adjusted according to wind speed and release height in order to obtain the overall view of seed dispersal processes.

2.4 Determination of trajectory and dispersal distance

Videos were analyzed by QuickTime player (Apple Macintosh, version 7.79.80.95, 2016) to determine the seed position and dispersal distance. As the video captured by camera was a 3-dimensional scene, coordinates transformation was conducted to obtain projected coordinates on tunnel wall based on perspective principle (Fig. 3). Every frame of the video was printed on a paper, then two marking lines GH and JK were drawn on the paper intersecting at the point V according to the perspective principle, i.e., the vanishing point. Line HK was an intersection line of side wall and the ground. The point A was a position of falling seed in the picture. Vertical line was drawn from the point A intersecting with the central line LM at point B. Point C was an intersection between line BV and HK. A vertical line was drawn from the 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 token, successive projected coordinates of every video frame were obtained. A projected trajectory of seed was drawn from the release point P_o (x_o, y_o) to the fall point P_t (x_t, 0) on the paper. The dispersal distance DP_t is (x_t-x_o) cm, where the x_t, and x_o is the abscissa of P_t and P_o (Fig. 3).

2.3 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)

166 to the trajectory modes of the 7 *Calligonum* species. Since four types of appendage
 167 structures and trajectory modes are not scaled attributes, we defined 4 variables for
 168 the occurrence of appendage structures, AS_1 , AS_2 , AS_3 and AS_4 , with the property that
 169 $AS_i=1$ if the appendage structure belongs to wings, bristles, membranous-saccate and
 170 wings +thorns, otherwise $AS_i=0$. For same token, we defined 4 variables for the
 171 occurrence of trajectory modes: concave upward, straight line, horizontal projectile
 172 and projectile, as TM_1 , TM_2 , TM_3 and TM_4 . Each explanatory power was tested to
 173 assess the contribution of various abiotic and biotic factors to the variation in dispersal
 174 trajectory shifts by using forward-selection procedures.
 175 Hierarchical clustering analysis was used to classify the dispersal distance of 7 species.
 176 A dendrogram was drawn by ward's method after transforming values of dispersal
 177 distance into standardized Z scores. The hierarchical clustering analysis, dendrogram
 178 plot and descriptive statistics were analysed using PASW Statistics Software version
 179 18.0 (IBM Corp., Armonk, New York, USA). Box plot, curve fit and scatter plot was
 180 drawn using SigmaPlot version 10.0 (Systat Software, Inc., USA).

181 **3. Result**

182 **3.1 Trajectory modes of 7 *Calligonum* species under different release heights and** 183 **wind speeds**

184 Four modes of moving trajectory, i.e., concave upward, straight line, horizontal
 185 projectile and projectile, were tracked under different release heights and wind speeds.
 186 The concave upward had the largest launching angle between horizontal and moving
 187 direction. The straight line had a constant and smaller included angle than that of
 188 concave upward. The horizontal projectile had the smallest launching angle
 189 (approximate to 0). The projectile had a launching angle above the horizontal
 190 direction (Fig. 4).

191 **3.2 Relationship between seed dispersal distance and dispersal trajectory mode**

192 The dispersal distance increased from concave upward, straight line, horizontal
 193 projectile to projectile. The concave upward trajectory had the dispersal distance

194 ranging from 10 cm to 260 cm (median 45 cm). The dispersal distance of straight line
195 mode ranged from 6 cm to 480 cm (median 105 cm). The horizontal projectile mode
196 dispersed 70 cm to 600 cm in distance (median 260 cm) and the projectile mode from
197 128 cm to 750 cm (median 337 cm) (Fig. 5).

198 **3.3 Occurrence probability of 4 trajectory modes under 4 wind speeds and 5** 199 **release heights**

200 Four modes of trajectory shifted with a probability of occurrence under each wind
201 speed and release height. With the increase in wind speed, the concave upward mode
202 showed random occurrence probability, ranging from 17.0%-32.0% (Fig. 6 A). The
203 straight line mode had a decreased probability, ranged from 31.6% to 18.3% (Fig. 6
204 B). The projectile and projectile modes showed increased probability, from 1.1% to
205 47.1% and from 2.3% to 50.6%, respectively. The accumulative probability of these
206 two modes was more than 80% when the wind speed was above 8 m s⁻¹ (Fig. 6 C and
207 D).

208 With the increase in release height, the concave upward mode significantly decreased
209 in occurrence probability, from 68.5% to 0, occurred mainly within 20-40 cm (Fig. 6
210 E). The occurrence probability of the straight line mode fluctuated slightly, from 17.4%
211 to 22.6% (Fig. 6 F). The horizontal projectile and projectile modes showed increasing
212 tendency from 9.6%-34.9% and 4.7%-31.7%, respectively. Each of these two modes
213 had the occurrence probability higher than 75% within the release height 60 cm to 100
214 cm (Fig. 6 G and H).

215 **3.4 Clustering of dispersal distance of 7 *Calligonum* species**

216 The 7 species could be classified into 3 groups according to the dispersal distance (Fig.
217 7). Group I included *C. arborescens*, *C. densum*, and *C. klementzii*, with bristles, big
218 mass and high terminal velocity (Table 1). Mean of dispersal distance was 124.3 cm
219 (standard deviation, 84.3) ranging from 10 cm to 395 cm (median 104.5 cm). Group II
220 included *C. mongolicum* and *C. rubicundum* with bristles and wings+thorns,
221 respectively. *C. mongolicum* had small mass and terminal velocity, while *C.*

222 *rubicundum* had big mass and terminal velocity (Table 1). Mean of dispersal distance
223 was 151.7 cm (standard deviation 108.8) ranging from 6 cm to 650 cm (median 124.0
224 cm). Group III included *C. aphyllum* and *C. junceum* with small mass and terminal
225 velocity. *C. aphyllum* had wings and *C. junceum* had balloon-like
226 membranous-saccate. Mean of dispersal distance was 181.0 cm (standard deviation
227 120.8) ranging from 18 cm to 750 cm (median 150.0 cm).

228 **3.5 Distribution of trajectory modes in 7 *Calligonum* species**

229 In group I, the modes of concave upward trajectory (>10%) and straight line trajectory
230 (>75%) accounted for more than 90% of total trajectories, while the modes of
231 horizontal projectile trajectory (<7.5%) and projectile trajectory (not found in the
232 three species) was less than 10% (Table 2). In group II, the concave upward and
233 straight line modes in two species occupied 58-85% of total trajectories and the
234 horizontal projectile and projectile 13.8%-41% (Table 2). In group III, the concave
235 upward and straight line modes in two species were less than 65% of the total
236 trajectories. The horizontal projectile and projectile modes made up more than 35% of
237 the total trajectories (Table 2).

238 We defined the proportion of trajectory modes in a species as the trajectory spectrum.

239 In group I, there is higher percentage of concave upward and straight line, and low
240 percentage of horizontal projectile and projectile in their spectrum, such as *C.*
241 *arborescens* and *C. densum* (Table 2). In group III, high percentage of horizontal
242 projectile and projectile occurs in their spectrum, such as *C. aphyllum* (Table 2).

243 **3.6 Relationship between wind speed, release height, seed morphological traits, 244 and trajectory modes**

245 The terminal velocity (TV), wings (AS₁), membranous-saccate (AS₃), release height
246 (RH) and shape index (SI) were positively linked with the modes of horizontal
247 projectile (TM₃) and projectile (TM₄), while negatively linked with the concave
248 upward (TM₁) and straight line (TM₂) (Fig. 8 A). The seed mass (SM), TV, bristles
249 (AS₂), wings+thorns (AS₄) and wind loading (WL) were negatively linked with

250 horizontal projectile (TM₃) and TM₄, and positively linked with TM₁ and TM₂ (Fig. 8
251 A).

252 For all 7 species, the explanatory power on the trajectory modes (TM) in descending
253 order was WS, SM, RH, TV, AS₄, SI and WL (Table 3). The WS has the most
254 explanatory power, explained 9.2% ($p=0.002$) of variation in trajectory modes. The
255 SM has the second explanatory power, explained 6.1% of the variation. The other
256 factors in descending order were RH, TV, AS and SI as well as WL, totally explained
257 6.3% of the variation (Table 3).

258 In group I, RH, TV, WS and SM were the significant explanatory variables ($p=0.002$),
259 explained 16.0% of the variation in trajectory modes (Table 3). The RH was positively
260 linked with TM₂, TM₃ while negatively linked with TM₁. The TV was positively
261 linked with TM₁ and negatively linked with TM₂. The WS was positively linked with
262 TM₃ and negatively linked with TM₂. The SM was positively linked with TM₂ and
263 negatively linked with TM₃ (Fig. 8 B). The RH was the most significant factor
264 explained 13.4% ($p=0.002$) of the variation in trajectory modes. While TV, WS and
265 SM only explained 2.5% (Table 3).

266 In group II, WS, SI and RH were the significant explanatory variables ($p=0.002$),
267 explained 32.4% of the variation in trajectory mode shifts (Table 3). The WS and RH
268 were positively linked with TM₃ and TM₄ and negatively linked with TM₁ and TM₂.
269 The SI was positively linked with TM₁ and TM₂ and negatively linked with TM₃ and
270 TM₄ (Fig. 8 C). The WS was the key factor, explained 20.5% of the variation. The SI
271 and RH explained 12.1% (Table 3).

272 In group III, the significant explanatory variables ($p=0.002$) were WS, RH and SI,
273 explained 23.3% of the TM variation (Table 3). The WS and RH were positively
274 linked with TM₃ and TM₄ and negatively linked with TM₁ and TM₂. The SI was
275 positively linked with TM₂ and negatively linked with TM₁, TM₃ and TM₄ (Fig. 8 D).
276 The WS was the key factor, explained 20.3% of the variation in trajectory modes. The
277 RH and SI explained 3.0% in total (Table 3).

4. Discussion

4.1 Contributions of wind speed, release height and morphological traits to trajectory modes

Our results showed that wind speed had the strongest effect on trajectory modes. The finding here support the general perception that wind is the key factor determining seed dispersal trajectory. The trajectory modes might be affected by not only horizontal wind but also turbulent fluctuations in vertical updrafts. Previous studies demonstrated that horizontal wind is an important environmental factor prompting the lateral dispersal (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). Fluctuations of shear-induced updrafts would increase with increasing horizontal wind speed (Greene, 2005). Thus, the trajectory modes might be strongly influenced by the fluctuations of updrafts with wind speed. Surprisingly, seed mass has the second explanatory power on trajectory modes though the seeds were selected within the same genus, *Calligonum*, which have little variation in seed mass among species. The high explanatory power of seed mass could be due to the fact that seed mass could influence lateral movement and rate of descent (Matlack, 1987, 1992). The findings are in consistent with the perception that small seeds disperse better than large seed because larger seed mass is poorly accelerated and dispersed by wind (Greene and Johnson, 1993; Thomson *et al.*, 2011). Different from our expectations, release height has the third explanatory power on trajectory modes instead of having the least effect on it. The reason might be that release height is strongly correlated with falling time of seed (Savage *et al.*, 2014). The falling time can change horizontal and vertical speed of seeds, and thus affect the trajectory modes.

The other seed morphological traits such as terminal velocity, appendage structure, shape index and wing loading explained 4.1% (accounting for 19.0% of total explanation) of the variation in trajectory modes. One possible reason is that these

306 factors have low variation across species, consequently contributing low variation to
307 the trajectory modes.

308 In this study, the redundancy analysis showed that the total explanation power of
309 abiotic and biotic factors on the variation in trajectory modes is from 16.0% to 32.4%.

310 There are two possible reasons for the low explanatory power occurred in the
311 experiment. Firstly, the occurrence of trajectory modes, such as straight line, varies
312 little with wind speed and release height, which decreases explanatory power of
313 independent variable on shifts of dispersal trajectory. Secondly, the wind loading may
314 be not appropriate for spherical seeds with complicated structures because its
315 projected area might be miscalculated.

316 **4.2 Effects of seed appendages on dispersal trajectory modes and spectrum**

317 Appendages of wind-dispersed seeds are designed for slowing descent rate by
318 lowering wing loading or increasing the roughness of seed surface and the chance of
319 exposure to wind (Andersen, 1993; Augspurger, 1986; Nathan *et al.*, 2011). Our
320 findings suggest that the key factors shaping primary dispersal trajectory might be
321 different for seeds with different morphological traits. The redundancy analysis
322 showed that the key factor is not terminal velocity but release height for seeds with
323 bristles. However, for seeds with wings, the key factor is wind speed. There are two
324 possible reasons. Firstly, seeds with bristles have high wind loading because the
325 bristles have so low projected area that low drag force is exerted by wind speed. Thus,
326 the trajectory modes are dependent on the release height rather than the terminal
327 velocity or wind speed. Secondly, wings decrease wing loading and obtain more drag
328 force from wind speed. So, wind speed has much effect on the trajectory modes of
329 seeds with wings.

330 Seed appendages have profound influence on the trajectory spectrum of species. The
331 trajectory spectrum is different between seeds with bristles and seeds with wings. The
332 proportion of concave upward and straight line for seeds with bristles (e.g. *C.*
333 *arborescens*) are higher than that for seeds with wings (e.g. *C. aphyllum*). Conversely,

the proportion of horizontal projectile and projectile for seeds with bristles are lower than that for seeds with wings.

4.3 The relationship between seed dispersal distance and trajectory modes

Previous studies demonstrated that wind speed is the most important determinant of seed dispersal distance (Soons *et al.*, 2004; Zhu *et al.*, 2016). The findings showed that the trajectory of concave upward and straight line tend to have short dispersal distance because wind speed has little influence on the occurrence of these two trajectories. And, concave-upward tend to have the shortest distance because it mostly occurs under the release heights below 40 cm which shortens the dispersal distance. However, the trajectory of horizontal projectile and projectile tend to have long dispersal distance because their occurrence probabilities are greatly affected by wind speed, and mostly occurred under wind speed over 8 m s⁻¹.

Obviously, different trajectory modes have different ranges of dispersal distance. However, the studies have adequately support the hypothesis that the same dispersal distance may be the results of different trajectory modes because the ranges of dispersal distance overlap each other among different trajectories, for example the overlap of the straight line (ranged from 6 cm to 480 cm) and horizontal projectile (70 cm to 600 cm) is from 70 cm to 480cm.

4.4 The relationship between seed dispersal capacity and trajectory spectrum

Previously studies showed that seed dispersal distance embody dispersal capacity (Thomson *et al.*, 2011). Therefore, the trajectory spectrum of a species can reflect its dispersal capacity. For example, *C. arborescens*, *C. densum* and *C. klementzii* have low dispersal capacity due to the high percentage of concave upward (>10%), low percentage of horizontal projectile (<7.5%) and projectile (0) (Table 2). On the contrary, *C. aphyllum* and *C. junceum* have high dispersal capacity since there are low proportion (<2%) of concave upward and high proportion of horizontal projectile (>25%) and projectile (>9%) in their spectrum (Table 2). The results suggest that the trajectory spectrum of each species might reflect the dispersal strategy due to

362 consequence of natural selection.

363 **5. Conclusion**

364 In virtue of the wind tunnel and video recording technique, concave upward, straight
365 line, horizontal projectile and projectile are tracked in the 7 species. Wind speed, seed
366 mass and release height are key factors determining seed dispersal trajectory modes.
367 Release height has main influence on primary dispersal trajectory of seeds with
368 bristles, while wind speed has it on that of seeds with wings. Concave upward and
369 straight line modes tend to exert short dispersal distances, the horizontal projectile and
370 projectile modes tend to exert long dispersal distances. Different trajectory modes
371 lead to different dispersal distances, but the same dispersal distance can be resulted
372 from different trajectory modes. Trajectory spectrum of species not only reveals its
373 dispersal capacity but also reflects its primary dispersal strategies and evolutionary
374 consequences. This study provides critical information for clarifying the mechanisms
375 of seed primary dispersal and predicting seed dispersal pattern.

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383 **Authors' contributions**

384 ZL, ML and QZ conceived the ideas and designed methodology; ZX, WL, XQ and
385 XC collected the data; JQ, YW, YZ and XL analyzed the data; QZ led the writing of
386 the manuscript. All authors contributed critically to the drafts and gave final approval
387 for publication.

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456 *Zygophyllum xanthoxylon* (Zygophyllaceae)? *Journal of Plant Ecology* **9**, 346-356.
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460 Tables and Figures:

461

462 Table 1 Morphological and aerodynamic characteristics of the seeds in the 7 studied

463 *Calligonum* species (Mean±SD)

Species	Structure	Length (mm)	Width (mm)	Height (mm)	Mass (mg)	PA (mm ²)	WL (mg/cm ²)	SI	TV (m/s)
<i>C. aphyllum</i>	wings	14.3±1.2	11.7±1.6	11.7±1.5	46.5±8.8	1.3±0.2	37.8±6.3	0.01±0.01	2.58±0.26
<i>C. arborescens</i>	Bristles	24.9±1.6	22.0±1.4	22.4±1.8	193.8±21.1	4.2±0.5	46.5±5.2	0.003±0.002	3.30±0.20
<i>C. densum</i>	Bristles	16.4±1.6	14.3±1.1	13.9±1.2	95.6±18.1	1.8±0.3	55.0±9.6	0.004±0.004	3.39±0.25
<i>C. junceum</i>	Membranous-saccate	11.9±0.6	9.6±1.4	8.7±1.6	35.0±7.6	0.8±0.2	44.2±7.8	0.02±0.01	3.23±0.50
<i>C. klementzii</i>	Bristles	20.6±2.1	20.5±2.1	19.8±2.0	103.8±14.3	3.3±0.6	32.5±5.0	0.002±0.002	3.31±0.26
<i>C. mongolicum</i>	Bristles	16.0±1.3	15.5±1.4	14.5±1.7	39.3±11.1	1.8±0.3	21.3±5.3	0.003±0.003	2.48±0.44
<i>C. rubicundum</i>	Wings +thorns	19.6±1.3	15.5±1.8	15.2±1.8	187.6±23.1	2.2±0.3	85.4±10.5	0.014±0.006	4.07±0.37

464 Abbreviations: PA, Projected area; TV, Terminal velocity; SI, Shape index; WL, Wing loading

465

466 Table 2 Number and proportion of 4 trajectory modes in each species.

Group	Species	Concave upward	Straight line	H-projectile	Projectile
Group I	<i>C. arborescens</i>	50 (12.5%)	345 (86.3%)	5 (1.2%)	0
	<i>C. densum</i>	82 (20.5%)	300 (75.0%)	18 (4.5%)	0
	<i>C. klementzii</i>	41 (10.2%)	329 (82.3%)	30 (7.5%)	0
Group II	<i>C. mongolicum</i>	5 (1.2%)	227 (56.8%)	162 (40.5%)	6 (1.5%)
	<i>C. rubicundum</i>	10 (2.5%)	335 (83.7%)	55 (13.8%)	0
Group III	<i>C. aphyllum</i>	5 (1.2%)	204 (51.0%)	149 (37.3%)	42 (10.5%)
	<i>C. junceum</i>	1 (0.3%)	252 (63.0%)	111 (27.7%)	36 (9.0%)

467

468

Table 3 Explanations and relative contributions of wind speed, release height and seed morphological traits to trajectory modes of 7 *Calligonum* species

Species	Explanatory factors	Explanation (%)	Contribution (%)	F value	<i>p</i> value
All 7 species	WS	9.2	42.4	283.0	0.002
	SM	6.1	28.1	201.0	0.002
	RH	2.2	10.2	75.0	0.002
	TV	1.9	8.9	36.4	0.002
	AS ₄	1.1	4.9	68.0	0.002
	SI	0.7	3.4	26.4	0.002
	WL	0.4	1.7	12.8	0.002
	Total (%)	21.6	99.6		
Group I	RH	13.4	84.1	186.0	0.002
	TV	1.2	7.5	16.7	0.002
	WS	1.0	6.6	14.8	0.002
	SM	0.3	1.9	4.3	0.028
	Total (%)	16.0	100		
Group II	WS	20.3	62.7	203.0	0.002
	SI	8.4	25.9	93.5	0.002
	RH	3.7	11.4	43.5	0.002
	Total (%)	32.4	100		
Group III	WS	20.3	87.2	204.0	0.002
	RH	1.9	8.2	19.6	0.002
	SI	1.1	4.6	11.2	0.002
	Total (%)	23.3	100		

473 Fig. 1 Side and top view of 7 species of *Calligonum*

474

475 Fig. 2 Sketch map of recording seed trajectory and dispersal distance in wind tunnel.

476 A: a pitot tube; B: differential pressure transmitter; C: a seed releaser; Z: detailed

477 structure of the releaser; D: a release controller with a wrench; E: a baffle plate

478 controlled by the wrench; F: a seed released from the releaser; H: release height; G: a

479 camera; M: a marker; L: the centre line of the tunnel ground; N: square grids scale; P:

480 a marking line.

481

482 Fig. 3 Sketch map of coordinate transformation of seed position from a 3-dimensional

483 scene into a 2-dimensional surface based on perspective principle. NHKQ: square

484 grids scale on the wall of wind tunnel; HGJK: ground of wind tunnel; HK and GH:

485 intersection lines of the side wall and the ground; LM: the centre line of the ground;

486 GH and JK: two marking lines; V: vanishing point, extended lines of GH, JK and their

487 parallel lines intersected at the point; O: seeds release point; A: any point in seed

488 dispersal trajectory; F: seed fall point; E and B: projected point of O and A on the

489 ground; D ($x_o, 0$), C ($x_i, 0$) and P_t ($x_t, 0$): intersection points of VE, VB and VF with

490 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

491 scale; R: a marker.

492

493 Fig. 4 Trajectory modes of primary seed wind dispersal of 7 *Calligonum* species under

494 release height of 20 cm (A), 40 cm (B), 60 cm(C), 80 cm (D) and 100 cm (E) under

495 the wind speed of 4, 6, 8 and 10 m s⁻¹.

496

497 Fig. 5 Relationship between trajectory modes and primary dispersal distance. Where,

498 CU: Concave upward; SL: Straight line; HP: Horizontal projectile; P: Projectile.

499

500 Fig. 6 Probability of the occurrence of 4 trajectory modes under 4 wind speeds and

501 5 release heights. The left panels (A~D) show probability of the occurrence of 4

502 trajectory modes under 4 wind speeds. The right panels (E~H) show probability of the
503 occurrence of 4 trajectory modes under 5 release heights.

504

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

508

509 Fig. 8 Relationship between wind speed, release height, seed morphological traits, and
510 shifts of trajectory mode of (A) 7 species (in total); (B) 3 species in group one; (C) 2
511 species in group two; (D) 2 species in group three. TM: trajectory mode; TM₁:
512 concave upward, TM₂: straight line; TM₃: horizontal projectile; TM₄: projectile; SM:
513 seed mass (mg); TV: terminal velocity (m/s); WL: wing loading (mg/cm²); SI: shape
514 index; RH: release height (cm); WS: wind speed (m/s); AS: appendage structure; AS₁:
515 wings; AS₂: bristles; AS₃: membranous-saccate; AS₄: wings+thorns. Explanatory
516 factors are indicated by red lines with hollow arrows. Trajectory modes are showed by
517 blue lines with solid arrows.

518

519

C. aphyllum *C. arborescens* *C. densum* *C. junceum* *C. klementzii* *C. mongolicum* *C. rubicundum*