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Samara size versus dispersal and seedling establishment in *Ailanthus altissima* (Miller) Swingle

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Abstract: *We have specifically carried out a greenhouse experiment to assess relationship between samara weight and seed success. Relationship assessed as dispersal potential, germination level, germination rate and early seedling mass for the invasive species Ailanthus altissima. For this purpose, we considered two close stands as seeds source. We found no correlation between samara size and neither germination level, germination rate, nor seedling mass, but a positive correlation with samara projected area. These results suggest that samara weight is not directly related to germination, dispersal and invasion potential neither. Nevertheless, stands differed in the invasion potential of their samaras; one stand presented samaras with higher projected area per weight unit whereas the other one presented samaras that produced heavier seedlings. Whatever the origin, (genetic or environmental) of this differences it should be advantageous for a colonizing invader species such as A. altissima since it could imply a wider range of habitats susceptible to invasion.*

Key words: *Plant invader, Germination rate, Seed size, Seed viability, Seedling biomass*
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Introduction

Plant invasions are drastically altering natural habitats and threatening biodiversity at both local and global levels producing strong economic and environmental impacts (Elton, 1958; Vitousek *et al.*, 1997; Wilcove *et al.*, 1998; Pimentel *et al.*, 2000; Gaskin and Schaal, 2002; Tilki and Dirik, 2007).

Even at local scale, successful invasion should involve three phases: dispersal, establishment of a self-sustained population and later spread to nearby habitats (Williamson, 1996; Kolar and Lodge, 2001; Leung *et al.*, 2002). Initial dispersal and seedling establishment seem to be the more critical phase in plant invasions and most management efforts should be developed at that early time to minimise the establishment of the invader (Mills *et al.*, 1993; Hobbs and Humphries, 1995; Pimentel *et al.*, 2000; Leung *et al.*, 2002; Simberloff, 2003). So the study of variation in seed and seedling features related to dispersal and seedling establishment should be a priority to understand invasion capability of an exotic species.

The ability of invasive plants to compete and to proliferate can be caused by intrinsic factors such as physiological or reproductive capabilities often associated with weedy species (Baker, 1965). In this sense, *Ailanthus altissima* (Miller) Swingle is considered a "weed" tree because of its capabilities to grow rapidly and to reproduce by seeds, stump sprouts, and suckers (Brizicky, 1962). Thus, *A. altissima* is one of the most dangerous plant invasive species in Mediterranean Islands (Hulme, 2004). It is a species in the *Simaroubaceae* (Quassia Family) originating from China and wide spread throughout Europe, North America and Australia as an invasive plant (Knapp, 2000). Female trees produce pistillate flowers and fruits and male trees produce staminate flowers (Hu, 1979). Fruits are 2-5 cm long brown thin papery samaras, with one seed in the centre of each wing.

Seedling recruitment and establishment is linked to (i) the dispersion of seeds and (ii) the probability of seedlings' survival (Akashi, 1997; Rose and Poorter, 2003). Variability in seed size seems to be related to both phenomenons in different ways. On one hand, lighter seeds disperse further (Howe and Westley, 1986; Troumbis and Trabaud, 1986; Willson, 1992) and, on the other hand heavier ones produce larger, more competitive seedlings (Gross and Kromer, 1986; Andersson, 1990; Tripathi and Khan, 1990; Shipley and Parent, 1991; Leishman and Westoby, 1994; Rose and Poorter, 2003). Therefore, seed weight is a quite reliable measure of dispersal ability, and also could be related to seedling's establishment opportunities. Nevertheless, weight by itself is not the only variable related to dispersal syndromes and the size and shape of seeds should also be taken into account (Reichman, 1984; Imbert, 2002).

In this work, we have specifically assessed if samara weight in *A. altissima* is related to samara size, germination level, germination rate and seedling mass. Our aim was to assess if samara features could be related to invasion potential in this exotic species.

Materials and Methods

Study area and plant material: Field work was carried out in December 2005 in the experimental fields of Instituto Madrileno de Investigacion y Desarrollo Rural, Agrario y Alimentario (IMIDRA) research institute located close to the city of Alcala de Henares (Madrid, Central Spain) at 610 m over sea level. Climate is semi-arid, continental, Mediterranean with mean average temperature T=13.5^{o}C and average annual rainfall 426 mm. The soil, a loamy

Table - 1: Mean values (±S.E.) of fruit and germination features of studied *A. altissima* stands. Different letters in the same column indicate significant differences

	Samara weight (mg)	Samara projected area (cm^2)	Germination percentage	Germination time 50	Seedling weight (mg)
Stand 1	0.304 ± 0.009[a]	3.088 ± 0.078[a]	90.67 ± 1.87	20.33 ± 0.25	0.407 ± 0.008[b]
Stand 2	0.354 ± 0.010[b]	3.601 ± 0.074[b]	91.38 ± 1.79	20.61 ± 0.25	0.365 ± 0.007[a]

Table - 2: Results of ANCOVA analyses on germination variables using average samara weight as covariate and stand as factor. Analyses were performed on transformed variables. All interactions were not significant

	Stand	Samara weight
Total germination percentage	$F_{1,22}$=1.64; p=0.213	$F_{1,22}$=2.95; p=0.099
Germination time 50	$F_{1,22}$=0.24; p=0.632	$F_{1,22}$=4.18; p=0.053
Projected area	$F_{1,22}$=6.71; p=0.016	$F_{1,22}$=38.67; P<0.001

Table - 3: Results of ANCOVA analyses on seedling weight using samara weight and seedling age as covariates and stand as factor. Analyses were performed on transformed variables. All interactions were not significant

	Seedling weight
Stand	$F_{1,21}$=15.63; p<0.001
Samara weight	$F_{1,21}$=1.876; p=0.185
Seedling age	$F_{1,21}$=0.014; p=0.906

silt, could be considered a moderately drained, xeric, Calcic Luvisol (FAO, 1998). Natural vegetation has been completely replaced by crop fields interspersed with strips of spontaneous vegetation.

Two close stands (about 160 m apart from each other, no topographic grade between them) located at both roadsides of the highway towards Madrid were selected as a source of samaras. With these purpose, a total of 25 female individuals (ramets) of *A. altissima* were randomly selected from both stands. A sample of 12 ramets were selected from Stand-1 (UTM: 30T475185-4486682) and a sample of 13 from Stand-2 (UTM: 30T475129-4486558). From each ramet a set of at least 200 samaras were collected to obtain a fruit pool. From each individual fruit pool, a subset of 25 samaras was randomly selected. Each samara were weighted separately, labelled with an identification number, and scanned using a flat bed scanner. After this process, each group of samaras was stored in paper bags in a dry place.

The samara is an indehiscent fruit and previous attempts to separate samara wings from seed produced seed coat breaking and even seed damage very often. So we decided to perform germination experiments using intact samaras. This way, the germination results obtained should not be altered by seed manipulation, making also easier to infer explanations to natural germination scenarios. As a drawback, we were not able to obtain direct measurements of seed weight.

On the 8 of June 2006, the 625 stored samaras were individually sowed at a depth of 0.5 cm into 450 cm^3 pots filled with a 1:1 mixture of fertilized peat (N:P:K; 16:10:20) and vermiculite substrate. Pots were kept in a greenhouse under natural light and they were watered daily; every 3 days, pots were randomly rotated in order to avoid position effects.

Data and statistical analysis: From the obtained image, the projected area of every samara was calculated using the ImageJ 1.36b software (National Institute of Health, USA). The surface of the samara is positively related to dispersal ability, increasing flying time and, therefore, flying distances (Minami and Azuma, 2003).

In order to avoid pseudoreplication, each batch of 25 seeds from each parent plant was considered as an independent replicate. Both, average samara weight and average samara surface for each parent plant was calculated as the arithmetic mean of the corresponding values of each group of 25 selected samaras. Seedling emergence was recorded daily. Two indexes were calculated:

(i) Germination level was calculated as the final cumulative percentage of germination (Herranz *et al.,* 1998). There was no germination after day 28 of sowing.

(ii) Germination time 50 (*i.e.* number of days elapsed to reach 50% of the germination percentage) was calculated as an index to compare relative rate of germination (Travlos *et al.*, 2007).

To assess successful establishment of seedlings from each parent plant, early seedling mass was recorded as it has been reported that heavier seedlings are better competitors and present higher herbivore tolerance (Gross and Kromer, 1986; Tripathi and Khan, 1990; Armstrong and Westoby, 1993; Gomez, 2004; Stougaard and Xue, 2004). A sample of 375 randomly selected pots was harvested on day 38 after sowing, 10 days after germination finished. Whole seedlings (*i.e.* leaves, stem and roots) were oven dried and weighted. An averaged seedling mass per parent plant was calculated as the average dry weight of seedlings from the same parent plant contained in the sample (12-18 seedlings per plant). Seedling age (in days) was also recorded in order to correct for ontogenetic differences when comparing different aged seedlings in analysis.

Differences in average samara weight between stands were assessed using univariate analysis of variance. The relationship between average samara weight and germination level and germination time 50 were analysed by means of analysis of covariance (ANCOVA) using stand as factor and average samara weight as covariable. Because not only samara projected area, but also samara weight is related to potential seed dispersal, we performed an ANCOVA using stand as factor and seed mass as covariate in order to assess differences in dispersal ability. Since seedling weight could be related to both seed size and seedling age, the relationship between average samara weight and seedling mass were analysed using stand as factor and both average samara weight and average seedling age (in days) as covariables.

Seedling age and germination time 50 were log-transformed and germination percentage arcsine-transformed to achieve normality and variance homogeneity. No transformation was required for the rest of the variables.

Results and Discussion

Differences on samara weight between the two analyzed stands were significant ($F_{1,23}$=12.65; p=0.002; Table 1) with seeds from Stand-2 being 14% heavier than those from Stand-1. Despite of these differences in samara weight between stands, ANCOVA results showed no differences in germination variables (Table 2). Furthermore, samara weight was unrelated to neither germination level or germination time 50 (Table 2) in both stands. On the other hand, there were differences in seedling mass between stands (Table 2), with those from Stand-1 achieving higher weight at harvest time in spite of its lighter samaras (Table 1). Furthermore, ANCOVA results show that seedling weight was unrelated to samara weight (Table 3). Finally, there were also differences in samara projected areas between stands (Table 2); although a positive correlation between samara mass and projected area existed, those from stand-2 presented proportionally wider wings (Fig. 1).

In the present study we were interested in correlations between samara features and invasion potential in *A. altissima*. We focused on the relationship between samara weight and seed success measured as dispersal ability, germination level, germination rate and seedling weight using samaras from two stands. Our results have shown that both stands differed in samara weight and that differences also exist in variables related to seed success such as seedling establishment and potential dispersal ability. Nevertheless, all relationships presented the same intensity in both stands (*i.e.* there were no interactions between stand and samara size).

We found no positive correlation between samara size and neither germination level, germination rate, nor seedling size. Positive relationships between seed size and seed fitness within a species have been reported often, mainly through correlations with seed germination and seedling survival (bigger seeds and seedlings growing from having a better performance, see *e.g.* Gross and Kromer, 1986; Andersson, 1990; Tripathi and Kahn, 1990; Shipley and Parent, 1991; Leishman and Westoby, 1994; Eriksson, 1999). Nevertheless, such pattern not always has been found because it is modulated by environmental conditions. For instance, several authors have shown that heavier seeds are only advantageous under competitive or harsh environments (Kalisz, 1989; Capuccino *et al.*, 2002). So, the lack of correlation between samara size and seed success found in our study, could be explained because seeds were subjected to optimal conditions in the greenhouse.

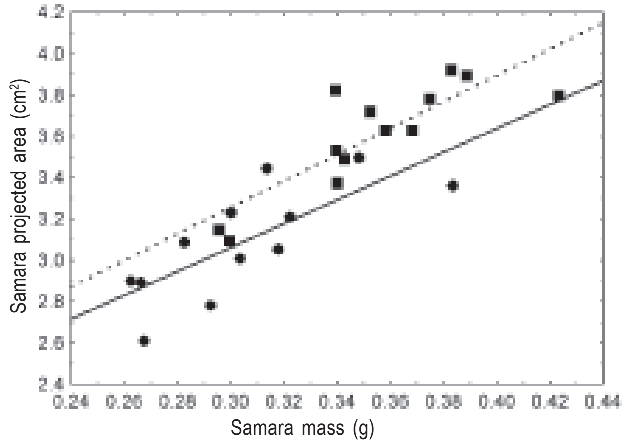

Fig. 1: Relationship between samara weight and seedling weight in the two studied stands. Stand-1 circles, solid line, Stand-2 quadrats, dashed line

On the other hand, there was a positive correlation between samara weight and samara size, suggesting that heavier samaras presented also wider wings maintaining dispersal ability throughout the whole seed range. In other words, there was no variation of weight/area ratio and therefore no differences in dispersal ability related to samara size. Nevertheless, there were differences between stands implying proportionally wider wings for one of the stands, which also produced significantly lighter seedlings.

Differences in seed dispersal and seedling weight between the two stands reported in this study suggest the existence of different reproductive strategies in *A. altissima* 1) plants producing samaras with higher dispersal potential, and 2) plants producing samaras that originate larger, more competitive seedlings. Differences between the two stands could be related to both genetic differences and maternal environmental effects, in spite of being located quite close and sharing mesoclimatic conditions (Galloway, 2005; Mousseau and Fox, 1998).

Independently of the origin (genetic or environmental) of these differences, they represent different extremes of the same continuum established through the existing trade off between seed dispersal and seedling establishment (Morse and Schmitt, 1985; Ezoe, 1998; Capuccino *et al.*, 2002) (i) higher dispersal ability but lower establishment success and (ii) lower dispersal distance but high competitive seedlings with increased establishment probability. From the perspective of a colonizing invader species such as *A. altissima*, it should be likely adaptive, generating a wider range of habitats susceptible to invasion. This set of habitats will comprise those recently disturbed patches with low competitors located at longer distances from mature established stands, and those closer patches colonized yet by competitors. The relative contribution of each strategy in the propagation of this species through an ecosystem would not be homogeneous but dependent on the spatial distribution of suitable patches and the existence or not of corridors connecting them. This could be especially relevant in the case of *A. altissima* due to its distribution pattern along roads, railways and streams (Merrian, 2003; Hulme, 2004) which are well known functional corridors (Parendes and Jones, 2000; Tikka *et al.*, 2001; Auld *et al.*, 2003; Christen and Matlack, 2006; Thomas *et al.*, 2006).

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