

Seed dispersal of the non-native invasive tree *Ailanthus altissima* into contrasting environments

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Abstract *Ailanthus altissima* has a long history of invasion in urban areas and is currently spreading into suburban and rural areas in the eastern U.S. The objectives of our study were to (1) determine whether *A. altissima* seed dispersal distance differed between populations on the edges of open fields and intact deciduous forest, and (2) determine whether dispersal differed for north and south winds. We also assessed the relationship between seed characteristics and distance from source populations in fields and forests, and whether seeds disperse at different rates throughout the dispersal season. Using two fields, two intact forest stands, and one partially harvested stand, we sampled the seed rain at 10 m intervals 100 m into each site from October to April 2002–2003. We compared seed density in field and intact forests using a three-way ANOVA with distance from source, wind direction, and environmental structure as independent variables. To assess the accuracy of common empirical dispersal models, mean seed density data at each site were fitted with alternative regression models. We found that mean seed dispersal distance depended on environmental

structure and wind direction, a result driven in large part by dispersal at a single site where seed density did not decline with distance. The two alternative regression models fit each site's dispersal curve equally well. More seeds were dispersed early than in mid- or late-season. Large, heavy seeds traveled as far as small light seeds. Turbulent winds appear to be necessary for seed release, as indicated by a wind tunnel experiment. *A. altissima* is able to disperse long distances into fields and into mature forests, and can reach canopy gaps and other suitable habitats at least 100 m from the forest edge. It is an effective disperser and can spread rapidly in fragmented landscapes where edges and other high light environments occur. These conditions are increasingly common throughout the eastern U.S. and in other temperate regions worldwide.

Keywords Empirical dispersal models · Forest edges · Seed rain · Topography · Wind direction

Introduction

Seed dispersal is an important component of plant demography and largely determines the spatial and temporal patterns of recruitment (Harper 1977; Schupp and Fuentes 1995). For an invasive species whose range is expanding, accurate

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estimates of seed dispersal distance are necessary to predict potential rates of spread. This is particularly important for wind dispersed “weedy” species such as *Ailanthus altissima* Swingle (Simaroubaceae) (Hu 1979) that may be capable of dispersing at different rates into a range of suitable environments. Understanding variability in seed dispersal is therefore a critical element in managing the invasion process in landscapes composed of heterogeneous suitable environments.

Dispersal can be difficult to quantify empirically, although seed density distributions estimated by the sampled seed rain depend on a combination of biological and physical factors that are themselves quantifiable (Levin et al. 2003). For wind dispersed (anemochorous) seeds, biological factors include the height of seed release, fecundity, and geometry of source plants (van der Pijl 1982; Tackenberg 2003), together with seed size, mass, shape, terminal velocity, and the strength of the physical connection to the infructescence (Augspurger and Franson 1987; Matlack 1987; Greene and Johnson 1992). Physical factors include local topography, the intensity and direction of dispersal events, landscape structure, and the structure of the environment within which dispersal occurs (Sharpe and Fields 1982; Nathan 2001; With 2002).

Environmental structure, defined as the spatial arrangement of physical objects in a habitat (McCoy and Bell 1991), can play an important role in the seed dispersal process because structure influences local wind velocity and direction (Coutts and Grace 1995), two factors that in turn affect the seed rain at various distances from their source, laying the template for recruitment (Levin et al. 2003). Despite its apparent importance, little is known about the relationship between environmental structure and seed dispersal in contrasting habitats. Environmental structure is ecologically important not only because it influences how far a seed travels but also because it determines the fate of the seed after its arrival (Chambers and MacMahon 1994). Understanding variability in seed dispersal patterns within and between habitats characterized by differences in structure allows general predictions of an invasive species’ rate of spread in landscapes composed of several different suitable habitat types. This may

be particularly important for recently arrived exotic invasive species for which little specific demographic information exists. Finally, because environmental structure acts on individual seeds as they disperse, it is important to describe how variability in seed size and weight are influenced by environmental structure.

Ailanthus altissima (Miller) Swingle, commonly called tree-of-heaven, is a dioecious deciduous tree in the Quassia family (Simaroubaceae) native to the temperate forests of central China (Hu 1979). In the U.S., it was originally planted in urban areas in the nineteenth and twentieth centuries because of a recognized tolerance of stressful urban growing conditions. Tolerant of infertile, compacted soils and capable of rapid growth (Feret 1985) and early maturity (Feret 1973), *A. altissima* is an aggressive competitor in disturbed environments. The presence of *Ailanthus* throughout the mid-Atlantic region’s interstate highway system, along with its recent discovery in harvested forest stands, mature second-growth forest (Kowarik 1995) and in old-growth forest canopy gaps (Knapp and Canham 2000) indicate that it is no longer confined solely to urban areas, road sides and edges, but is also spreading into relatively intact forest communities more common in rural areas.

In addition to its rapid development, *Ailanthus* has several characteristics often associated with highly invasive, “weedy” plant species. Mature females produce up to 300,000 anemochorous seeds (Bory and Clair-Maczulajtys 1980) that are dispersed from late summer to spring in the mid-Atlantic region of the U.S. Seeds are capable of germinating in a variety of habitats and soil conditions (Hu 1979), showing very high germination rates in disturbed environments including clear-cuts and partially harvested stands (Kota et al. 2007). Capable of prolific vegetative reproduction from stumps and roots, it commonly forms dense clones that inhibit or eliminate native plants (Mergen 1959). Known to be tolerant of various air pollutants including ozone (Davis et al. 1978), sulphur dioxide (Kim 1975), and dust (Klincsek 1976), it is a strong competitor along roadside and highway edges as well as in urban, suburban, and rural areas where air pollution is significant. In addition to its weedy characteristics,

A. altissima has allelopathic chemicals in its roots and leaf exudates (Heisey 1990; Lawrence et al. 1991) that have demonstrated inhibitory effects on over 35 species of hardwoods and 34 species of conifers (Mergen 1959).

In the present study, we deployed dense arrays of seed traps to characterize *A. altissima*'s seed rain in order to better understand potential rates of invasion in three common habitat types in the mid-Atlantic region of the eastern USA. This region is experiencing rapid population growth and associated changes in land uses, including sprawl development in the eastern part (U.S. Census Bureau 2001) and high rates of timber harvesting in the western portion of the region (Luppold et al. 1998). These land use changes could favor invasive species as relatively undisturbed areas of forest and farmland are fragmented and developed.

In this study, we addressed the following four questions: (1) what is the shape of the dispersal curve, and is this species capable of primary dispersal 100 m from the source? Information on dispersal pattern will help in understanding the potential local pattern of invasion. (2) Is there an effect of environmental structure on seed dispersal distance? Seeds dispersing into fields or clear-cuts may be expected to travel farther than those dispersing into a closed canopy forest, suggesting that these habitats would be more rapidly invaded. (3) Does seed dispersal vary with wind direction? A consistent effect of wind direction would indicate that *A. altissima* might not be spreading at the same rate in all directions across the landscape. (4) Does seed dispersal vary seasonally? Early dispersing seeds may suffer higher rates of predation by rodents and birds relative to those that are available for a relatively short time before germinating.

Materials and methods

Study sites and regional wind environment

Five seed dispersal sites (Table 1) were identified in August, 2002 in north-central West Virginia, USA (W 79°50', N 39°37'). The area is characterized by a mixture of woodland, pasture-grassland,

and populated areas with mixed land cover, with gently rolling topography with relief of approximately ± 200 m. Sites contained a focus population of at least three mature female *A. altissima* ≥ 10 m in height, and an adjacent 50 m by 100 m (0.5 ha) seed dispersal sampling area extending 100 m into the respective forest or field. Female *A. altissima* trees in each focus population existed within 2 m of the linear 50 m boundary, on the edge of the forest or field where dispersed seeds were sampled, and can be considered as a line source rather than a point source. To reduce the possibility of seed trap contamination from nearby trees, all other female *A. altissima* trees within 300 m of the focus population were felled and left on site. Two focus populations were adjacent to intact forest and were separated by a distance of 0.5 km, two were next to open fields and were separated by 4 km, and one was adjacent to a recent timber harvest and was 8 km from the most proximal site. The two intact forest stands were approximately 100-year-old mixed-species deciduous forest comprised predominantly of sugar maple (*Acer saccharum*), tulip tree (*Liriodendron tulipifera*), black cherry (*Prunus serotina*), oaks (*Quercus* sp.), and hickory (*Carya* sp.). The recently harvested stand was similar in species composition to the intact stands and was partially cut in 1998; approximately half of the basal area had been removed. The two hay fields were used for convenience to approximate dispersal conditions that might occur with a clear-cut or old-field. To examine the effect of wind direction, one field and one intact forest were located north of the focus population, to capture seeds dispersing on a south wind. One field and one forest were located south of the focus population, to capture seeds dispersing on a north wind. The recently harvested stand was located west of the focus population to capture seeds dispersing on infrequent east winds that may occur during winter storms. Seeds dispersed on north and south winds were sampled because these wind directions represent orthogonal contrasts, permitted replication, and occur throughout the dispersal season (NOAA 1998).

Detailed local climatological data records from the National Oceanic and Atmospheric Administration (NOAA) weather station in Morgantown, WV (N 39°38'40", W 79°55'10') were used to

Table 1 The environmental setting of seed dispersal sample sites

Environment and wind direction	Slope	Aspect	Topographic position of focus population †	Number of reproductive females
Field – North	0%	None, flat	Plateau	4
Field – South	3–4%	180°	Mid-slope	13
Forest – North	4–5%	180°	Upper-slope	4
Forest – South	4–5%	360°	Upper-slope	9
Harvest – East	6–7%	270°	Upper-slope	11

Sites are comprised of a single *Ailanthus altissima* focus population and respective seed dispersal sampling area. The focus population at each site can be considered a dispersed line source located at the 50 m edge of the 50 × 100 m seed sampling area

† Position of reproductive female *Ailanthus altissima* trees relative to local relief in the landscape. “Plateau” indicates no local relief. “Mid-slope” indicates that the focus population and sampling area are located between hilltop and lower slope. “Upper-slope” indicates the focus population and respective sampling area are located near the hilltop

characterize wind direction and velocities at the five sample locations during the sampling period. The weather station is located within 3 km of the intact forest sites and open field sites, and 15 km from the partially harvested stand site. The data included daily observations of maximum speed and direction of 5-s and 2-min sustained wind gusts, taken 10 m above the ground surface. Wind directions (bearings) were given in degrees and converted to either northerly or southerly. While we expected local deviations from the absolute values observed at the NOAA site, these data were used only to broadly characterize the regional wind environment.

Seed dispersal sampling design

A total of 275 circular 0.25-m² seed traps were constructed using 13-cm-wide aluminum flashing for sides and a fine nylon mesh screen bottom. Traps were anchored to the soil surface using 18” surveying flags.

Five seed traps were placed randomly along each of 11 transects per site (55 traps per site). Transects were 50 m in length and located at 10 m intervals parallel to the edge, and thus parallel to the female trees comprising each focus population. The first transect was located at 0 m, and the 11th was located 100 m from the focus population. Sampling began on October 19th 2002, at the beginning of the dispersal season and was terminated on April 9th 2003 after > 95%

of the seeds had dispersed. Sampling occurred every 14–15 days, except between January and March, when two 28-day sampling intervals occurred. Sampling consisted of collecting all *A. altissima* seeds at each trap and cleaning the traps of other debris (seeds, leaves, snow). When snow was present, it was carefully sifted to capture all *A. altissima* seeds.

To determine whether seeds were being lost from traps once captured, 10 samaras were marked with permanent green ink and placed in a randomly selected trap on the 0, 50, and 100 m transect at one forest and one field location. Their presence was determined by counting the seeds during each sampling period. Between October and April, only one seed was lost at the field site, and no seeds were lost at the forest site. To determine whether secondary dispersal into traps was occurring, 10 samaras were marked with red ink and scattered within 1 m of the perimeter of a randomly selected trap on the 0, 50, and 100 m transect at the same forest and field location. These were checked concurrently with the seed loss experiment. No marked seeds moved into the seed traps during the sampling period.

Immediately following collection, all seeds were taken to the laboratory, air-dried at 20°C and 60% relative humidity (10.5 g m⁻³) for 2 weeks to remove weight variation caused by variable wetting, counted, and weighed. Random samples of five intact samaras per trap per sampling period were also imaged with a Canon

Powershot G4 digital camera with a fixed focal length mounted on a tripod. A ruler was included in all images for calibration. If there were fewer than five intact samaras per sampling period, all were photographed. Images were imported to a PC, calibrated, and samara size was estimated using the formula for an ellipse by taking the maximum length and width of each samara in pixels (Scion Image 2000). This method was selected as the most accurate 2D estimate of size, although samaras are not perfect two-dimensional ellipses as they are slightly irregular in shape and may be twisted along the long axis. These data were used to estimate samara size, mass, and wing loading, the samara mass: size ratio (DeBain et al. 2003). Samara terminal velocity was measured using 20 ripe seeds per site, gathered directly from trees in October 2003. Seeds were gathered from trees because the shape and aerodynamics of intact seeds sampled in the seed traps may have been altered in the dispersal and sampling process, affecting their performance. Terminal velocity was calculated by releasing seeds from 4 m above the ground and allowing them to descend 2 m before timing began (Greene 1989). A mean velocity was calculated using $n = 5$ trials per samara. Only those trials where samaras achieved full rotation at the start of timing were used in the analysis. Time of descent was measured with a digital stopwatch.

Wind tunnel experiment

The relationship between seed release rate and wind speed was analyzed in a low turbulence wind tunnel at West Virginia University. Seed clusters were randomly sampled from two trees in Morgantown, West Virginia after trees senesced in November 2002. The sample was split randomly, with four clusters assigned to a “dry” and the remaining three clusters assigned to “wet” treatment. Wet clusters were soaked in water for 30 min and allowed to air-dry for 1 h to simulate conditions following a heavy autumn rainfall event. Seed release rate was analyzed by exposing each cluster to wind speeds of 0–40, 0–80, 0–120 and 0–160 km h⁻¹ and holding them at each respective terminal velocity for 3 min. Time to maximum velocity was held constant at 30 s for

each sample. The total number of seeds released per cluster after 3 min at terminal velocity was counted as a measure of wind speed effect.

Data analysis

Regression was used to model seed dispersal as a function of distance from each of the five source populations. Mean seed density m⁻² was calculated using the five seed traps located at each distance category (from 0–100 m). Means from 10–100 m were then expressed relative to the mean at the 0 m, creating a relative measure of seed density and controlling for initial differences in seed number at each source population. Relative density was modeled using inverse power and negative exponential regression (Burnham and Anderson 1998). These models are simple, can be directly compared using coefficients of determination, and have been used to model a range of seed dispersal data (Levin et al. 2003). Data for mean seed density at the origin ($x = 0$ m) was plotted but excluded from each regression model. By modeling dispersal distance at each site, model types could be compared to uncover patterns within and between the contrasting environments.

Model fits to each respective data set were determined both qualitatively and quantitatively. Initially, each model was assessed qualitatively by evaluating its respective fit across the range of distance from source. For instance, if predicted seed densities were either higher or lower across a range of distances, the utility of that particular model was considered to be of limited value. We used two quantitative measures to compare models. The first comparison was based on the relative strength of each respective model's coefficient of determination (R^2), using the square root of the coefficient of determination following transformation of R to z^* -scale for small samples and applying a t -test (Sokal and Rohlf 1995). In contrast to the parametric method, the second comparison employed an information-theoretic approach (Akaike 1973; Burnham and Anderson 2002), referred to as AIC, “an information criteria” (Akaike 1973). We used AIC_c which applies a correction that adjusts for small sample size (Sugiura 1978; Akaike 1992; Johnson and

Omland 2004). Using this approach, models are ranked based on the empirical data and the model with lowest value is deemed the better fit. However given that all models are simplifications of a complex reality, it is possible that both models could fit a given data set equally well (Burnham and Anderson 1998), and that different parts of the dispersal curve could be fit with different functions.

To assess whether mean seed dispersal distance varied quantitatively between the five sample populations, we examined the interaction between site and mean dispersal distance by applying a two-way factorial model. The model was applied using both negative exponential and power transformations on the relative seed density data from 10 to 100 m from each source. The main effects of site and distance were treated as fixed factors, and distance was modeled continuously.

A three-way factorial model I analysis of variance with replication was used to determine whether the effect of distance on the seed rain differed with forest structure (distance \times environment effect). The dependency of the distance effect on wind direction (distance \times direction interaction) was examined as well. To be consistent with our prior use of regression analysis to model the tails of the density distribution, the mean seed density at $x = 0$ m was excluded from the factorial model. Distance was treated as a continuous variable. All main effects were treated as fixed factors, and the data were log-transformed to meet the assumption of normality. Because the number of reproductive female trees at each site varied (and thus the number of seeds would be expected to differ), analysis of the model's main effect 'environment' was not considered relevant with respect to the dependent variable, seed rain. Because there was only one harvested stand, and it was sampled along a different wind direction gradient than the others, this site was excluded from this analysis. For the remaining four sites, only one site having each combination of environmental structure and wind direction was sampled due to the constraints on availability of accessible field sites and the ability to sample traps in a reasonable time frame. This meant that the design was pseudoreplicated (Hurlbert 1984) with respect to the environment \times wind direction and

environment \times distance terms in the model (although F -tests could be performed since distance was considered a continuous variable). These limitations narrowed the scope of inference possible from this experiment to only these four populations for these two model terms. Therefore, we interpreted them conservatively.

Seed size and mass were analyzed using one-way ANOVA, with focus population as the main effect. Data used in the size and mass analysis were randomly selected subsamples of dispersed seeds and only included samaras that were intact. Seed size and mass were also regressed against distance from source population to examine how these two important seed traits are related to dispersal distance at each sampling location. To remove the inherent variability in samara size and mass at each site and to determine whether average dispersal distance varied by environment and wind direction for a standardized seed, wing 'loading' was analyzed in a three-way ANOVA (with the same limitations described previously). Seed terminal velocity was not analyzed statistically because seeds were not randomly sampled. The data were compared to terminal velocity estimates for *A. altissima* cited in the literature.

To better understand the timing of dispersal and determine whether dispersal timing varied between forests and fields and with wind direction (north versus south), we divided the total dispersal season into three periods, termed 'early', 'mid', and 'late' seasons. The early season had 61 days (Oct 19–Dec 19). Mid-season had 53 days (Dec 19–Feb 10). Late season had 58 days (Feb 10–Apr 9). The seasonal total number of seeds trapped at each site was converted to proportions of the total seeds trapped over the entire season. Proportions were arcsine square root transformed to meet the assumption of normality (Sokal and Rohlf 1995) and analyzed using a three-way ANOVA with season, wind direction, and environment as independent variables. Due to a lack of replication, and given the experimental interest in the season \times environment and season \times wind direction interactions, we omitted the 3-way interaction and confined our analysis to the 2-way terms.

For the wind tunnel study, the number of wet and dry seeds released per cluster at each wind velocity (40, 80, 120, and 160 km h⁻¹) was counted following exposure of the cluster for 3 min. The dependent variable ‘proportion of seeds released’ per cluster for each wind speed was arcsine transformed and analyzed using a 2-way ANOVA with treatment (wet versus dry) and wind speed as factors. All statistical models were analyzed in SAS JMP software (version 5.1, SAS Inc. 2004).

Results

Regional wind environment

Wind gusts throughout the dispersal season were primarily from the southwest (Fig. 1), yet strong north and south gusts occurred throughout the dispersal season. Of the upper 90th percentile of maximum daily 5-s gusts recorded locally, 76% were from a southerly direction. Furthermore, 65% of the strongest maximum daily 2-min sustained gusts were from the south. Although both 5-s and 2-min southerly gusts were more

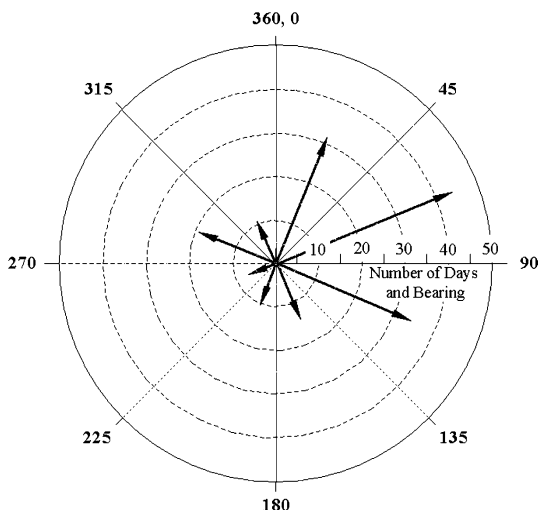


Fig. 1 Vectors of 2-min daily maximum wind gusts showing wind direction and number of days. Vectors represent wind direction $\pm 22.5^\circ$. Vector length represents the number of days with a daily maximum gust in that direction. The 5-s wind gust speeds were highly correlated with 2-min gust speeds ($R^2 = 0.94$) and are not shown

frequent than northerly gusts of the same duration, there was no difference in the average strength between northerly and southerly wind gusts of either duration.

Timing of dispersal

In total, 3332 *A. altissima* seeds were collected in the 275 traps (total area = 68.75 m²) between October 21st 2002 and April 9th 2003 for an average seed density of 48.5 seeds m⁻² in the five 50 × 100 m areas adjacent to the five focus populations. Seeds were dispersed more frequently in the early season ($F = 25.58$, $P = 0.04$) (Fig. 2a), with approximately half of the total seeds in our sample trapped in October and November. The timing of dispersal was not significantly different for forest and field environments ($F = 0.0018$, $P = 0.97$; Fig. 2b), and showed no differences with wind direction ($F = 0.0018$, $P = 0.97$; Fig. 2c).

Seed dispersal curves

Dispersal curves at four of the five sites demonstrated a significant decline in seed density with increasing distance from source populations, although the pattern of decline varied in type and degree (Fig. 3). The most striking pattern was found at the Forest-North site (Fig. 3c), where seed density was independent of distance from seed source across our sampling range and the two models were qualitatively indistinguishable. The two south wind sites, however, were very similar in their general pattern (Fig. 3b, d), characterized by relatively steep declines in seed density from 10 to 40 m compared to changes in density in their respective far tails. This change in density over the 10–40 m range was greater at the south wind sites than at the two north wind and single east wind sites, due in large part to their respective seed density at 10 m from each source. At all sites where seed densities declined with increasing distance from their source, the two models fit seed density values in the far tail more accurately than their fit near the source. The fit in the far tail at the two intact forest sites was comparable to the fit at the field sites.

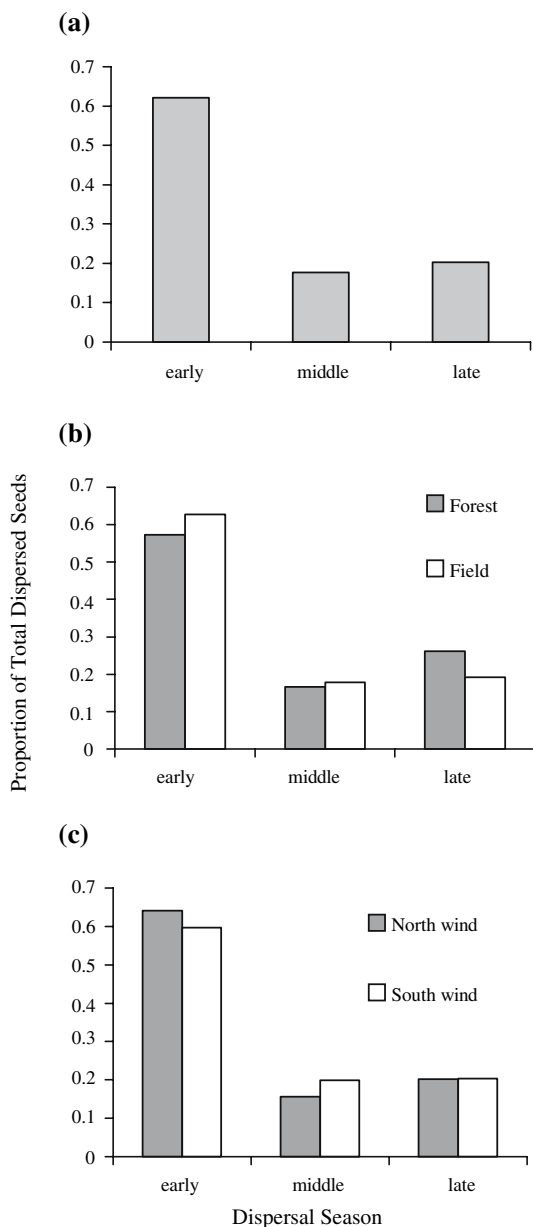


Fig. 2 Proportion of seeds dispersed (a) during the early (Oct 19–Dec 19), middle (Dec 19–Feb 10), and late (Feb 10–Apr 9) sampling periods, and as a function of (b) environmental structure, and (c) wind direction

There was no significant difference in fit between the exponential and power functions at the five sites using model R^2 t -values as a comparison (Table 2), yet AIC_c values indicate that both of the field sites and the forest-south site

were better fit by the exponential model. Qualitatively the two models differ somewhat at each site, particularly near each source. Generally, the exponential model appeared to fit the data in the near tail at each site more accurately. The dispersal curve generated by the east wind at the partially harvested stand was the noted exception. Here, the power model fit the data very well across the entire sample range (Fig. 3e), offering a better fit than the exponential model in the 10–40 m near tail area. In the far tail at the east wind site, both models fit the data from 70 to 100 m from the source.

Differences in mean seed dispersal between populations

As anticipated, the mean dispersal distance depended on site as estimated by the slopes of the negative exponential and power function models, respectively ($F = 12.226$, $P < 0.0001$; $F = 14.036$, $P < 0.0001$). The most notable difference between the five populations existed at the Forest-North population. Here, seed densities varied dramatically but showed no consistent relationship with increasing distance from their source.

Dispersal into contrasting environments

The three-way ANOVA provided evidence for significant variation in seed dispersal patterns in field and forest environments. As expected, mean relative seed density decreased significantly with increasing distance, but the rate of decline depended on both environment (distance \times environment) and wind direction (distance \times direction) (Table 3). Due substantially to the non-declining seed density at the Forest-North site, seeds traveled farther in the forest than in the field as indicated by the shallower slope (Fig. 4a), and traveled farther on a north wind than on a south wind (Fig. 4b). The distance that seeds traveled depended on environment and the direction of the wind, yielding a unique dispersal curve at each site. Other factors such as slope and topographic position of the trees in the landscape (Table 1) also may have influenced seed distance.

Fig. 3 Regressions of mean relative seed density as a function of distance from source population at each of the five sites, represented by the power function (—) and the exponential function (...). Data are expressed relative to the mean seed density m^{-2} at 0 m from each source population. The 0 m datum is plotted but not used in the models. Sampling occurred between Oct 19, 2002 and Apr 9, 2003

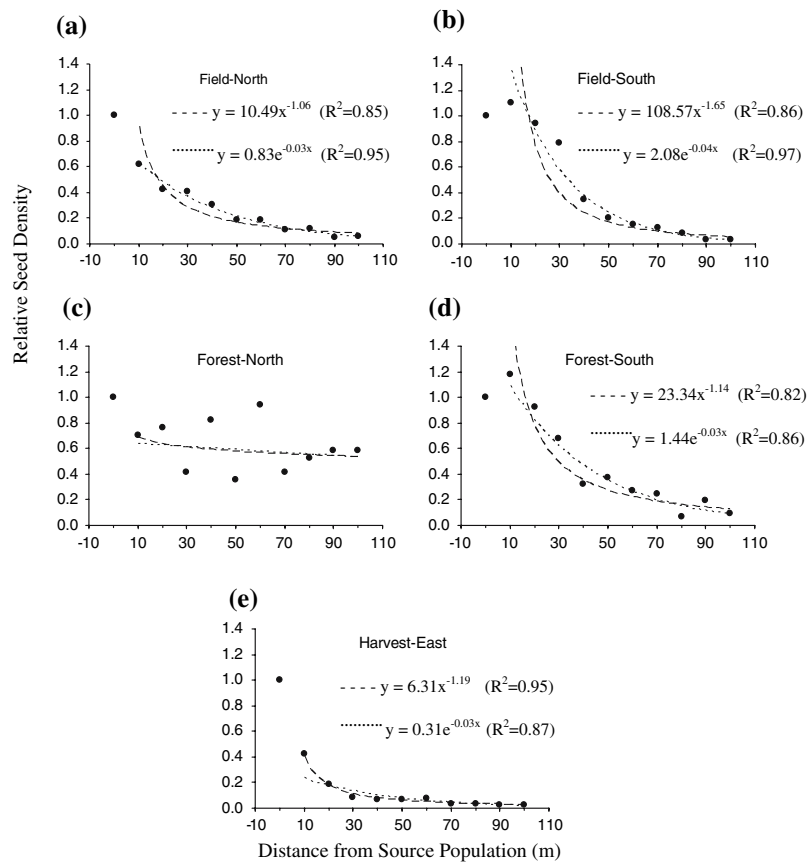


Table 2 Statistics and comparisons of each model applied to each site’s relative seed density from 10–100 m from the focus population

Environment and wind direction	Model and statistics			
	Exponential	Power	Ho: $\rho_{exp} = \rho_{power}$	AIC _c
	R^2, p	R^2, p	t -value, p	Exponential, Power
Field – North	0.95, <0.0001	0.85, 0.0002	1.095, 0.3	-17.31 , -5.22
Field – South	0.97, <0.0001	0.86, 0.0001	1.549, 0.13	-14.25 , 3.02
Forest – North	0.03, 0.60	0.06, 0.50	-0.038, >0.5	-5.77, -6.01
Forest – South	0.86, 0.0001	0.82, 0.0003	0.240, >0.5	-4.24 , -1.79
Harvest – East	0.87, <0.0001	0.95, <0.0001	-0.829, >0.5	-5.68, -14.91

The lower of the two AIC_c values, in bold, indicates the better fit

Samara size, mass, wing-loading, and terminal velocity

Samara size and mass varied by focus population (size, $F = 26.48, P < 0.001$; mass, $F = 79.93, P < 0.0001$) (Fig. 5a, b, respectively). Although size and mass varied between populations, neither variate demonstrated a strong or consistent

pattern with distance from their respective source population. Mass declined with increasing distance only at the Field-North site ($r^2 = 0.46, P = 0.02$), and showed no effect of distance at the remaining four sites. Conversely, size increased with distance at the Forest-North site ($r^2 = 0.38, P = 0.04$). The lack of a consistent pattern was substantiated by the factorial model

Table 3 Three-way ANOVA of relative seed density m^{-2}

Source of variation	df	SS	F ratio	P value
Environment	1	0.882	16.97	0.0002
Wind direction	1	0.012	0.34	0.56
Distance	1	4.69	125.57	<0.0001
Environment*Wind direction	1	0.44	11.70	0.0008
Environment*Distance	1	0.20	5.46	0.02
Wind direction *Distance	1	1.02	27.31	<0.0001
Environment*Wind direction*Distance	1	0.04	1.12	0.29
Error	192	7.175		

The seed density data at each sampling location from 10 to 100 m from source populations were divided by the seed density at the source at each site (0 m). The 0 m data were excluded from the model, and the data were log-transformed to improve the normality of model residuals. The partially harvested stand was excluded from the analysis

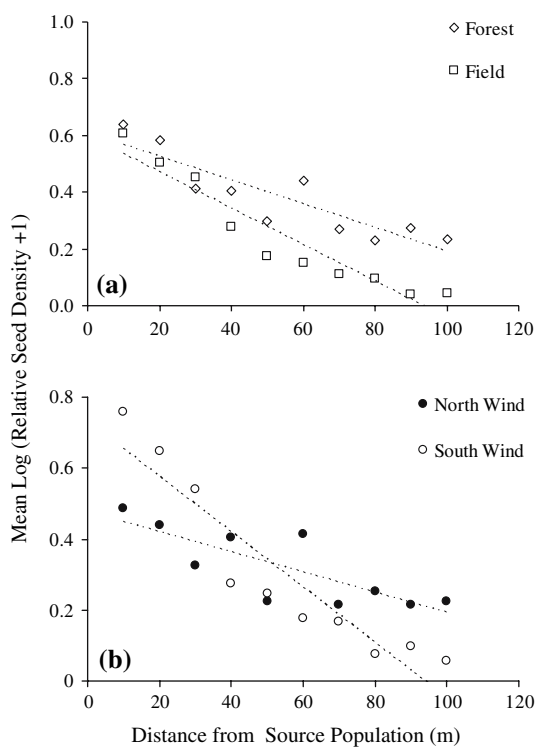


Fig. 4 Two-way interactions between (a) environmental structure and distance from source populations, and (b) wind direction and distance from source populations at the intact forest and open field four populations. The data from the partially harvested forest stand at the east wind site was not included in the analysis

that showed no effect of either distance ($F = 0.59$, $P = 0.44$) or environment ($F = 3.06$, $P = 0.09$) on wing-loading (Fig. 5c). Samara terminal velocity ranged from a mean of $0.65\text{--}0.88\text{ m s}^{-1}$, between the values described by Matlack (1987) and Schmidt (1918).

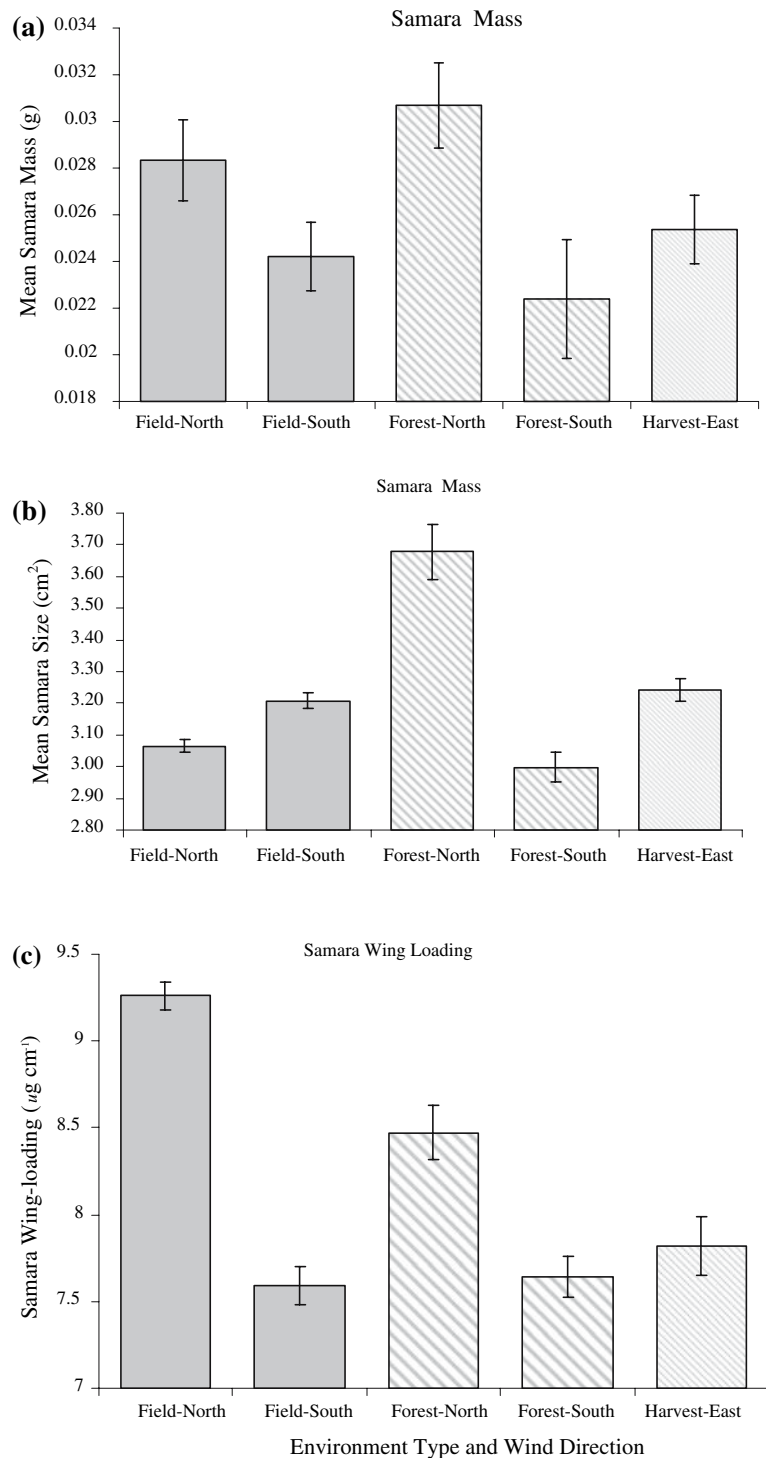
Seed release in non-turbulent winds

In the laminar flow winds produced in the wind tunnel, seed release was very low at all wind speeds from 0 to 160 km h^{-1} . Wind speed was a statistically significant factor, with the highest proportion of seeds released at 160 km h^{-1} winds ($F = 15.39$; $P = 0.0006$). Wet seeds were released at higher rates than dry seeds ($F = 6.97$; $P = 0.01$), but the treatment \times wind speed interaction was non-significant ($F = 2.33$; $P = 0.14$). Over 95% of the seeds remained attached at maximum wind velocity of 160 km h^{-1} , indicating that wind speed alone does not adequately explain seed release in *A. altissima*. Observation accompanied by video imagery of the seed clusters revealed that the laminar flow in the wind tunnel caused clusters to compress, such that many seeds were protected from the direct force of the moving air.

Discussion

Seed dispersal links the spatial pattern of adult trees to that of their offspring, laying the template for establishment (Harper 1977; Schupp and Fuentes 1995; Nathan and Muller-Landau 2000). Thus seed dispersal distance, acting together with rapid local population growth, largely determines the rate of invasion (Clark et al. 1998). Most wind-dispersed tree seeds travel only a short distance from their source, often a few meters to tens of meters. Distant dispersal events are rare (Greene and Johnson 1995; Portnoy and Willson

Fig. 5 Mean samara size (a) mass (b) and wing-loading (c) sampled at the five focus populations. Error bars represent one standard error of the mean



1993) and therefore difficult to quantify accurately (Silvertown 1991), however they may not be as rare as previously thought (Clark 1998;

Horn et al. 2001). Yet, despite the difficulty in quantification, such events play a critical role in determining invasion and range expansion rates

(Clark et al. 1998; Higgins and Richardson 1999; Cain et al. 2000; Nuebert and Caswell 2000). This may be particularly true for highly effective dispersers that are positively associated with intermediate levels of disturbance and landscape fragmentation (With 2002), and where forest and field edges are common.

As estimated by their respective R^2 values, the two dispersal curves at each site were fit equally well by the negative exponential and power functions. However, the AIC_c comparison revealed that the exponential model was a closer approximation to actual seed density at both field sites and the forested site where seed density declined with increasing distance. The power function tended to overestimate seed densities at 10 m and underestimate density in the middle of the curve. The single exception to this was at the partially harvested stand where seeds were trapped on the east wind. Here the power function, with its characteristic steep decline near the seed source followed by a relatively fat tail, fit exceptionally well across the entire sampling range. This pattern may have been due to infrequent easterly winds associated with mid-Atlantic coastal storms.

Since predictions at the extreme tail are the basis for estimates of range expansion, inaccurate reflection of these values could result in either liberal or conservative estimates of range expansion. Recent attempts at curve fitting have had some success either by mixing several dispersal kernels (Clark et al. 1999; Higgins and Richardson 1999; Bullock and Clarke 2000) or by restricting their fitting exercise to a specific section of the curve (Portnoy and Willson 1993). Both methods have their respective strengths and limitations. Given the natural variability in the factors that influence seed shadows, ecologists and land use managers should ascertain the range of values associated with these factors in their particular system. Understanding this variability, and how it can influence dispersal, is most important.

Whatever the precise best-fit function in a given section of the dispersal curve, *A. altissima* is clearly capable of dispersing 100 m and very likely much farther, in fields (Kota et al. 2007) and mature deciduous forest. Seeds were consistently sampled at 100 m in both environments, as

well as in the partially harvested stand representing intermediate structure. Relative to the density of seeds sampled at 0 m (at their source), the density of seeds dispersed 100 m varied between 2 and 58%, representing 1–16 seeds m^{-2} , with the latter figure depending in part on source density. Distant dispersal also occurred frequently throughout the dispersal season at all sites; seeds dispersed at least 100 m in 42% of the seed trap sampling events, and dispersed at least 70 m in 80% of the sampling events.

Dispersal distance is determined by seed characteristics, release height, and wind dynamics, including both speed and turbulence (Greene and Johnson 1995; Horn et al. 2001). Wind speeds tend to be higher in an opening than in an adjacent stand (Raynor 1971; Nathan et al. 2002) because tree canopies create friction and dissipate wind energy (Coutts and Grace 1995). Within stands, winds are highest in the upper canopy and decrease exponentially with increasing depth (Grace 1977). Factors such as seed release height and seed terminal velocity being equal, average seed dispersal distance should be significantly less in a forest, including in a leafless deciduous stand, than in an open field. Nonetheless, canopy generated wind turbulence (Finnigan 1985), particularly at the edges of a forest (DeWalle 1983), can effectively lift seeds to various heights above the canopy where they then travel long distances (Horn et al. 2001; Nathan et al. 2002).

An *A. altissima* samara is somewhat asymmetrical, falcate, and twisted at its free end. Although it has properties of both the “roller” (*Fraxinus*, *Liriodendron*) and “autogyro” (*Pinus*, *Acer*) categories of wind-dispersed seeds or fruits (Augsburger 1986), it has distinct aerodynamic behavior, which differs from both rollers and autogyros. After release, it auto-rotates about its long axis in the manner of a Flettner rotor (Vogel 1981), while simultaneously descending in a spiraling helix approximately 50 cm in diameter. The resulting flight pattern creates significant drag that slows the seed’s descent in still air. In turbulent conditions, however, the samaras stop rotating and spiraling (“stall”) and are transported rapidly down-wind (Norberg 1974; McCutchen 1977).

McCutchen (1977) also noted that a fraction of *A. altissima* samaras do not spiral but only autorotate and descend at approximately 45° to the horizontal in a straight glide path. Assuming the 45° angle of descent, a seed released from the top of a 15 m tall tree would travel 15 m in still air, without any assistance from wind. Although the probability of an *A. altissima* samara being released in still air is extremely low, a seed released under gusty conditions and subsequently deposited into a low wind environment (e.g., under a dense canopy), could continue to travel some distance before alighting.

Large, light seeds would be expected to travel farther than small, heavy seeds because lighter seeds and/or seeds with lower wing-loadings have lower terminal velocities (Augspurger and Franson 1987). Although samara size, mass, and wing-loading varied among the five populations, there was no consistent relationship between any of these characteristics and dispersal distance. Large, heavy samaras may travel as far or farther than light samaras, on average, because of the amount of turbulent force required to release the samaras from the tree (Greene and Johnson 1992, 1995). In *A. altissima*, samaras do not have an abscission layer. Rather the sessile samaras are attached to the gynophore disk, and wing tissue begins to tear free from the marginal fibrovascular bundles when the samara is subjected to mechanical stress, such as wind. As indicated by our wind tunnel results, the samara is held firmly by these vascular strands and only liberated when the force is sufficiently strong to snap the fibrous strands. Thus, most seeds do not break free until strong, turbulent wind gusts occur, winds capable of transporting seeds of variable wing-loading equally far (Augspurger and Franson 1987; Horn et al 2001). In fact, the largest, heaviest seeds, seeds characterized by intermediate wing-loading values, traveled the farthest distance at the north wind, intact forest site, supporting our contention of more turbulent winds at this site.

Environmental structure and wind direction did affect the dispersal pattern of *A. altissima*, but not in the manner we had predicted. In our forest samples, neither forest stand inhibited dispersal vis-a-vis open fields. The reduction in seed densities we observed with distance depended in part

on environmental structure and in part on wind direction such that each dispersal curve was unique. Turbulence likely played a significant role at all five sites, but appeared to be particularly important in the intact forest stand where seed density showed no decline with increasing distance from source. Local gusts may have produced this dispersal pattern because of the site's hilltop topography. An additional factor is that average samara release height was higher here, exposing seeds to more turbulent winds. Indeed, parent trees at this site were taller, on average, than at the other sites (Forest-North mean tree height = 14.0 m; Mean height for remaining stands = 10.3 m). Although seeds dispersed farther on north winds than on south winds, the difference depended on environmental structure. It would be useful to know if this pattern is repeated at similar 'forest-north' sites, or is a function of a unique local wind anomaly. In our single documented case, it suggests that under certain conditions *A. altissima* seeds may disperse great distances and thus potentially spread very rapidly. How far they are capable of traveling is unknown but likely depends on local turbulent wind conditions (Horn et al. 2001), which may themselves be influenced by environmental structure. The implications of this unique dispersal kernel suggest that *A. altissima* poses significant, and costly, management challenges in areas where it currently exists.

In the mid-Atlantic region of the eastern U.S., *A. altissima* seeds disperse from the time of fruit ripening in September–October until the final seed is shed in April–May. This pattern of prolonged dispersal has both advantages and disadvantages. First, a long period of release will increase the variability in distance and direction of dispersal, and therefore area covered, because winds of different direction and speed will be involved (Canham and Marks 1985). This increases the probability of landing in a suitable site (Harper 1977). Although not requiring stratification (Graves 1990), seeds that disperse early will likely have higher germination rates because of their longer contact with moist soils and litter (Little 1974). In addition, time is required for seeds to infiltrate the litter layer. Conversely, seed exposure to predators and disease increases with

time following dispersal (Janzen 1971; Chambers and MacMahon 1994). In temperate climates where snow covers the ground intermittently, as it does in the mid-Atlantic region, a long dispersal season increases the probability that some fraction of wind-dispersed seeds will experience secondary dispersal across the snow surface, possibly traveling hundreds or even thousands of meters (Matlack 1989).

Wind speed, direction, and environmental structure act on seed dispersal distance in complex ways. Although certain general seed distribution patterns were revealed, the result is that each seed dispersal curve is unique. Empirically modeling dispersal demonstrates this inherent complexity and forces an examination, optimally under replicated experimental control, of the mechanisms and their associated interactions that combine to explain a significant proportion of the potential rate of spread. Such information could be used in constructing a spatially explicit model of invasion potential. From an applied perspective, a better understanding of dispersal patterns is important for land managers interested in controlling the spread of exotic invasive species such as *A. altissima*, particularly in areas where these species are associated with field and forest borders, roadsides, power line corridors, and other juxtaposed habitats characterized by contrasting structures. As demonstrated most clearly by the Forest-North site, a 100-m buffer zone around areas where timber harvest is being planned is insufficient to reduce the possibility of invasion and establishment. To maximize the effectiveness of pre-emptive management efforts, mature female trees should be farther than 200 m (Kota 2005) from timber harvests. As one of the most invasive tree species in the eastern deciduous forest of North America, this information could be used to slow the spread and reduce future infestations that impart a high economic cost on ecosystem services and reduce biodiversity.

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