Simulating the dispersal of hemlock woolly adelgid in the temperate forest understory

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Abstract
The hemlock woolly adelgid (HWA), *Adelges tsugae* Annand (Hemiptera: Adelgidae), has spread rapidly across the eastern USA since its introduction from Japan 60 years ago, causing widespread mortality of both eastern hemlock [*Tsuga canadensis* (L.) Carrière] and Carolina hemlock [*Tsuga caroliniana* Engelm. (Pinaceae)]. Although HWA spread patterns have been repeatedly analyzed at regional scales, comparatively little is known about its dispersal potential within and between hemlock stands. As the small size and clonal nature of HWA make it nearly impossible to identify the source populations of dispersing individuals, we simulated intra-stand HWA movement in the field by monitoring the movement of clumps of fluorescent powder that are slightly larger than HWA, but much easier to detect in the forest understory. Using three hemlock trees with three colors of fluorescent powder as source populations, we detected dispersal events at the farthest distances within our trapping array (400 m). However, more than 90% of dispersal events were <25 m. Dispersal patterns were similar from all three source trees and the distribution of dispersal distances in all cases could be described by lognormal probability density functions with mean dispersal distance of 12–14 m, suggesting that dispersal was relatively independent of location of source trees. In general, we documented tens of thousands of passive dispersal events in the forest understory despite the presence of a dense forest canopy. Thus, even under relatively light-wind conditions, particles of similar dimensions to HWA are capable of intra-stand movement, suggesting that a large population of HWA could rapidly infest other trees within several hundred meter radius, or beyond.

Introduction

The hemlock woolly adelgid (HWA), *Adelges tsugae* Annand (Hemiptera: Adelgidae), is an invasive hemipteran native to Japan (Havill et al., 2006), that was first detected in the eastern USA 60 years ago in Virginia (Souto et al., 1996). This small insect feeds on both eastern hemlock [*Tsuga canadensis* (L.) Carrière] and Carolina hemlock [*Tsuga caroliniana* Engelm. (Pinaceae)], and has caused the decline of both tree species throughout much of their range (Orwig & Foster, 1998). Infested trees apparently possess inadequate defenses against HWA, and high-density infestations are capable of killing mature trees in as little as 4 years (McClure, 1991).

Hemlock woolly adelgid has two generations per year in its invaded range. In the spring, eggs laid by the overwintering sistens generation hatch and produce progrediens generation crawlers that either settle immediately on hemlock foliage or are passively dispersed via wind, birds, or animals (McClure, 1990). Crawlers that find a suitable hemlock host become sessile adults that reproduce asexually. In their native range, overwintering sistens also produce sexual winged offspring called sexuparae that feed on spruce trees (McClure, 1989a). As suitable spruce hosts are lacking in the northeastern USA, however, this sexual phase is a demographic 'dead end' and HWA is therefore parthenogenetic in the invaded range. Mature progrediens lay eggs in the summer that hatch into passively dispersed sistens crawlers that settle, overwinter, and complete the

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cycle by producing progrediens the following spring (McClure, 1989a).

Since arriving in Virginia in the 1950s, HWA has rapidly expanded its invaded range. Models parameterized using county-level data on HWA spread estimate that this species' range is expanding at a rate of 10–30 km per year, with the rate of spread varying by geographic location (Ward et al., 2004; Evans & Gregoire, 2007; Morin et al., 2009; Fitzpatrick et al., 2010). Spread dynamics at the landscape scale have been relatively well studied; however, there has been little effort to quantitatively assess HWA movement within and between hemlock stands.

Quantifying dispersal of any organism represents a major technical challenge and tracking HWA dispersal is particularly difficult. Although sophisticated mathematical models have substantially increased our ability to model dispersal under a wide range of conditions (Nathan et al., 2005), field experiments provide the most accurate information on dispersal patterns for organisms at a particular time and place. In particular, properly designed field studies can not only inform models of dispersal, but also provide critical tests of their predictions. As dispersing crawlers are small (ca. 0.4-mm long; McClure, 1989a), nearly transparent, and extremely fragile, traditional techniques for tracking the fate of individuals (e.g., Eizaguirre et al., 2004; Guichard et al., 2010) cannot be employed. Monitoring trees for changes in infestation status offers one means of inferring dispersal. However, low-density infestations are difficult to detect (Fitzpatrick et al., 2009) and only provide a record of successful dispersal events. Even if dispersing crawlers are detected, their source population cannot be definitively established. Although the advent of DNA microsatellite technology as a tool for linking individual dispersers to their 'parent' populations has allowed researchers to quantitatively assess pollen dispersal (Ashley, 2010), HWA is clonal on the east coast of the USA and possesses virtually no microsatellite variation in its invaded range (reviewed in Sanchez & Keena, 2009). Such challenges may account for why only two published studies have attempted to directly assess HWA dispersal (McClure, 1989b, 1990). These studies documented between-stand dispersal of crawlers by both wind and biotic vectors (birds and deer), but did not provide a quantitative estimate of the frequency distribution of dispersal distances. Because of this, neither of the study can be used to determine the likelihood of HWA crawlers traveling a given distance.

Although these difficulties make direct assessment of HWA impractical, our interest in understanding the potential for HWA dispersal led us to conduct a 'field simulation' in which we tracked the movement of HWA-crawler-sized clumps of fluorescent powder in the temperate forest understory. Specifically, we 'infested' three source hemlock trees with a distinct color of fluorescent powder and documented powder movement through the use of sticky traps located in multiple transects extending from each of the three source trees. Infesting multiple trees in different locations with a distinct color powder allowed us to assess whether passive movement (dispersal) differed in space. We addressed three key questions: (1) What is the propensity for HWA-sized-clumps of fluorescent powder to disperse between hemlock trees in the forest understory? (2) What is the shape of the function describing the distribution of dispersal distances? and (3) Do patterns of dispersal differ in space? Although there are several potential differences between our proxy and HWA crawlers, a better understanding of how passively dispersed propagules move with respect to a single initial source population can only help to inform HWA monitoring efforts. More generally, such information may also prove useful in understanding how similarly small organisms are dispersed within the temperate forest understory.

Materials and methods

Study site

Our experiment was conducted in the Simes tract (42°30′N, 72°12′W), a 125-ha research area of hemlock-hardwood forest managed by Harvard Forest (Petersham, MA, USA). This area is near the current northern border of HWAs invaded range in Massachusetts; a survey of ca. 200 mature hemlocks in this area found light to moderate HWA infestations on 70% of trees (JL Turner, MC Fitzpatrick & EL Preisser, unpubl.). A detailed description of this site is provided elsewhere (Busby et al., 2009); briefly, this mature hardwood stand is dominated by red oak (*Quercus rubra* L.), red maple (*Acer rubrum* L.), and American beech (*Fagus grandifolia* Ehrh.), with small stands of mature eastern hemlock clustered in mesic sites. We selected three mature (12–14 m tall) hemlocks separated by deciduous species as the 'source' trees for our experiments. All source trees were of similar height and diameter and appeared virtually identical in structure, foliar cover, etc. The source trees were located 240 m from each other along a north–south axis, with the most southerly tree being 240 and 470 m from the middle and most northerly tree, respectively.

We used data from a weather station located ca. 0.5 km from our study site to conduct a multi-year analysis of wind data for the months of June through August (HFL-TER, 2010). This weather station was chosen because of its proximity and the fact that it is located in a forested area similar in age and species composition to our study site. The analysis revealed that wind movement (including

storm gusts) during this period occurred predominantly in a southwest to northeast direction (Figure 1A). To confirm that passive dispersal occurred primarily in the directions indicated by the weather station data, we then conducted a 2-week pilot study. For the pilot study, we monitored the movement of fluorescent powder in all cardinal directions and at distances up to 50 m from a single source tree, following the same procedures for the application and trapping of powder as described below in 'Dispersal material and monitoring'. This study confirmed that the vast majority (>93%) of particle movement occurred in the dominant southwest to northeast wind direction. Based on this information, we focused our sampling along a series of transects placed at multiple distances from each of the three source trees. The pilot study also

facilitated the selection of distances at which one could place traps.

Dispersal material and monitoring

We used fluorescent powders as proxies for dispersing HWA. Powder is similar to small passively dispersed organisms in that it remains on the tree until either wind or another vector dislodges it. Nonetheless, there are clearly differences in the physical attributes of powder and HWA that could produce differences in dispersal patterns. To account for these differences, we took steps to ensure that we measured only movement of propagules of similar size to dispersing HWA (see below).

Our experiment used three colors of DayGlo fluorescent powder (DayGlo, Cleveland, OH, USA): aurora pink, arc yellow, and fire orange. We chose these colors because we were able to clearly differentiate between them in the field and under ultraviolet light. We used thin-gauge nylon line to establish 'trapping arrays' with seven individual trap lines at distances of 5, 15, 25, 33, 50, 75, and 100 m from each of the three source trees. Given the dominant winds in the study area, we placed one trapping array to the north of the southernmost tree, one trapping array to the south of the northernmost tree, and one trapping array each to the north and south of the middle tree, for four trapping arrays total. As the hemlocks were within several hundred meters of each other, each trapping array could also be used to monitor powder dispersal from each of the three source trees and thereby increased the maximum trapping distance to 400 m. Trap lines were strung horizontally at 1.5 m above the forest floor between deciduous trees and were placed such that the trap line was perpendicular to the prevailing southwest-northeast wind direction. Sixteen equally spaced whitefly sticky cards (7.62 × 12.70 cm; Ben Meadows, Janesville, WI, USA) were hung on the nylon line at each distance, in each array (16 cards per distance × 7 distances per array × 4 trapping arrays = 448 total traps). As the cards were adhesive on both sides, we were able to capture passively dispersed propagules from each of the three source trees; each trap was also initially covered with a removable non-adhesive plastic sheet to prevent accidental contamination. The traps were installed with the coversheets in place, and the coversheets were removed at the beginning of the experiment.

Once the trapping arrays were installed (but the traps were not yet 'opened'; see below for details), we began the experiment by applying a distinct color of fluorescent powder to each of the three source trees. We spread the powder on each tree using a 5-m extension pole with a color-specific measuring cup attached to the end. This allowed us to cover the lowest branches to ca. 6 m above the forest floor. Powder was applied evenly in 2-l
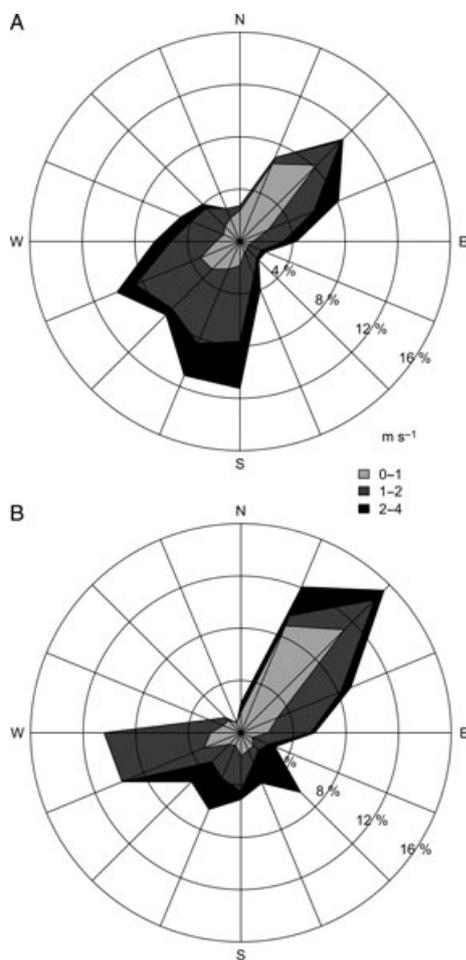

Figure 1 Wind roses showing wind patterns in the vicinity of the study site for (A) the average conditions for June through August in years 2001–2004, and (B) during the sampling period, 6–15 July 2009.

increments on all sides of the tree at the beginning of the sampling period. To prevent contamination of the traps during powder application, we wore disposable rubber gloves and color-specific disposable Tyvek coveralls (DuPont, Wilmington, DE, USA) for applying the powder to each source tree. The rubber gloves and Tyvek coveralls were changed for each tree, and the extension pole was cleaned before leaving each source tree. A day after adding the powder to each of the trees, we began the experiment by removing the non-adhesive plastic sheet from both sides of each of the 448 traps. This allowed airborne powder to settle prior to the beginning of the experiment, and reduced the likelihood of accidental contamination as a result of the powder application process.

The experiment ran for a 9-day sampling period, 6–15 July 2009, during which we documented wind speed and direction using a local weather station (HFLTER, 2010). As this time period coincides with the emergence of sistens-generation crawlers, the observed dispersal patterns we observed are likely to be most indicative of this generation. As sistens are 8–10× more fecund than progrediens-generation adults (McClure, 1989a), the dispersal (and ensuing settlement) of sistens-generation crawlers is likely to play an important role in the colonization of new trees both within and between hemlock stands. All cards were collected at the end of the experiment. As some cards were lost during the experiment, we gathered data from a total of 440 traps. Each card was sealed in a single transparent plastic sandwich bag in the field to guard against cross-contamination, leaving the card's sticky surfaces covered with a washable transparent coating.

Dispersal assessment

After cleaning the outer plastic coating of each card with a mild soap and water solution to remove any accumulated dirt or other particles, both sides of each card were photographed in a photography box under UV light. We used a Nikon D3 camera (Melville, NY, USA) with a 70-mm lens and polarizing filter. Each photograph was analyzed using Adobe Photoshop CS3 Extended (Adobe, San Jose, CA, USA) to select like-colored pixels for each of the three powder colors. We ensured that any clump of powder detected by the program was equal to or larger than the size of a sistens crawler by adjusting the resolution of our digital analysis as follows. First, we determined the average size of a sistens crawler using data provided in McClure (1989a), where measurements of 100 sistens crawlers averaged 44-μm long × 27-μm wide (1 188 μm²). Each card was 96.774 cm² (9.6774×10^9 μm²), and we set the program to record data on 4.673×10^6 pixels per card. Each pixel thus measured 2 071 μm² and an average sistens

crawler covered less (57.4%) than the area of a single pixel. To account for undocumented differences in the mass and buoyancy between particles of powder and dispersing HWA, we assumed that only particles larger than 10 pixels could be considered a dispersal event. As such, our analysis is probably a conservative estimate of dispersal. Nonetheless, we ran the statistical analysis with and without this correction and found virtually no difference in the results.

Data analysis

We assessed patterns of dispersal for each of the three trees by comparing the fit of four candidate functions representing the frequency distribution of dispersal distances, hereafter termed the distance probability density function or 'distance pdf' (technically not a dispersal kernel, which describes the density of propagules as a function of the distance x from a source; Cousens et al., 2008) to the field data and estimated parameters that characterize the dispersal distance and shape. To find the best functional form of the distance pdf, we compared the fit of the frequency distribution of observed dispersal distances to the following four candidate functions: Weibull, inverse Gaussian, lognormal, and negative exponential (Table 1). These 'fat-tailed' functions are commonly used to model dispersal (Cousens et al., 2008) as they allow for rare events at extreme distances. We obtained parameter estimates for these dispersal functions by numerically minimizing the negative log-likelihood using the Nelder-Mead simplex algorithm from the mle2 function in the bbmle library (Bolker B & R Development Core Team, 2011) in R 2.11.0 (R Development Core Team, 2009). Confidence intervals for the estimated parameters were calculated by numerical approximation of the Hessian, a matrix (or single number in the case of the single-parameter negative exponential function) of second partial derivatives of the log-likelihood surface with respect to the parameters at the maximum-likelihood estimate. The inverse of the Hessian, estimates the asymptotic variance-covariance matrix, from which variances can be obtained to calculate 95% confidence intervals for all parameters (Bolker, 2008). We used Akaike's Information Criterion (AIC) to determine the model best supported by the data (Burnham & Anderson, 2002).

Results

Wind patterns in the vicinity of the study site were broadly similar during the 9-day sampling period to those of the multi-year average for June through August (Figure 1). In particular, wind speeds fell in the same range and did not exceed 4 m s^{-1} for either period. There were similarities in

Table 1 Candidate functions used to fit dispersal data

Function	Equation	Mean dispersal distance	Parameters
Lognormal	$f(x) = \dfrac{1}{\sqrt{2\pi}\ \sigma x} e^{-\left(\frac{(\ln x - \mu)^2}{2\sigma^2}\right)}$	$e^{\left(\mu + \frac{\sigma^2}{2}\right)}$	μ = mean, σ = standard deviation
Inverse Gaussian	$f(x) = \sqrt{\dfrac{\lambda}{2\pi x^3}} e^{-\left(\frac{\lambda(x-\mu)^2}{2\mu^2 x}\right)}$	m	μ = mean, λ = shape
Weibull	$f(x) = \dfrac{\lambda}{k}\left(\dfrac{x}{k}\right)^{\lambda-1} e^{\left(-\left(\frac{x}{k}\right)^\lambda\right)}$	$k\Gamma\left(1 + \dfrac{1}{\lambda}\right)$	λ = shape, k = scale
Negative exponential	$f(x) = \dfrac{1}{k} e^{-\frac{x}{k}}$	k	k = scale

The shape parameter (λ) determines the shape of the function, whereas the scale parameter (k) determines how concentrated or spread out the function is, with larger values of k producing more spread out functions.

wind direction as well, but during the sampling period winds came out of the southwest less frequently and out of the west more frequently than the multi-year average.

We detected movement of powder from source trees at a maximum distance of 400 m, the greatest distance our trapping array was able to measure (Figure 2A). Dispersal events of this distance were extremely rare, however, with >90% of dispersal events occurring within 25 m of source trees. Although source trees were widely separated from one another, the form of the best-supported model was the same for all source trees (Table 2). Model comparison by ΔAIC and normalized Akaike model selection weights (Burnham & Anderson, 2002) revealed that a lognormal function best described the distribution of dispersal distances regardless of location of the source tree. For all three source trees, the AIC weights (a measure of the relative goodness-of-fit of the four candidate functions) were approximately equal to 1 for the lognormal functions, confirming the strength of its support relative to the Weibull, inverse Gaussian, and negative exponential functions. Further, the parameter values for (and thus the shapes of) the three lognormal functions were generally similar (Figure 2B), with mean dispersal distance of 12–14 m for all three source trees (Table 2).

Discussion

We documented numerous dispersal events within a closed-canopy setting. In general, there was a high abundance of powder within 25 m of each of the three source trees, followed by a sharp decline beyond this distance. Of particular ecological interest was the fact that powder was captured 400 m from the source trees, the farthest possible distance our trapping array was capable of measuring. This

suggests that small particles may be capable of traveling beyond our sampling array. This fact is notable in the context of dispersal of HWA, given that our experiment took place over a relatively short (9-day) period; in contrast, sistens crawlers are present in New England throughout June and July (McClure, 1989a, 1991).

Our finding that passively dispersed material can move long distances from source hemlock trees agrees with the findings of previous research on HWA dispersal (McClure, 1989b, 1990). A study of springtime crawler dispersal found individuals that had apparently travelled >1 200 m from an infested hemlock stand through a largely hemlock-free hardwood forest (the infested stand was assumed to be the source of all dispersing crawlers; McClure, 1990). Earlier work (McClure, 1989b) also apparently documented crawler dispersal >1 000 m from the edge of the same infested stand, but provided no information regarding the timing or length of the study. Both these studies assumed that passive crawler dispersal occurred primarily in the late spring, before leaf-out of deciduous trees in the forest canopy reduces wind velocity in the forest understory. In contrast, we documented a considerable amount of passive dispersal in the forest understory, despite the presence of a dense forest canopy. This suggests that even under relatively light-wind conditions, lightweight particles of similar dimensions to dispersing adelgids may be capable of spreading quickly throughout (and presumably between) hemlock stands. This information is particularly important because, unlike many other insect pest species, HWA is obligately asexual in its invaded range (McClure, 1989a). Although there is considerable variation in HWA settlement (Butin et al., 2007) and crawlers experience high mortality rates (McClure, 1991), even single individuals that successfully settle
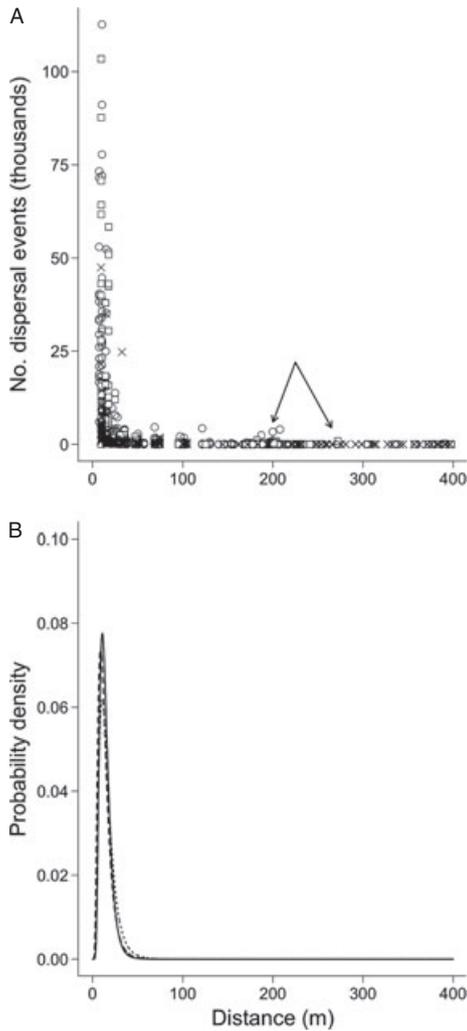
Figure 2 (A) Observed dispersal events and the (B) best-fitting dispersal probability density functions for each color of powder and source tree (lognormal in all three cases). Orange: open circles, solid line. Yellow: open squares, dashed line. Pink: crosses, dotted line. Arrows in (A) indicate dispersal events associated with flying insects. The probability that a dispersing particle will travel a given set of distances (e.g., between 50 and 60 m) can be approximated by integrating the probability densities [y-axis of (B)] over the distance interval.

source trees was best modeled using a lognormal function with similar parameter values suggests that dispersal was relatively independent of location of the source tree, at least over the duration of our study. Given the observed dispersal distances, our findings indicate that passive dispersal from a small number of HWA-colonized host trees could quickly lead to stand-level infestations. This suggests that efforts to detect, manage, and eradicate HWA infestations are more likely to succeed when conducted at the stand level (Costa, 2005).

Hemlock woolly adelgid crawlers may be primarily wind-dispersed, but vectored dispersal on birds and deer has also been observed (McClure, 1990). We did not observe vertebrate dispersal, but did document a number of cases of powder dispersal via flying insects. During our experiment, we observed large dipterans (primarily members of the family Tipulidae) flying through the understory with powder adhering to their legs and body. A number of such powder-bearing insects were caught on our trapping array, and were responsible for a few long-distance dispersal events (see arrows in Figure 2A), suggesting that large flying insects could in principle serve as dispersal vectors for adelgids. Although individual insects are unlikely to transport more than a few dispersing crawlers, the high abundance and diversity of flying invertebrates in the forest understory suggests that they may serve as important, but undocumented vectors of HWA spread.

Although the use of fluorescent powder is common in studies of pollination or other ecological processes (e.g., Waser & Price, 1982; Vicens & Bosch, 2000), its use to simulate within-stand HWA dispersal has a number of potential drawbacks. If HWA crawlers and clumps of fluorescent powder differ considerably in their aerodynamic qualities, their tendency for within-stand movement might also diverge. Although we attempted to correct for such differences by only tracking powder clumps whose two-dimensional surface area (length × width) was equal to or greater than that of HWA crawlers, ensuring that both moved at a similar rate and would ultimately require wind-tunnel tests. Another potential problem is that some wind-dispersed arthropods may actually resist being blown off a suitable host. 'Ballooning' organisms like spiders are more likely to enter the wind column when air speeds are moderate, and actively avoid being dislodged from a host at high-wind speeds (Suter, 1999; Reynolds et al., 2007). Although adelgid crawlers do not balloon, we are unaware of any research exploring the potential for crawler behavioral responses to different wind speeds and are thus unable to determine whether this might be a concern. Even if both concerns are valid, however, our study suggests the potential for particles of similar dimensions to HWA to spread rapidly between hemlock stands.

on hemlock trees are potentially capable of starting an infestation. At the landscape scale, a rare long-distance dispersal event of a single individual eventually may yield multiple isolated infestations substantially in advance of the invasion 'front'. Precisely such a pattern has been documented in surveys of HWA spread in southern New England (Preisser et al., 2008).

Our ability to distinguish between propagules from different trees enabled us to determine the shape of the dispersal distance pdf. The fact that dispersal from all three

Table 2 Best-supported distance probability functions and parameter estimates

Distance probability dispersal function	ΔAIC	w	μ	σ	Mean distance (m)
Pink					
Lognormal	0	1	2.637	0.533	13.98 [13.95, 14.00]
Inverse Gaussian	1935	<0.001			
Weibull	195992	<0.001			
Negative exponential	284636	<0.001			
Yellow					
Lognormal	0	1	2.563	0.436	12.98 [12.97, 12.99]
Inverse Gaussian	153673	<0.001			
Weibull	1137193	<0.001			
Negative exponential	1420590	<0.001			
Orange					
Lognormal	0	1	2.461	0.530	11.72 [11.71, 11.73]
Inverse Gaussian	255281	<0.001			
Weibull	1791806	<0.001			
Negative exponential	1936114	<0.001			

Variables are: ΔAIC, Akaike's information criterion (AIC) for each model, minus the AIC of the model with minimum AIC; w, normalized model selection weights; μ and σ, the mean and standard deviation of the natural logarithm of the dispersal distances. Distances in brackets represent estimates of the 95% confidence limits of the mean distance.

The relative ease with which we used fluorescent powder in our simulation of HWA dispersal suggests that this technique may provide a simple and affordable means for investigating other passive dispersal events in the field. The powder is similar to HWA crawlers and other small passively dispersed organisms in that it remains on branches until either wind or another vector removes it. Unlike HWA crawlers or organisms like the elongate hemlock scale (another invasive herbivore that competes with HWA; McClure, 1977; Preisser & Elkinton, 2008), fluorescent powder is easily visible and the source population can be clearly identified. Finally, the use of fluorescent powders allows the number of dispersing particles to be controlled by measuring the amount of powder applied. Given the tremendous volume of particles that can be used in the field, a very large source population can be established with little effort, which increases the probability of detecting rare long-distance dispersal events without the need to increase trap area.

More broadly, the quantification of dispersal processes is key to understanding many biologic processes, most notably the dynamics of spatial spread. In a statistical and modeling context, so-called 'fat-tailed' functions with relatively high proportions of long-distance dispersal events, such as the lognormal, may better describe patterns of dispersal. In the context of HWA, our results suggest that in only a few days, a single source population could infest other trees within several hundred meter radius, or beyond.

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