

DIFFERENCES IN SEEDLING DISTRIBUTION PATTERNS BETWEEN WIND-DISPERSED *LIQUIDAMBAR FORMOSANA* AND RODENT-DISPERSED *QUERCUS ACUTISSIMA*

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Abstract

Plants rely on a variety of dispersal vectors to transport their seeds, including both abiotic and biotic vectors. Distribution patterns of seedlings may be different owing to these differences in seed dispersal vectors; however, few studies have examined this assumption. In this study, we compared several seedling parameters (number, diameter, height, and distance from the mother tree) between a wind-dispersal species, *Liquidambar formosana*, and a rodent-dispersal species, *Quercus acutissima*, growing in the same bamboo forest and also examined how the type of dispersal vector influenced the spatial distribution of seedlings. One-hundred and seventy-four individual *L. formosana* seedlings and 84 individual *Q. acutissima* seedlings were recorded, and the average diameter and height of *Q. acutissima* seedlings were significantly larger than those of *L. formosana* seedlings. The seedling density of *L. formosana* showed a single-peak whereas *Q. acutissima* showed multiple peaks at different distances from the parent plant. The average dispersal distance of *Q. acutissima* seedlings (11.13 ± 9.45 m) was much further than that for *L. formosana* (7.71 ± 6.74 m). The results of this study suggest that rodent-dispersed plants may have an increased chance of survival and a longer dispersal distance than wind-dispersed plants, and that animal-dispersal might be more conducive to the spread and regeneration of plant populations.

Key words: Wind-dispersed; Rodent-dispersed; Seedling distribution pattern; *Quercus acutissima*; *Liquidambar formosana*.

Introduction

Seed dispersal is the movement or transport of seeds away from the parent plant, and it is a key life-history stage in plants (Nathan & Muller-Landau, 2000; García *et al.*, 2011). Plants have very limited mobility and consequently rely on a variety of vectors for their seed dispersal, including both abiotic (e.g. gravity, wind, ballistic and water) and biotic (eg. animals) vectors (Tol *et al.*, 2017). Seeds can be dispersed away from the parent plant individually or collectively, as well as dispersed both spatially and temporally (Plue & Cousins, 2018). The spatial distribution pattern of seedlings is determined, in large part, by the dispersal mechanism, for example the dispersal distance of seeds, seed predation and whether the microhabitat where the dropped seed is suitable for its germination (Ran *et al.*, 2000). The process of seed dispersal is complex and there are differences in the spatial distribution of seedlings between different dispersal vectors. Previous studies have shown that certain seed characteristics are important in affecting the spatial distribution of seedlings (Ghersa *et al.*, 2010; Xiao *et al.*, 2015). For example, seeds adapted for wind dispersal are small in volume or light, which increases the seed quantity per unit area and forms a leptokurtic seedling distribution with a peak near the parent plant (Gómez-Aparicio *et al.*, 2007). As for rodent dispersed seeds, seed size will influence the costs incurred by the rodent in terms of handling and transporting the seed, thereby affecting rodent selection of seeds and the distribution of seedlings (Cao *et al.*, 2016; Zhang *et al.*, 2016). Likewise, traits of dispersal vectors can also influence the spatial distribution of seedlings (Quick *et al.*, 2017). For wind-dispersed species, some studies have concluded that spatial distribution of seedlings is influenced by wind speed, wind direction, vertical turbulence, vegetation types, and the traits of plant (e.g.

size, height) (Heydel *et al.*, 2014; Savage *et al.*, 2014). Rodent behavior can affect the spatial distribution of seedlings (Muñoz & Bonal, 2011; Steele *et al.*, 2014), as where they move and store seeds depends on the result of a trade-off between the foraging benefit and predation risk (Suselbeek *et al.*, 2014; Yang *et al.*, 2016). For instance, Steele *et al.*, (2014) found that eastern gray squirrels (*Sciurus carolinensis*) dispersed larger, more profitable acorns of oaks (*Quercus* spp.) into open habitat, where the probability of predation was lower.

Different dispersal vectors and mechanisms result in different seedling distribution patterns. Many studies have examined the seedling distribution patterns of wind-dispersed plants (Fernandes *et al.*, 2016) and rodent-dispersed plants (Sunyer *et al.*, 2015; Hao *et al.*, 2017), however, few studies have examined the differences between wind-dispersed and rodent-dispersed seedling distribution patterns with in the same habitat.

Formosan gum (*Liquidambar formosana*) and Sawtooth Oak (*Quercus acutissima*) are dominant tree species widely distributed in China (Zhang *et al.*, 2014; Sun *et al.*, 2016). The former has very light seeds (0.31-0.55g/100 grain) and relies on wind to disperse. The large acorns (83.55-636.78g/100 grain) of the latter are rich in starch and rely on rodents to disperse (Liu *et al.*, 2009). In Xia-shu forest farm, the mother trees of these two species are simultaneously distributed above the hill road, and bamboo forests are situated below the hill road. Due to the characteristics of the mountain, the seedlings of *Q. acutissima* and *L. formosana* are simultaneously recruited in the bamboo forest (Wang, 2017). In this study, we measured seedling number, diameter, height, and distance from the mother trees for these two tree species, and compared the spatial distribution of seedlings. We addressed the hypotheses that the dispersal distance and distribution pattern of rodent-disperse seedlings would be larger than wind-dispersed seedlings.

Materials and Methods

Study area: This study was conducted in the Xia-shu forest farm (119°12'E, 32°07'N) in Jurong City, Jiangsu Province, East China, which has a total area of 314.4 ha. This region experiences a subtropical monsoon climate region, with an annual average temperature of 15.2°C, and an extreme temperature range from -6.7°C in January to 39.6°C in July. The annual average rainfall is 1055.6 mm, and this mainly falls in a period of 6-8 months. The annual total temperature is 4859.6°C, and the average annual hours of light is 2157 h. The annual average relative humidity is more than 79%, and there are 233 d frost-free days per year on average. The local vegetation consists of evergreen and deciduous broad-leaved mixed forests, and the dominant tree species are *Pinus massoniana*, *Quercus acutissima* and *Koelreuteria paniculata* (Jiang *et al.*, 2011).

Data collection: We established one ha fixed plots (100 small quadrats of 10×10m) perpendicular to the dividing line between the bamboo forest and hill road in April 2018, and used vernier calipers to measure the diameter (height 1cm above the ground, DGH) and height (H) of all seedlings (of height ≤30 cm) from two trees in each quadrat. We took the south-west angle of the sample as the origin, the east-west direction as the X axis, the south-north direction as the Y axis, and used the resulting coordinates (X, Y) to record the position of the seedlings (Yang *et al.*, 2014). Meanwhile, we used a meter-rule to measure the distance between the seedling and the mother tree.

Statistical analyses: We divided diameter into three levels with the intervals of 0.1 cm: I: 0 cm < DGH ≤ 0.1 cm; II: 0.1 cm < DGH ≤ 0.2 cm; III: 0.2 cm < DGH ≤ 0.3 cm; and divided height into three levels with the intervals of 10 cm: I: 0 cm < H ≤ 10 cm; II: 10 cm < H ≤ 20 cm; III: 20 cm < H ≤ 30 cm, and counted of the numbers of seedlings in each level, respectively. We used Chi-square tests to analyze the differences in the number of the two species' seedlings between different diameter and height levels, respectively. In addition, we used Mann-Whitney tests to compare the difference in the diameter, height and dispersal distance between the two species' seedlings. A p-value of <0.05 was considered to be statistically significant for all statistical analyzes according to Khan *et al.*, (2018), and figures were made using the statistical programming language R (v. 3.1.0).

Results

Seedling characteristics of two species of trees: A total of 174 *L. formosana* seedlings and 84 *Q. acutissima* were recorded in the bamboo forest. There were significant differences in the number of *L. formosana* seedlings between the different diameter levels ($\chi^2=11.483$, $df=2$, $p=0.003$) and height levels ($\chi^2=12.655$, $df=2$, $p=0.02$), and significant differences in the number of *Q. acutissima* seedlings between different diameter grades ($\chi^2=28.500$, $df=2$, $p<0.01$) and height levels ($\chi^2=25.929$, $df=2$, $p<0.01$) (Fig. 1). Furthermore, there were significant differences in the diameter ($Z=-6.326$, $p<0.01$) and height ($Z=-2.522$, $p=0.012$) between the two species' seedlings, and the average diameter (1.56 ± 0.05 vs 1.42 ± 0.06 cm) and height (0.20 ± 0.05 vs 0.14 ± 0.07 cm) of *Q. acutissima* seedlings were significantly larger than those of *L. formosana*.

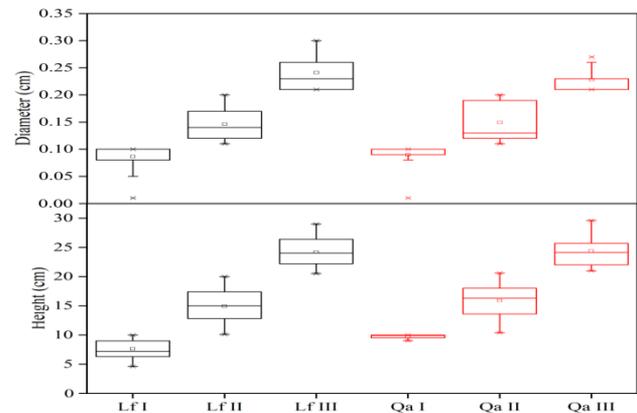


Fig. 1. Height and diameter of *Liquidambar formosana* and *Quercus acutissima* seedlings in the bamboo forest of Xia-shu forest farm, China.

(Lf: *Liquidambar formosana*; Qa: *Quercus acutissima*; Diameter: I: 0cm < DGH ≤ 0.1cm; II: 0.1cm < DGH ≤ 0.2cm; III: 0.2cm < DGH ≤ 0.3cm; Height: I: 0cm < H ≤ 10cm; II: 10cm < H ≤ 20cm; III: 20cm < H ≤ 30cm).

Seedling distribution patterns: 74% of *L. formosana* and 59.52% of *Q. acutissima* seedlings at a distance of 0-10m from the parent tree showed a significant aggregation pattern, but the degree of aggregation was more obvious in the former, with a significantly random pattern (Fig. 2). The seedling densities (seedling number per m²) of *L. formosana* and *Q. acutissima* were 0.07/m² and 0.03/m², respectively. The distribution pattern of *L. formosana* showed a single-peak and *Q. acutissima* showed multiple-peaks at different distance scales (Fig. 3). There was significant difference in the dispersal distance between the two species ($Z=-2.958$, $p=0.003$), with averages 7.71 ± 6.74 m and 11.13 ± 9.45 m for *L. formosana* and *Q. acutissima*, respectively. Seedling number was decreased with increased dispersal distance in both species.

Discussion

In general, *L. formosana* produces several times more seeds than *Q. acutissima*, therefore the number of seedlings was much larger than that for *Q. acutissima*. However, our results showed that there was no significant difference in seedling number between the two species, and this may be due to differences in the characteristics of their respective dispersal vectors. In wind-dispersed species, this may be due to variation and unpredictability in wind direction and velocity, therefore not all seeds can be deposited in potential recruitment sites (Tiawoun *et al.*, 2017), and wind-dispersed seeds tend to aggregate in space. This results in higher density-dependent mortality rates and the number of seedling was lower (Nathan & Muller-Landau *et al.*, 2000). However, rodents can carry seeds to a suitable microhabitat for effective burial. This not only shelters seeds from harsh physical conditions (e.g. ultra violet light, desiccation), but also provides a suitable seedbed for seed germination (Dracxler & Forget, 2017), thus rodent-dispersed seeds have a high survival rate. Furthermore, the seedlings of *Q. acutissima* were significantly larger diameter and taller than those of *L. formosana*. This may be because the embryos of *Q. acutissima* seeds contain a large amount of starch, which is beneficial for seedling growth.

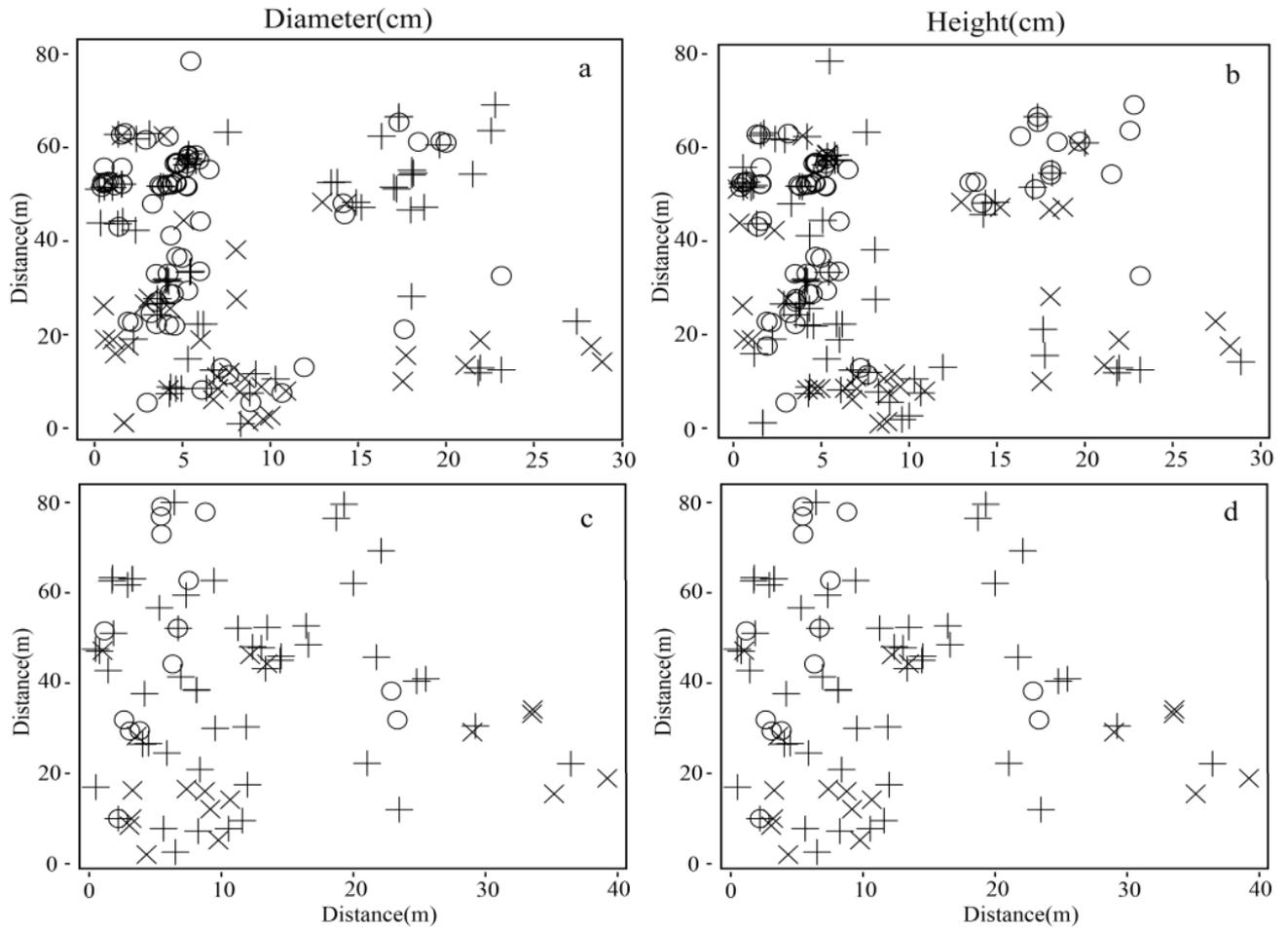


Fig. 2. Diameter and height spatial distribution of *Liquidambar formosana* (a, b) and *Quercus acutissima* (c, d) in the bamboo forest of Xia-shu forest farm, China.
 (Diameter: \circ $0\text{ cm} < \text{DGH} \leq 0.1\text{ cm}$; $+$ $0.1\text{ cm} < \text{DGH} \leq 0.2\text{ cm}$; \times $0.2\text{ cm} < \text{DGH} \leq 0.3\text{ cm}$; Height: \circ $0\text{ cm} < H \leq 10\text{ cm}$; $+$ $10\text{ cm} < H \leq 20\text{ cm}$; \times $20\text{ cm} < H \leq 30\text{ cm}$)

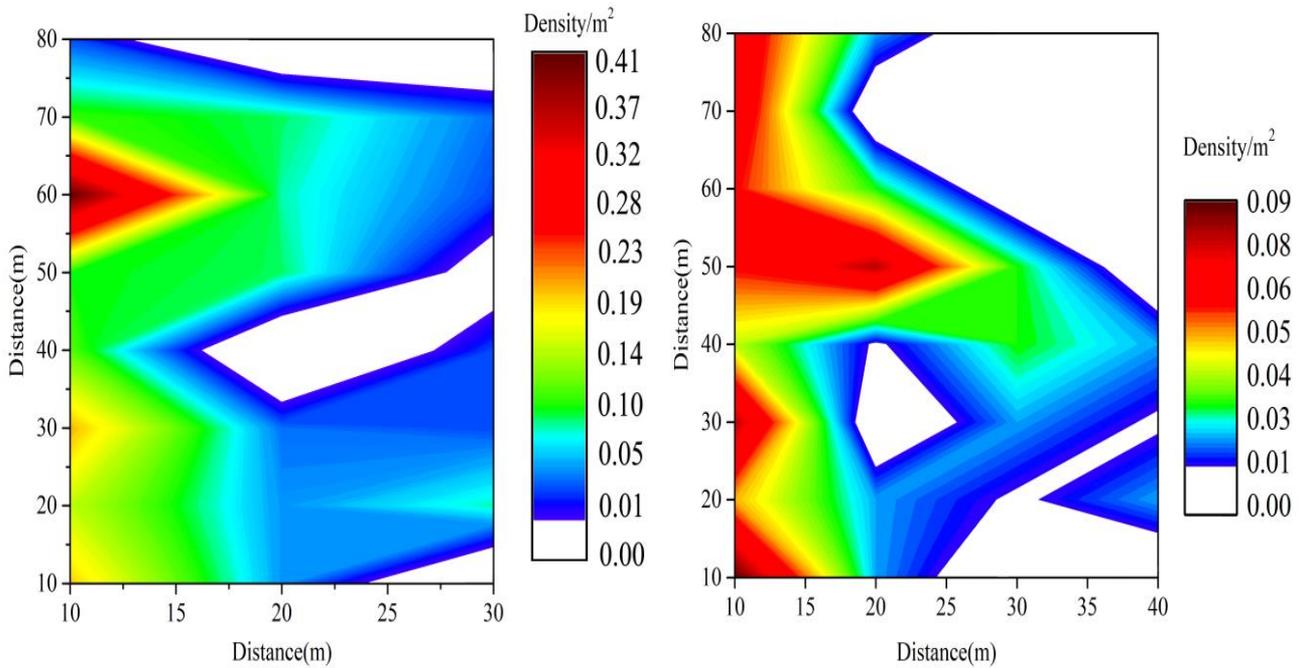


Fig. 3. Seedling densities of *Liquidambar formosana* (a) and *Quercus acutissima* (b) at different distance scales in the bamboo forest of Xia-shu forest farm, China.

The density distribution pattern of *L. formosana* seedlings showed a single-peak, whereas *Q. acutissima* seedlings showed multiple-peaks (Fig. 3), and this was consistent with our hypotheses. This may be related to dispersal vectors and seed characteristics. The seeds of *L. formosana* are very light, and wind speed is greatly affected by the surrounding vegetation (Zhang *et al.*, 2010), therefore its seedlings tend to aggregate in space and form a single peak near the parent plant. On the other hand, the seeds of *Q. acutissima* mature in the autumn and are rich in starch, so they are often moved and stored to act as a buffer for food shortages that may occur during harsh weather conditions or less productive years (Kim *et al.*, 2016). Rodents often adopt scatter-hoarded strategy when caching seeds in order to protect seeds and reduce stealing by other rodents (Steele *et al.*, 2015), thus rodent-dispersed seedlings have multiple peaks in spatial distribution.

The average dispersal distance of *Q. acutissima* (11.13 ± 9.45 m) seedlings was further than that of *L. formosana* (7.71 ± 6.74 m) seedlings, and this result supports our hypotheses. This may have been influenced by characteristics of the species' different vectors. For wind-dispersed plants, some studies have shown that the wind speed is the most important factor in determining seed dispersal distance, followed by plant traits such as seed release height and vegetation height (Marushia and Holt, 2006), and terminal velocity (Soons *et al.*, 2004). Other studies have shown that terminal velocity plays the most important role in determining seed dispersal distances, followed by wind speed (Caplat *et al.*, 2012) or release height (Thomson *et al.*, 2011). In our study, the presence and height of vegetation surrounding the mother tree may have influenced the dispersal distance of *L. formosana*. Vegetation was dense in the bamboo forest, which could significantly reduce dispersal distance through dramatically changing wind velocity. The fact that no *L. formosana* seedlings were found in oak forests on the slope also indicated that vegetation can obstruct the path of dispersing seeds. On the other hand, the factors influencing the dispersal distance of *Q. acutissima* may have been related to predation risk. The mature seeds of *Q. acutissima* naturally fall mainly on the left side of round hill road, where there is more human disturbance and a higher predation risk, so rodent often carry seeds to a safer place (e.g. bamboo forest) for feeding or storage, thus increasing the dispersal distance of seeds.

Conclusions

The average diameter and height of *Q. acutissima* seedlings were significantly larger than those of *L. formosana* seedlings. The seedling density of *L. formosana* showed a single-peak compared to multiple peaks at difference distances from the parent tree for *Q. acutissima*, and average dispersal distance of *Q. acutissima* (11.13 ± 9.45 m) seedlings was much further than that for *L. formosana* (7.71 ± 6.74 m) seedlings. Our results indicate that rodent-dispersed plants may have a higher chance of survival and have longer dispersal distances than wind-dispersed plants, and that animal-dispersal might be more conducive to the spread and regeneration of plant populations.

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