Seed Viability and Dispersal of the Wind-Dispersed Invasive *Ailanthus altissima* in Aqueous Environments

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Abstract: In mesic forest environments, seeds of wind-dispersed plant species may frequently be deposited in aqueous environments (e.g., lakes and rivers). The consequences of deposition in an aqueous medium depend on whether seed viability is maintained. If seeds survive there, secondary dispersal in water may transport seeds long distances to suitable habitats. Using the exotic species, tree-of-heaven (*Ailanthus altissima* [Mill.] Swingle), in this study we estimated seed dispersal into water as a function of distance and experimentally tested seed buoyancy, secondary dispersal, and germinability after dispersal in water and on land. We found that biologically significant numbers of seeds disperse directly into water, remain buoyant, and are transported long distances by water. Germination rates for seeds that were kept in aqueous environments (Cheat Lake and the Monongahela River, near Morgantown, WV) were found to be similar to or higher than those in nearby terrestrial controls ($F = 10.94$, $P = 0.0057$). Seeds kept in aqueous environments retained high germination rates (94.4 ± 1.1%) even after 5 months. Although *A. altissima* may not disperse primarily through water environments, this study suggests that secondary dispersal by water is possible and may allow for long-distance dispersal more than two orders of magnitude farther than recorded primary dispersal. FOR. SCI. 54(5):490–496.

Keywords: hydrochory, secondary dispersal, long-distance dispersal, seed cage

THE LOW OBSERVED RATES of plant dispersal are insufficient to explain historical migration rates (Reid 1899, Skellman 1951, Clark et al. 1998). Many studies have investigated dispersal distances and suggest that the rapid rates of spread, often observed in invasive species, may require rare long-distance dispersal events (e.g., Ritchie and MacDonald 1986, Lonsdale 1993, Cain et al. 1998), but these events are difficult to observe (Clark 1998, Higgins and Richardson 1999). The inability to accurately sample and subsequently predict how a species will disperse into and colonize new environments has hampered the parameterization of migration rate modeling in a constantly disturbed and dynamic environment (Higgins and Richardson 1999).

How a community responds to disturbance (e.g., flooding, logging) depends largely on what species arrive and colonize the open niches (Grubb 1977, He and Mladenoff 1999, Lockwood et al. 2005). The "regeneration niche" concept posits that early-established species have a greater chance to preempt resources than species establishing at a later time (Belyea and Lancaster 1999). Understanding the ability of a species to disperse to these open environments becomes essential, and in many cases species with long dispersal distance and high propagule pressure will have the greatest opportunity for establishment (Lockwood et al. 2005). Species with these characteristics, many of which are invasive, are increasingly being recognized as a threat to biodiversity (Rejmánek and Richardson 1996, Mack et al. 2000), and the prevalence of invasive species in disturbed environments continues to grow at alarming rates (Higgins et al. 1999, Parendes and Jones 2000, Hutchinson et al. 2004). Many invasive species such as the widespread terrestrial tree, tree-of-heaven (*Ailanthus altissima* [Mill.] Swingle), are poised to expand into new locations throughout the United States (Kota 2005, Kota et al. 2007, Landenberger et al. 2007). The ability to predict where and how quickly the establishment of an invasive species will occur can improve the effectiveness of conservation management (Mack et al. 2000, Rejmánek 2000) but requires quantification of the dispersal tail (Bullock and Clarke 2000).

The difficulty of quantifying long-distance dispersal empirically is twofold: the frequency of long-distance dispersal is low (Bullock and Clarke 2000, Clark et al. 2005, Landenberger et al. 2007) and the mechanism of dispersal may not be the obvious "primary " mode (Pakeman 2001). Multiple studies have shown that seeds can be dispersed by more than one mechanism (e.g., Darwin 1859, Welch 1985, Myers et al. 2004, Couvreur et al. 2005). Rather than being the exception, this polychory has been shown to be the rule in some plant communities (Ozinga et al. 2004). Each secondary dispersal mechanism such as animals (both internal and external) and water provides greater opportunity for long-distance dispersal events as suggested by Hampe (2004) in a dispersal study of glossy buckthorn (*Frangula alnus*), in which propagules dispersed by frugivorous birds were unidirectionally re-dispersed by hydrochory.

Hydrochory has long been proposed as an important mechanism explaining the global distribution of plants (Darwin 1856). However, limited experimental work has been published on dispersion in aquatic environments

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(Barrat-Segretain 1996, Andersson and Nilsson 2002, Boedeltje et al. 2003, Truscott et al. 2006). Water could be an important vector because it flows long distances in a single season via connected corridors and can carry debris with little friction (Vogt et al. 2004). Seeds accumulate in aqueous environments through primary dispersal directly into water or by secondary movement spurred by animals, wind, or rain wash, often assisted by gravity. In essence, for hydrochory to occur, three conditions must be met: seeds must be able to reach water; seeds must retain viability while in the water; and seeds must be able to be deposited in a suitable habitat.

This study focuses on whether the conditions of hydrochory occur for *A. altissima*, an invasive terrestrial "wind-dispersed" species. We hypothesized that the first two requirements of hydrochory occur at measurable levels and assume that, if these requirements are met, on at least some occasions the third will also be met, i.e., seeds will occasionally be deposited (e.g., by flooding events) in suitable habitat, increasing the frequency of long-distance dispersal for this species.

Methods

Study Species and Area

A. altissima grows rapidly in a wide variety of environments in the eastern United States (Feret 1985), limited primarily by shade intolerance, low water availability, and severe cold temperatures (Feret 1985, Kowarik and Säumel 2007). Copious amounts of seeds borne by mature females ripen, desiccate, and start to disperse starting in September (Kaproth 2008). Desiccated seeds used for the following experiments were collected from four populations in Monongalia County, WV, mixed, and kept at room temperature. Previous work has shown that there was no difference in germination rate in terrestrial environments between maternal seed sources (Kota et al. 2007).

Investigations of *A. altissima* hydrochory occurred at two study sites, one located in and along the Monongahela River neighboring the Core Arboretum of Morgantown, WV (39°38′31″N and −79°58′37″W at an elevation of 238 m), and the other 10 km to the northeast in and along the river-fed impoundment of Cheat Lake, WV (39°38′53″N and −79°58′41″W at an elevation of 271 m). Temperatures of both water bodies ranged from 1 to 19°C during November to April 2006, although Cheat Lake water temperature averaged 1°C lower than that of the Monongahela River, 5 and 6°C, respectively. Mean low monthly air temperatures for Morgantown, WV, range from −6 to 4°C during November to April and are 3°C lower at Cheat Lake, WV (J.B. McGraw, personal observation, 2006).

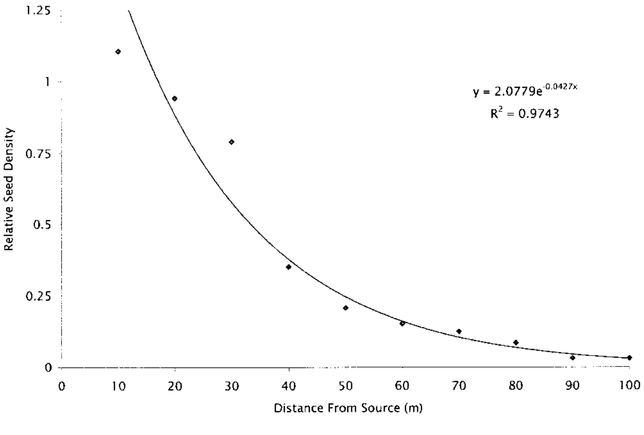

Figure 1. Log-linear curve fit to observed primary dispersal of *A. altissima*, relative to densities found at parent (0 m) to 100 m in an open field environment. Adapted from Landenberger et al. 2007.

Estimating Direct Primary Dispersal into Nearby Water

Knowing the primary seed dispersal curve function of *A. altissima* derived from a log-linear curve fit of the well-characterized primary dispersal curve out to 100 m (Landenberger et al. 2007) (Figure 1), we estimated the expected proportion of seeds landing directly in water as a function of distance from the water's edge:

$$\frac{2\left[\displaystyle\int_{\theta=0}^{\theta=\cos^{-1}(d/100)}\int_{r=d/\cos\theta}^{r=100}\frac{2.0079e^{-0.0427r}}{2\pi r}\,r\,\mathrm{d}r\,\mathrm{d}\theta\right]}{\displaystyle\int_{r=0}^{r=100}2.0779e^{-0.0427r}\,\mathrm{d}r}. \quad (1)$$

In the calculation of this estimate (Equation 1), cylindrical coordinates were used in an assumed environment in which all seeds came from a point source, the shoreline was straight, the water continued out 100 m, and the seed shadow was equal in all directions (Figure 2). In Equation 1, d is the shortest distance from the point source to the water's edge, θ is the angle between the perpendicular dispersal vector and the seed dispersal vector, and r is the radius along which seeds disperse (Figure 2). The constants were derived from the previously published regression equation (Landenberger et al. 2007). The numerator of the equation

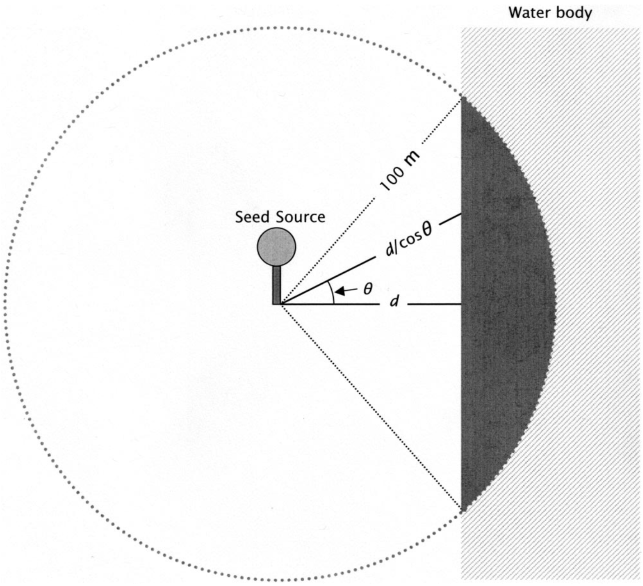

Figure 2. Primary dispersal into water, assuming equal dispersal in all directions.

determines the seed rain falling directly into the water body as a function of d and the denominator estimates total seed rain, within a 100-m radius.

In an effort to derive an empirical estimate of the number of seeds that could be deposited in water from the primary dispersal estimate (Equation 1), a single 100-m wide survey was conducted on February 24, 2007, along the east shore of a 1-km stretch of the Monongahela River near Morgantown, WV. The location and dbh of each reproducing *A. altissima* female present was recorded. Distance of each tree from the water was determined using a global positioning systems (GPS) and mapped using geographic information systems (ESRI ArcView 9.1). Each individual's total seed count was estimated from a linear relationship (Equation 2) between dbh (x in cm) and the natural log of total tree seed count (y) for 14 various sized *A. altissima* females in September 2006 (Kaproth 2008):

$$y = 0.08797x + 7.91856. \qquad (2)$$

Buoyancy Studies

To determine the period of potential buoyancy of *A. altissima* seeds in moving water, 400 intact seeds were divided evenly into four covered 100-L containers filled to a depth of 30 cm with tap water and stirred once daily for 5 seconds to break surface tension (as adapted from Boedeltje et al. 2003). After stirring, the number of buoyant propagules was recorded every day for the 1st week and thereafter once a week for a month. The containers were kept in an unheated greenhouse in which water temperatures were similar to outdoor aqueous environment temperatures during November and February–April (6–19°C). Differences in buoyancy over time were analyzed using logistic regression (JMP version 5.1.2; SAS). Statistical significance for all tests was recognized when $P \leq \alpha = 0.05$. After 1 month, 25 randomly sampled seeds were harvested from each container, bisected across the endosperm, and exposed to 0.1 M triphenyl tetrazolium chloride for 24 hours to test whether viability was retained (Watkinson 1978).

In a parallel study, seed buoyancy was tested after being marked with fluorescent spray paint, to determine whether it would be possible to do a realistic mark-recapture study in a calm water body. Paint markings remain on seeds <2 months, with no perceived effect on germination. A total of 600 intact *A. altissima* seeds were divided evenly into three marking treatments: yellow-fluorescent Rust-Oleum paint, orange-fluorescent Rust-Oleum paint or unmarked. The intact seeds of each painted treatment were lightly sprayed and dried, adding <0.1 g per seed. Seed treatments were divided, exposed to water, measured, and analyzed using methods similar to those described previously for the potential buoyancy study in moving water; however, the containers were not stirred.

Observing Hydrochory

To determine the potential movement of *A. altissima* propagules through hydrochory, a mark-recapture study was used (Nilsson et al. 1991). A weight-estimated total of 10,000 yellow-painted seeds were scattered at one location on the water's surface in the center of the Monongahela River along Morgantown, WV, on June 29, 2006. After 24 hours, the banks of the river were surveyed downstream for a distance of 8.1 km. The position of any marked seeds was noted using GPS.

Measuring Secondary Dispersal on Land

In northern West Virginia, the majority of mature *A. altissima* seeds dehisce from October through April (Landenberger et al. 2007, Kaproth 2008), with a peak of 40% of total seed rain occurring in November (Kota 2005). *A. altissima* germination does not begin before late May (Kota et al. 2007, Kaproth 2008), allowing up to 7 months of secondary dispersal events. To determine the rate at which seeds landing in terrestrial environments might move downhill into streams, rivers, or lakes, a short-term study was conducted on a closed canopy floor of Morgantown, WV's Core Arboretum, by evenly placing 6,000 painted seeds over six 5-cm wide × 4-m long transects on January 16, 2007. Transects were placed in pairs oriented along three continuous contours (9, 33, and 48% slope). After 1 month, seed positions were recorded. Differences in dispersal distances among slopes were analyzed using a nonparametric nested analysis of variance (ANOVA) (JMP version 5.1.2), with the effect of transect nested within slope class.

Germinability after Dispersal in Water

To determine whether *A. altissima* seed germinability was affected by continuous exposure to an aqueous environment, a seed cage study was set up using 60 buoyant cages on November 1, 2005. Each cage was made from a 3.8-L plastic container, kept buoyant by two 5-cm × 5-cm × 10-cm foam pieces (Dow Styrofoam), and covered in nylon mesh bags (as adapted from Edwards et al. 1994). This design kept seeds near the water's surface, as would occur when the seeds were floating, driven by current or wind, and when they washed up to the shoreline strand, along the water's edge. Twenty-six containers were deployed in the Monongahela River, Morgantown, WV, whereas another 26 were tethered in Cheat Lake, WV. An additional four containers per site were packed with leaf litter and placed under the neighboring forest canopy to serve as terrestrial controls. Each container included 50 mature *A. altissima* seeds harvested from three Morgantown, WV, sources 1 week before deployment, providing 50 seeds × 60 cages = 3,000 seeds total.

Every 2 weeks thereafter, two submerged containers were removed from each site until April 4, 2006. Two terrestrial controls were removed after 2 and 22 weeks from each site. The seeds remaining in each container were transferred into trays of moist sand and allowed to stratify for 5 weeks at 4°C. After stratification, trays were placed under fluorescent lights at room temperature (22–25°C) and allowed to germinate for at least 4 weeks. Differences in germination rates between environment (aquatic versus terrestrial) and incubation site (Cheat versus Monongahela) were determined through a two-way ANOVA, with harvest

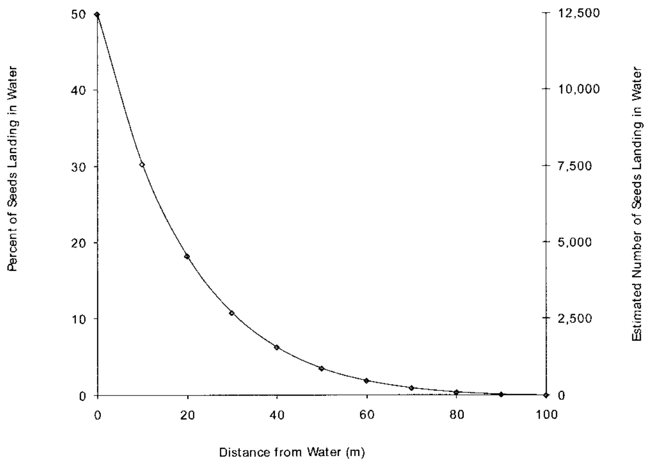

Figure 3. Percentage (left axis) and estimated number (right axis) of seeds dispersing into water as a function of tree distance from water's edge, based on a tree of 25 cm dbh.

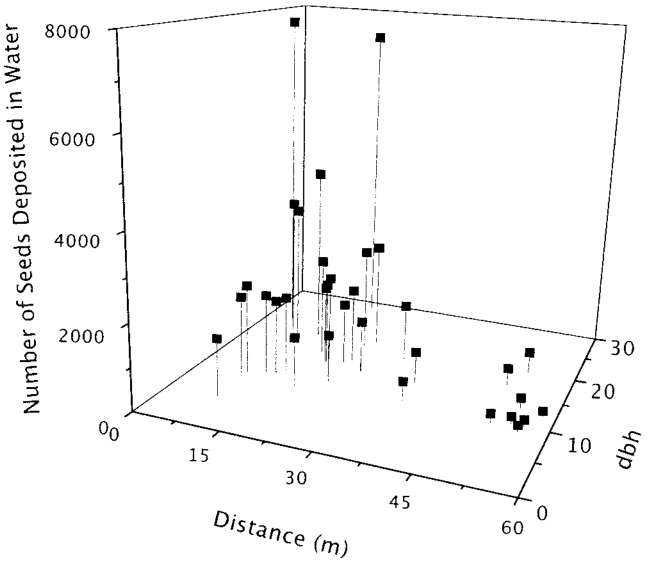

Figure 4. Relationship of individual *A. altissima* dbh (cm) and distance from water on the number of seeds deposited directly into water as a function of Equation 1.

date as a "covariate" and observations weighted by sample size. In addition, differences in germination among the aqueous sites as a function of harvest date were analyzed using a two-way ANOVA (JMP version 5.1.2).

Results

Estimating Direct Primary Dispersal into Nearby Water

The proportion of a plant's seed shadow predicted to be deposited in a neighboring water body decreased exponentially with distance from the water body (Figure 3). The proportion of an individual's seeds primarily dispersed into water dropped to 18.2% at a distance of 20 m.

In a single 100-m-wide, 1-km-long survey along the one side of the Monongahela River, 33 female *A. altissima* trees were found at a mean distance of 26.9 m from water. Provided the assumptions of the primary dispersal model are met (Equation 1) (Figure 2), varying seed totals (Equation 2) and distances from water for each tree (Figure 4), an estimated population total of 62,124 seeds (17.8%) would be deposited into the water through primary dispersal in 1 year along this 1-km stretch of urban/suburban riparian forest along the river.

Buoyancy Studies

Buoyancy of unmarked *A. altissima* seeds in stirred water decreased with the number of days exposed (likelihood ratio, $X^2 = 1{,}767.911$, $P < 0.0001$), with a predicted 50% of seeds remaining buoyant after 1.5 days. After 7.0 days, only 2% of seeds remain buoyant. All seeds exposed to triphenyl tetrazolium chloride were viable, regardless of buoyancy retention. In contrast, when in still water, buoyancy was retained in all seeds after 1 day, regardless of paint treatment.

Observing Hydrochory

Of the 10,000 seeds released, 565 were recovered over a distance of 8.1 km of shoreline after 24 hours. Retrieved propagules traveled a mean distance of 4.05 km; however, the first group found (88.5% of recovered seeds) were 3.95 km downstream. An additional 65 seeds were recovered at six locations with a maximum dispersal distance of 6.8 km. The seeds retained buoyancy and were found in caches of debris only on the western (outer) edge of the river. Wind was negligible during the study period. The surface flow rate (~0.5 m/s) and discharge (650 m^3/s) of the Monongahela River during seed release was above average for summer conditions, but within the normal range of conditions for winter (US Geological Survey National Water Information System).

Measuring Secondary Dispersal on Land

After 27 days, secondary seed dispersal of *A. altissima* on land varied by slope ($F = 108.6699$, $P < 0.0001$). The greatest seed movement occurred along the steepest slopes, with 5.7% of all seeds traveling >0.25 m, including the maximum distance traveled for one seed at 10 m (Figure 5). Only 3.4% of all seeds on a 33% slope traveled >0.25 m, whereas no seeds on a 9% slope traveled >0.25 m (Figure 5). Secondary dispersal distance varied by transect within slope class ($F = 71.9895$, $P < 0.0001$). Although normal precipitation levels occurred throughout the study period (totaling 70 mm), leaf litter and seed movement appeared highest where surface water moved ephemerally during snow melting events.

Germinability after Dispersal in Water

Seeds recovered from submerged cages retained high germinability (94.4 ± 1.1%), showing no significant decline over a 5-month period (Figure 6). On dates when terrestrial controls were sampled, seeds that had been exposed to aqueous environments germinated at a 15.5% higher rate than those in terrestrial environments ($F = 10.94$, $P = 0.0057$). Furthermore, the effect of environment on seed germinability depended on site ($F = 6.88$, $P = 0.0210$) (Figure 7). Seeds germinated at a lower rate if incubated on land (relative to

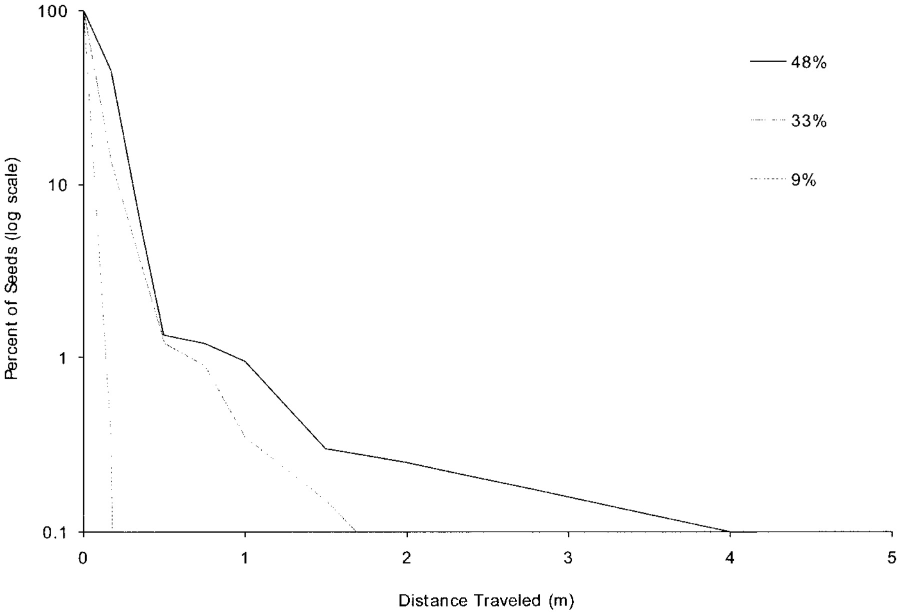

Figure 5. Percentage of seeds traveling a certain distance downhill through secondary dispersal events in a terrestrial environment over 1 month as a function of slope.

those incubated in water) at Cheat Lake, but this pattern was not observed at the Monongahela River site.

Discussion

The results of our dispersal and germination studies suggest that the prerequisites for dispersal of *A. altissima* by water are present as hypothesized. Within 20 m of the shoreline, high proportions of an individual's seeds were estimated to disperse directly into water (18.2% at 20 m and 3.5% at 50 m). Overall, an *A. altissima* population will contribute a considerable number of seeds because of overall high fecundity. Although we found minimal secondary dispersal on land in our short-term study, some additional seeds are likely to reach aquatic environments by this route. The population's estimated seed rain into the water along just 1 km of the Monongahela River suggests a high likelihood that this secondary mechanism of dispersal is frequent. Similar relationships between the number of collected diaspores downstream and stand distance from water (negative) or seed production (positive) were found for riparian species (Boedeltje et al. 2003).

Second, *A. altissima* seeds submerged in water retained consistently high rates of germinability over 5 months and may retain viability in aqueous environments for longer periods, even if submerged (Lazenby 1955). In addition, seeds can float on still water under controlled conditions for 1 month and retain buoyancy in moving water under controlled and riverine conditions for at least 24 hours.

Given that seeds can reach aqueous environments and some retain viability, the only sine qua non of hydrochory is deposition into a suitable habitat. Provided that a species has high propagule pressure, such as *A. altissima*, it appears that the opportunity for safe site deposition and germination along riparian zones is possible (Barrat-Segretain 1996, Von Holle and Simberloff 2005). In addition, successful

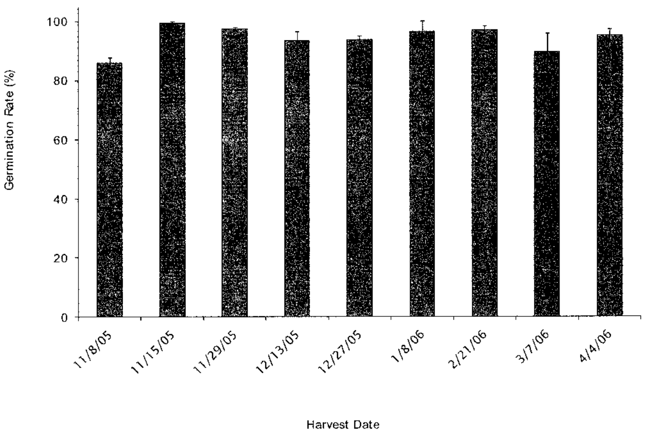

Figure 6. Mean (±2 SE) germination rate of *A. altissima* seeds incubated in aqueous conditions over 5 months.

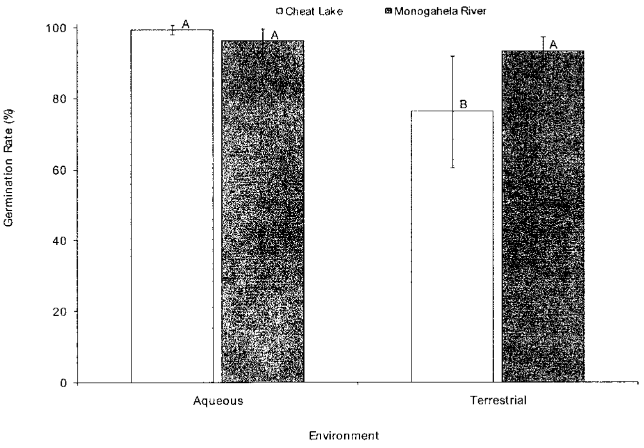

Figure 7. The effect of environment and location on the mean germination (±2 SE) of *A. altissima* seeds near Morgantown, WV. Columns with different letters are significantly different from one another (Tukey-Kramer honestly significant difference a posteriori test).

hydrochory would probably enhance with flooding conditions as increased flow rate and volume would transport seeds farther and permit deposition at high-water elevations in newly disturbed habitat (Middleton 2002, Boedeltje et al. 2004). Because *A. altissima* is not typically a riparian species, deposition during high water or movement to higher ground by wind or animals would increase the probability of successful establishment. Individual *A. altissima* plants have been observed at sites that have periodic flooding.

Within the estimates and observations presented in this study, buoyant propagules of *A. altissima* can be dispersed long distances at greater frequencies than primary dispersal. Although we know that *A. altissima* seeds can disperse at least 200 m through primary dispersal (Kota 2005), hydrochory can carry seeds distances two orders of magnitude farther over a short time (7.2 km in approximately 4 hours at measured rates). These long-distance dispersal events may be occurring at similar rates throughout much of the United States and other countries, as disturbances (e.g., flooding, railroads, and anthropogenic activity) are typically created along river gradients and are frequently dominated by invasive species (Parendes and Jones 2000).

The observed variation in seed germination rates was unexpected. Seeds incubated in aqueous environments did not differ in germination rates, whereas seeds kept at one terrestrial site germinated at lower rates. Low temperature limitations have been previously noted for *A. altissima* (Kowarik and Säumel 2007) and the Cheat Lake terrestrial treatment also experienced lower temperatures than any other site. Owing in part to the temperature-buffering ability of water, the submerged seeds at Cheat Lake may have experienced limited temperature variation and had restricted exposure to severe low temperatures compared with terrestrial controls. These results indicate that aqueous bodies may provide large, temperature-insulating transient seed banks that can disperse propagules long distances throughout mesic environments (Gurnell et al. 2007).

Although *A. altissima* is described as a wind-dispersed invasive species; the description can be misleading. Although its seed structure initially facilitates wind dispersal, the structure should not be assumed to imply that primary dispersal is the only, let alone most important, means of long-distance dispersal. This study provides evidence that hydrochory may be an important mechanism for migration of *A. altissima,* and we expect that these findings may apply to other wind-dispersed, native and non-native species as well (Boedeltje et al. 2003, Ozinga et al. 2004, Nathan 2006). Previous studies have shown that parameterization of a species' seed dispersal curve is vital for forecasting range movement and establishment with changing environmental conditions (Higgins et al. 2003, Lyford et al. 2003). These models of spread are particularly sensitive to how long a dispersal tail is (Clark 1998), and for some terrestrial wind-dispersed species hydrochorous secondary dispersal may provide the mechanism for long-distance dispersal.

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