

## Estimating wind dispersal potential in *Ailanthus altissima*: The need to consider the three-dimensional structure of samaras

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### Abstract

Plant dispersal is a very important ecological phenomenon, as it can enable species to move away from the parent plant. This contributes to shaping communities, determining patterns of distribution, landscape configuration, plant invasions and evolutionary processes. Measuring dispersal distance directly is difficult and thus, diaspore morphology can be used to make estimates. Previous research on the topic often resorts to analysing the diaspore's morphology as if it was a bi-dimensional structure; when in many cases, diaspores have three-dimensional qualities. In this study, we show how estimates of wind dispersal potential of *Ailanthus altissima* can be considerably improved using morphological variables that succeed in describing the three-dimensional nature of samaras. We suggest that this reasoning could be extensively applied to research involving not only other species, but also multi-specific scenarios with a wide range of diaspore morphologies.

**Keywords:** *Ailanthus altissima*, diaspore morphology, samara, three-dimensional structure, wind dispersal potential

### Introduction

Diaspore dispersal enables species to augment their area of distribution and move farther away from their parent plant, making it an extremely important process in the evolution of organisms and in the resilience and spatio-temporal structure of ecosystems worldwide (Nathan et al. 2008). The ecological importance of the dispersal capacity of diaspores has been long supported (Darwin 1859) and is currently treated as a crucial factor in explaining many ecological processes. These include shaping the assembly of communities (Howe & Smallwood 1982; Nilsson et al. 2010), determining patterns of distribution (Nathan & Muller-Landau 2000; Drezner et al. 2001; Levin et al. 2003), population dynamics (Levin et al. 2003), landscape configuration (Thompson & Katul 2009), colonisation (Howe & Smallwood 1982), habitat loss and fragmentation (Nathan et al. 2008; Hampe 2011), invasions (Kowarik & Sämel 2008) and genetic flow (Nathan & Muller-Landau 2000).

Plant dispersal is a complex stochastic multi-scale process, and for this reason, it is very complicated

to make direct measurements (Nathan et al. 2008). Many efforts have been made to directly measure dispersal through field experiments by tagging diaspores with paint to visually observe their movement (Sämel & Kowarik 2010; Kowarik & Von der Lippe 2011; Sämel & Kowarik 2013; von der Lippe et al. 2013; Cabra-Rivas et al. 2014). Other methods resort to using seed traps at different distances from the parent plant (Bullock & Clarke 2000; von der Lippe et al. 2013) or attaching metal tags and then using magnetic locators (Alverson & Diaz 1989). Finally, genetic analysis has also been used to determine which diaspores correspond to which mother plant (Godoy & Jordano 2001; Jordano et al. 2002), but the costs and time required make this useful only in limited situations.

To overcome the difficulties in direct field measurement of dispersal distance (Nathan 2006), researchers can use controlled environments to apply two different approaches: (1) determination of the velocity of a falling diaspore and (2) the use of indirect measurements, in which a relationship is established between the dispersal distance and

another variable that is easier to measure. The first approach consists of determining the terminal velocity, i.e. the maximum speed of a falling diaspore in still air, which is negatively related to dispersal distance. Its exact determination involves corrections of the initial acceleration, which requires the use of aerodynamic equations and discretised simulations (Schäfer 2002). For this reason, terminal velocity is usually substituted with descent velocity (Greene & Johnson 1993; Landenberger et al. 2006), which also presents an inverse relationship with dispersal distance (Greene & Johnson 1989; Nathan et al. 2011).

For the second approach, many different variables have been reported to be related to dispersal distance and, therefore, have been used to estimate dispersal potential. For instance, some studies infer dispersal distance from plant taxonomy (Tamme et al. 2014), frugivore density (Morales & Carlo 2006), population density (Spiegel & Nathan 2012), plant height (Tackenberg 2003; Thomson et al. 2011), diaspore morphology (Nathan et al. 2008; Sämel & Kowarik 2013) or from a combination of several traits (Vittoz & Engler 2007).

Many wind-dispersed species have diaspores with wing-like structures that increase the surface area to reduce descent velocity in air. Therefore, diaspore morphology is usually characterised as if it is a bi-dimensional structure. For instance, most studies estimate dispersal potential using only a diaspore's surface area and mass – or their ratio, also known as wing loading (Augspurger 1986; Matlack 1987; Delgado et al. 2009). However, the true structure of most diaspores is spatially organised over three dimensions; they have twists, bumps and other traits that may be key in making a better estimation of dispersal distance. For example, in the case of samaras, the way they are twisted (a three-dimensional quality) is essential in determining autorotation speed and therefore, descent velocity (Yasuda & Azuma 1997; Minami & Azuma 2003; Lentink et al. 2009). However, this is not usually considered when assessing their dispersal potential (Augspurger 1986; Matlack 1987; Minami & Azuma 2003).

The aims of this work are to assess the relationship between the morphology of the samaras from the invasive tree *Ailanthus altissima* (Mill.) Swingle and their wind dispersal potential. We have specifically addressed the following questions: (1) identifying which morphological traits are more relevant in predicting the wind dispersal potential of *Ailanthus altissima* samaras and (2) determining whether the inclusion of variables describing the three-dimensional arrangement of samaras improves potential dispersal distance estimates.

## Methods

### Study area and species

Fieldwork was carried out on the campus of the Complutense University of Madrid located in an urban area of the city of Madrid (Central Spain, 40° 27' 4" N, 3° 43' 35" W, at 645 m over the sea level). The climate is Mediterranean, semi-arid and continental with a mean annual temperature and rainfall of 14.6°C and 530 mm, respectively.

*A. altissima* is a tree from the Simaroubaceae family native to China that is currently widespread across all continents except in Antarctica. It is classified as a “noxious weed” and invasive species in many regions due to its rapid growth, allelopathic effects, extensive root system and ability to reproduce quickly via seeds and clonal growth (Lawrence et al. 1991; Kowarik & Sämel 2007). The plant grows 8–18 m tall, with females producing up to 325,000 samaras per year (Bory & Clair Maczulajtys 1981). These samaras are adapted to wind dispersal and have one seed in the centre of each wing. The samaras rotate along their axis and are rigid and sturdy (Kowarik & Sämel 2007) to enable a variety of flying methods, with autorotation being the most common (Yasuda & Azuma 1997; Lentink et al. 2009).

### Sampling, measurements and analysis

In January 2013, we randomly selected five female *A. altissima* trees growing spontaneously in open spaces on the campus. From each tree, we collected a set of 50 ripened samaras to obtain a fruit pool. All damaged samaras were discarded, and thus 200 samaras were ultimately used for the measurements (40 samaras per tree). Each samara was weighed to the nearest 0.1 mg and individually stored in paper bags.

To obtain detailed information on samara morphology, including their three-dimensional arrangement, we took measurements from two different viewpoints; a frontal view and a side view. All pictures were taken with a tripod at the same distance using the same focal length. A scaled ruler was included in every image as a reference to subsequently calculate lengths and areas. We processed each image with

Table I. Average measurements  $\pm$  their standard deviation for all 200 samaras of *A. altissima*.

Frontal area (cm <sup>2</sup> )	2.901 $\pm$ 0.567
Frontal perimeter (cm)	10.551 $\pm$ 0.958
Width (cm)	1.202 $\pm$ 0.176
Length (cm)	4.363 $\pm$ 0.416
Side area (cm <sup>2</sup> )	1.222 $\pm$ 0.279
Side perimeter (cm)	9.379 $\pm$ 0.893
Side height (cm)	0.628 $\pm$ 0.133
Mass (mg)	33.765 $\pm$ 7.684
Average descent velocity (m s <sup>-1</sup> )	1.095 $\pm$ 0.194

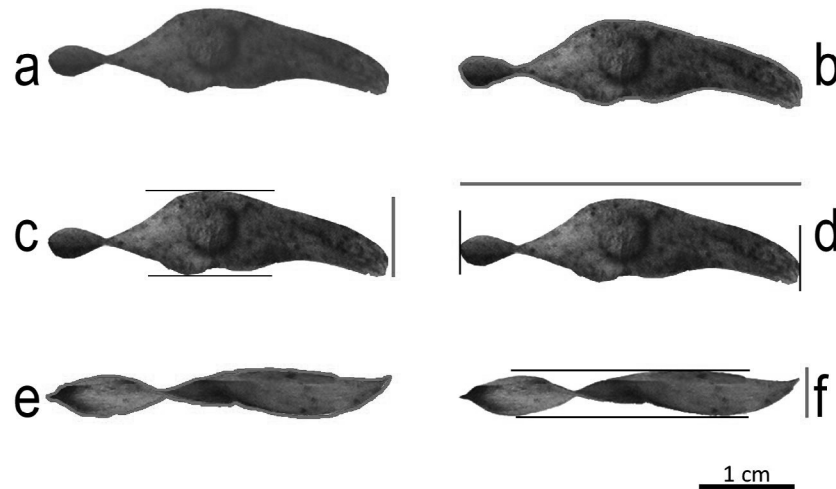


Figure 1. Morphological measurements taken are marked as follows: (a) frontal area; (b) frontal perimeter; (c) width; (d) length; (e) side perimeter; (f) side height.

Adobe Photoshop CS6 and Image J v1.47. We specifically took the following measurements (Table I and Figure 1): (a) frontal area, which is related to the flying capabilities of samaras by augmenting the surface area (Nilsson et al. 2010; Säumel & Kowarik 2013); (b) frontal perimeter, which is also related to the surface area of the samara; (c) width, which is closely related to the autorotation capabilities of the samara, affecting wind dispersal potential (Lentink et al. 2009); (d) length; (e) side area, which could be related to the surface area of the samara and thus affect flying capabilities; (f) side perimeter, which is positively related to the magnitude of the samara's spiral twist. This spiral shape is closely related to the autorotation capacity of the samara, affecting wind dispersal potential (Lentink et al. 2009) and increasing dispersal distance (Matlack 1987); and, finally, (g) side height, which informs us of the deviation of that spiral twist from its axis, as samaras with an intense deviation will give the impression of having a greater height when seen from the side as compared to more regular samaras. An irregular spiral twist is not able to generate as many autorotations as a regular symmetrical twist, consequently generating higher descent velocities (Lentink et al. 2009) and reducing dispersal distance.

As a previous statistical analysis to assess if samara morphology varied significantly amongst the studied trees of *A. altissima*, a MANOVA was performed ( $F_{48, 1126} = 11.97, p < 0.0005$ , Wilks' Lambda = 0.483), showing that individuals have different samara morphologies. Differences in samara morphology have already been described for this plant (Bory & Clair Maczulajtys 1981; Klotz et al. 2002; Delgado et al. 2009).

To estimate the samaras' wind dispersal capabilities, we measured their descent velocity. To measure the duration of the flight of the samaras, we dropped them inside an airtight and sealed chamber (Greene & Johnson 1993) with no air currents from a height of 2.0 m. Following the protocol of Landenberger et al. (2006), each samara was dropped in the exact same manner five times consecutively and the time it took to reach the ground was recorded with a stop watch (Greene & Johnson 1993; Landenberger et al. 2006). We then averaged the five measurements of each samara and calculated their average descent velocity as "height/average time to reach the ground" in (m/s).

Throughout the course of this study, samaras were not painted, coloured, written on, modified or altered in any way. We maintained their individual identification by placing each of them inside a spacious, conveniently labelled paper bag.

#### Statistical analysis

The repeatability and consistency of our protocol to measure descent velocity was assessed by means of an intraclass correlation coefficient (ICC) analysis. The relative influence of the morphological characteristics of the samara on its flying capabilities was analysed by multiple linear regressions. The lack of multicollinearity was assessed through the variance inflation factor (VIF). The adjusted  $R^2$ , the Akaike information criterion (AIC) and the cross-validated  $R^2$  (obtained by means of a 10-fold and leave-one-out cross-validation) were used to evaluate the quality of the different proposed models. All analyses were performed with SPSS v21 (IBM).

## Results

The ICC on descent velocity was 0.8, indicating that measurements are consistent between repetitions and that samara characteristics were preserved throughout the course of the experiment (Fleiss & Cohen 1973; Lew & Doros 2010).

Samara morphology and average descent velocities are summarised in Table I.

The lack of multicollinearity between the variables was assessed through the VIF. As seen in Table II, values are between 1 and 5, indicating a very weak correlation between the variables (Belsley et al. 2005).

The results of the multiple linear regression on the standardised variables in Table III indicate which morphological variables have a significant effect in determining the flying capabilities of the samara. Mass has the largest positive effect on descent

velocity, followed by side height and width, while frontal area and side perimeter have negative effects on descent velocity. The other variables (side area, length and frontal perimeter) had no significant effect on descent velocity ( $p > 0.05$ ).

Tables IV and V summarise different linear regression models sorted according to their adjusted  $R^2$  values. The first model (AE) includes only the variables that are commonly used in research on dispersal distance (mass and surface area of the samara). The rest of the models incorporate successively the side perimeter (ACE), the side height (ACDE) and the width of the samara (ABCDE) including all the morphological variables that have a significant effect in determining flying capabilities.

There is an increase of 57% in the prediction capacity of wind dispersal potential of samaras using the model that includes the side perimeter (ACE) as compared to the conventional model (AE), which only considered the mass and the surface area of the samara. Adding the variable side height (model ACDE) only entails a 14% increase in prediction capacity over the previous model (ACE). Finally, the addition of samara width generates model ABCDE, improving the prediction potential of the previous model (ACDE) by just 7% (Figure 2).

## Discussion

Diaspore mass and surface area (or the ratio between them, the wing loading) have often been used to estimate wind dispersal potential (Augspurger 1986; Matlack 1987; Minami & Azuma 2003). Nevertheless, our results show that in *A. altissima* samaras, the prediction capacity of a regression model with these variables is quite low, even under controlled conditions (Table V). We also found that

Table II. Variance inflation factor (VIF) values for the independent variables studied in *A. altissima*.

Frontal area	4.26
Frontal perimeter	2.08
Width	2.12
Length	3.16
Side area	2.03
Side perimeter	2.75
Side height	1.54
Mass	3.66

Table III. Multiple linear regression results showing which morphological characteristics of samaras in *A. altissima* have a significant effect in determining their descent velocities.

	$p$ value	$\beta$ (standardised)
Frontal area	<0.0001	-0.453
Side perimeter	<0.0001	-0.371
Width	0.043	+0.165
Side height	<0.0001	+0.240
Mass	<0.0001	+0.692

Table IV. Different regression models generated to explain average descent velocity of samaras of *A. altissima*,  $n = 200$ .

Variables	Regression model
ABCDE	Average descent velocity = $1.272 - 0.155 \times A + 0.182 \times B - 0.081 \times C + 0.352 \times D + 0.017 \times E$
ACDE	Average descent velocity = $1.427 - 0.125 \times A - 0.086 \times C + 0.332 \times D + 0.019 \times E$
ACE	Average descent velocity = $1.601 - 0.136 \times A - 0.090 \times C + 0.022 \times E$
AE	Average descent velocity = $1.020 - 0.149 \times A + 0.015 \times E$

Notes: A = frontal area; B = width; C = side perimeter; D = side height; E = mass.

Table V. Adjusted and cross-validated  $R^2$  values and AIC values for the different models used to explain average descent velocity of samaras of *A. altissima*,  $n = 200$ .

Variables	Adj $R^2$	AIC	$R^2$ prediction <sup>a</sup>	$R^2$ prediction <sup>b</sup>
ABCDE	0.280	-3.540	0.257	0.266
ACDE	0.268	-3.534	0.247	0.255
ACE	0.228	-3.490	0.213	0.217
AE	0.147	-3.399	0.133	0.138

Notes: A = frontal area; B = width; C = side perimeter; D = side height; E = mass.

<sup>a</sup>Leave-one-out cross-validation.

<sup>b</sup>10-fold cross-validation.

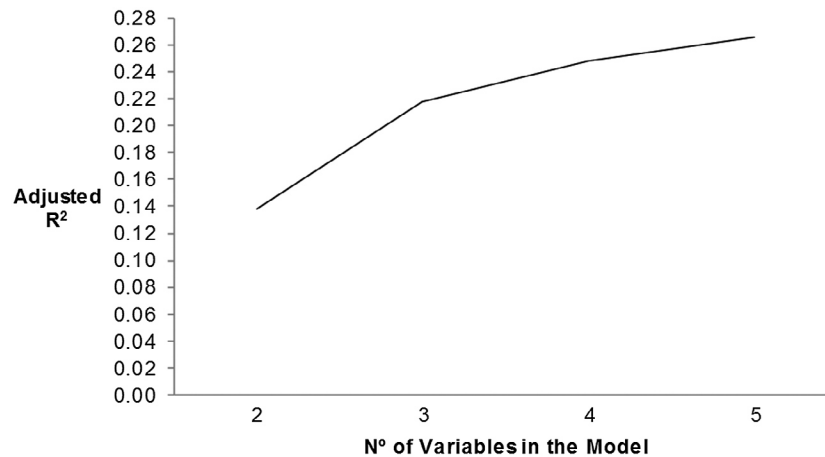


Figure 2. Changes in the value of the adjusted  $R^2$  depending on the number of variables included in the models that explain the average descent velocity of samaras of *A. altissima*.

the side perimeter and the side height of the samara, both related to their three-dimensional arrangement, are relevant variables in explaining their descent velocity. In addition, the inclusion of the side perimeter of the samara in the regression model drastically increased its prediction capacity for wind dispersal potential (Figure 2).

Further cumulative inclusion of a samara's side height and width fails to create such a considerable improvement in the subsequent models. Although we did not use an accuracy-to-cost trade-off approach, it could be expected that the inclusion of more variables in the model increases the statistical error of the estimate and could require a disproportionate amount of effort for only a small improvement in prediction (Kuyah & Rosenstock 2015).

There is a well-known relationship between the existence of a spiral twist along the samara's longitudinal axis (e.g. *Fraxinus* spp. and *A. altissima*) or a pitch in the samara's wing (*Acer* spp.) and their ability to autorotate and, therefore, to decrease their descent velocity (Matlack 1987; Lentink et al. 2009). Surprisingly, the consideration of these traits to estimate the samara's dispersal potential has often been discarded. Our results support the need for considering the use of morphological variables that are able to portray the three-dimensional nature of *A. altissima* samaras to improve the prediction capacity of their dispersal potential. We believe that the side perimeter is an easy-to-take measurement whose inclusion provides a notable increase in prediction power.

The improvement of dispersal estimates through the consideration of the three-dimensional morphology of the diaspore should not be restricted to *A. altissima*, but rather should be used for species with other samaras capable of autorotation (such as those from the genera *Acer*, *Fraxinus* or *Tipuana*) as well as other types of winged diaspores with varying flying methods

(such as in *Picea*, *Pinus*, *Alsomitra*, *Liriodendron*, *Ptelea* or *Ulmus*). This can also be very relevant in other wind-dispersed diaspores with a more pronounced three-dimensional arrangement. This is the case of *Cavanillesia* fruits with several wings arranged along different planes, the two-winged fruits of *Gyrocarpus* and *Dipterocarpus* with a single seed and two long wings, or even the infrutescences of *Tilia*, in which the flower bract forms the wing. Diaspores with the same wing-loading could differ greatly in their dispersability because of the influence of the three-dimensional arrangement on the descent velocity. Therefore, we suggest that an effort be made to find appropriate variables to summarise the effect of the three-dimensional morphology of the diaspore in the estimates of dispersal potential.

These considerations are not only relevant when comparing dispersal potential amongst individuals of the same population or between populations under different environmental conditions but also for community studies. Relative dispersability of species is key to assessing the regional coexistence and the consequences of fragmentation (Johnson 1988). Therefore, the study of relative dispersability within communities has received much attention (such as in Augspurger (1986); Augspurger (1988); Azuma and Yasuda (1989); Ozinga et al. (2004)). If in the community there are species with flat diaspores and others with a relevant three-dimensional arrangement, the use of wing loading would generate more accurate predictions of dispersal potential in the former than in the latter. Predictions derived from the use of their relative dispersability would be affected by the different levels of accuracy.

In conclusion, the use of morphological variables that reflect the three-dimensional qualities of diaspores can render future research on dispersal distance more accurate, especially when it involves

multi-specific scenarios with a wide range of diaspore morphologies. The portrayal of the three-dimensional morphology will particularly improve the dispersal distance estimates in diaspores with a strong volume or three-dimensional morphology, as the benefit was significant even in the case of *A. altissima*, which has relatively flat diaspores as compared to other species. This work provides new insights into the need to evaluate three-dimensional morphology to predict dispersal distance. Future research could focus in the most appropriate way of describing and measuring the three-dimensional nature of other types of diaspore morphologies to improve dispersal distance estimates.

## Acknowledgements

We would like to thank Sarah Young for helping in polishing and improving our English.

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