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Original article

Gone with the wind and the stream: Dispersal in the invasive species *Ailanthus altissima*☆

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ABSTRACT

Dispersal is a key process in plant invasions and is strongly related to diaspore morphology. Often, dispersal comprises more than one step, and morphologies adapted to a primary dispersal mechanism can aid or detract from a secondary one. The aim of this work was to assess the relationship between primary wind dispersal and secondary water dispersal in *Ailanthus altissima*, an invasive tree species. Wind and water dispersal potential and their association with the morphological characteristics of samaras were assessed under controlled conditions to ensure the repeatability of the measurements. We found a direct positive relationship between primary wind and secondary water dispersal in *A. altissima*. The main morphological characteristics of the samara that affected the success of the two types of dispersal were side perimeter and mass. However, a possibility of dispersal specialisation exists, as one morphological characteristic (samara width) affects wind dispersal negatively but water dispersal positively, and dispersal potential and samara morphology have been shown to differ across individuals.

1. Introduction

A successful invasion comprises three stages: dispersal of diaspores, formation of a new self-sufficient population and, finally, the spread of this new population to nearby habitats (Leung et al., 2002; Williamson and Fitter, 1996). Therefore, diaspore dispersal mechanisms are crucial processes in understanding plant invasions, and as such, their study is key to managing plant invasions effectively (Leung et al., 2002).

Seed dispersal syndromes define the dispersal strategy of a diaspore and have been studied in depth on numerous occasions (Howe and Smallwood, 1982; Van der Pijl, 1982; Wheelwright and Orians, 1982). Diaspores may be dispersed ballistically, in which case fruits spring open abruptly and explosively release them. Animals can also disperse diaspores that are partly edible or that attach to them by means of hooks or sticky surfaces. Wind-dispersed diaspores, on the other hand, commonly have light structures that can act as wings, plumes or balloons, thus decreasing fall velocity and increasing dispersal distance (Augspurger, 1986; Matlack, 1987). Diaspores can also be dispersed by water, if they are able to float and resist water damage (Säumel and Kowarik, 2013).

Diaspore dispersal is not always a single-step process, and multiple vectors (animals, wind or water) may be involved (Vander Wall et al., 2005). While primary vectors move diaspores away from the parent plant, secondary vectors can dramatically increase the transport distances (Nathan et al., 2008; Säumel and Kowarik, 2013). Although if there is promising research in estimating dispersal distance (Soons et al., 2004; Tackenberg, 2003; Tackenberg et al., 2003), the relationship between dispersal and diaspore morphology is not yet completely understood (Higgins et al., 2003), as it is a complex multi-scale process that may involve different vectors (Nathan et al., 2008). Furthermore, diaspore morphologies adapted for a primary dispersal mechanism can indirectly favour or dampen secondary dispersal mechanisms (Hintze et al., 2013; Kowarik and Säumel, 2008).

Many invasive tree species have diaspores adapted for wind dispersal (Burrows, 1986). The morphological adaptations for wind dispersal can also render diaspores well adapted for dispersing through water, since features such as a low mass or a high surface area are suited to both (Nilsson et al., 2010; Säumel and Kowarik,

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☆ All authors have approved the final version of this article and declare to have participated equally in its design, accomplishment and preparation.

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2013). Wind can move diaspores long distances (Thomson et al., 2011; Vittoz and Engler, 2007), and those that fall along a watercourse could potentially disperse even further (Poschlod and Bonn, 1998; Säumel and Kowarik, 2013). The relationship between wind and water dispersal remains uninvestigated, as is the influence of diaspore morphology on each dispersal mechanism (Higgins et al., 2003). Nonetheless, selective pressure will likely benefit plants that are good at both methods of dispersal. Since wind dispersal is multi-directional, it can enable propagules to land in a wide range of new habitats, while water dispersal increases the probability of propagules landing in a suitable area (i.e. close to a water source) and can amplify wind dispersal transport distances by a factor of at least 20 (Säumel and Kowarik, 2013).

Here we evaluate the relationship between dispersal and diaspore morphology in the invasive tree *Ailanthus altissima* (Miller) Swingle. This species uses wind as primary and water as secondary dispersal vector (Kowarik and Säumel, 2008). It has also been reported to spread along roads, railways and water courses (Kowarik and Säumel, 2007; Merriam, 2003), where the relative relevance of the two mechanisms should vary. In this study, we consider the following: 1) the relationship between wind dispersal potential and water dispersal potential in *A. altissima*, 2) the role of samara morphology in both types of dispersal and 3) differences in the dispersal capabilities of individual *A. altissima* trees.

2. Materials and methods

2.1. Study area and species

Field work was carried out on the campus of the Complutense University of Madrid. This is an urban campus located in the city of Madrid (Central Spain, 40° 27′ 4″ N, 3° 43′ 35″ W, at 645 m above 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. Soils are characterised as luvisols (FAO-UNESCO soil classification system) and are siliceous, sandy and nutrient-poor with a slightly acidic pH (Nombela et al., 1994). Structurally, they are highly developed soils with good air diffusion and low waterlogging capabilities.

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 for its rapid growth, allelopathic effects, extensive root system and ability to reproduce quickly via diaspores and clonal growth (Kowarik and Säumel, 2007; Lawrence et al., 1991). The plant grows 8–18 m tall, with females producing up to 325,000 samaras per year (Bory and Clair Maczulajtys, 1981). These samaras are adapted to wind dispersal and have one seed in the centre of each wing. Diaspores rotate along their axis and are rigid and sturdy (Kowarik and Säumel, 2007) which enables a variety of flying methods, with autorotation being the most common (Lentink et al., 2009; Yasuda and Azuma, 1997). Water dispersal has also been reported in this species (Kaproth and McGraw, 2008; Kowarik and Säumel, 2008).

2.2. Sampling, measurements and analysis

In January 2013, we randomly selected seven female *A. altissima* trees growing spontaneously in open spaces in the campus. We collected roughly 50 samaras from each tree, discarded the damaged ones, and retained 242 samaras for our measurements (40 samaras per tree except for two trees, from which only 19 and 23 samaras were used). Samaras were weighed to the nearest 0.1 mg and individually stored in paper bags until morphological and dispersal measurements were taken.

Samara morphology was described from a frontal and a side view (Fig. 1). Pictures of individual samaras were taken from a tripod placed at a fixed distance and using a fixed focal length. We included a scaled ruler as a reference to calculate distances with Adobe Photoshop CS6 and Image J v1.47. In this way, we measured specific morphological attributes of samaras that are related to wind and/or water dispersal. They included frontal area, side area and frontal perimeter, which are closely related to the wind and water dispersal potential of samaras as the total surface area is a function of these values (Nilsson et al., 2010; Säumel and Kowarik, 2013); and samara width, which is closely related to the autorotation and flotation potential of the samara (Lentink et al., 2009). We also measured other morphological variables to obtain a more complete description of the samaras' morphology (Tables 1 and 2).

We estimated samara wind dispersal potential by measuring their average descent velocity (Greene and Johnson, 1993; Landenberger et al., 2006). This trait is inversely related to dispersal distance (Greene and Johnson, 1989; Nathan et al., 2011; Tackenberg, 2003), and it was quantified by dropping the samaras inside an airtight and sealed chamber (Greene and Johnson, 1993) from a height of 2.0 m. Each samara was dropped in the same manner three times, and the time it took to reach the ground was recorded with a stop watch (Greene and Johnson, 1993; Landenberger et al., 2006). Descent velocity was calculated as height divided by time to reach the ground. Average descent velocity for all 242 samaras was 1.106 ± 0.215 m/s (range 0.703–1.705 m/s; Table 1).

The water dispersal potential of the samaras was inferred from their drifting velocity and floating time, which respectively relate to their ability to drift downstream and the length of time they can be transported by flotation.

To measure drifting velocity we built a polypropylene channel, square in cross section, 4 m long, 0.09 m wide and 0.05 m high. Water flow was empirically measured to be 0.108 L/s (roughly 0.25 m/s) across the whole channel profile and 0.591 m/s at the water surface. We recorded the time it took for each samara to traverse the 4 m channel and calculated drifting velocity as channel length divided by the time recorded. Each samara was released from the same place in the same position three times; between measurements they were allowed to dry in the open air for a week. Average drifting velocity for all 242 samaras was 0.530 ± 0.011 m/s (range 0.481–0.554 m/s; Table 1).

To measure the floating capabilities of samaras, we placed them in individual water containers with 55 ml of distilled water. We then placed the containers in an orbital shaker at 150 rpm for

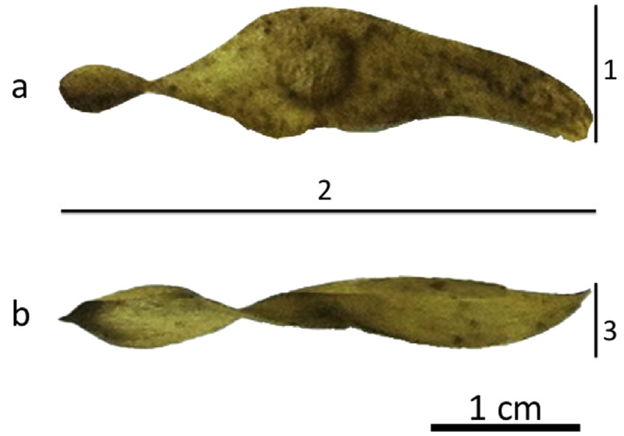

Fig. 1. Some morphological measurements of the samaras from a frontal view (a) and side view (b): width (1); length (2); side height (3).

Table 1
Average measurements ± standard deviations and range of the variables used to characterise samaras of *A. altissima* ($n = 242$). Measurement units are shown in parentheses.

Variable description	Average ± SD	Range
Morphology		
Frontal area (cm^2)	2.957 ± 0.581	1.397–4.398
Frontal perimeter (cm)	10.529 ± 0.966	7.797–13.321
Width (cm)	1.225 ± 0.181	0.698–1.764
Length (cm)	4.371 ± 0.415	3.293–5.391
Side area (cm^2)	1.259 ± 0.284	0.700–2.664
Side perimeter (cm)	9.506 ± 0.920	7.095–11.85
Side height (cm)	0.635 ± 0.127	0.323–1.233
Mass (mg)	34.3 ± 7.6	20.70–59.10
Dispersal		
Descent velocity (m/s)	1.106 ± 0.215	0.703–1.705
Drifting velocity (m/s)	0.530 ± 0.011	0.481–0.554
Floating time (days)	2.074 ± 0.589	1.0–4.0

Table 2
Intraclass correlation coefficient (ICC) results and average measurements of each repetition for wind and water dispersal. ICC results are calculated from the individual values of each of the 242 samaras from each repetition.

	Descent velocity (m/s)	Drifting velocity (m/s)	Floating time (days)
ICC	0.8	0.3	0.7
Repetition 1	1.07 ± 0.22	0.56 ± 0.13	2.16 ± 0.53
Repetition 2	1.01 ± 0.24	0.54 ± 0.14	1.95 ± 0.60
Repetition 3	1.11 ± 0.23	0.50 ± 0.14	2.14 ± 0.50

12 min to allow the floating samaras to become fully impregnated with water. In this way we eliminated differences in floating time due to the way the samara lands in the water (i.e., whether the samara breaks the water surface tension). Finally, we placed the containers into an airtight chamber which was observed at 24 h intervals and registered the time it took for the samaras to sink. This process was repeated three times, allowing the samaras to dry for a week between measurements. Average floating time for all 242 samaras was 2.074 ± 0.589 days (range 1–4 days; Table 1).

We performed three different measurements of each dispersal variable to test the repeatability and consistency of our protocol and, at the same time, to generate for each samara an average value to be used in the statistical analyses. Throughout the course of this experiment, samaras were not painted, coloured, written on, modified or altered in any way. They were placed inside labelled paper bags for individual identification.

2.3. Statistical analysis

The consistency and repeatability of our dispersal measurements were evaluated in terms of the intraclass correlation coefficient (ICC) for the repeated measurements made on each samara. The relationship between wind and water dispersal was assessed by Pearson correlation analyses. To explore the potential effect of each morphological variable on dispersal estimates, we used single regression analysis. Then, the best models relating dispersal estimates and the morphological attributes of samaras were obtained using an information-theoretical approach and identity as the link function, since dispersal estimates were normally distributed. The selection of the most parsimonious set of parameters was based on fit to the data and number of variables of the model, according to the Akaike information criterion corrected for small sample sizes (AICc; Johnson and Omland, 2004). Although the lowest AICc indicates the model that best fits the data (Hosmer and Lemeshow, 2004), models with ΔAICc ≤ 2.0 are considered equally informative (Burnham and Anderson, 2003). Wald statistics were used to assess the significance of regression coefficients in the selected models. Collinearity amongst independent variables was assessed with the variance inflation factor (VIF). To test for differences in samara morphology between individual *A. altissima* trees, MANOVA and principal component analysis (PCA) were used. Finally, to test for differences in dispersal potential between individual trees, MANOVA was used followed by univariate ANOVAs and Tukey's HSD tests. All analyses were performed with SPSS v21 (IBM).

3. Results

The ICC results (Table 2) show that, except for drifting velocity, our dispersal measurements were consistent across repetitions (Fleiss and Cohen, 1973; Lew and Doros, 2010). The lack of consistency in measurements of drifting velocity could be mainly due to subtle changes in water velocity during the three experimental trials, rather than being the effect of repeated rewetting of samaras, as no trend was found when we later performed the floatability measurements.

Pearson correlation results showed a significant inverse relationship between descent velocity and floating time ($p = 0.001$; $r = -0.206$), meaning that samaras with slower descent rates will have longer flotation times (Fig. 2). On the other hand, there was a positive relationship between descent velocities and drifting velocities of samaras ($p = 0.05$; $r = 0.189$; Fig. 2). Finally, there was no statistically significant relationship between drifting velocities and floating times ($p = 0.48$).

Fig. 3 shows the relationship of each morphological variable and dispersal capabilities. Mass had the largest positive effect on descent velocity, followed by width and side height, while frontal area and side perimeter had negative effects on descent velocity. Moreover, drifting velocity was only influenced by side perimeter, which had a negative effect. Finally, the flotation time of samaras was inversely related to mass and, to a lesser extent, positively related to side perimeter and width. It must be highlighted that all of those linear regressions were significant because of the large number of points, but the R^2 values were extremely low.

The results of the best subset procedure are shown in Table 3. For descent velocity, six models with ΔAICc ≤ 2.0 were obtained, but using the criteria of model complexity, two models with five variables each were considered as the most parsimonious ones (Table 3). Both included frontal area and side perimeter (with negative coefficients), side height and mass (with positive coefficients), and differed in the inclusion of samara width or side area (with positive and negative coefficients; Table 4). There were more than ten models selected for drifting velocity (ΔAICc ≤ 2.0), but two of them were considered to be the most parsimonious because of their lower number of variables. In fact, both only selected one variable: the side perimeter or the length of the samara (Table 3), and both were negatively related to drifting velocity (Table 4). Finally, although seven models for floating time presented ΔAICc ≤ 2.0, just one of them was considered the most plausible model because of its lower number of variables (Table 3). Floating times of samaras were negatively correlated to mass and

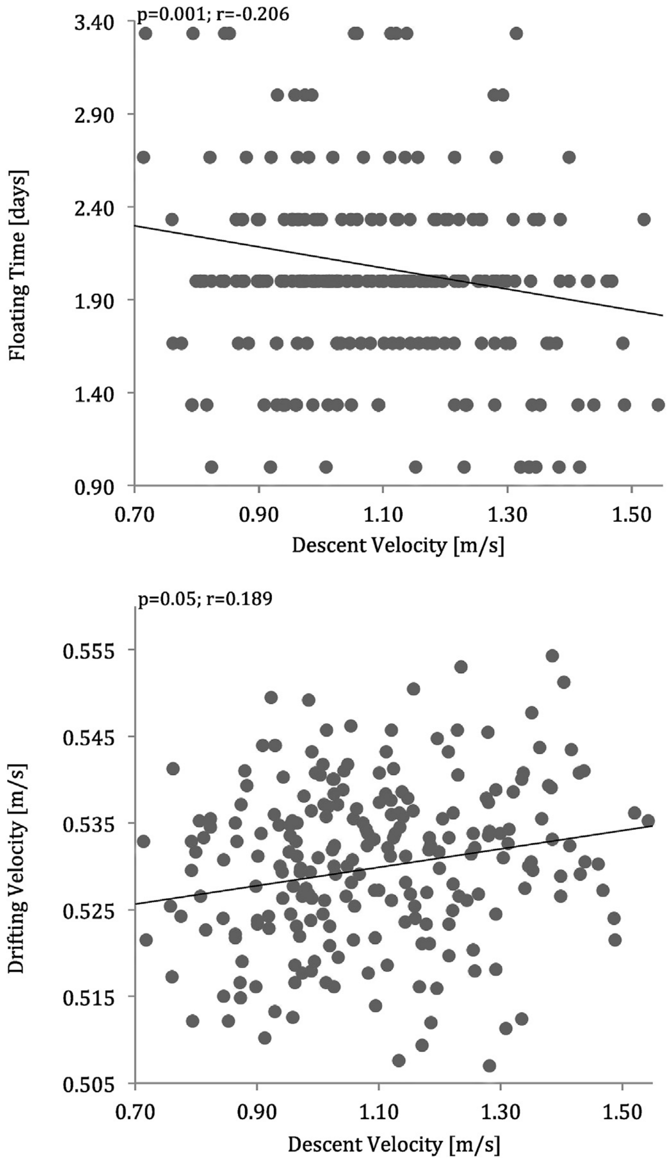

Fig. 2. Relationship between wind and water dispersal in *A. altissima*.

positively to width and side perimeter (Table 4). Ordinary linear regression models performed with the same subset of variables showed a relevant improvement of prediction power in relation to that of single variables, but adjusted R^2 values were still low (Table 3).

The variance inflation factor (VIF) ranges from 1 to 5 (frontal area = 4.66; frontal perimeter = 2.02; width = 2.22; length = 3.88; side area = 2.04; side perimeter = 2.83; side height = 1.52; mass = 3.67), indicating a weak correlation among the independent variables (Belsley et al., 2005).

Samara morphology was significantly different among the studied trees of *A. altissima* (MANOVA, $F_{48,1126} = 11.97$, $p < 0.0005$, Wilks' lambda = 0.483). The PCA resulted in two factors with eigenvalue >1, explaining 71.2% of the variance. The main principal component was positively related ($p < 0.01$ in all cases) to mass ($r = 0.885$), frontal area ($r = 0.876$), side perimeter ($r = 0.827$), width ($r = 0.660$) and side height ($r = 0.425$). The second component was related ($p < 0.01$ in all cases) positively to side height ($r = 0.751$) and mass ($r = 0.170$) and negatively to width ($r = -0.321$) and frontal area ($r = -0.247$). Within the samara trait space, individual trees were segregated on the first axis according to the size of the samaras, whereas on the second axis they were segregated mainly according to their side perimeter (Fig. 4). These results show that there were no large differences in samara morphology within individual trees, but that across individuals there may be great differences. Nevertheless, some individuals had a broader spectrum of samara morphologies than others (see e.g. plant 2 versus plant 4 in Fig 4).

Dispersal capacity was also significantly different among the studied trees of *A. altissima* (MANOVA, $F_{18,660} = 23.76$, $p < 0.0005$, Wilks' lambda = 0.032). Further univariate ANOVAs tell us that individuals differ in the three types of dispersal (Table 5). These results suggest that different dispersal capacities are expected depending on the individual (Fig. 5).

4. Discussion

Our results suggest that wind dispersal as a primary vector and water dispersal as a secondary vector are positively correlated in *A. altissima.* Samaras with slower descent velocities also showed longer floating times. It has previously been reported that plants whose primary dispersal method is wind may also be effectively dispersed by water (Soomers et al., 2012). Our results showed such a positive relationship at the level of individual samaras within a single species. From an evolutionary standpoint, this positive relationship between wind and water dispersal suggests that there may be a selective pressure to simultaneously improve both dispersal potentials in some anemochorous species. This is further supported if we take into account that both kinds of dispersal are governed, at least in *A. altissima,* by similar morphological characteristics of the samaras.

Diaspore mass is negatively correlated to both kinds of dispersal, as reported for many wind- and water-dispersed species (Nilsson et al., 2010; Säumel and Kowarik, 2013). The greater the mass, the shorter the distance the diaspore will be able to fly (Greene and Johnson, 1993) and the faster it will sink in water. Diaspore mass has been reported to evolve quickly in wind-dispersed species (Cheptou et al., 2008), but there was a wide variation in this trait in the studied population of *A. altissima* (Table 1). These results suggest that there is not a strong selective pressure on diaspore mass to increase dispersal distance. Alternatively, variation in samara mass in the studied population could be the result of two counteracting selective pressures: 1) to reduce samara mass and, therefore, increase dispersal distance; and 2) to increase samara mass and produce heavier, more competitive seedlings (Delgado et al., 2009).

On the other hand, there was a positive correlation between descent and drifting velocities, suggesting a negative correlation between wind and water dispersal in moving water. This suggestion will need further research however, since in our study drifting velocities were inconsistent between repetitions, and the effects of side perimeter or length of the samara on this measure of dispersal were very weak. In addition, although side perimeter was positively related to wind dispersal and negatively to drifting velocity, it was also positively related to floating time, so there was not a consistent opposite effect of this variable on wind and water dispersal. Furthermore, in field conditions, the weak effect of side perimeter or samara length on drifting velocity might have little effect in determining water transport due to the combined effects of current, waves and wind (Wang et al., 2015). As a consequence, differences in dispersal could depend mainly on river characteristics (Säumel and Kowarik, 2013).

Samara width clearly affected dispersal via wind and water differently in *A. altissima*. Although it was one of the less important characteristics in determining both water and wind dispersal capabilities, it opens up a possibility for differentiation in dispersal

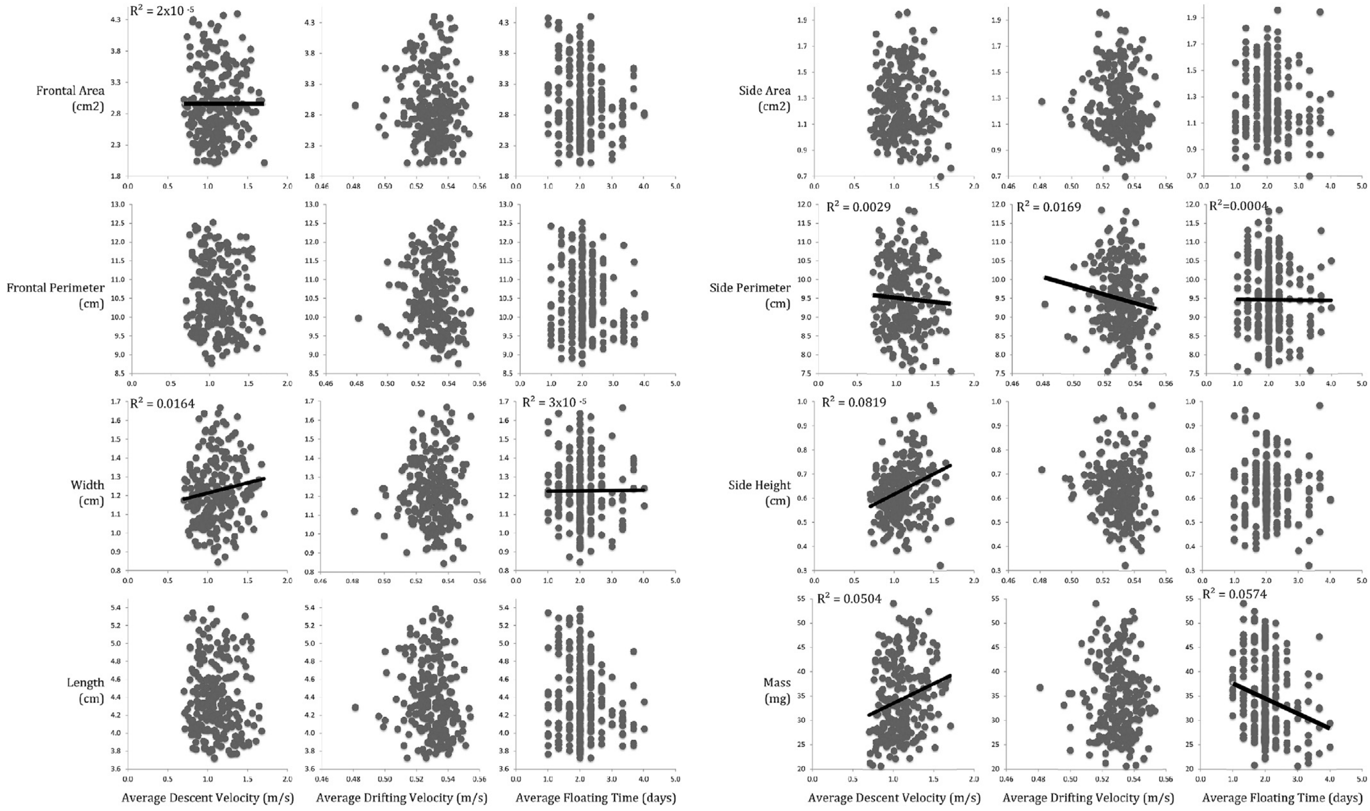

Fig. 3. Relationship between samara morphology and dispersal potential in *A. altissima*. Trendlines are shown for significant relationships (n = 242).

Table 3
Model selection showing which combinations of morphological traits best explain each samara dispersal variable. Models displayed are the ones with the lowest number of variables as long as their ΔAICc < 2.

Model	Predictors	AICc	Adjusted R^2[a]
Descent velocity			
A	1 5 6 7 8	−803.719	0.239
B	1 3 6 7 8	−803.574	0.239
Drifting velocity			
A	6	−2196.939	0.013
B	4	−2196.679	0.012
Floating time			
A	3 6 8	−284.417	0.130

Predictors: (1) frontal area; (2) frontal perimeter; (3) width; (4) length; (5) side area; (6) side perimeter; (7) side height; (8) mass.

[a] The adjusted R^2 values were calculated by means of ordinary least squares regression to better determine the predictive value of each model.

Table 4
Parameter estimates for the predictor variables included in the best models for descent velocity, drifting velocity and floating time.

Variable	Estimate	Standard error	Wald test	P
Descent velocity – Model A				
Intercept	1.367	0.147	86.53	<0.001
Frontal area	−0.139	0.033	17.81	<0.001
Side area	−0.134	0.059	5.10	0.024
Side perimeter	−0.069	0.021	11.31	0.001
Side height	0.471	0.115	16.82	<0.001
Mass	0.020	0.003	45.96	<0.001
Descent velocity – Model B				
Intercept	1.312	0.156	70.44	<0.001
Frontal area	−0.172	0.037	21.65	<0.001
Width	0.208	0.094	4.95	0.026
Side perimeter	−0.086	0.019	21.13	<0.001
Side height	0.371	0.103	12.99	<0.001
Mass	0.018	0.003	38.08	<0.001
Drifting velocity – Model A				
Intercept	0.544	0.007	5919.79	<0.001
Side perimeter	−0.002	0.001	4.15	0.042
Drifting velocity – Model B				
Intercept	0.544	0.007	57,040.60	<0.001
Length	−0.003	0.002	3.89	0.049
Floating time				
Intercept	0.823	0.434	3.59	0.058
Side perimeter	0.196	0.054	13.11	<0.001
Mass	−0.046	0.007	39.23	<0.001
Width	0.798	0.244	10.68	0.001

strategies: narrower samaras dispersing better by wind than by water. Therefore, samara morphology could suffer opposite selection pressures depending on the relevance of each dispersal mode in each habitat type (Venable, 1985).

It must be highlighted that, although several morphological characteristics were significantly related to dispersal capabilities in *A. altissima*, there was a large variability in all these cases (i.e. low R^2 values). In other words, every independent variable is a poor predictor of the dispersal capability of the samara. These results are surprising since morphological variables were, and still are, widely used as surrogates of seed dispersal capabilities in both interspecific (Hintze et al., 2013; Smith et al., 2015) and intraspecific comparisons (Bartle et al., 2013; Delgado et al., 2009). The use of diaspore characteristics to assess dispersal potential seems to be promoted because they are easily measurable traits rather than because they are highly correlated to dispersal (Hintze et al., 2013). Obtaining direct dispersal measures is an overwhelming task and thus beyond the scope of many studies, however, single characteristics should not be relied on when inferring dispersal capabilities from diaspore morphology. The simultaneous use of several

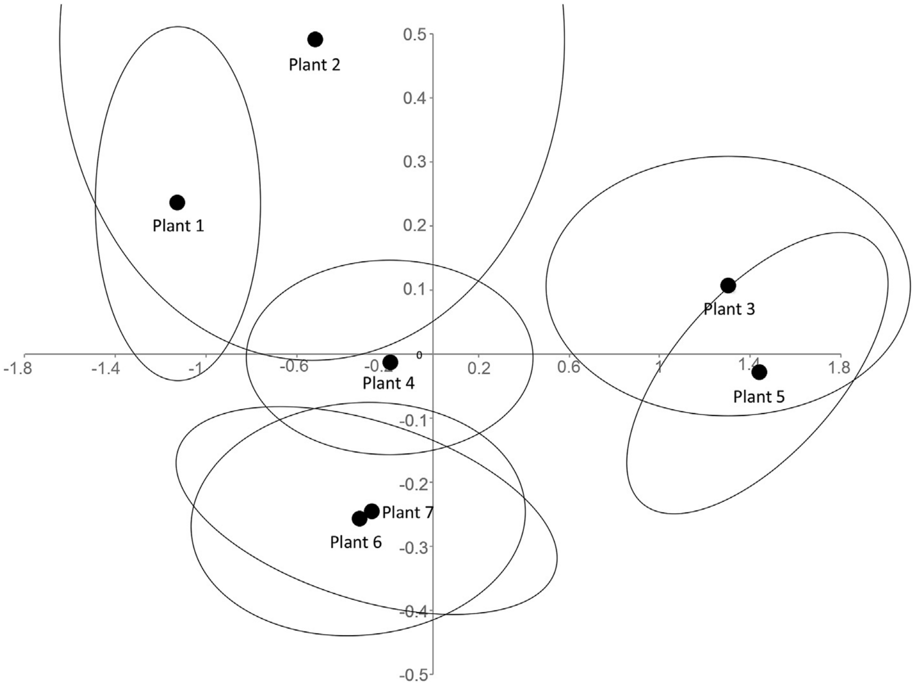

Fig. 4. Distribution of individual trees (and their 95% confidence ellipses) in the samara morphology space.

Table 5
Univariate ANOVA results for wind and water dispersal.

	p value	$F_{6,\ 235}$
Descent velocity	<0.0005	11
Drifting velocity	<0.0005	16
Floating time	<0.0005	5

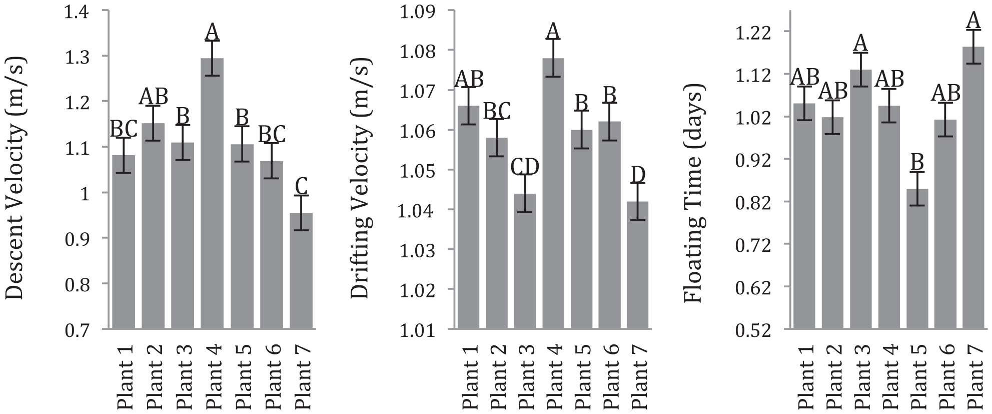

Fig. 5. Average values and standard deviations of descent velocity, drifting velocity and floating time per plant. Tukeys HSD's homogeneous plant subsets are ordered by descending mean values and labelled with letters. For all plants n = 40 except plants 2 and 3 (n = 19 and n = 23 respectively).

morphological characteristics substantially increased prediction power as shown in our results.

We found that individual plants under the same mesoclimatic conditions had different samara morphologies and consequently differed in their dispersal potential by wind and by water. In addition, strong differences in samara characteristics (area per unit of weight and total weight) have already been described for nearby stands of this plant, indicating that they differ in invasion potential (Delgado et al., 2009). This could be due to genetic or maternal environmental effects even in shared mesoclimatic conditions (Galloway, 2005; Mousseau and Fox, 1998). From the perspective of an invasive species, this broad spectrum of plant traits and dispersal capabilities might be beneficial as it could enable successful settlements in a wide range of habitats (Constán-Nava and Bonet, 2012; Williamson and Fitter, 1996).

In conclusion, our results suggest that primary wind dispersal and secondary water dispersal are usually positively correlated in *A. altissima* since most morphological characteristics of samaras affect both dispersal modes in the same way. Samaras with low mass and a large side perimeter had larger dispersal potentials both by wind and by water. The width of samaras in contrast affected the two types of dispersal in opposite ways, allowing differentiation in the dispersal strategies of this invasive species. Furthermore, variation in samara morphology within individuals of *A. altissima* was quite low, supporting the specialization of individuals in different dispersal modes. For instance, it could be suggested that *A. altissima* trees producing narrower samaras would be favoured if they occur close to water courses, whereas those producing wider samaras would be favoured in open areas or roadsides. To what extent variations in the morphology of samaras and, consequently, their dispersal capabilities could be due to adaptation to different environments could be an interesting topic for future research.

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