Postprint: Dispersal Characteristics of Dimorphic Fruits in Fraxinus velutina

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Abstract

The occurrence of polymorphic fruits or seeds holds significant importance for plant population dispersal. Fraxinus velutina produces fruits with dimorphic characteristics, primarily distinguished by the number of wings, which are defined as two-winged and three-winged fruits. To compare the differences in wind dispersal between these two fruit types, we examined fruit morphology, wing structure, dispersal distance, and dispersal duration. In a large enclosed basement, airflow generated by an electric fan at different speed settings served as the wind source; fruits were manually released from heights of 2, 1.5, and 1 m, and dispersal distances and durations were compared at wind speeds of 0, 4.6, 6.5, and 7.3 m/s. Linear correlation analysis between morphological characteristics and dispersal traits was subsequently performed. The results indicated that at the same release height and wind speed, the horizontal dispersal distance of three-winged fruits was significantly greater than that of two-winged fruits, while their corresponding dispersal duration was shorter than that of two-winged fruits. Under identical conditions, the settling velocity of three-winged fruits was significantly higher than that of two-winged fruits. For both fruit types, dispersal distance and duration increased correspondingly with increasing release height; both parameters also increased with increasing wind speed. The mass of three-winged fruits was significantly higher than that of two-winged fruits, whereas the length and width of three-winged fruit wings were significantly smaller than those of two-winged fruits. The wing cell structure was identical in both types, with air sac-like structures inside cells and streamlined longitudinal ridges along the wing surface in the longitudinal axis direction. Linear correlation analysis revealed that wing type was the most significant morphological characteristic affecting dispersal distance and duration; compared with fruit release height, wind speed was the most significant environmental factor influencing the dispersal distance and duration of Fraxinus velutina fruits. The key to three-winged fruits of Fraxinus velutina dispersing farther than two-winged fruits lies in their possession of three wings, which re-

spond instantaneously to gusts, resulting in higher settling velocity that enables rapid dispersal to greater distances under instantaneous wind action. The combination of three-winged and two-winged dispersal modes enhances the survival and colonization opportunities of Fraxinus velutina.

Full Text

Preamble

Study on Dispersal Traits of Dimorphic Fruits of *Fraxinus velutina*

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Abstract

Seed dispersal is a critical stage in the plant life cycle, playing a vital role in the colonization and expansion of plant populations. Fruit dimorphism is a widespread phenomenon in plants, with significant differences in dispersal distance and in-flight behavior between normal and heteromorphic fruits. This morphological variation allows for multiple dispersal modes within a single species, thereby enhancing dispersal efficiency, range, reproductive success, and ultimately, evolutionary potential. Fruit features, release height, and wind speed are among the key factors influencing seed or fruit dispersal.

Fraxinus velutina exhibits dimorphic fruits characterized by differences in wing number, which we define as two-winged (the normal samara type) and three-winged morphs. However, few studies have investigated the dispersal differences between these two samara types. The present research aimed to compare the dispersal performance of these two samara types under different wind speeds and release heights to better understand how dispersal is affected by samara type and morphological/structural characteristics.

In a large basement chamber, air currents were generated by an electric fan with adjustable speed settings (0, 4.6, 6.5, and 7.3 m/s) to simulate wind. Fruits were manually released from heights of 2, 1.5, and 1 m, and dispersal distance and in-flight duration were measured. Linear correlation analysis explored relationships among samara traits (wing type, fruit weight, wing width, and wing length) and dispersal parameters (release height, wind speed, dispersal distance, and in-flight duration).

Results showed that at the same release height and wind speed, the horizontal dispersal distance of three-winged fruits was significantly greater than that of two-winged fruits, while their corresponding in-flight duration was shorter. The terminal velocity of three-winged fruits also significantly exceeded that of two-winged fruits under identical conditions. Both dispersal distance and duration increased correspondingly with increasing release height and wind speed. The three-winged fruit type had significantly higher fruit weight than the two-winged type, but lower wing length and width. The cellular structure of the wings was identical between both types, with numerous air sacs permeating the wing tissue and streamlined ridges along the longitudinal axes. Correlation analysis revealed that phenotypic traits strongly correlated with dispersal performance, with wing type being the primary morphological factor significantly affecting dispersal distance and duration. Compared to release height, wind speed was the most significant environmental factor influencing dispersal distance and duration in *F. velutina*.

The key to the superior dispersal distance of three-winged fruits lies in their faster response to gusts, resulting in higher terminal velocity that enables rapid propagation to distant locations under instantaneous wind conditions. The combination of three-winged and two-winged fruit dispersal mechanisms enhances survival and colonization opportunities for *F. velutina*.

Keywords: *Fraxinus velutina*; dimorphic fruit; dispersal distance; in-flight duration; wing type

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1. Introduction

Seed dispersal represents a crucial phase in plant life histories, with profound implications for species survival, reproduction, physiological ecology, and evolution. Effective dispersal enables seeds to escape natural enemies, reduce sibling competition, avoid density-dependent predation or parasitism, and increase the probability of colonizing canopy gaps. Dispersal also influences spatiotemporal settlement patterns, determining the distance from maternal plants, the type of habitats seeds reach, and the competitive environment seedlings will face, thereby affecting seedling survival and population structure. Ultimately, dispersal potential influences species distribution and abundance, as well as gene flow and speciation processes.

Morphological variation in wind-dispersed seeds and fruits significantly affects dispersal capacity and flight characteristics. Intraspecific variation in seed size on individual plants also markedly influences dispersal distance. Dimorphic fruits (also termed fruit heteromorphism or heterocarpy) refer to plants producing two or more distinct fruit morphs on a single individual, which has attracted ecologists' attention for decades due to differences in morphology, physiology, and ecology between morphs. These heteromorphic fruits exhibit significant differences in dispersal distance, and any change in their proportions may affect dispersal fitness.

Fraxinus species primarily disperse via wind and water. Previous research on ash samaras has focused on flight trajectories and aerodynamics, revealing that ash fruits typically exhibit spiral dispersal patterns and that intraspecific variation exists in wing morphology. Several studies have documented heteromorphic fruits in the genus: Tang Jin reported a three-petal variant in *Fraxinus chinensis* from Hebei; Hong Yaping observed three-carpel fruits; Yang Xin et al. reported twin-seed phenomena in *Fraxinus rhynchophylla*; and Wang Guangqin and Fan Wei documented heteromorphic fruits in *Fraxinus hopeiensis*. These findings indicate that dimorphic or polymorphic fruits are relatively common in *Fraxinus* and represent significant adaptations for seedling colonization and dispersal, reflecting alternative dispersal strategies.

We discovered that *Fraxinus velutina* produces two distinct wing morphologies—two-winged and three-winged samaras—with substantial numbers of heteromorphic fruits produced annually. However, detailed studies on the dispersal characteristics of heteromorphic ash fruits are lacking. This research investigates the dispersal capabilities of these two fruit morphs in *F. velutina*, examining horizontal dispersal distance and duration, and analyzing how fruit morphology and environmental factors influence dispersal patterns to provide a scientific basis for understanding the ecological adaptation mechanisms of heteromorphic fruits in this species.

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2. Materials and Methods

2.1 Fruit Collection and Processing

Fraxinus velutina fruits were collected in mid-October when seeds matured. The collection site was a mixed plantation in Taigu County, Shanxi Province, China, where *F. velutina* grew interspersed with other tree species. Collected fruits were spread in thin layers for natural drying indoors. Damaged samaras were discarded, while intact fruits were stored in cardboard boxes at room temperature.

2.2 Morphological Characteristics Observation

Random samples of 100 fruits from each morph type were selected for measurements. Fruit mass was determined using an electronic balance. Following methods by Yilmaz and Jarni, wing length and width were measured with vernier calipers. Wing width was measured at the widest point; for three-winged fruits, width was measured as the distance between any two wings. Microscopic and scanning electron microscope (SEM) observations were conducted on samara wings. Each measurement was replicated 30 times per seed.

2.3 Dispersal Characteristics Experiment

To compare dispersal traits between the two wing morphs, experiments were conducted in a large, enclosed basement room (~100 m^2) in the Science and Technology Building of Shanxi Agricultural University, following methods by Cheng Xiaojun and Guo Qiang. Fruits used in dispersal trials were from the same batch used for morphological measurements.

Based on the lowest fruit-bearing position on maternal trees (~2 m) and for measurement convenience, fruits were released from heights of 2, 1.5, and 1 m. An electric fan provided horizontal airflow at three settings (high, medium, low). Wind speeds were measured at the release point using an anemometer, yielding values of 0, 4.6, 6.5, and 7.3 m/s.

Each fruit was released individually by hand at the same position, held by the pedicel end with the wing plane perpendicular to wind direction. A stopwatch was started at release and stopped when the fruit landed, recording in-flight duration. Dispersal distance was measured from the vertical projection of the release point to the landing position.

2.4 Statistical Analysis

Data were analyzed using SPSS 22.0 software. Wing type was coded as a categorical variable (two-winged = 1, three-winged = 2) for analysis. Dispersal duration and distance were analyzed using hierarchical grouping methods. Linear correlation analysis was performed between fruit morphological traits (phenotypic characteristics) and dispersal parameters.

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3. Results

3.1 Fruit Morphological Characteristics

Fraxinus velutina samaras possess apical wings attached to one end of the seed, extending bilaterally from the seed' s central longitudinal axis and flattening into wing structures. The two-winged morph represents the common samara type. In three-winged fruits, an additional wing differentiates on the surface of the common flat wing, with angles of 120° between any two wings.

Microscopic examination of paraffin sections revealed that both two- and three-winged samaras have aerenchymatous, air-sac-like cells within the wing tissue, with some vascular bundle cells distributed along the wing margins. SEM observations showed streamlined ridges along the longitudinal axes of all wing surfaces.

Fruit weight ranged from 11.5–34.2 mg for two-winged fruits and 14.1–46.8 mg for three-winged fruits, with three-winged fruits being significantly heavier (Table 1). Wing length of three-winged fruits ranged from 2.188–3.814 cm, while two-winged fruits ranged from 2.180–3.528 cm; two-winged fruits had significantly longer wings. Wing width ranged from 0.31–0.60 cm for two-winged fruits and 0.322–0.67 cm for three-winged fruits, with two-winged fruits having significantly greater width.

Table 1 Phenotypic traits of dimorphic fruits of *Fraxinus velutina*

Trait	Three-winged	Two-winged	F-value
Fruit weight (mg)	27.30±0.50	20.60±0.40	1205.692
Samara length (cm)	2.98±0.02	3.09±0.02	178.734
Samara width (cm)	0.47±0.01	0.50±0.01	141.208

3.2 Horizontal Dispersal Distance and Duration

At 1 m release height, differences in dispersal distance between three- and two-winged fruits were not highly significant, though both distance and duration differences were extremely significant, indicating that release height affects dispersal. At 1.5 m and 2 m heights, three-winged fruits showed significantly greater dispersal distances than two-winged fruits, but with significantly shorter dispersal durations.

With increasing wind speed, both dispersal distance and duration increased significantly. Wind speed had a pronounced effect on dispersal performance (Table 2).

Table 2 Dispersal distance and in-flight duration of *Fraxinus velutina* fruits falling from different heights under various wind speeds

Release height (m)	Wind speed (m/s)	Dispersal distance (cm)	In-flight duration (s)
		Three-winged	Two-winged
2.0	0	12.23±0.89	7.97±0.55
	4.6	104.79±2.18	79.45±2.18
	6.5	123.36±2.89	88.82±2.71
	7.3	131.09±3.30	97.32±2.57
1.5	0	10.66±0.81	5.76±0.55
	4.6	107.18±2.58	88.27±2.54
	6.5	125.20±2.99	110.84±2.15
	7.3	135.59±3.10	119.77±3.47
1.0	0	7.35±0.64	5.64±0.53
	4.6	97.45±2.27	94.08±2.16
	6.5	118.26±2.84	110.36±2.66
	7.3	120.01±2.54	120.33±2.78

3.3 Fruit Settling Velocity

Settling velocity, calculated as the ratio of release height to dispersal duration under windless conditions, was significantly greater for three-winged fruits than for two-winged fruits at all release heights. Both morphs showed increased settling velocity with increasing release height (Table 3).

Table 3 Terminal velocity of *Fraxinus velutina* samaras without wind

Release height (m)	Wind speed (m/s)	Terminal velocity (m/s)
		Three-winged
2.0	0	2.63±0.04
1.5	0	1.46±0.02
1.0	0	1.55±0.03

3.4 Correlations Between Phenotypic and Dispersal Traits

Correlation analysis revealed that wing type was the most significant morphological factor affecting dispersal distance and duration. Wing type correlated negatively with fruit weight (three-winged heavier) and positively with dispersal distance (three-winged dispersed farther). Wing type correlated positively with wing length and width (two-winged having larger dimensions) and positively with in-flight duration (two-winged remaining airborne longer).

Fruit weight correlated positively with wing length and width, indicating significant relationships between mass and wing dimensions. Fruit weight correlated negatively with in-flight duration, suggesting heavier fruits spend less time airborne. Both wing length and width correlated positively with in-flight duration, consistent with two-winged fruits having longer dispersal times.

Wind speed showed extremely significant positive correlations with both dispersal distance and duration, confirming experimental results (Table 4).

Table 4 Correlation between samara traits and dispersal characteristics of *Fraxinus velutina*

Index	Wing type	Fruit weight	Samara length	Samara width	Release height	Wind speed	Dispersal distance	In-flight duration
Wing type	1	-0.543**	0.242**	0.216**	0.000	0.000	-0.131**	0.566**
Fruit weight		1	0.264**	0.189**	0.000	0.000	0.034**	-0.359**
Samara length			1	0.428**	0.000	0.000	-0.044**	0.128**
Samara width				1	0.000	0.000	-0.022**	0.191**
Release height					1	0.000	0.028**	-0.450**
Wind speed						1	0.752**	0.136**
Dispersal distance							1	0.003

Index	Wing type	Fruit weight	Samara length	Samara width	Release height	Wind speed	Dispersal distance	In-flight duration
In-flight duration								1

Note: ** indicates significance at p < 0.01 level.

4. Discussion

4.1 Wing Type Variation in *Fraxinus velutina*

Both two- and three-winged fruit types exhibit a range of intramorph variation, primarily in fruit mass, wing length, and width. These findings align with studies on other *Fraxinus* species including *F. wilcoxiana*, *F. mandshurica*, *F. ornus* subsp. *cilicica*, and American ash (*F. americana* and *F. pennsylvanica*), which show significant morphological variation influenced by provenance.

The occurrence of three-winged fruits in *Fraxinus* has been previously documented. Sun Sansheng proposed that ash gynoecia typically develop from 2-carpel fusion (producing two-winged fruits) or 3-carpel fusion (producing three-winged fruits). Tang Jin considered this a floral morphological variation, while Hong Yaping confirmed 3-carpel structures. Such structural diversity is often linked to diversified seed/fruit dispersal mechanisms. The emergence of three-winged fruits in *F. velutina* thus enhances dispersal mechanism diversity.

Seed dispersal represents the only means of escaping unfavorable environments across space and time. Dispersal-related traits are largely under maternal control, with plasticity regulated by maternal effects—particularly when maternal trees experience environmental stress. In our study, *F. velutina* maternal trees were noticeably shaded by surrounding vegetation with suboptimal light conditions. The production of three-winged fruits may thus represent an adaptive strategy to increase dispersal distance under unfavorable environmental conditions.

4.2 Fruit Settling Velocity

Three-winged fruits exhibited greater settling velocity than two-winged fruits, and both morphs showed velocities greater than those reported for *Fraxinus griffithii* (112 cm/s) by Guo Qiang. Settling velocity is a key determinant of dispersal distance; under identical conditions, slower settling velocities and longer airborne periods generally increase dispersal distance. Each wind-dispersed seed evolves traits for minimal settling velocity and maximal flotation according to its environment.

Paradoxically, two-winged fruits showed longer in-flight duration than three-winged fruits, yet three-winged fruits achieved significantly greater dispersal distances at the same release height and wind speed. This apparent contradiction may be explained by research indicating that wind speed exerts a more significant influence on dispersal distance than settling velocity alone.

4.3 Effect of Release Height on Dispersal

Release height directly determines airborne time and is a crucial factor affecting dispersal distance. Plant size and growth form correlate with dispersal patterns and influence the evolution of dispersal characteristics. Higher fruit positions on trees facilitate access to high-velocity wind currents, promoting longer-distance dispersal.

Fraxinus velutina fruits are concentrated at 2–3 m height on maternal trees with pendulous infructescences, and trees are often shaded by taller neighboring vegetation. While both dispersal distance and duration increased with release height in our experiments, the correlation between release height and dispersal distance was not statistically significant. This suggests that although release height promotes dispersal, its effect on distance is less pronounced than other factors.

4.4 Effect of Wind Speed on Dispersal

In the absence of wind, both fruit types fell nearly vertically with minimal dispersal distance. Under windy conditions, dispersal distance and duration increased correspondingly with wind speed. *Fraxinus* fruits typically require strong winds to detach from trees and initiate dispersal. Our collection site in Jinzhong, Shanxi (112.32°E, 37.26°N) experiences fruit maturation in mid-October, with dispersal occurring primarily between October and November, often associated with gusts or rainfall. Many fruits may persist on trees for extended periods, sometimes coexisting with the following year’ s crop.

The substantially greater dispersal distance of three-winged fruits demonstrates that wing morphology differentially affects wind response. Three-winged fruits respond more rapidly to wind gusts, and higher wind speeds amplify this advantage, carrying them considerably farther than two-winged fruits.

4.5 Influence of Phenotypic Traits on Dispersal

Both fruit morphs exhibit streamlined shapes with favorable aerodynamic properties. During flight, the rigid, conical seed apex splits the air, creating faster airflow over the wing surface than underneath, generating lift according to Bernoulli’ s principle. The wings are smooth, thin, and internally aerenchymatous, reducing mass, while longitudinal vascular bundles form ridges that reduce air resistance and maintain suspension.

Dispersal mode is determined by dispersal vectors and fruit/seed characteristics, with seed size, pericarp structure, and dehiscence patterns playing decisive roles. In *F. velutina*, morphological traits including wing type, length, and width all influence dispersal, but wing type shows the strongest correlation with dispersal distance. Although two-winged fruits have greater individual wing length and width, three-winged fruits possess an additional wing, creating greater total wing area and a more aircraft-like configuration that enhances flight performance. This larger surface area likely increases the "sail area" exposed to wind, generating greater kinetic energy upon initial airflow contact and enabling rapid, far-distance dispersal.

The longer in-flight duration of two-winged fruits may result from their spiral autorotation during descent in calm or weak wind conditions, which prolongs suspension and increases the probability of encountering turbulent currents for secondary dispersal. This provides opportunities for continued dispersal when new air currents are encountered. The combination of two distinct dispersal behaviors—rapid long-distance dispersal by three-winged fruits and prolonged suspension with secondary dispersal potential by two-winged fruits—enhances overall dispersal success for *F. velutina*.

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5. Conclusion

The dimorphic characteristic of *Fraxinus velutina* is expressed through fruit wing number, defined as two-winged and three-winged types. Three-winged fruits have significantly greater mass, while two-winged fruits have significantly greater wing length and width. These phenotypic differences collectively influence dispersal distance and duration, with wing type being the primary determinant.

The three-winged morphology inherently determines flight behavior, enabling rapid response to instantaneous wind gusts. Wind speed and release height significantly promote dispersal, with dispersal distance increasing as wind speed or release height increases. Under identical conditions, three-winged fruits achieve significantly greater horizontal dispersal distances than two-winged fruits. However, two-winged fruits have longer in-flight durations, providing opportunities for secondary dispersal.

The combination of these two dispersal mechanisms helps *F. velutina* avoid sibling competition and enhances population diffusion and reproduction. This dual strategy aligns with the dispersal characteristics of polymorphic seeds, with two- and three-winged fruits partitioning the risks of spatiotemporal environmental variation to improve survival and colonization success.

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