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**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, 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 by 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.

1

INTRODUCTION

2Diaspore dispersal enables species to augment their area of distribution and move
3farther away from their parent plant, making it an extremely important process in the
4evolution of organisms and in the resilience and spatio-temporal structure of
5ecosystems worldwide (Nathan et al. 2008). The ecological importance of the
6dispersal capacity of diaspores has been long supported (Darwin 1859) and is
7currently treated as a crucial factor in explaining many ecological processes such as:
8shaping the assembly of communities (Howe & Smallwood 1982; Nilsson et al.
92010), determining patterns of distribution (Nathan & Muller-Landau 2000; Drezner
10et al. 2001; Levin et al. 2003), population dynamics (Levin et al. 2003), landscape
11configuration (Thompson & Katul 2009), colonisation (Howe & Smallwood 1982),
12habitat loss and fragmentation (Nathan et al. 2008; Hampe 2011), invasions (Kowarik
13& Säumel 2008) and genetic flow (Nathan & Muller-Landau 2000).

14Plant dispersal is a complex stochastic multi-scale process and for this reason it is
15very complicated to measure it directly (Nathan et al. 2008). Many efforts have been
16made in directly measuring dispersal through field experiments by tagging diaspores
17with paint to visually observe their movement (Säumel & Kowarik 2010; Kowarik &
18Von der Lippe 2011; Säumel & Kowarik 2013; von der Lippe et al. 2013; Cabra-
19Rivas et al. 2014). Moreover, other methods resort to using seed traps at different
20distances from the parent plant (Bullock & Clarke 2000; von der Lippe et al. 2013) or
21attach metal tags and then use magnetic locators (Alverson & Diaz 1989). Finally,
22genetic analysis has also been used to determine which diaspores correspond to which

23mother plant (Godoy & Jordano 2001; Jordano et al. 2002), but the costs and time
24required make this useful only in limited situations.

25To overcome the difficulties in direct field measurement of dispersal distance (Nathan
262006), researchers can use controlled environments to apply two different approaches:
271) Determination of the velocity of a falling diaspore and 2) the use of indirect
28measurements, in which a relationship is established between the dispersal distance
29and another variable easier to measure. The first approach consists of determining the
30terminal velocity, i.e. the maximum speed of a falling diaspore in still air, which is
31negatively related to dispersal distance. Nevertheless, its exact determination involves
32corrections of the initial acceleration, which requires the use of aerodynamic
33equations and discretized simulations (Schäfer 2002). For this reason, terminal
34velocity is usually substituted by descent velocity (Greene & Johnson 1993;
35Landenberger et al. 2006), which also presents an inverse relationship with dispersal
36distance (Greene & Johnson 1989; Nathan et al. 2011).

37For the second approach, many different variables have been reported to be related to
38dispersal distance and, therefore, have been used to estimate dispersal potential. For
39instance, some studies infer dispersal distance from plant taxonomy (Tamme et al.
402014), frugivore density (Morales & Carlo 2006), population density (Spiegel &
41Nathan 2012), plant height (Tackenberg 2003; Thomson et al. 2011), diaspore
42morphology (Nathan et al. 2008; Säumel & Kowarik 2013), or from a combination of
43several traits (Vittoz & Engler 2007).

44Many wind-dispersed species have diaspores with wing-like structures that increase
45the surface area to reduce descent velocity in air. Therefore, diaspore morphology is
46usually characterised as if it was a bi-dimensional structure. For instance, most studies

47estimate dispersal potential using only a diaspore's surface area and mass - or their
48ratio, also known as wing loading (Augspurger 1986; Matlack 1987; Delgado et al.
492009)). However, the real structure of most diaspores is spatially organised over three
50dimensions; they have twists, bumps and other traits that may be key in making a
51better estimation of dispersal distance. For example, in the case of samaras, the way
52they are twisted (a three-dimensional quality) is essential in determining autorotation
53speed and therefore, descent velocity (Yasuda & Azuma 1997; Minami & Azuma
542003; Lentink et al. 2009). However, this is not usually considered when assessing
55their dispersal potential (Augspurger 1986; Matlack 1987; Minami & Azuma 2003).

56The aims of this work are to assess the relationship between the morphology of the
57samaras from the invasive tree *Ailanthus altissima* (Mill.) Swingle and their wind
58dispersal potential. We have specifically addressed the following questions: 1) which
59morphological traits are more relevant in predicting the wind dispersal potential of
60*Ailanthus altissima* samaras and 2) if the inclusion of variables describing the three-
61dimensional arrangement of samaras improves potential dispersal distance estimates.

62

63

METHODS

64 *Study area and species*

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

70 *A. altissima* is a tree from the Simaroubaceae family native to China that is currently
71 widespread across all continents except in Antarctica. It is classified as a "noxious
72 weed" and invasive species in many regions for its rapid growth, allelopathic effects,
73 extensive root system and ability to reproduce quickly via seeds and clonal growth
74 (Lawrence et al. 1991; Kowarik & Säumel 2007). The plant grows 8-18m tall, with
75 females producing up to 325000 samaras per year (Bory & Clair Maczulajtyš 1981).
76 These samaras are adapted to wind dispersal and have one seed in the centre of each
77 wing. The samaras rotate along their axis and are rigid and sturdy (Kowarik & Säumel
78 2007) to enable a variety of flying methods, with autorotation being the most common
79 (Yasuda & Azuma 1997; Lentink et al. 2009).

80 *Sampling, measurements and analysis*

81 In January 2013, we randomly selected 5 female *A. altissima* trees growing
82 spontaneously in open spaces on the campus. From each tree, we collected a set of 50
83 ripened samaras to obtain a fruit pool. All damaged samaras were discarded, and thus
84 200 samaras were ultimately used for the measurements (40 samaras per tree). Each
85 samara was weighed to the nearest 0.1mg and individually stored in paper bags.

86To obtain detailed information on samara morphology, including their three-
87dimensional arrangement, we took measurements from two different viewpoints; a
88frontal view and a side view. All pictures were taken with a tripod at the same
89distance using the same focal length. A scaled ruler was included in every image as a
90reference to subsequently calculate lengths and areas. We processed each image with
91Adobe Photoshop CS6 and Image J v1.47. We specifically took the following
92measurements (Table 1, Figure 1): **a)** Frontal area, which is related to the flying
93capabilities of samaras by augmenting the surface area (Nilsson et al. 2010; Säumel &
94Kowarik 2013); **b)** Frontal perimeter, which is also related to the surface area of the
95samara; **c)** Width, which is closely related to the autorotation capabilities of the
96samara, affecting wind dispersal potential (Lentink et al. 2009); **d)** Length; **e)** Side
97area, which could be related to the surface area of the samara and thus affect flying
98capabilities; **f)** Side perimeter, which is positively related to the magnitude of the
99samara's spiral twist. This spiral shape is closely related to the autorotation capacity of
100the samara, affecting wind dispersal potential (Lentink et al. 2009) and increasing
101dispersal distance (Matlack 1987); and, finally, **g)** side height, which informs us of the
102deviation of that spiral twist from its axis, as samaras with an intense deviation will
103give the impression of having a greater height when seen from the side as compared
104to more regular samaras. An irregular spiral twist is not able to generate as many
105autorotations as a regular symmetrical twist, consequently generating higher descent
106velocities (Lentink et al. 2009) and reducing dispersal distance.

107To estimate the samaras' wind dispersal capabilities, we measured their descent
108velocity. To measure the duration of the flight of the samaras, we dropped them inside
109an airtight and sealed chamber (Greene & Johnson 1993) with no air currents from a
110height of 2.0m. Following the protocol of Landenberger et al. (2006), each samara

111 was dropped in the exact same manner 5 times consecutively and the time it took to
112 reach the ground was recorded with a stop watch (Greene & Johnson 1993;
113 Landenberger et al. 2006). We then averaged the five measurements of each samara
114 and calculated their average descent velocity as “height / average time to reach the
115 ground” in (m/s).

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

119 *Statistical analysis*

120 The repeatability and consistency of our protocol to measure descent velocity was
121 assessed by means of an Intraclass Correlation Coefficient (ICC) analysis. The
122 relative influence of the morphological characteristics of the samara on its flying
123 capabilities was analysed by multiple linear regressions. The lack of multicollinearity
124 was assessed through the Variance Inflation Factor (VIF). The adjusted R^2 , the
125 Akaike Information Criterion (AIC) and the cross-validated R^2 (obtained by means of
126 a 10-fold and leave-one-out cross validation) were used to evaluate the quality of the
127 different proposed models. All analyses were performed with SPSS v21 (IBM).

128

RESULTS

129The Intraclass Correlation Coefficient (ICC) on descent velocity was 0.8, indicating
130that measurements are consistent between repetitions and that samara characteristics
131were preserved throughout the course of the experiment (Fleiss & Cohen 1973; Lew
132& Doros 2010).

133Samara morphology and average descent velocities are summarised in Table 1.

134The lack of multicollinearity between the variables was assessed through the Variance
135Inflation Factor (VIF). As seen in Table 2, values are between 1 and 5, indicating a
136very weak correlation between the variables (Belsley et al. 2005).

137The results of the multiple linear regression on the standardised variables in Table 3
138indicate which morphological variables have a significant effect in determining the
139flying capabilities of the samara. Mass has the largest positive effect on descent
140velocity, followed by side height and width, while frontal area and side perimeter
141have negative effects on descent velocity. The other variables (side area, length and
142frontal perimeter) had no significant effect on descent velocity ($p > 0.05$).

143Tables 4 and 5 summarise different linear regression models sorted according to their
144adjusted R^2 values. The first model (AE) includes only the variables that are
145commonly used in research on dispersal distance (mass and surface area of the
146samara). The rest of the models incorporate successively the side perimeter (ACE),
147the side height (ACDE) and the width of the samara (ABCDE) including all the
148morphological variables that have a significant effect in determining flying
149capabilities.

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

157

DISCUSSION

158Diaspore mass and surface area (or the ratio between them, the wing loading) has
159often been used to estimate its wind dispersal potential (Augspurger 1986; Matlack
1601987; Minami & Azuma 2003). Nevertheless, our results show that in *A. altissima*
161samaras the prediction capacity of a regression model with these variables is quite
162low, even in controlled conditions (Table 5). We also found that the side perimeter
163and the side height of the samara, both related to their three-dimensional arrangement,
164are relevant variables in explaining their descent velocity. In addition, the inclusion of
165the side perimeter of the samara in the regression model drastically increased its
166prediction capacity of wind dispersal potential (Fig 2).

167Further cumulative inclusion of samara's side height and width fails to create such a
168considerable improvement in the subsequent models. Although we did not perform an
169accuracy-to-cost trade-off approach, it could be expected that the inclusion of more
170variables in the model increases the statistical error of the estimate and could require a
171disproportionate amount of effort for only a small improvement in prediction (Kuyah
172& Rosenstock 2015).

173There is a well-known relationship between the existence of a spiral twist along the
174samara's longitudinal axis (e.g. *Fraxinus* spp and *A. altissima*) or a pitch in the
175samara's wing (*Acer* spp.) and their ability to autorotate and, therefore, to decrease
176their descent velocity (Matlack 1987; Lentink et al. 2009). Surprisingly, the
177consideration of these traits to estimate the samara's dispersal potential has often been
178discarded. Our results support the need for considering the use of morphological
179variables that are able to portray the three-dimensional nature of *A. altissima* samaras
180in order to improve the prediction capacity of their dispersal potential. We believe that

181the side perimeter is an easy-to-take measurement whose inclusion provides a notable
182increase in prediction power.

183The improvement of dispersal estimates through the consideration of the three-
184dimensional morphology of the diaspore should not be restricted to *A. altissima*, but
185rather should be used for species with other samaras capable of autorotation (such as
186those from the genus *Acer*, *Fraxinus*, or *Tipuana*) as well as other types of winged
187diaspores with varying flying methods (such as in *Picea*, *Pinus*, *Alsomitra*,
188*Liriodendron*, *Ptelea* or *Ulmus*). This can also be very relevant in other wind-
189dispersed diaspores with a more pronounced three-dimensional arrangement. This is
190the case of *Cavanillesia* fruits with several wings arranged along different planes, the
191two-winged fruits of *Gyrocarpus* and *Dipterocarpus* with a single seed and two long
192wings, or even the infrutescences of *Tilia*, in which the flower bract forms the wing.
193Diaspores with the same wing-loading could differ largely in their dispersability
194because of the influence of the three-dimensional arrangement on the descent
195velocity. Therefore, we suggest that an effort be made to find appropriate variables to
196summarise the effect of the three-dimensional morphology of the diaspore in the
197estimates of dispersal potential.

198These considerations are not only relevant when comparing dispersal potential among
199individuals of the same population or between populations under different
200environmental conditions but also for community studies. Relative dispersability of
201species is key to assessing the regional coexistence and the consequences of
202fragmentation (Johnson 1988). Therefore, the study of relative dispersability within
203communities has received much attention (such as in Augspurger (1986); Augspurger
204(1988); Azuma and Yasuda (1989); Ozinga et al. (2004)). If in the community there
205are species with flat diaspores and others with a relevant three-dimensional

206arrangement, the use of wing loading would generate more accurate predictions of
207dispersal potential in the former than in the latter. Predictions derived from the use of
208their relative dispersability would be affected by the different levels of accuracy.

209In conclusion, the use of morphological variables that are able to portray the three-
210dimensional qualities of diaspores can render future research on dispersal distance
211more accurate, especially when it involves multi-specific scenarios with a wide range
212of diaspore morphologies. The portrayal of the three-dimensional morphology will
213particularly improve the dispersal distance estimates in diaspores with a strong
214volume or three-dimensional morphology, as the benefit was significant even in the
215case of *A. altissima*, which has relatively flat diaspores as compared to other species.
216Although this work provides new insights on the need of evaluation of the three-
217dimensional morphology in order to predict dispersal distance, future research is
218needed to determine the most appropriate way of describing and measuring the three-
219dimensional nature of other types of diaspore morphologies in order to improve
220dispersal distance estimates.

221

222

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336

337

Table 1 Average measurements \pm their standard deviation for all 200 samaras of *A. altissima*.

Frontal Area (cm ²)	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 ²)	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 ⁻¹)	1.095 \pm 0.194

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339

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Table 2 Variance Inflation Factor (VIF) values for the independent variables studied in *A. altissima*.

Frontal Area
Frontal Perimeter
Width
Length
Side Area
Side Perimeter

Side Height

Mass

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342

343

Table 3 Multiple linear regression results showing which morphological characteristics of samaras in *A. altissima* have a significant effect in determining their descent velocities.

	P value	β (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

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Table 4 Different regression models generated to explain average descent velocity of samaras of *A. altissima*, n=200.

A=Frontal Area; **B**=Width; **C**=Side Perimeter; **D**=Side Height; **E**=Mass

Variables	Regression Model
ABCDE	Average Descent Velocity = 1.272 – 0.155*A + 0.182*B – 0.081*C + 0.352*D + 0.017*E

ACDE	Average Descent Velocity = $1.427 - 0.125*A - 0.086*C + 0.332*D + 0.019*E$
ACE	Average Descent Velocity = $1.601 - 0.136*A - 0.090*C + 0.022*E$
AE	Average Descent Velocity = $1.020 - 0.149*A + 0.015*E$

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Table 5 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=242.

A=Frontal Area; **B**=Width; **C**=Side Perimeter; **D**=Side Height; **E**=Mass

Variables	Adj R^2	AIC	R^2 Prediction ^(a)	R^2 Prediction ^(b)
ABCDE	0.26578	-3.55698	0.246398	0.249178
ACDE	0.24793	-3.53975	0.231784	0.233675
ACE	0.21809	-3.51058	0.204845	0.207934
AE	0.13867	-3.41377	0.119488	0.120078

a Leave-one-out cross-validation; **b** 10-fold cross-validation

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1 cm

359 **Figure 1** Morphological measurements taken are marked as follows: **a)** Frontal area;
 360 **b)** Frontal perimeter; **c)** Width; **d)** Length; **e)** Side perimeter; **f)** Side height

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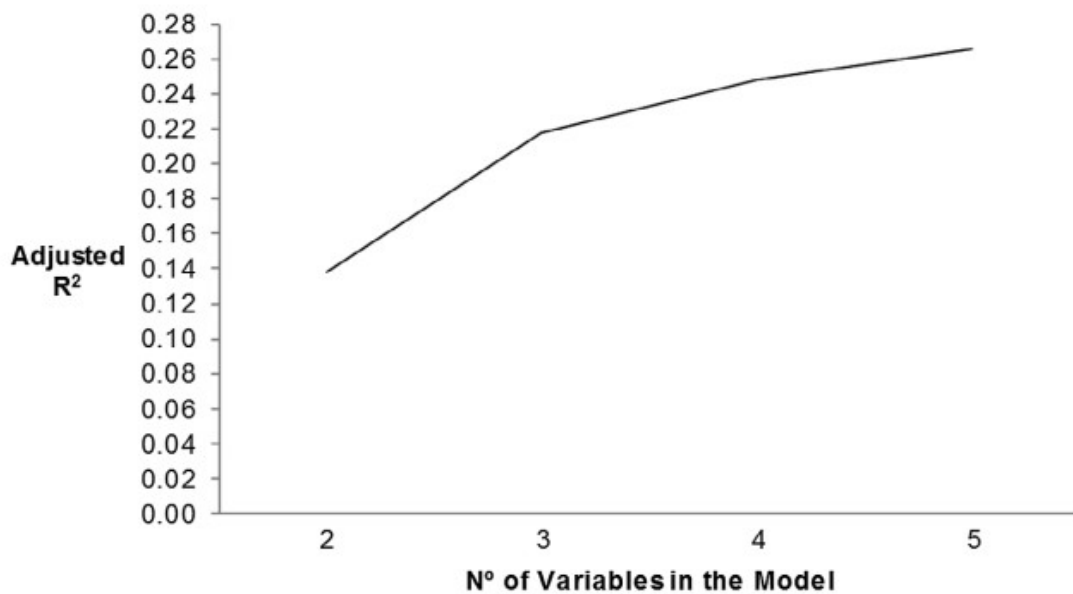
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368 **Figure 2** Changes in the value of the adjusted R² depending on the number of
 369 variables included in the models that explain the average descent velocity of samaras
 370 of *A. altissima*.