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Research Article

Does stream structure affect dispersal by water? A case study of the invasive tree *Ailanthus altissima* in Spain

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Abstract

Riparian zones are highly susceptible to invasion by alien plants. For both invasive and non-invasive plants, water has been proved to be an important vector for seed dispersal, connecting distant populations and, therefore, contributing to the downstream expansion of invaders. However, the effect of intrinsic factors of watercourses, such as habitat quality, on the invaders' dispersal ability is largely unknown. We compared the dispersal ability of *Ailanthus altissima* fruits through a release experiment in two contrasting 100 m-long stretches of a near-natural and a degraded reach of the same river. One hundred fruits were released in the centre of the channel and allowed to float during 90 minutes. Results showed that fruit retention was five times lower in the degraded reach, suggesting that the loss of complexity in the fluvial habitat structure may increase dispersal distances of *A. altissima* fruits in headwater streams of similar characteristics. The lack of potential depositional zones, such as pools, meanders, or biological structures in the degraded reach increased the water dispersal success of *A. altissima* fruits. Among the studied retentive structures, macrophytes were found to be the main natural barrier to limit dispersal of *A. altissima* fruits. Velocities of dispersed fruits were highly variable within each reach but did not depend on the habitat quality. This study provides reasons to consider the heterogeneity and complexity of riparian and fluvial habitat to control the dispersion of fruits of the invasive tree *A. altissima*.

Key words: tree of heaven, hydromorphological quality, invasive species, riparian ecosystems, hydrochory

Introduction

Riparian ecosystems have been the focus of intense human activity for many centuries (Washitani 2001). Consequently, many have been highly degraded (Holmes et al. 2005; Richardson et al. 2007). Currently, these ecosystems are recognized as highly prone to invasion by alien plants (Müller and Okuda 1998; Chytrý et al. 2008; Eschtruth and Battles 2011). According to the resource fluctuation hypothesis, disturbances make available resource pulses that allow niches to be temporarily exploited by alien plants (Davis et al. 2000). Also the absence of environmental stressful conditions (e.g. pronounced drought or low nutrient availability) and the higher propagule pressure resulting from intense human activity in floodplains, may explain the high degree of invasion of these ecosystems (Kolar and Lodge 2001; Chytrý et al. 2008).

Water is an important downstream dispersal agent of propagules (Pyšek and Prach 1995). Rivers can transport millions of propagules and deposit them hundreds of kilometres away from their sources (Merritt and Wohl 2006). Thus, riparian habitats can act as 'conveyor belts' for propagules (Richardson et. al 2007), and implies they might be important corridors for seed dispersal, both for native and alien species (Pyšek and Prach 1995; Stohlgren et al. 1998).

Many alien species spread along watercourses (Richardson et al. 2000), and their invasion success largely depends on their dispersal ability (Pyšek and Prach 1995). *Ailanthus altissima* (Mill.) Swingle (tree of heaven) (Simaroubaceae) is a wind-dispersed tree that has been long recognized as a very aggressive invader in different regions (Kowarik and Säumel 2007), including riparian zones (Müller and Okuda 1998). This species is in the list of the 100 worst aliens in Europe (DAISIE

Figure 1. Degraded reach, in Sigüenza (A) and near-natural reach, in Baides (B) of the Henares river in Guadalajara province, Spain, as study sites. Photographs by Isabel Cabra Rivas.

European Invasive Alien Species Gateway 2012). In Spain, it naturalizes in almost every temperate region, grows in thick stands, quickly expands its populations, and displaces native vegetation (Sanz-Elorza et al. 2004; Constán-Nava et al. 2008). Although wind-dispersed *A. altissima* fruits may reach distances further than 100 m away from their source (Portnoy and Willson 1993; Kota 2005; Landenberger et al. 2007), Landerberger et al. (2007) found very low densities of seeds 50 m away from the source. Accordingly, Cho and Lee (2002) found that 75% of *A. ailanthus* seedlings appeared within the first 20 m of the parent tree. Nevertheless, long-distance dispersal events also happen, leading to population spread and to colonization of new habitats (Nathan et al. 2008). Previous studies suggested that water may be an important and effective fruit dispersal agent, allowing *A. altissima* fruits to be dispersed through longer distances, even kilometres (Kaproth and McGraw 2008; Säumel and Kowarik 2010; Säumel and Kowarik 2013). Except for a recent study (Säumel and Kowarik 2013), most experiments on seed dispersal by water have focused on large channelized rivers (Kowarik and Säumel 2008; Säumel and Kowarik 2010), where the chances of a fruit being intercepted by retentive structures could be lower than in small or non-channelized rivers. Moreover, the dispersal efficiency of small rivers may be largely influenced by the heterogeneity and complexity of both the river and the riversides. Different hydromorphological properties defining the ecological quality of rivers and riversides (e.g. aquatic and terrestrial vegetation cover and structure, substrate composition, frequency of pools and riffles, etc) may affect the process of fruit transport/deposition, therefore affecting invasion processes by exotic riparian plants. Understanding how these properties affect fruit dispersal of exotic trees may help to plan effective measures to prevent invasions along rivers and floodplains.

This study aims to assess the effects of riparian and fluvial habitat heterogeneity and complexity on the dispersal of fruits of the invasive tree *A. altissima* by water. Specifically we address the following questions: 1) Are small streams good dispersal agents of *A. altissima* fruits? 2) Does the stream and riparian habitat complexity and heterogeneity (hydromorphological quality) affect the success of *A. altissima* hydrochorous dispersal? 3) What particular structures are involved in the retention of *A. altissima* fruits when dispersed by flowing water? We hypothesize that near-natural streams will reduce the downstream transport of *A. altissima* fruits, as their higher heterogeneity would provide more retention structures. This knowledge can be applied when trying to mitigate the colonization of downstream habitats by this alien species.

Materials and methods

Study area

The study area was located in the Mediterranean Region, in the centre of the Iberian Peninsula, Guadalajara Province (Spain), within the Henares

River basin (Figure 1). In this region, the hydromorphological quality has been shown to be deficient to moderate in 82% of the surveys (MAGRAMA 2012). We selected two headwater second-order reaches (according to Strahler 1964) of the Henares River, 17 km apart, with 3–12% slopes and contrasting complexity and heterogeneity of fluvial and riparian structure. The upper reach, located in Sigüenza (41º04'33"N, 2º37'50"W, 990 m.a.s.l.), exhibited a poor hydromorphological quality. This degraded reach underwent a rectification process (removal of meanders to expand arable and grazing lands) and lacks of pools and riffles. Due to agricultural and grazing uses, riparian vegetation was removed, with only a narrow linear strip 1m wide of *Populus* spp. remaining. The riverbed was mainly constituted of fine sediment (<2 mm). The lower reach, located in Baides (41º00'13"N, 2º45'50"W, 860 m.a.s.l.), was considered as a reach of high hydromorphological quality. This was a free-flowing sinuous reach, with an alternation of riffles and pools and covered by a riparian forest canopy, dominated by *Populus* spp and *Fraxinus angustifolia*. Fine-grained sediments prevailed over gravel and boulders in the riverbed.

Experimental design

We collected ripened fruits from five mature *Ailanthus altissima* trees in Alcalá de Henares (Madrid, Spain) during October - November 2010 and let them dry at ambient temperature in the laboratory. Fruits had a mean length (±SD) of 4.5±0.3 mm (n=100), a mean dry weight of 0.038±0.007 g (n=750), and a mean area of 3.42± 0.21 cm^2 (n=100). We spray-painted (Pinty Plus Basic, Novasol Spray, Spain) sets of 100 fruits in bright colours (pink, orange, and red) in order to facilitate their subsequent location in the river. Other studies found no effect of tagging fruits with spray paint on their floating ability (Kaproth and McGraw 2008; Säumel and Kowarik 2010; Säumel and Kowarik 2013).

A fruit release experiment was conducted in a 100 m-long stretch of the near-natural and degraded reaches. Near-natural and degraded reaches were divided into 10 sections of 10 m long each. We released 100 fruits from the inner channel, in the upper part of the reach and allowed them to float during 90 minutes. During this time, two observers, situated 100 m downstream of the releasing point, collected all fruits arriving at this point (referred to as *non-retained fruits* hereafter) by means of a hand net and registered their arrival time. Afterwards, the two observers walked up the 100 m stretch searching for retained fruits. Distance from the releasing point and properties of the retentive sites (see below) were recorded for all the retrieved fruits (3 to 23% of the released fruits were not retrieved). This protocol was repeated three times for each reach (15th, 16th and 18th February 2011, no change of river discharge occurred between these dates). See Table 1 for details on river characteristics. Overall, 300 seeds (100 per colour) were released in each reach.

Measured variables

We used the River Habitat Index (IHF) and the Riparian Quality Index (QBR) to assess the hydromorphological quality of each reach. These are the two hydromorphological indices currently used in Spain to assess the ecological status of rivers in accordance with the European Water Framework Directive. These indices (ranging from 0-100) take into account all the characteristics that reflect habitat quality (see Appendix 1 in Supporting Information). Categories of IHF classify river habitats within a gradient from "very low habitat diversity" (scores under 30) to "very high habitat diversity" (≥90). QBR index classifies riparian habitat quality from terrible status (scores <25) to natural status (>95). For more details see Jáimez-Cuéllar et al. (2002). To estimate water velocity and the discharge in each reach, three parallel transversal transects were set out per reach prior to fruit release. Ten measurements were taken per transect with a water velocitymeter (Series P 600, DOSTMANN electronic GmbH, Wertheim) at approximately 1/3 of the section depth (Förch meter) (Table 1). Water velocity was estimated as the mean velocity of the 30 measures per reach. Dispersal velocity (m/s) of non-retained fruits was calculated by dividing the reach length (100 m) by the time elapsed to cover that distance.

Sites where fruits were retained were characterised on the basis of the following properties: (i) position within the channel (shore vs. centre), (ii) morphological unit (riffle-zone with turbulences vs. pool zone without turbulences), (iii) position within the water column (submerged vs. floating) and (iv) retentive structure (e.g. macrophytes, logs, branches, twigs diameter < 0.5 cm, stones, woody roots, non-woody roots, or leaf litter).

Data analysis

Analyses conducted only considered retrieved fruits (including those retained in the 100 m stretch and those exceeding this distance). The percentage of non-retained fruits and water velocity were compared between reaches by means of a Student's t-test (data fulfilled test assumptions of normality (Shapiro-Wilk) and homocedasticity (Bartlett test)), while dispersal velocity of non-retained fruits was compared by means of a Wilcoxon test. The proportion of fruits retained in different structures (macrophytes/ logs/ branches/ twigs/ stones/ woody roots/ non-woody roots/ leaf litter) was compared separately for each reach with a Kruskal-Wallis test. The degree of association of the major retentive structure with morphological units (riffles vs.pools) was tested using a Fisher's exact test. Finally, to make predictions about the fate of the fruits, we compared i) the position of retained fruits in the water column (floating vs. submerged) and ii) the position of retained fruits (shore vs. centre of the channel) between reaches by means of a Wilcoxon test. All statistical analyses were carried out with R 12.15.1 (R Foundation for Statistical Computing, Vienna, Austria).

Results

Dispersal efficiency (percentage of fruits moved to the end of the 100 m-reach) of *A. altissima* fruits differed between reaches; with the percentage of fruits that travelled at least 100 m being five times greater in the degraded than in the near-natural reach (t=-9.051; P<0.01) (Figure 2). Mean dispersal distance of retained fruits was not significantly different between reaches (28.2±14.5 m and 26.9±5.4 m in the near-natural and in the degraded reach respectively). In the near-natural reach, 89.3%±0.2 of the retained fruits were recovered in two sections (0-10 m and 70-80 m) that corresponded with the locations of the largest pools.

Mean water velocity was two times higher in the near-natural reach (0.5 m/s) (t=4.03, P<0.001). However, fruit transport velocity of non-retained fruits did not differ between reaches (0.26±0.16 and 0.21±0.17 m/s for degraded and the near-natural reach respectively, W= 422.5; P>0.05). The first fruit arriving at the end of the reach spent less than 4 minutes covering 100 m (41.67 cm/s), whereas the last fruit to appear spent more than 70 minutes (<2.38 cm/s).

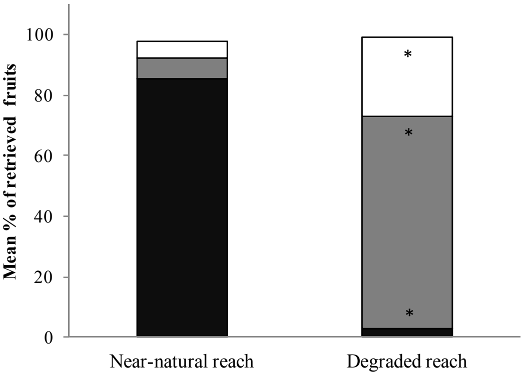

Figure 2. Mean percentage of retained and non-retained (white) fruits in the degraded reach and near-natural reach. Retained fruits are expressed as mean percentage of fruits retained in the centre (grey) or on the shore (black) of the reach. Asterisks indicate significant differences (P<0.05) between reaches (n=3).

In the degraded reach, only three types of structures (macrophytes, branches, and twigs) retained *A. altissima* fruits. Although the near-natural reach had eight different retentive structures, macrophytes, branches, and twigs retained most of the recovered fruits also (Table 2). Rooted macrophytes trapped the most fruits, among all the studied structures, in both the near-natural ($\chi^2_{(7)}$ = 15.41, P<0.05) and the degraded reach ($\chi^2_{(2)}$ = 7.2, P<0.05). In the near-natural reach, macrophytes were positively associated with pools (P<0.001), as 93.2%±4.5 of the fruits retained in macrophytes were also retained in pools. Fruits were rapidly trapped (several minutes) and exceptionally remobilized in these macrophyte-dominated pools. Fruits in the degraded reach were retained in the centre of the channel which aided their ability to float downstream relatively unobstructed (96%±3), whereas in the near-natural reach, fruits were mainly trapped in the channel margins (92%±14) (Figure 2). More than two thirds of the fruits remained on the water surface, regardless of the reach hydromorphological quality (W=6.0; P>0.05).

Discussion

Hydrochory has been shown to play a major role in transporting and depositing seeds along river corridors (Merrit and Wolk 2002; Boedeltje et al. 2003; Vogt et al. 2004; Truscott et al. 2006). We have found that small rivers or streams can also transport *A. altissima* fruits over distances longer than 100 m, in accordance with what Säumel and

Table 1. Location, physical fluvial and riparian status (IHF and QBR), and physical properties of the degraded and near-natural reaches including mean wetted channel width (MWCW), mean channel depth (MCD), mean water velocity (MWV), and mean discharge (MD) are shown as mean (±SD) for N = 3.

Reach	Location	IHF	QBR	MWCW (m)	MCD (cm)	MCV (m s^{-1})	MD (m^3 s^{-1})
Degraded	Sigüenza	42	10	3.3±0.44	41.5±0.36	0.24±0.03	0.41±0.17
Near-natural	Baides	81	90	4.1±0.78	35.7±14.6	0.50±0.16	0.66±0.23

Table 2. Mean percentages of fruits (±SD) trapped by various retentive structures in the study streams for a total number of 232 fruits in the degraded reach and 290 fruits in the near-natural reach (N = 3 replicates).

	Macrophytes	Logs	Branches	Twigs	Stones	Woody roots	Non-woody roots	Leaf Litter
Degraded reach	68.5 (± 10.5)	-	8.78 (±8.30)	24.1 (±5.93)	-	-	-	-
Near-natural reach	68 (±9.3)	3.2 (±2.0)	11.6 (±8.7)	13.0 (±11.8)	1.0 (±0.8)	1.9 (±0.8)	1.8 (±1.6)	0.5(±0.8)

Kowarik (2013) found in a river with a similar width in Berlin. We also found a high influence of the hydromorphological quality on the dispersal process. Our results support the hypothesis that, in headwater streams, a poor hydromorphological quality enhances the hydrochorous dispersal of *A. altissima* fruits. Indeed, the likelihood of *A. altissima* fruits being moved over distances longer than 100 m is five times higher in the degraded system than in the near-natural reach. This can be attributed to the low within-channel heterogeneity of the former, which was characterized by a scarcity of pools and low riparian and aquatic vegetation cover which lead to a decrease in the presence of structures acting as barriers for seed dispersal (i.e. logs, branches, exposed roots, etc).

Literature shows that water, as a secondary dispersal mechanism, may transport wind-dispersed propagules at greater distances than wind (Imbert and Lefèvre 2003; Säumel and Kowarik 2010). *A. altissima* fruits can be transported several kilometres downstream by large rivers (Kaproth and McGraw 2008; Säumel and Kowarik 2010). In our study, performed in a small headwater river with high hydromorphological quality, less than 25% of the fruits dispersed further than 100 m, resembling the distances reported for wind-dispersed *A. altissima* fruits (Kota 2005; Landenberger et al. 2007). However, these results contrast with other studies (Säumel and Kowarik 2013) where nearly 40% of the fruits were transported at least 1200 m in a similar river. This disparity suggests that the transport distance by hydrochory depends on other factors apart from the magnitude of the river. Differences concerning heterogeneity of fluvial and riparian habitat between their study system and ours could be behind these contrasting results, but, unfortunately, Säumel and Kowarik (2013) did not describe the hydromorphological characteristics of their rivers. Even if fruits had been observed for longer (>90 minutes), we would not expect many more of them to be transported further than 100 m in our study systems, as most were efficiently trapped soon after release. Nevertheless, a higher discharge flow, instead of an increase in observing time, could be a more determinant factor that would enhance fruit remobilization after being trapped, contributing to longer transport distances and likely would increase the contrast between the degraded and near-natural reach.

In the near-natural reach, fruits were deposited along the outer side of channel meanders. By contrast, in the straight channel of the degraded reach, the centre of the stream was the main depositional zone. In both cases, water velocity was low as pools and macrophytes slowed down water velocity. Other studies have highlighted the contribution of channel structures (Bilby and Likens 1980) and channel morphology (Gomi et al. 2002) to the retentive capacity of rivers (Engström et al. 2009). Pools are considered to have greater retention capacity due to deeper water and the lower water velocity (Prochazka et al. 1991). Macrophytes, strongly associated with pools in the well preserved reach, showed the highest retention of *A. altissima* fruits. This is due to the ability of the macrophytes to trap the fruits in their structures but also to the indirect effect of the macrophytes decreasing the water velocity (Horvath 2004; Rodriguez-Barrios and Ospina 2007). In reaches with a low cover of riparian vegetation, and consequently, lower chances of biological structures (e.g. logs, branches, leaf litter) falling into the channel acting as seed traps, macrophytes from the channel can be an important element (Friedman and Lee 2002) and play a key role in the structure and functioning of reaches (Barrat-Segretain 1996). Given the importance of channel complexity in propagule dispersal (Engström et al. 2009), our study suggests that the presence of macrophytes may limit dispersal of *A. altissima* fruits, especially in degraded rivers lacking pools.

Water streams may disperse both asexual and sexual propagules of *A. altissima* (Kowarik and Säumel 2007). While asexual propagation is useful to quickly increase the local abundance of a population, seed dispersal allows the species to spread over longer distances, especially by water. Moreover, *A. altissima* fruits have been found to remain viable after floating in water or being submerged for five months (Kaproth and McGraw 2008; Kowarik and Säumel 2008). Thus, hydrochory increases the chances for successful recruitment in new downstream locations, far from the initial focus of invasion. For a terrestrial plant, such as *A. altissima*, the possibility of water dispersal means that this species has the advantage of a rapid spread. Nevertheless, *A. altissima* fruits retained in river structures need to be able to reach available, safe microsites in the floodplain in order to germinate. High discharges that may increase flow rates could increase the chances for floating fruits to reach available microenvironments with suitable conditions for germination and establishment (i.e. canopy gaps or highly disturbed forests) (Kota 2005; Kota et al. 2007), even along rivers and floodplains (Stromberg and Chew 2002; Merriam 2003).

The poor hydromorphological quality of the river may also increase the chances of any plant dispersing downstream. However, *A. altissima* is known to outcompete native species for space or resources under certain environmental conditions (Kowarik 1995; Knapp and Canham 2000). Given the high number of seeds produced by this species (Bory and Clair-Maczulajtys 1980) and their high germination rates in disturbed environments (Kota et al. 2007), it is likely that *A. altissima* will become a successful invader in downstream open areas (Kowarik 1995; Kaproth and McGraw 2008). This poses a possible threat to disturbed native forests downstream of existing *A. altissima* populations and highlights the importance of maintaining a minimum degree of fluvial habitat complexity as a preventive action to avoid further undesirable *A. altissima* spread. Special care should be taken concerning the non-invaded open forests downstream of invaded sites, as they may be favorable sites for propagule deposition and establishment of this alien plant.

Conclusions

Our study has shown that headwater streams can contribute to long distance dispersal of *A. altissima* fruits. The naturalness of riparian and fluvial habitats plays an important role in the dispersal of *A. altissima* fruits. Poor hydromorphological quality may enhance the transport of fruits downstream. For most invasive species, eradication is not affordable, so maintaining fluvial ecosystems in a near-natural status may became an alternative to decrease the spread of *A. altissima* and other exotics.

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Appendix 1. Hydromorphological indexes applied to assess the conservation status of the studied streams, detailing the factors they account for and the quality categories corresponding to different indexes scores.

	Index	
	IHF (River Habitat Index)	**QBR** (Riparian Quality Index)
Assessed factors	Sedimentation in pools Riffles frequency Substrate composition Velocity and depth regimes Heterogeneity elements in the channel bed Channel shade percentage Aquatic vegetation cover	Channel naturalness Extent of the riparian vegetation cover Structure of the riparian vegetation cover Quality of the riparian vegetation cover
Index Ranges and Quality Categories	≥90: Very high habitat diversity 70-89: High habitat diversity 50-69: Mid habitat diversity 30-49: Low habitat diversity < 30: Very low habitat diversity	>95: natural status 95-75: good quality 70-55: acceptable quality 50-30: bad quality <25: terrible status