Plant Diversity 43 (2021) 234–238

Contents lists available at ScienceDirect

Plant Diversity

journal homepage: http://www.keaipublishing.com/en/journals/plant-diversity/ http://journal.kib.ac.cn

Research paper

Dispersal and germination of winged seeds of *Brandisia hancei*, a shrub in karst regions of China

Yongquan Ren [a,*], Chengling Huang [a], Jiaming Zhang [a], Yongpeng Ma [b], Xiaoling Tian [c,**]

[a] College of Eco-Environmental Engineering, Guizhou Minzu University, Guiyang 550025, China
[b] Yunnan Key Laboratory for Integrative Conservation of Plant Species with Extremely Small Populations, Kunming Institute of Botany, Kunming 650201, China
[c] The College of Humanities and Science of Guizhou Minzu University, Guiyang 550025, China

A R T I C L E I N F O

Article history:
Received 30 June 2020
Received in revised form
6 November 2020
Accepted 11 November 2020
Available online 26 November 2020

Keywords:
Anemochory
Hydrochory
Membranous wing
Seed dispersal
Winged seed

A B S T R A C T

Brandisia hancei (Paulowniaceae) is a widely distributed shrub in karst regions in southwestern China. Its seeds have a membranous wing, and they mature just before the rainy season begins. To assess the effect of the wing on seed dispersal and germination of *B. hancei*, we measured the dispersal distance at varying wind speeds and release heights, falling duration from different release heights, floating duration on still water, rates of imbibition of water, and drying and soil adherence to seeds. Germination experiments were conducted on intact and de-winged seeds immediately after harvest. The wing increased the falling duration in still air and the floating ability on water. Dispersal distance of winged and de-winged seeds did not differ at a wind speed of 2.8 m s^{-1}, but at 3.6 and 4.0 m s^{-1} dispersal distances were greater for de-winged than for winged seeds. Seed wing had little effect of absorption and retention of water, but significantly increased soil adherence to the seeds. Mature seeds were non-dormant and germinated to over 90% with a mean germination time of about 10 days. By combining the environmental conditions in karst habitat with the seed traits of *B. hancei*, we conclude that dispersal and germination of winged seeds are adapted to the precipitation seasonality in heterogeneous habitats absence of soil.

1. Introduction

Seed dispersal is a key process in the life history of plants. Abiotic agents can spread seeds over long distances, with the most common means of dispersal being anemochory and hydrochory (Vargas et al., 2012). Anemochory is the most frequent dispersal strategy, especially in dry, open conditions (Soons et al., 2004; Jara-Guerrero et al., 2011), and the presence of a seed wing usually increases seed buoyancy and thus dispersal distance by wind (Minami and Azuma, 2003; Eriksson and Kainulainen, 2011; Zhang et al., 2014). Water is also an important agent even for seed dispersal on dryland, and hydrochory enables long-distance dispersal before seeds are deposited in suitable sites for plant growth (Cabra-Rivas et al., 2014; Kehr et al., 2014). Seeds of many plant species have the ability to float, and seed morphological traits influence floating time and thus dispersal distance by water (Guja et al., 2010; Carthey et al., 2016). Often, seed dispersal occurs in more than one step, and hydrochory can act as an additional mode after anemochory, thereby dispersing seeds longer distances than anemochory alone (Kowarik and Säumel, 2008; Säumel and Kowarik, 2010).

Brandisia hancei Hook. f. (Paulowniaceae) is an evergreen shrub that grows up to 2 m in height. Plants grow in forests or along forest edges with a wide distribution, primarily in karst regions of SW China (Hong et al., 1998), where microhabitats are highly heterogeneous due to discontinuous soil cover and a shallow layer of soil. *B. hancei* usually grows on the lower and gentle part of karst hillslopes. *B. hancei* flowers in winter, and seeds are mature by April (Ren et al., 2016). The flat, oval-shaped seeds of *B. hancei* are 3–4 mm in length and 1–2 mm in width. The seed is surrounded by a membranous wing, which is formed from the outer integument of the seed coat. After wing removal, the elongated-oval de-winged seeds are only about 1 mm in length.

Seeds with low mass and/or a wing have been selected for increased buoyancy, and thus dispersal by wind (Eriksson and

* Corresponding author.
** Corresponding author.
E-mail addresses: renyqcn@163.com (Y. Ren), lengyan1112@163.com (X. Tian).
Peer review under responsibility of Editorial Office of Plant Diversity.

https://doi.org/10.1016/j.pld.2020.11.006
2468-2659/

Kainulainen, 2011). However, dispersal of seeds by anemochory alone is often for only short distances, and the effect of the wing on seed dispersal by wind is not obvious (Jongejans and Telenius, 2001; Säumel and Kowarik, 2010). In addition, the effectiveness of wind dispersal of seeds of shrubs growing in the understory of forests is likely to be limited by their small stature and also by the low wind speeds in their habitats (Sypka and Starzak, 2013; Suetsugu, 2018). Anemochory therefore may not be the only dispersal strategy in *B. hancei*. The winged seeds of this species mature and disperse in April, just at the transition from the dry to rainy season in SW China, during which time (May to August) there is considerable surface runoff of water in its habitat (Tu et al., 2016). Thus, the seed wing may contribute to dispersal by both anemochory and hydrochory; however, the full dispersive potential of seeds has not been characterized for *B. hancei*.

Despite the high annual precipitation in the karst regions in SW China, the soil water storage capacity is very low because soil depth is usually shallow. Therefore, plants frequently suffer from a deficiency of soil moisture (Jiang et al., 2014). A membranous wing on seeds has been reported to be an adaptation for floating on water, seed dispersal, water uptake and soil adhesion, which would improve germination in a dry environment (Western, 2012; Chen et al., 2016). Because seed maturity of *B. hancei* occurs at onset of the rainy season, we investigated the role of the seed wing in dispersal by wind and water. We tested two hypotheses. 1) The seed wing functions as a dispersal mechanism and plays a key role in both anemochory and hydrochory. 2) The seed wing contributes to absorption and retention of water, as well as adherence of soil, and thus facilitates timely germination in karst habitats.

2. Materials and methods

2.1. Materials

Mature seeds of *Brandisia hancei* were collected from a natural population of plants growing in Guiyang, Guizhou, China (26.36°N, 106.66°E, elevation: 1250 m). A germination experiment was conducted immediately after seed collection in April 2019, while seeds for other experiments, except those for water absorption and retention studies, were stored in paper envelops for about 3 months. The water absorption and loss experiments were conducted with seeds collected in April 2020, which were also stored in paper envelops for about 2 months.

2.2. Dispersal potential of anemochory and hydrochory

To determine the effect of the seed wing on dispersal potential via anemochory, falling duration and dispersal distance were measured and compared for intact and de-winged seeds of *Brandisia hancei* in a windless laboratory. The seed wing was rubbed off by hand at first and then further removed with a needle. Falling duration was measured for 50 intact seeds and 50 de-winged seeds. Seeds were released one by one from 60 cm, 120 cm and 180 cm above the floor, and falling duration was recorded with a stopwatch. Dispersal distance in still air was measured for 100 intact seeds and 100 de-winged seeds. Seeds were released one by one from a height of 60 cm, 120 cm and 180 cm above a point on the floor, and the distance from the point to where each seed landed was measured.

Dispersal distance under different wind speeds was also measured to evaluate the influence of the wing on dispersal distance. One hundred intact seeds and 100 de-winged seeds were released one by one at 60 cm above a point on the floor in a room exposed to three wind speeds (2.8 $m \cdot s^{-1}$, 3.6 $m \cdot s^{-1}$ and 4.0 $m \cdot s^{-1}$) generated by using different settings on an electric fan. An anemometer was used to measure the wind speed at the release point.

To investigate the role the seed wing played in dispersal by hydrochory, 100 intact seeds and 100 de-winged seeds were placed in two glass beakers filled with tap water to assess buoyancy. The containers were placed on a laboratory bench under ambient conditions (~25 °C) and their position randomized every 2 days. Surface tension was deliberately disrupted when replacing or adding water to containers. Sunken seeds were counted every day. Mean floating duration (MFD) was calculated as: $MFD = \Sigma (t_i * n_i) / \Sigma n_i$, where t_i is the duration of experiment (days), n_i is the number of seeds sunk at t_i. The floating duration experiment was conducted in five replicates of 100 seeds each.

2.3. Water absorption and retention

Rates of imbibition and drying were determined for four replicates of 2000 intact and 2000 de-winged seeds. Each replicate was weighed with an electronic balance (0.1 mg accuracy) and then placed into a beaker filled with water. At one-hour intervals, water was poured out of the beaker, wet seeds were patted dry with filter paper and weighed; this procedure was repeated until seeds stopped increasing in mass. At constant wet mass, seeds were allowed to dehydrate at room temperature (~25 °C). Seeds were weighed at one-hour intervals until seed mass was constant.

2.4. Soil adherence to imbibed seeds

To determine the effect of the wing on soil adherence to imbibed seeds, 1000 intact and 1000 de-winged dry seeds were weighed and allowed to imbibe water for 24 h. Then, the imbibed seeds were placed on wet soil collected from the habitat of *B. hancei*. After the seeds had been mixed with the soil for about one minute, they were removed one by one and allowed to dry at ambient room conditions, after which they were weighed to determine how much soil adhered to them. The experiment was repeated five times.

2.5. Seed germination

A germination experiment for both intact and de-winged seeds was conducted starting on 15 April 2019, one day after seed collection. Each treatment had five repetitions of 100 seeds each. Seeds were incubated in 9-cm Petri dishes on medical cotton moistened with distilled water at ambient room conditions. Germination was recorded daily, and a seed was considered germinated when the length of the emerged radicle was about 1 mm. Germinated seeds were counted and removed from the Petri dishes daily. When no seeds germinated for five consecutive days, the test was terminated. Germination percentage (GP) and mean germination time (MGT) were calculated as: $GP = \Sigma n_i / 100$ and $MGT = \Sigma (t_i * n_i) / \Sigma n_i$, where t_i is the number of days from start of experiment and n_i the number of seeds germinated at t_i.

2.6. Data analysis

An independent samples-T test was conducted to compare differences between intact seeds and de-winged seeds. All analyses were performed by SPSS v.19.0 for Windows (IBM, Chicago, IL, USA), and all data presented as well as figures are given as mean ± standard error.

3. Results

3.1. Dispersal potential of anemochory and hydrochory

Intact seeds had longer fall duration than de-winged seeds in still air (Fig. 1). This result was supported by experiments from all three release heights: 60 cm ($t = 17.375$, $P < 0.001$), 120 cm ($t = 26.300$, $P < 0.001$), and 180 cm ($t = 29.073$, $P < 0.001$). Compared to intact seeds, de-winged seeds had a shorter dispersal distance (Fig. 2) when released from 60 cm ($t = 2.490$, $P = 0.014$) to 120 cm ($t = 5.223$, $P < 0.001$) or 180 cm ($t = 6.366$, $P < 0.001$) in a windless laboratory condition.

Higher wind speeds increased dispersal distances for both intact and de-winged seeds; however, higher wind speeds increased dispersal of de-winged seeds more than of intact seeds (Fig. 3). Without wind, intact seeds were dispersed further than de-winged seeds ($t = 2.490$, $P = 0.014$). At a wind speed of 2.8 $m \cdot s^{-1}$, dispersal distances of intact and de-winged seeds did not differ ($t = 0.026$, $P = 0.979$). At wind speeds of 3.6 $m \cdot s^{-1}$ ($t = 5.318$, $P < 0.001$) and 4.0 $m \cdot s^{-1}$ ($t = 6.258$, $P < 0.001$), dispersal distances of de-winged seeds were greater than those of intact seeds. Winged seeds showed a complex falling trajectory compared to de-winged seeds. Observations of seeds exposed to higher wind speeds indicated that winged seeds rolled as they fell, whereas the trajectory of de-winged seeds was more stable.

Intact seeds showed considerable buoyancy on water and did not begin to sink until the fifth day, with an average floating duration of 12.8 days. About half the seeds remained buoyant for 12–15 days, and the longest floating time was 19 days. However, all de-winged seeds sank within 15 min.

3.2. Water absorption and retention

The mass of intact seeds was very low, with the wing mass being about 15% of total seed mass (Table 1). Seeds imbibed water readily, and de-winged seeds reached a constant mass in less time than did intact seeds (Fig. 4). There was no difference between water absorption in intact and de-winged seeds; the wing contributed little to water absorption (Table 1). After saturation, both winged and de-winged seeds lost water quickly, and returned to their original dry mass within six hours (Fig. 4).

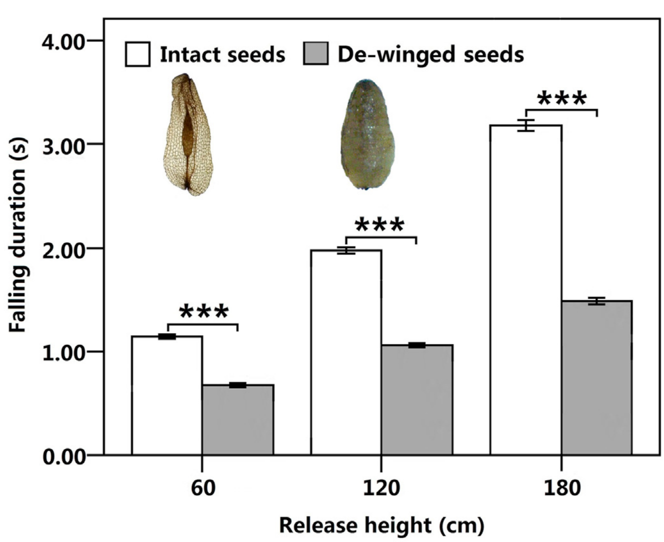

Fig. 1. Falling duration of *Brandisia hancei* seeds in still air after release from different heights. *** indicates $P < 0.001$.

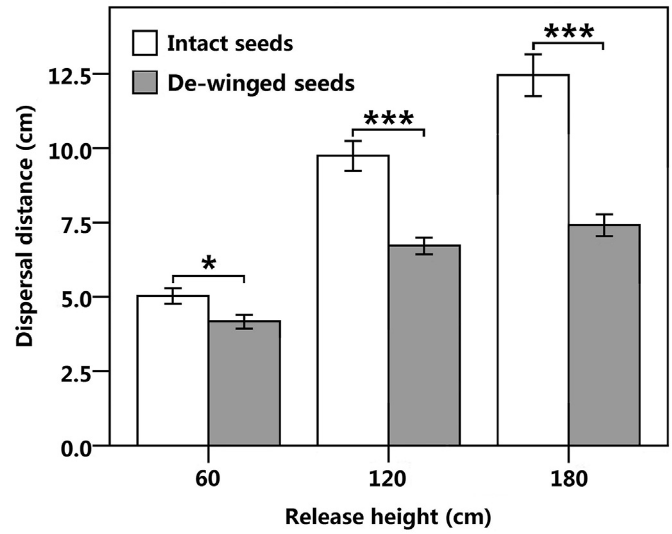

Fig. 2. Dispersal distance of *Brandisia hancei* seeds in still air after release from different heights. * indicates $P < 0.05$, *** indicates $P < 0.001$.

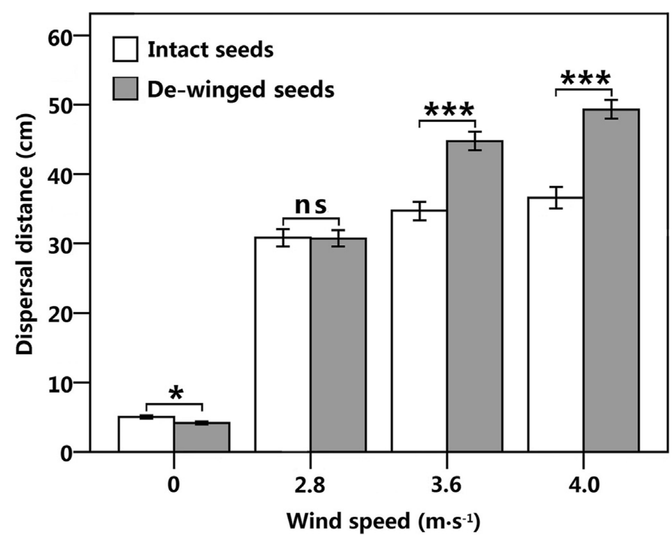

Fig. 3. Dispersal distance of *Brandisia hancei* seeds at different wind speeds. * indicates $P < 0.05$, *** indicates $P < 0.001$, ns represents non-significance.

3.3. Soil adherence to imbibed seeds

The soil adhered to seeds was as much as eight times the dry mass of intact seeds, but it was less than twice the dry mass of de-winged seeds (Table 1).

3.4. Seed germination

Both intact and de-winged seeds germinated to more than 90% (Table 2). Intact seeds began to germinate in 7 days, and the MGT was 10.2 days. De-winged seeds began to germinate in 4 days with an MGT of 8.4 days.

4. Discussion

Brandisia hancei produces seeds with low mass, which are expected to fall more slowly than those with high mass and thus are more likely to be dispersed further than high-mass seeds. Seed

Table 1
Seed mass, water imbibition and soil adhesion to seeds of *Brandisia hancei*.

	Intact seeds	De-winged seeds	t	P
Mass of 2000 seeds (g)	0.1304 ± 0.0005	0.1108 ± 0.0006	26.190	0.000
Water imbibed by 2000 seeds (g)	0.0908 ± 0.0023	0.0911 ± 0.0026	0.072	0.945
Soil adhesion (g·g-1)	7.9871 ± 1.0544	1.9029 ± 0.0678	5.758	0.004

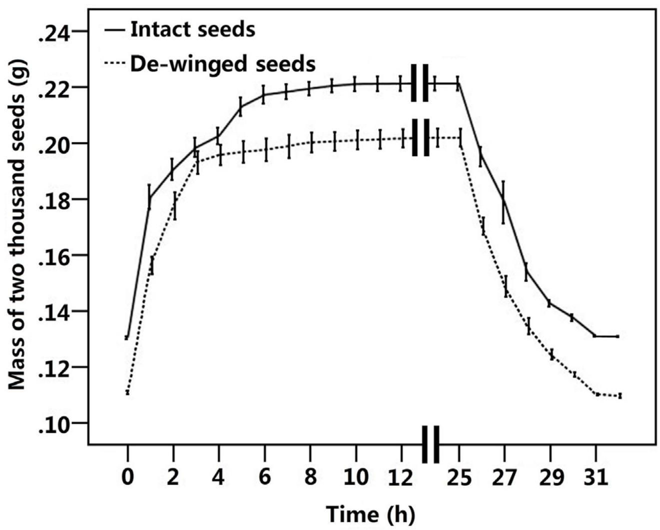

Fig. 4. Water absorption and loss from intact and de-winged seeds of *Brandisia hancei*.

Table 2
Germination percentage and mean germination time of *Brandisia hancei* seeds.

	Intact seeds	De-winged seeds	t	P
Germination percentage	93.00 ± 1.79	91.00 ± 2.35	0.678	0.517
Mean germination time (d)	10.18 ± 0.09	8.44 ± 0.34	4.935	0.006

wings are known to enhance seed buoyancy, and are thus thought to increase dispersal distance by wind (Nathan et al., 2002; Eriksson and Kainulainen, 2011; Zhang et al., 2014). In our study, low-mass seeds with a membranous wing had a low falling velocity; thus, they fell slowly and were dispersed further in windless conditions than de-winged seeds (Figs. 1 and 2). Increased wind speed resulted in further seed dispersal distances for both intact and de-winged seeds of *B. hancei*. Notably, at higher wind speeds, de-winged seeds dispersed further than intact seeds (Fig. 3). This result does not agree with the general hypothesis that the presence of a seed wing facilitates aerodynamic dispersal (Heydel et al., 2014; Zhang et al., 2014).

One possible explanation for this result is the complex effects of turbulence on seeds during wind dispersal. High winds are necessarily turbulent due to the shear force. Vertical turbulence does not only retard seed sinking, but it may lift seeds via updrafts; it can also accelerate seed sinking by downdrafts (Horn et al., 2001). Furthermore, the turbulence generated by wind is stronger when wind velocity increases, but the tendency for turbulence becomes more intermittent, resulting in less effectiveness for seed dispersal (Heydel et al., 2014). In our study, higher wind speeds increased dispersal distances for both intact and de-winged seeds (Fig. 3). Thus, the differences in dispersal distance between intact and de-winged seeds cannot be explained by the intermittence of turbulence caused by strong wind. At wind speeds of 3.6 $m \cdot s^{-1}$ and 4.0 $m \cdot s^{-1}$, winged seeds show a more complex falling trajectory than de-winged seeds, with obvious rolling and whirling. The complex falling patterns of winged seeds may consume more energy, resulting in shorter dispersal distances than in de-winged seeds.

There may be a critical value of wind speed that affects falling trajectory of the winged seeds of *Brandisia hancei*. In windless conditions, the wing enhances seed dispersal, while intact and de-winged seeds have similar dispersal distances as the wind speed increases to 2.8 $m \cdot s^{-1}$. The average wind speed in the habitat is less than 2.5 $m \cdot s^{-1}$ (Shang et al., 2019), which suggests that the presence of a wing plays a positive role in anemochory in the natural environment of *B. hancei*. Turbulence, especially updraft, plays an importance role in wind dispersal of light and/or winged seeds (Nathan et al., 2002; Tackenberg et al., 2003; Heydel et al., 2014). *B. hancei* usually grows on slopes, where updraft is likely to occur. Considering the low wind speed and potential updraft in the habitat, we conclude that the presence of a wing is critical for anemochory of this tiny seed.

Seed dispersal by anemochory is often for only short distances, and secondary dispersal, or the movement of the seeds from the initial dispersal point to microhabitats suitable for establishment, can be more important than primary anemochory dispersal (Jongejans and Telenius, 2001; Säumel and Kowarik, 2010). Seeds are often dispersed by more than one mechanism, and water can be an effective vector for long distance secondary dispersal (Säumel and Kowarik, 2010; Cabra-Rivas et al., 2014). The average wind speed in the habitats of *Brandisia hancei* is relatively low (Shang et al., 2019), and the small stature of this shrub (usually 1–2 m in height) is likely to further limit the effectiveness of wind dispersal (Sypka and Starzak, 2013; Suetsugu, 2018). However, surface runoff easily forms in habitats of *B. hancei*, due to concentrated rainfall after seeds mature (Tu et al., 2016). Seeds with a membranous wing can float for more than 10 days. Thus, high seed buoyancy may enhance the possibility of hydrochory via surface runoff, which could be of great importance in dispersal of *B. hancei* seeds. Because this species is self-compatible and can produce seeds through delayed selfing (Ren et al., 2016), there is reduced risk of pollen limitation after long-distance seed dispersal and plant establishment far from source populations.

The membranous wing contributes little to the absorption and retention of water by the seed, but it enhances soil adherence to the seed. Seeds mature at the beginning of the rainy season, when soil water content would be sufficient for germination of *Brandisia hancei* seeds. However, shallow soil may constrain seedling establishment of *B. hancei*. Thus, soil instead of water is the main factor limiting seedling establishment in the rainy season. *B. hancei* usually grows on slopes, where rapid surface runoff could result in a large number of seeds being removed from the original point after dispersal by anemochory. Without some mechanisms to help it stay in the soil, a seed would easily be removed by rain to unfavorable habitats without soil in karst regions. The ability of seed adhesion to soil is greatly promoted via mucilage production (Sun et al., 2012). Without mucilage, seed adherence to the soil seems to be enhanced by the surface area of the wing in *B. hancei*. In addition, small or flat elongated seeds are more likely to be buried than large or spherical seeds (Liang et al., 2019). Thus, both the membranous wing and flat elongated shape promote good seed contact with soil in microhabitats suitable for germination in *B. hancei*. There is usually more soil in the lower and gentle part of karst slopes due to the erosion of surface runoff, and good seed-soil contact increases the probability of seeds being retained in this microhabitat after dispersal by anemochory and hydrochory; this is consistent with the distribution pattern of *B. hancei*.

Seeds that disperse at the beginning of the rainy season are usually non-dormant, and can germinate quickly when the soil moisture content is adequate for seedling development (Ramos et al., 2017; Escobar et al., 2018). In *Brandisia hancei*, seeds mature and disperse just before rainy season, and freshly matured seeds germinate to a high percentage in a short time. These life-history traits are adaptive to seasonal precipitation, which is the most important factor affecting the survival of *Brandisia hancei*. The presence of a wing in some species has been reported to hinder germination by inhibition of water absorption and the presence of chemical substances (Xing et al., 2013; Bhatt et al., 2017). Given that germination percentages of intact and de-winged seeds of *B. hancei* do not differ, there does not seem to be a chemical inhibitor in the wing.

In conclusion, a membranous wing on *Brandisia hancei* seeds enhances dispersal potential by wind as well as by water. After dispersal by anemochory, it is possible for winged seeds to be dispersed over long distances by hydrochory. The seed wing functions little in water absorption and has no function in retention of seed moisture, but its presence promotes soil adherence to the seed. Freshly matured seeds are non-dormant, and can germinate at the beginning of the rainy season. Therefore, seed dispersal and adherence to soil after dispersal are enhanced by the membranous wing, and dispersal and germination traits are adapted to the precipitation seasonality in the heterogeneous habitats of *B. hancei*.

Authors' contributions

YR and XT designed the study; YR, CH and JZ performed experiments; YR analyzed the data; YR and YM wrote the manuscript.

Declaration of competing interest

None.

Acknowledgements

We thank Prof. Carol C. Baskin who greatly improved the manuscript with constructive suggestions. We also acknowledge the support for this work from Yu He, Na Gao, Zhengquan Chen and Chengqian Yang. This research was funded by the National Natural Science Foundation of China to Xiaoling Tian (No. 31901237), and it was supported by the Young Academic and Technical Leader Raising Foundation of Yunnan Province to Yongpeng Ma (No. 2018HB066).

References

Bhatt, A., Phartyal, S.S., Nicholas, A., 2017. Ecological role of distinct fruit-wing perianth color in synchronization of seed germination in *Haloxylon salicornicum*. Plant Species Biol. 32, 121–133.

Cabra-Rivas, I., Alonso, Á., Castro-Díez, P., 2014. Does stream structure affect dispersal by water? A case study of the invasive tree *Ailanthus altissima* in Spain. Manag. Biol. Invasion. 5, 179–186.

Carthey, A.J.R., Fryirs, K.A., Ralph, T.J., et al., 2016. How seed traits predict floating times: a biophysical process model for hydrochorous seed transport behaviour in fluvial systems. Freshw. Biol. 61, 19–31.

Chen, X., Lu, J., Chen, C., et al., 2016. Anatomic structure of seed coat ornamentation and mucilage of *Peganum multisectum* and its ecological adaptation to seeds dispersal and germination. Acta Bot. Boreali Occident. Sin. 36, 930–937.

Eriksson, O., Kainulainen, K., 2011. The evolutionary ecology of dust seeds. Perspect. Plant Ecol. 13, 73–87.

Escobar, D.F.E., Silveira, F.A.O., Morellato, L.P.C., 2018. Timing of seed dispersal and seed dormancy in Brazilian savanna: two solutions to face seasonality. Ann. Bot. 121, 1197–1209.

Guja, L.K., Merritt, D.J., Dixon, K.W., 2010. Buoyancy, salt tolerance and germination of coastal seeds: implications for oceanic hydrochorous dispersal. Funct. Plant Biol. 37, 1175–1186.

Heydel, F., Cunze, S., Bernhardt-Römermann, M., et al., 2014. Long-distance seed dispersal by wind: disentangling the effects of species traits, vegetation types, vertical turbulence and wind speed. Ecol. Res. 29, 641–651.

Hong, D.Y., Yang, H.B., Jin, C.L., et al., 1998. Scrophulariaceae. In: Wu, Z.Y., Raven, P.H. (Eds.), Flora of China, vol. 18. Missouri Botanical Garden Press, St. Louis, Beijing, pp. 6–9. Science Press.

Horn, H.S., Nathan, R., Kaplan, S.R., 2001. Long-distance dispersal of tree seeds by wind. Ecol. Res. 16, 877–885.

Jara-Guerrero, A., Cruz, M.D.L., Méndez, M., 2011. Seed dispersal spectrum of woody species in south Ecuadorian dry forests: environmental correlates and the effect of considering species abundance. Biotropica 43, 722–730.

Jiang, Z., Lian, Y., Qin, X., 2014. Rocky desertification in southwest China: impacts, causes, and restoration. Earth Sci. Rev. 132, 1–12.

Jongejans, E., Telenius, A., 2001. Field experiments on seed dispersal by wind in ten umbelliferous species (Apiaceae). Plant Ecol. 152, 67–78.

Kehr, J.M., Merritt, D.M., Stromberg, J.C., 2014. Linkages between primary seed dispersal, hydrochory and flood timing in a semi-arid region river. J. Veg. Sci. 25, 287–300.

Kowarik, I., Säumel, I., 2008. Water dispersal as an additional pathway to invasions by the primarily wind-dispersed tree *Ailanthus altissima*. Plant Ecol. 198, 241–252.

Liang, W., Liu, Z., Liu, M., et al., 2019. How do diaspore traits, wind speed and sand surface configuration interact to determine seed burial during wind dispersal? Plant Soil 440, 357–368.

Minami, S., Azuma, A., 2003. Various flying modes of wind-dispersal seeds. J. Theor. Biol. 225, 1–14.

Nathan, R., Katul, G.G., Horn, H.S., et al., 2002. Mechanisms of long-distance dispersal of seeds by wind. Nature 418, 409–413.

Ramos, D.M., Diniz, P., Ooi, M.K.J., et al., 2017. Avoiding the dry season: dispersal time and syndrome mediate seed dormancy in grasses in Neotropical savanna and wet grasslands. J. Veg. Sci. 28, 798–807.

Ren, Y.Q., Xu, Y.P., Zhang, T., et al., 2016. Growth discrepancy between filament and style facilitates self-fertilization in *Brandisia hancei* (Paulowniaceae). Plant Species Biol. 31, 153–158.

Säumel, I., Kowarik, I., 2010. Urban rivers as dispersal corridors for primarily wind-dispersed invasive tree species. Landsc. Urban Plann. 94, 244–249.

Shang, Y., Song, D., Pei, X., et al., 2019. Multi-scale variation of ozone concentration and its relationship with meteorological conditions in Guiyang. Chin. Agr. Sci. Bull. 35, 95–101.

Soons, M.B., Heil, G.W., Nathan, R., et al., 2004. Determinants of long-distance seed dispersal by wind in grasslands. Ecology 85, 3056–3068.

Suetsugu, K., 2018. Independent recruitment of a novel seed dispersal system by camel crickets in achlorophyllous plants. New Phytol. 217, 828–835.

Sun, Y., Tan, D.Y., Baskin, C.C., et al., 2012. Role of mucilage in seed dispersal and germination of the annual ephemeral *Alyssum minus* (Brassicaceae). Aust. J. Bot. 60, 439–449.

Sypka, P., Starzak, R., 2013. Simplified, empirical model of wind speed profile under canopy of Istebna spruce stand in mountain valley. Agric. For. Meteorol. 171–172, 220–233.

Tackenberg, O., Poschlod, P., Kahmen, S., 2003. Dandelion seed dispersal: the horizontal wind speed does not matter for long-distance dispersal—it is updraft! Plant Biol. 5, 451–454.

Tu, C., Lu, X., Liu, R., et al., 2016. Output characteristics of surface runoff in typical karst watershed. Resour. Environ. Yangtze Basin 25, 1879–1885.

Vargas, P., Heleno, R., Traveset, A., et al., 2012. Colonization of the Galápagos islands by plants with no specific syndromes for long-distance dispersal: a new perspective. Ecography 35, 33–43.

Western, T.L., 2012. The sticky tale of seed coat mucilages: production, genetics, and role in seed germination and dispersal. Seed Sci. Res. 22, 1–25.

Xing, J., Cai, M., Chen, S., et al., 2013. Seed germination, plant growth and physiological responses of *Salsola ikonnikovii* to short-term NaCl stress. Plant Biosyst. 147, 285–297.

Zhang, X., Zhang, Z., Stützel, T., 2014. Ontogeny of the ovule and seed wing in *Catha edulis* (Vahl) Endl. (Celastraceae). Flora 209, 179–184.