Dispersal of *Agrilus planipennis* (Coleoptera: Buprestidae) From Discrete Epicenters in Two Outlier Sites

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ABSTRACT Emerald ash borer, *Agrilus planipennis* (Fairmaire) (Coleoptera: Buprestidae), a phloem-feeding beetle native to Asia, has become one of the most destructive forest pests in North America. Since it was first identified in 2002 in southeast Michigan and Windsor, Ontario, dozens of isolated *A. planipennis* populations have been discovered throughout Michigan and Ontario, and in 12 other states and the province of Quebec. We assessed realized *A. planipennis* dispersal at two discrete outlier sites that originated 1 yr and 3 yr earlier from infested nursery trees. We systematically sampled ash trees within an 800 m radius of the origin of each infestation to locate galleries constructed by the progeny of dispersing *A. planipennis* adults. Our sampling identified eight trees at the 1 yr site infested with a mean ± SE of 11.6 ± 8.4 *A. planipennis* larvae and 12 trees at the 3 yr site with 25.8 ± 11.1 larvae per meter squared. Dendroentomological analysis indicated that *A. planipennis* populations were predominantly undergoing a 2 yr (semivoltine) life cycle at both sites. Colonized trees were found out to 638 and 540 m from the epicenters at the 1 yr and 3 yr sites, respectively. Logistic regression was used to determine whether the likelihood of *A. planipennis* colonization was affected by wind direction, ash phloem abundance, distance from the epicenter, or land-use type (i.e., wooded, residential, agricultural, or urban). Results show that the probability of *A. planipennis* colonization was significantly affected by ash phloem abundance and decreased with distance from the epicenter.

KEY WORDS *Agrilus planipennis*, biological invasion, dendroentomology, emerald ash borer, eradication

Emerald ash borer, *Agrilus planipennis* (Fairmaire) (Coleoptera: Buprestidae), has become one of the most destructive forest pests in North America. It was first identified in July 2002 as the cause of widespread ash (*Fraxinus* spp.) mortality in southeast Michigan and Windsor, Ontario, Canada (Cappaert et al. 2005, Poland and McCullough 2006). As of July 2009, *A. planipennis* populations had been identified in at least 12 additional states and the province of Quebec (EAB Information 2009).

In its native range in Asia, *A. planipennis* is not a significant pest and there was little to no information available related to the biology, survey methods, or control options when *A. planipennis* was discovered in North America (Poland and McCullough 2006). Initial studies in North America suggested *A. planipennis* required a year to complete development (Cappaert et al. 2005, Poland and McCullough 2006 and references therein). Generally, larvae feed on ash phloem from mid to late summer, complete four instars by autumn, overwinter as prepupae in either the thick outer bark or outer sapwood of the tree, then pupate in spring. Adult beetles, active for much of the summer, feed on ash foliage for 2–3 wk before laying individual eggs under bark flakes and in bark crevices from late June through mid August. Serpentine galleries excavated by larvae feeding in the phloem and cambium often score the outer sapwood, disrupting nutrient and water transport, leading to canopy dieback and, eventually, tree mortality. As of July 2009, this invasive pest had killed tens of millions of ash trees in forested and urban settings in Michigan and Ohio alone (EAB Information 2009).

Following identification of *A. planipennis* in late 2002, federal, state and provincial quarantines were imposed to limit transport of ash nursery trees, logs, firewood, or related materials from areas known to be infested. Regulatory personnel also initiated surveys to detect and delineate outlier populations of *A. planipennis* that originated when infested ash nursery trees were transplanted or infested ash logs or firewood were moved. Survey efforts were complicated by the difficulty of iden-

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tifying newly infested trees that typically exhibit no external symptoms (McCullough et al. 2009a). *A. planipennis* beetles do not appear to produce long-distance pheromones (Rodriguez-Saona et al. 2006) and effective traps and lures were not available. Virtually nothing was known about *A. planipennis* dispersal behavior or host selection by ovipositing female adults. Scientists speculated that *A. planipennis* dispersal could either be random, determined by prevailing winds or directed toward the concentrations of ash trees in the vicinity, but few data were available to address any of the hypotheses.

In October 2003, regulatory trace-backs of ash nursery trees originating within the known *A. planipennis* infestation in southeast Michigan led to the discovery of a discrete, localized *A. planipennis* outlier population that had become established when infested nursery trees were planted at the site in autumn 2002. A second outlier site, initiated by infested ash nursery trees planted in October 2000, was subsequently identified in November 2003. Because the infestations were relatively recent, discrete and well beyond the known *A. planipennis* infestation in southeast Michigan, regulatory officials targeted both outlier sites for eradication. Officials determined that all ash trees within 800 m of the origin of each infestation would be felled, chipped, and burned in an effort to destroy potentially infested but nonsymptomatic trees.

Eradication activities at the two outlier sites, however, provided a unique opportunity to assess realized dispersal of *A. planipennis* in areas where the origin and year of establishment of the infestations were known. The landscape at each site was heterogeneous, encompassing a variety of wooded, residential, agricultural, and highly developed urban areas. In cooperation with regulatory officials who provided access to private land, and contractors who assumed the challenges and liability associated with felling municipal and private trees, we systematically sampled individual ash trees within the 800 m radius established around the origin of each infestation.

Our goal was to assess realized dispersal of *A. planipennis* by examining the spatial distribution of trees with larval galleries, constructed by the progeny of the emerged adult beetles, in relation to the epicenter of each infestation. Our main objectives were to determine whether ash trees beyond the immediate vicinity of the epicenter had been colonized by *A. planipennis* and whether dispersal appeared to be random or influenced by prevailing winds or ash abundance. Another objective was to determine whether the broadly classified land-use types (i.e., wooded, residential, agricultural, and urban) affected the likelihood of *A. planipennis* colonization. Additionally, density and life stages of *A. planipennis* larvae on infested trees were recorded to learn more about the biology and development of this recent invader.

Materials and Methods

Study Sites. The two isolated *A. planipennis* outlier infestations were located in (1) the unincorporated community of Shields, in Saginaw County in eastern mid-

Fig. 1. Location of the *A. planipennis* outlier sites at Shields and St. Joseph, MI, where sampling and eradication activities occurred in 2004. The six counties originally quarantined for *A. planipennis* in 2002 are outlined by the bold line.

Michigan [43.42° N, 84.07° W]; and (2) the city of St. Joseph, in Berrien County in southwestern lower Michigan [42.08° N, 86.48° W] (Fig. 1). The Shields site (Fig. 2a) became infested in spring 2003 when adult beetles emerged from 12 ash nursery trees planted by landscapers the preceding autumn at a restaurant. Similarly, the St. Joseph site (Fig. 2b) had become infested in spring 2001 after adult *A. planipennis* emerged from six nursery trees planted in autumn 2000 at a restaurant. At each site, the infested ash nursery trees were planted in an area that was <0.4 ha in size. The infested nursery trees were 3–5 cm in caliper diameter and were apparently healthy, with no obvious canopy dieback or external symptoms of *A. planipennis* infestation at the time of planting. The nursery trees at both sites were destroyed in 2003 by Michigan Department of Agriculture (MDA) personnel when life stages collected from the trees were determined to be *A. planipennis.* Using methods described in McCullough and Siegert (2007) and reports from the MDA inspectors, we estimated phloem area and the potential number of adult *A. planipennis* that could have emerged from the infested nursery trees at each site. At Shields, where only a single generation of *A. planipennis* emerged, we assumed that up to 50% of the potential number of beetles that could have developed on the trees had emerged in 2003 before the trees were destroyed and that 50% of the emerged adults would have been female. Based on these estimates, ≈35 adult female *A. planipennis* likely emerged from the 12 nursery trees at the Shields site. At the St. Joseph site, where up to three generations of beetles could have emerged from the nursery trees at the time of our sampling (Fig. 3), we assumed that 100% of the potential beetles that could

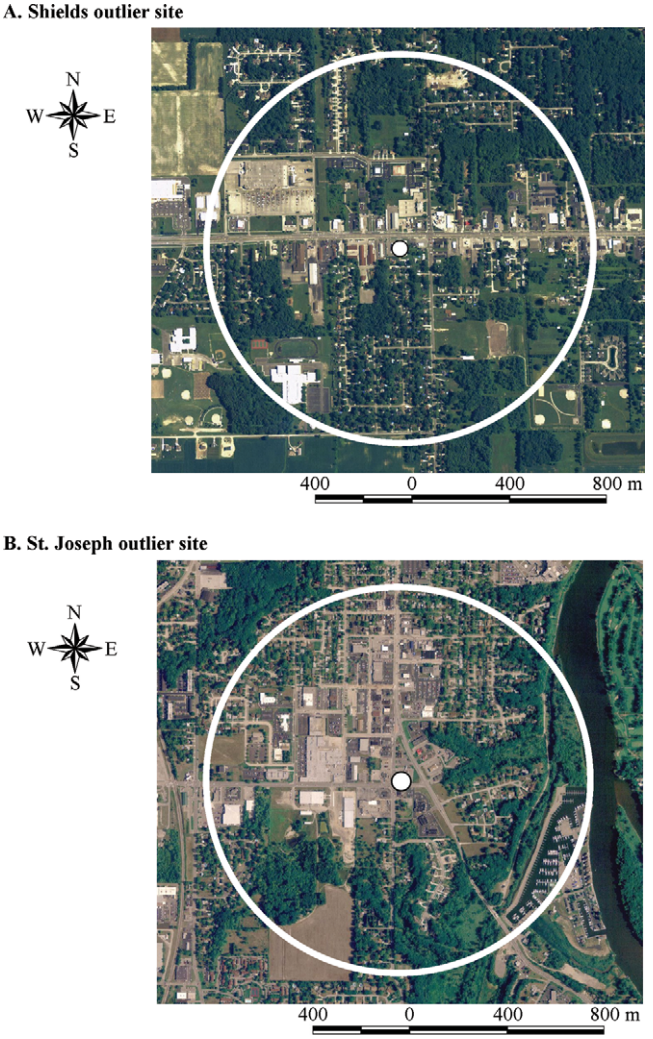

Fig. 2. Aerial photos of the (A) Shields and (B) St. Joseph sites, with the respective origins of the *A. planipennis* infestations and 800 m sampling radii denoted in white. (Online figure in color.)

have developed on the infested nursery trees emerged before the trees were destroyed and that 50% were female, yielding a total of ≈35 adult female *A. planipennis* over 3 yr.

Eradication protocols enacted by federal and state regulatory officials included removal and destruction of all ash trees ≥2.5 cm in caliper diameter within 800 m of any tree found to be infested during initial delimitation surveys. Personnel from the MDA marked and tallied ash trees by diameter class in each 100 × 100 m cell of a grid overlaid on the 2.0 and 2.2 km^2 areas delineated at Shields and St. Joseph, respectively (McCullough and Siegert 2007). The MDA personnel also classified each 100 × 100 m cell as primarily 'wooded' (e.g., woodlots without residences), 'residential' (e.g., private homes with yard trees), 'agricultural' (e.g., cropland or pasture), or 'urban' (e.g., commercial development) because different specifications and contracts were established for ash tree removal in forested areas and in residential or urban areas where structures, wires, and other hazards were common. Ash trees at both sites were predominantly green ash (*F. pennsylvanica* Marshall) although some white ash (*F. americana* L.) were present at the St. Joseph site.

Sampling Methods. Realized dispersal of *A. planipennis* adult females was assessed by identifying the location of ash trees infested with *A. planipennis* larvae in relation to the origin of each infestation. Trees were sampled from 23 to 27 February 2004 and from 4 to 9 April 2004 at the Shields and St. Joseph sites, respectively. Limited funds, time, and regulatory issues (e.g., unauthorized removal of felled ash material from the eradication area) required that our sampling and the subsequent eradication activities be completed as quickly as possible. Contractors felled, removed, and destroyed ash trees in both eradication areas immediately following our sampling.

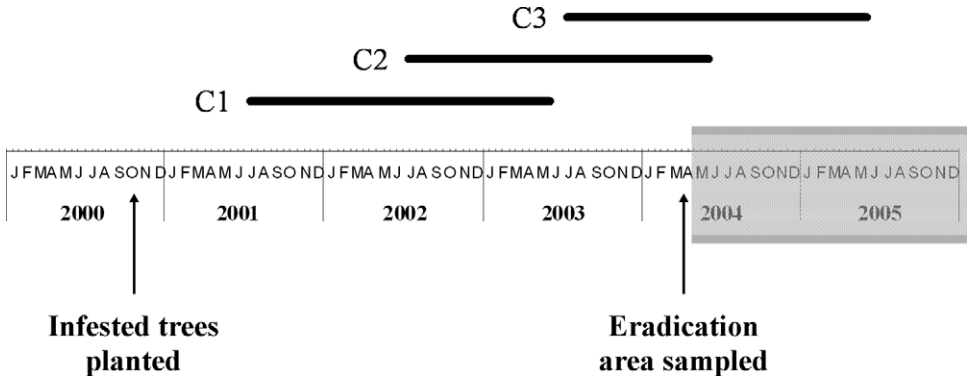

Fig. 3. Timeline of the three *A. planipennis* cohorts (C_1, C_2, and C_3) at the St. Joseph site. The shaded portion of the timeline denotes that ash trees in the study area were no longer present following eradication activities in April 2004.

At least one ash tree in each 100 × 100 m cell in the 800 m radius plot centered at the origin of each site was identified for sampling using a randomly selected direction and number of paces from the center or a corner of each cell. At the Shields site, a single ash tree was selected in each grid cell for sampling; in a few cells, an additional tree was also felled and sampled. At the St. Joseph site, if no *A. planipennis* larvae were found on the first tree, a second tree in the grid cell was sampled. Trees were felled by contractors working immediately ahead of our sampling crews. Diameter at breast height (DBH) was measured on all sample trees. When multiple trunks occurred, DBH of each trunk was recorded and summed. Ash phloem area was calculated using DBH of each tree with models developed by McCullough and Siegert (2007).

To sample trees for *A. planipennis* larvae, we delineated at least four sample areas, each ≥500 cm^2 in size, positioned 1–3 m apart on the trunk(s) and on all first-order branches ≥8 cm in diameter. Each sample area encompassed at least the upper half of the circumference of the trunk or branch. Sample areas were evenly spaced from 1.6 m aboveground to the upper canopy on the main leader(s) and along each large branch. Small trees (≤10 cm DBH) had a minimum of four sample areas while large trees had up to 24 sample areas. Each sample area was carefully debarked, using drawknives and chisels, and the exposed area was measured. Since there was more than one *A. planipennis* cohort at the St. Joseph site (see below), sample areas were selected and then intensively examined before debarking to determine whether exit holes created during *A. planipennis* adult emergence were present. Density of *A. planipennis* life stages on each infested tree was standardized per meter squared of sample area by dividing the total number of larvae found by the area of phloem exposed in the sample areas.

Dendrochronological Reconstruction of *A. planipennis* Cohorts at St. Joseph. At the St. Joseph site, we sampled an additional 48 ash trees growing at a shopping center, directly across the street from the restaurant where the infestation originated (Fig. 4). All 48 trees were within 300 m of the origin of the infestation. Thirty-five of the 48 additional trees were small trees (mean ± SE of 5.6 ± 0.30 cm DBH) that had been planted along the parking lot border or in parking lot islands. Some of these trees exhibited external symptoms of *A. planipennis* infestation including D-shaped exit holes caused by emerging adult beetles or splits in the bark that covered old *A. planipennis* galleries. We felled the 35 trees and completely debarked the trunk and main leader, down to 5 cm diameter. The other 13 trees were slightly larger (mean ± SE of 11.3 ± 1.1 cm DBH) and were growing in landscaped areas around the perimeter of the shopping center. These 13 trees were felled and at least four

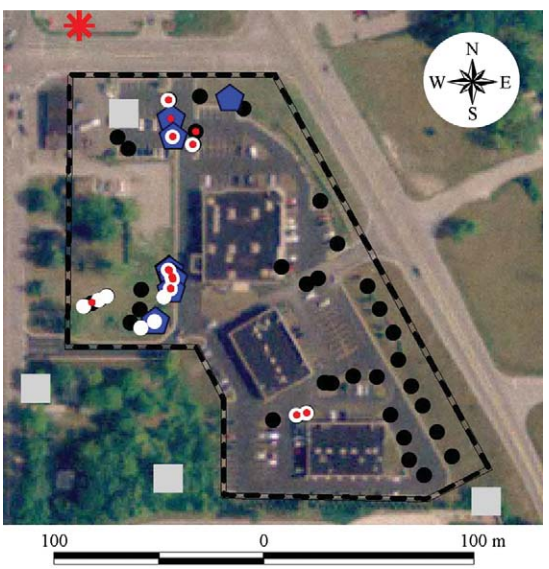

Fig. 4. Location of additional ash trees sampled at the shopping center (outlined with dashed line) adjacent to the epicenter of the St. Joseph outlier site (red asterisk). Trees with *A. planipennis* exit holes, prepupae, and larvae are denoted with blue pentagons, white circles, and red points, respectively. Black circles denote ash trees at the shopping center that did not have *A. planipennis* exit holes or life stages present, while gray squares denote the location of sample trees from the main grid sampling. (Online figure in color.)

sample areas per tree were debarked, using the methods described above for the grid sampling. Density of *A. planipennis* exit holes, prepupae and larvae were determined for all 48 trees.

One or more cross-sections collected from infested portions of the trees sampled in the main grid sampling and the 48 additional trees at the shopping center were used to reconstruct *A. planipennis* population dynamics after introduction. Cross-sections were sanded smooth with successively finer grit sandpaper and then examined under a microscope. Scars from *A. planipennis* galleries or cells excavated by prepupal larvae were dated to determine the year of infestation, duration of larval development, and subsequent emergence of *A. planipennis* adults.

Spatial Distribution of Colonized Trees. To assess the spatial distribution of trees with *A. planipennis* galleries, we calculated the center of mass of the infestation, along with its associated weighted and unweighted mean vectors, at the Shields and St. Joseph sites. Center of mass calculations represent the overall movement of a population and incorporate the rectangular coordinate (i.e., x_i and y_i) spread of the population from the epicenter and *A. planipennis* densities along each vector (Batschelet 1965). The weighted center of mass calculation of the *A. planipennis* distribution takes into account the density of *A. planipennis* in each grid cell, whereas the unweighted center of mass calculation treats each positive grid cell equally (Batschelet 1965).

Given n observations with rectangular coordinates x_i and y_i, the components of the unweighted center of mass of a distribution are:

$$x = n^{-1}(x_1 + x_2 + x_3 + \ldots + x_n), \quad [1]$$

$$y = n^{-1}(y_1 + y_2 + y_3 + \ldots + y_n). \quad [2]$$

The components of the weighted center of mass of a distribution are:

$$x = (M_1x_1 + M_2x_2 + M_3x_3 + \ldots)/(M_1 + M_2 + M_3 \ldots) = (\sum M_ix_i)/(\sum M_i), \quad [3]$$

$$y = (M_1y_1 + M_2y_2 + M_3y_3 + \ldots)/(M_1 + M_2 + M_3 \ldots) = (\sum M_iy_i)/(\sum M_i), \quad [4]$$

where M = the *A. planipennis* density in the grid cell.

Variables that could potentially influence dispersal of *A. planipennis* beetles and the distribution of colonized trees within each site were tested using logistic regression to evaluate the significance of specific predictor variables (R Core Development Team 2009). Because relatively few grid cells at either site had a colonized tree, we used a penalized maximum likelihood estimation of the logistic model to avoid inflated standard errors resulting from the high number of grid cells with a value of zero (Heinze 2006, Heinze and Schemper 2002, Heinze and Ploner 2003). Variables evaluated in our model included prevailing wind direction, ash phloem abundance, distance from the epicenter and land-use type (i.e., wooded, residential, agricultural, urban).

To evaluate effects of prevailing, southwesterly winds on beetle dispersal and location of colonized trees, we created a variable for the logistic regression by coding grid cells with at least one ash tree by its cardinal or intercardinal direction (i.e., north, northeast, east, southeast, south, etc.) from the epicenter. We effectively used the variable to test a linear contrast, in which the highest colonization likelihood would be expected northeast of the epicenter (e.g., beetle flight with the wind) and lowest colonization would be expected southwest of the epicenter (e.g., beetle flight against the wind). Grid cells in intermediate directions (i.e., north or east of the epicenter) would be expected to have higher colonization rates than grid cells which were perpendicular to prevailing wind direction (i.e., northwest or southeast of the epicenter), but lower than cells to the northeast. Similarly, grid cells to the south and west would presumably have higher probabilities of colonization than grid cells to the southwest but lower than cells to the northwest or southeast. Grid cells with no ash were treated as missing.

To assess the potential effect of ash phloem abundance on the spatial distribution of colonized trees, total area (m^2) of ash phloem per grid cell was calculated as per McCullough and Siegert (2007), using ash inventory data collected by the MDA survey crews and the midpoint of each diameter class. Frequency histograms were plotted to examine distribution of ash phloem by site and land-use type. Ash phloem area was subsequently rescaled (per 100 m^2) to avoid extremely small coefficients and then $\ln(x)$ transformed before inclusion in the logistic model. This transformation substantially reduced the skewness of the phloem variable and changed the meaning of the phloem coefficient to represent the effect of a *one percent* increase in phloem rather than the effect of a *one unit* increase in phloem (Vittinghoff et al. 2005). Distance of the center point of each grid cell from the epicenter was also rescaled (per 100 m), as described for ash phloem. Land-use classes (i.e., wooded, residential, agricultural, and urban) were included as dummy variables in the logistic model, with agricultural serving as the reference category. The significance of the interaction of ash phloem abundance and distance from the epicenter was of a priori interest and included in the model.

We used the odds ratios (OR) to explore the probability implications of the significant predictor variables from the logistic regression following methods described in Liberman (2005). We calculated the probability pair at the center of the probability range by taking the square root of the odds ratio value, equivalent to the centered risk ratio (RR), then determining the centered p_L as $1/(1+\sqrt{OR})$ and the centered $p_H = 1\text{-}p_L$. The difference between p_L and p_H represents the difference in probability of colonization with an incremental change in the predictor variable (Liberman 2005).

Table 1. Percentage of ash phloem (m^2) available for *A. planipennis* colonization within 200 m of the origin of the infestation by ash diam class for each secondary intercardinal direction at the Shields and St. Joseph sites

Site	Secondary intercardinal direction	Ash diam class (DBH)			
		2.5–25 cm (1–10 in)	26–42 cm (11–17 in)	43–60 cm (18–23 in)	>60 cm (>23 in)
Shields	NNE	100	0	0	0
	ENE	10	0	0	90
	ESE	80	20	0	0
	SSE	60	20	10	10
	SSW	70	10	20	0
	WSW	70	30	0	0
	WNW	100	0	0	0
	NNW	0	0	0	0
St. Joseph	NNE	40	60	0	0
	ENE	50	40	0	10
	ESE	70	0	0	30
	SSE	45	35	20	0
	SSW	45	35	20	0
	WSW	100	0	0	0
	WNW	100	0	0	0
	NNW	100	0	0	0

Results

Shields Site. At Shields, a total of 20,083 ash trees with 83,410 m^2 of phloem area, occurred in 155 of the 265 grid cells (58.5%) within the 2.0 km^2 area inventoried around the origin of the infestation (Fig. 2a). Small ash trees (≤25.4 cm DBH) were much more abundant than larger trees and comprised 96.4% of all ash at the site. Within the first 200 m radius of the origin of the *A. planipennis* infestation, these small trees accounted for at least 70% of the ash phloem area in all directions except the ENE direction, where most of the ash phloem was provided by large trees (>60 cm DBH) (Table 1). Trees of merchantable size (>25.4 cm DBH) amounted to only 3.6% of the ash and trees ≥43 cm DBH comprised only 1% of the ash trees. Of the 155 grid cells with ash present, 57 were categorized as wooded, 79 were categorized as residential, six were categorized as agricultural, and 13 were categorized as urban. Agricultural and urban cells only contained 1.0 and 1.8%, respectively, of the total ash phloem, while the cells classified as residential and wooded contained 29.7 and 67.5% of the ash phloem, respectively.

A total of 121.7 m^2 of ash phloem was exposed on the 143 green ash trees that were sampled at Shields. *A. planipennis* larvae were found on eight of the sampled trees. Infested trees ranged in DBH from 10.2 to 50.8 cm with a mean ± SE of 27.2 ± 5.78 cm, while DBH of uninfested trees ranged from 3.0 to 63.5 cm (mean ± SE of 24.0 ± 1.2 cm DBH). On average, we debarked and sampled a mean ± SE of 1.2 ± 0.3 m^2 (range of 0.5–3.6 m^2) of phloem area on each of the positive trees.

We found a total of 58 *A. planipennis* larvae or galleries on the eight positive trees at Shields. These larvae were the progeny of beetles that dispersed from the nursery trees that initiated the infestation and all initiated their feeding in 2003. Mean ± SE density of *A. planipennis* on the positive trees was 11.6 ± 8.4 beetles per meter squared of phloem. The overall mean *A. planipennis* density at the Shields site, however, was strongly influenced by a single tree, 15.0 cm DBH, located 220 m from the infestation origin. This was the only ash tree in our sample that was obviously stressed. It was growing on a property boundary and was half girdled by a woven wire mesh fence that had been nailed to the trunk several years before our sampling; part of the main leader and at least one large branch had died and broken off. We found 36 larvae in the area sampled on the stressed tree, equivalent to a density of 70.3 larvae per meter squared. Three of the *A. planipennis* were overwintering as fourth-instars while the rest were prepupal larvae (92%). In contrast, 17 of the 22 larvae (77%) found on the other seven infested trees at Shields were overwintering as early instars (Fig. 5). On those seven apparently healthy trees, larval density ranged from 0.8 to 6.3 larvae per meter squared, with a mean ± SE of 3.2 ± 0.8 larvae per meter squared.

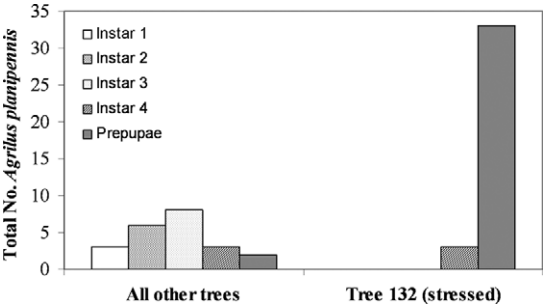

Fig. 5. Distribution of *A. planipennis* larval stages in positive trees sampled at the Shields outlier site. All larvae began feeding in 2003.

The *A. planipennis* beetles that emerged from infested nursery trees at Shields in 2003 oviposited on trees located 91–638 m away from the origin of the infestation (Fig. 6a). Distance of positive trees from the origin averaged 357.9 ± 71.2 m. There were two, three, one, and two positive trees within the 0–200, 201–400, 401–600, and 601–800 m radii around the origin, respectively. One positive tree occurred in a grid cell classified as wooded, while two positive trees, including the stressed tree with the high *A. planipennis* density, were in landscape trees around commercial buildings in cells classified as urban. Five positive trees were growing in lawns in cells classified as residential. The weighted center of mass of the *A. planipennis* distribution indicated that the overall movement of the infestation was 210 m toward the southwest, while the unweighted center of mass indicated the direction of movement was 270 m toward the south (Fig. 6a).

Number and size of ash trees, and subsequently the amount of ash phloem available to be potentially colonized by *A. planipennis*, varied considerably among the 100 × 100 m grid cells at the Shields outlier site (Fig. 7a). In the first 200 m radius, ash trees were positioned primarily toward the south (i.e., ESE, SSE, SSW, and WSW), with few positioned north of the origin (Table 1; Fig. 7a). Overall, however, the highest density of ash and the greatest amount of ash phloem

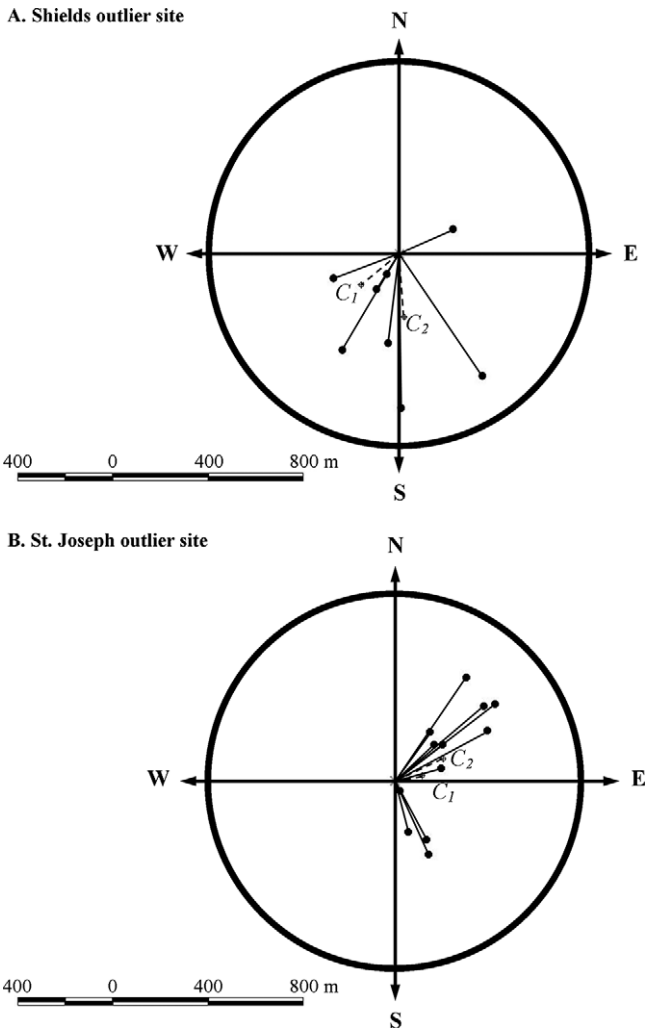

Fig. 6. Distribution of sampled trees with *A. planipennis* (black points) in relation to the origin at (A) the Shields site and (B) the St. Joseph site, with center of mass calculations. The weighted center of mass, C_1, accounts for the density of *A. planipennis* found in each positive sample tree, while the unweighted center of mass, C_2, treats each positive tree equally.

occurred in wooded areas that were northwest, northeast, and southwest of the origin (Table 2; Fig. 7a).

St. Joseph Site. At the St. Joseph site, a total of 21,429 ash trees with 68,131 m^2 of phloem area occurred in 140 of the 260 grid cells (53.8%) within the 2.2 km^2 area inventoried around the origin of the infestation (Fig. 2b). Distribution of ash trees by diameter size class and ash phloem by land-use at St. Joseph was similar to that at the Shields site. At the St. Joseph site, small ash trees (≤25.4 cm DBH) comprised 93.7% of all ash in the project area. Trees of merchantable size (>25.4 cm DBH) amounted to 6.3% of all ash and only 1.3% of the ash trees were >43 cm in DBH. Of the 140 grid cells with ash present, 65 were categorized as wooded, 58 were categorized as residential, nine cells were categorized as agricultural, and eight were categorized as urban. Cells classified as agricultural and urban contained only 1.3 and 0.5% of the total ash phloem, respectively, while the cells classified as wooded and residential contained 82.3 and 15.9% of the total ash phloem, respectively. Within the first 200 m radius of the origin, small trees (≤25.4 cm DBH) contained 40–100% of the ash phloem in all directions (Table 1). Ash trees ≥26 cm DBH occurred within 200 m of the origin in all directions except WSW, WNW, and NNW (Table 1).

A total of 138.7 m^2 of ash phloem was exposed on the 220 trees that were felled and sampled in the 260 grid cells at St. Joseph. On average, a mean ± SE of 1.2 ± 0.2 m^2 (range of 0.5–2.0 m^2) of phloem was exposed on the positive trees. We found 12 positive trees in 12 different grid cells; 10 of the infested trees were green ash and two were white ash. The 12 positive trees ranged in DBH from 22.9 to 55.9 cm (mean ± SE of 35.7 ± 2.52 cm). For the uninfested trees, DBH ranged from 3.0 to 91.4 cm (mean ± SE of 29.0 ± 1.2 cm). Only 12 of the negative trees were white ash; the other 196 negative trees were green ash.

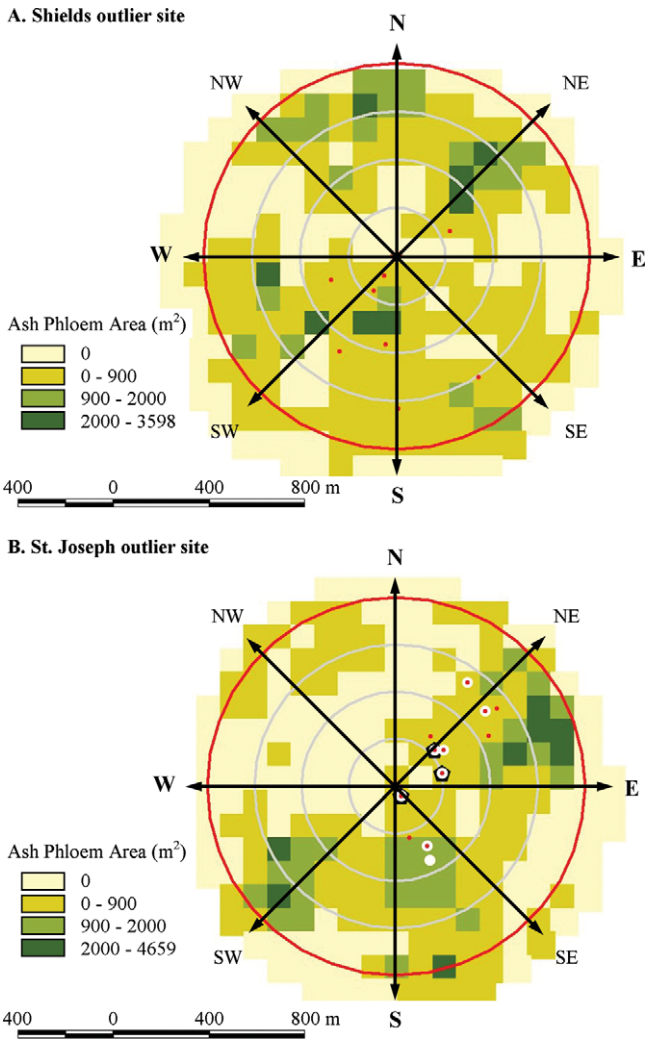

Fig. 7. Distribution and density of ash phloem per 100 × 100 m grid cell and the corresponding locations of sampled trees with *A. planipennis* exit holes (black pentagons), prepupae (white circles), and larvae (red points) within 200, 400, 600, and 800 m radii from the origin of the (A) Shields and (B) St. Joseph sites. Areas extending beyond the 800 m radius at either site were not included in analyses. (Online figure in color.)

We recorded a total of 346 *A. planipennis* larvae (including 63 prepupae), 58 exit holes left by emerged adults and 20 woodpecker attacks on late instar larvae on the 12 positive trees. Overall, *A. planipennis* density (including emerged adults) in the sampled trees averaged 25.8 ± 11.1 per meter squared. Positive trees were in two cells classified as urban, four cells classified as wooded and six cells classified as residential.

Dendrochronological analysis indicated that three separate *A. planipennis* cohorts occurred at St. Joseph between October 2000 when the infested trees were planted and April 2004, when we sampled the eradication area (Fig. 3). The first *A. planipennis* cohort, as evidenced by the presence of exit holes on three sample trees, was generated by adult *A. planipennis* that emerged from the original nursery trees in 2001. There was no evidence of emergence by this cohort until 2003 when 58 beetles emerged. The second cohort at the St. Joseph site likely represented progeny of adult *A. planipennis* beetles that emerged from the original nursery trees in 2002 (Fig. 3). A total of 93 overwintering fourth-instar and prepupae, which would have emerged as adults in summer 2004, were recorded on eight of the 12 infested trees. The third *A. planipennis* cohort represented the progeny of adult beetles that emerged in 2003 (Fig. 3) from both the original nursery trees and from established trees that became infested in 2001. The 272 *A. planipennis* larvae in the third cohort were overwintering as early instars on all 12 of the infested trees and would have continued to feed under the bark through 2004, overwinter and emerge as adults in 2005. Four of the 12 infested trees at St. Joseph had only early instars present and would not have produced any adult beetles until 2005.

Table 2. Amount of ash phloem (m^2) available for *A. planipennis* colonization within 200 m intervals for each secondary intercardinal direction at the Shields and St. Joseph sites

Site	Secondary intercardinal direction	Distance interval from epicenter (m)				
		0–200	200–400	400–600	600–800	0–800
Shields	NNE	5	876	6863	3494	11,239
	ENE	24	3698	5095	4447	13,265
	ESE	178	884	649	597	2308
	SSE	467	1039	993	3680	6179
	SSW	905	4453	3013	4111	12,482
	WSW	61	1175	6611	5071	12,918
	WNW	4	122	228	1422	1776
	NNW	0	1277	4841	9817	15,936
St. Joseph	NNE	104	250	563	1585	2503
	ENE	142	1334	6307	14810	22,594
	ESE	30	212	1553	785	2580
	SSE	336	3241	6759	6003	16,340
	SSW	84	1102	2674	4200	8060
	WSW	0	305	4780	4292	9378
	WNW	0	0	235	334	569
	NNW	0	0	151	1337	1488

A. planipennis life stages were found on trees located 50–540 m away from the origin of the infestation, with an average distance of 322.3 ± 44.0 m (Fig. 6b). There were three, six, four, and zero positive trees in the 0–200, 201–400, 401–600, and 601–800 m radii around the origin, respectively. Four positive trees occurred in grid cells classified as wooded, while two positive trees were landscape trees in cells classified as urban. Six positive trees were growing in yards in cells classified as residential. Only three trees had exit holes and all were located within 225 m of the origin. All positive trees were located within 600 m of the origin. Generally, movement of the population over the three years that the site was infested was 128 m toward the east (weighted) or 229 m toward the east-northeast (unweighted) (Fig. 6b).

Similar to the Shields site, the number and size of ash trees, and subsequently the amount of ash phloem available to be potentially colonized by *A. planipennis*, varied considerably among the 100 × 100 m grid cells at St. Joseph (Fig. 7b). The ash trees closest to the origin of the infestation were in grid cells positioned primarily toward the southeast and east-northeast of the epicenter (Table 1; Fig. 7b). Overall, however, the highest density of ash and the greatest amount of ash phloem occurred in wooded areas that were east-northeast, south and southwest of the infestation origin (Table 2; Fig. 7b).

Additional Sampling Near the Epicenter of the Infestation at St. Joseph. We found 21 of the 48 trees growing at the shopping center across from the origin of infestation had been colonized by *A. planipennis* (Fig. 4). All 13 of the larger landscape trees and eight of the 35 smaller trees were infested. Overall, *A. planipennis* density (including emerged adults) in the 21 positive trees from the shopping center averaged 32.6 ± 6.1 per meter squared.

Progression of the *A. planipennis* cohorts that developed as a result of the infested nursery trees planted in October 2000 was reconstructed through intensive dendrochronological analysis of cross-sections collected from the 21 positive trees at the shopping center (Fig. 3). Results indicated that three separate *A. planipennis* cohorts had been initiated on the trees at the shopping center in 2001, 2002, and 2003. We found no evidence of *A. planipennis* adult emergence from the trees at the shopping center until 2003, suggesting that the first two cohorts were progeny of beetles that emerged from the infested nursery trees planted at the restaurant in October 2000 (Fig. 3). In 2003, 50 of these larvae completed development and emerged from the shopping center trees as adult beetles (Fig. 3). We also recorded a total of 181 fourth-instars or prepupae overwintering in the shopping center trees. These larvae were the progeny of beetles that emerged from the infested nursery trees and reproduced in 2002. This cohort would have emerged as adults in May or June of 2004 (Fig. 3). The 81 *A. planipennis* that were overwintering as early instars when we sampled the trees in April 2004 would likely have continued to feed through 2004, overwinter and emerge as adult beetles in 2005. These early instars represented the progeny of beetles that emerged in 2003 from either the infested nursery trees or other trees infested by the first *A. planipennis* cohort, including those at the shopping center (Fig. 3).

Spatial Distribution of Colonized Trees. The potential influence of prevailing wind direction, ash phloem abundance, distance from the epicenter and land-use type on dispersal of *A. planipennis* beetles and the distribution of colonized trees within each site were tested using logistic regression. Results indicated that ash phloem abundance, distance from the epicenter, and the interaction of ash phloem abundance by distance from the epicenter significantly influenced dispersal of *A. planipennis* ($P < 0.05$) (Table 3). The effect of site was also significant, indicating that trees were more likely to be colonized by *A. planipennis* at the 3 yr old infestation in St. Joseph compared with the Shields site that was infested for only 1 yr ($P = 0.03$). Prevailing wind direction and land-use type at Shields and St. Joseph did not significantly influence dispersal of *A. planipennis* ($P > 0.05$) (Table 3). Interpretation of the odds-ratios associated with the main effects of phloem abundance and distance via the calculation of the probability pairs (Liberman 2005) suggests that a 1% change in the rescaled phloem abundance (measured in 100 m^2 units) would increase the probability of encountering an infested tree in our sampling by up to 25%, whereas a 100 m increase in distance from the epicenter would decrease the probability of colonization by up to 20%. However, the significant interaction between these two factors indicates that differences in phloem abundance matter substantially more at short distances than at longer distances. The predicted probability of *A. planipennis* colonization increases with greater abundance of ash phloem at several distances (Fig. 8). Because of the nonlinear nature of the ln(x) transformation used on ash phloem abundance, back-transforming the phloem values to more interpretable units (Fig. 8b) clarifies the nature of the interaction substantially. At short distances (0–200 m), the probability of *A. pla-*

Table 3. Coefficients, standard errors, upper and lower 95% confidence intervals (CI), χ^2 statistics, *P* values, and OR coefficients and 95% CIs for variables tested in a penalized max likelihood logistic regression to assess the likelihood of an ash tree colonized by *A. planipennis* occurring in a grid cell at two outlier sites

Factor	Coefficient	SE	Lower 95% CI	Upper 95% CI	χ^2	*P*	OR Coefficient	OR CI lower	OR CI upper
(Intercept)	−0.321	1.820	−5.410	2.630	0.0354	0.8506	0.73	0.00	13.87
Sites	1.254	0.586	0.121	2.516	4.734	0.0296	3.50	1.13	12.38
ln(phloem/100)	1.0183	0.340	0.371	1.738	9.667	0.0019	2.77	1.45	5.69
Distance/100	−0.815	0.171	−1.205	−0.497	31.049	<0.0001	0.44	0.30	0.61
Wind	0.157	0.204	−0.248	0.572	0.579	0.4468	1.17	0.78	1.77
Residential	1.150	1.708	−1.438	6.154	0.606	0.4364	3.16	0.24	470.40
Urban	1.652	1.806	−1.233	6.733	1.124	0.289	5.22	0.29	840.06
Wooded	−0.125	1.757	−2.917	4.907	0.005	0.9413	0.88	0.05	135.30
ln(phloem/100) × Distance/100	−0.199	0.065	−0.332	−0.062	7.620	0.0006	0.82	0.72	0.94

nipennis colonization rapidly increases with ash phloem abundance and ash trees in grid cells containing more than ≈1,000 m^2 of phloem were quite likely to be colonized. At longer distances from the epicenter, even very large amounts of ash phloem did not lead to a high probability of colonization (Fig. 8b). The main effect of site, however, alters those probability curves somewhat, suggesting that at St. Joseph, the site that had been infested longer, trees in distant grid cells that had large amounts of ash phloem were at greater risk of *A. planipennis* colonization than at the Shields site.

Discussion

Information about *A. planipennis* dispersal in localized outlier sites is critically needed as more states and provinces contend with this invasive pest. Understanding how far *A. planipennis* beetles may disperse and whether site-related factors influence dispersal could help officials develop appropriate protocols for *A. planipennis* detection, delimitation surveys and regulatory activities. Such information is also needed to accurately predict the rate and pattern at which *A. planipennis* infestations expand spatially.

Unfortunately, accurate assessments of *A. planipennis* dispersal are difficult to acquire. Efforts to visually monitor activity of the small, strong-flying *A. planipennis* beetles with high-powered, stabilized binoculars and scopes or electronically with micro-antennae in the field have not been successful (D.G.M. and T.M.P., unpublished data). Trees with low densities of *A. planipennis* exhibit virtually no external symptoms of in-

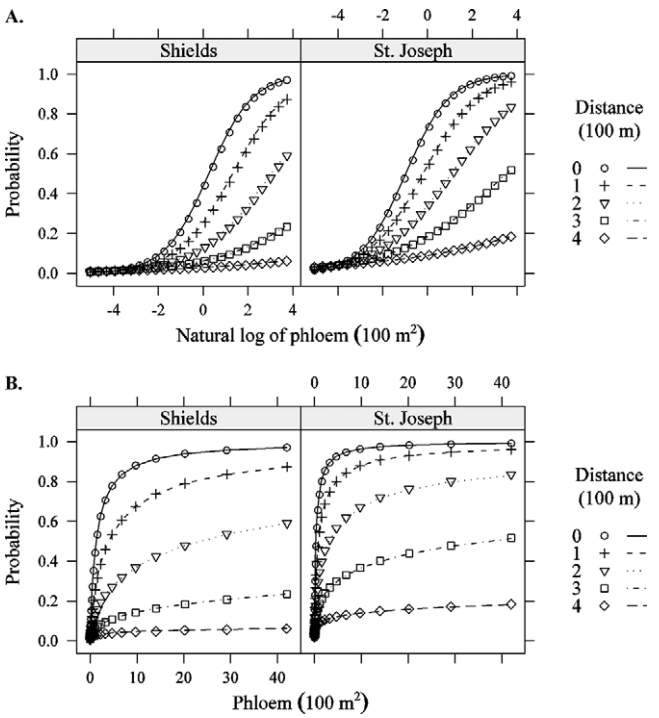

Fig. 8. Relationship between the probability of colonization by *A. planipennis* and (A) ln(x) transformed ash phloem abundance and (B) nontransformed ash phloem abundance, for five distances from the epicenter.

festation. Removing bark to locate larval galleries, as we did in these studies, is highly labor intensive and obviously destructive. Nevertheless, the information we collected by felling and sampling ash trees represents realized dispersal and reproduction of *A. planipennis* females, which determines the spatial and numerical progression of an infestation.

Previous efforts to assess *A. planipennis* dispersal have included flight mill studies in laboratory settings and mark-recapture studies in the field. Taylor et al. (2007) reported that mated females tethered to a flight mill were capable of flying twice as far as younger, unmated females. Maximum total flight recorded was 9.8 km (6.1 miles) by a mated female who flew 8 h per day for 5 consecutive days. Flight mill data, however, are best suited for relative comparisons, such as between sexes or between mated and unmated beetles. As noted by Taylor et al. (2007), results from flight mills cannot be calibrated with flight in the field, where beetles may be influenced by numerous biotic and abiotic factors.

Mark-recapture studies have been used to assess dispersal of numerous insects including rangeland grasshoppers and scolytid bark beetles (e.g., Cronin et al. 1999, Narisu et al. 1999). Fraser et al. (2007a,b) marked *A. planipennis* beetles reared from infested ash logs, and then released the marked beetles from a central point surrounded by sticky traps attached to trees in concentric circles around the release point. In 2005, 3.5% of 6,000 marked beetles were captured and the most distant beetle was trapped 60 m from the release point. In 2006, 3.6% of ≈18,800 marked beetles were captured; the furthest capture was 305 m from the release point. Dispersal appeared to be random with no pattern discernable and no differences between sexes. Both studies, however, were apparently conducted in sites with heavily-infested, declining ash trees (Fraser et al. 2007a,b). Stress caused by high densities of *A. planipennis* larvae, girdling or other injuries alters the volatile profile of ash trees (Rodriguez-Saona et al. 2006, Crook et al. 2008). Adult *A. planipennis* respond to stress-related foliar volatile compounds in laboratory tests (Rodriguez-Saona et al. 2006) and are attracted to stressed trees in the field (McCullough et al. 2009b). Volatiles emitted by infested, declining ash trees in these sites presumably could have affected dispersal behavior of the marked *A. planipennis* beetles.

Dispersal of *A. planipennis* was also evaluated in two field studies that used methods similar to those reported here to assess realized reproduction by recording the density and distance of larval galleries produced by a single cohort of adults emerging from a known origin (Mercader et al. 2009). In contrast to Shields and St. Joseph, however, ash trees in these two sites were distributed linearly, along a drainage ditch in one case and along a highway right-of-way in the other. Galleries were found on trees out to 750 m from the origin in one site and 240 m from the origin in the other. More than 80% of the larvae, however, were within 100 m of the origin at both sites and the distribution of larval galleries was well described by a negative exponential function (Mercader et al. 2009). While these studies were informative, the linear distribution of the ash trees likely functioned to direct beetle dispersal, similar to the corridor effect described by Shigesada and Kawasaki (1997). The Shields and St. Joseph sites, with a heterogeneous distribution of ash in all directions around a known origin, represent situations that are more commonly encountered in forest and urban settings.

Our sampling design incorporated two potential sources of variability including the likelihood of finding *A. planipennis* life stages on a tree that had been colonized and the likelihood of sampling a colonized tree in a grid cell. We are confident that when trees were actually infested, our sampling was sufficiently intense to locate larvae, even at ultra-low *A. planipennis* densities. At Shields, for example, we found a single first-instar larva overwintering on a large ash tree. Most of the bark on the other branches and trunk of the tree was subsequently removed but no additional larvae were found. We have successfully used similar sampling protocols in other low density sites to delimit recently established *A. planipennis* infestations or to assess effects of management strategies (McCullough and Siegert 2007; D.G.M. and N.W.S., unpublished data). Potential variability among ash trees within a grid cell is more difficult to address. Trees within grid cells were randomly selected for sampling and we effectively allocated similar sampling effort across the 2.0–2.2 km^2 sites defined by the 800 m radius around the origin of each infestation. We sampled only 0.8 and 0.7% of the total number of ash trees, however, at the Shields and St. Joseph sites, respectively. We cannot discount the possibility that colonized ash trees occurred but were not sampled in some grid cells nor can we be certain that some proportion of female beetles did not disperse beyond 800 m. The sampling effort that would have been necessary to sample all trees within grid cells or to locate infested trees beyond 800 m was well beyond our available financial and physical resources.

The weighted center of mass and logistic regression analyses showed that *A. planipennis* females did not disperse randomly from the infested nursery trees that initiated the infestations. There was no evidence that dispersal was influenced by prevailing wind direction nor did tree size appear to affect *A. planipennis* host selection at either site. The significant interaction between ash phloem abundance and distance from the epicenter, however, indicates that differences in phloem abundance mattered substantially more at short distances than at longer distances. Locations of the infested trees at both sites indicate beetle dispersal was directed toward areas where ash phloem was relatively abundant within 200 m of the origin. Whether ash phloem was abundant beyond 200 m in any given direction was less important. In other words, at short distances (0–200 m), the probability of *A. planipennis* colonization rapidly increased with ash phloem abundance and ash trees in grid cells containing more than ≈1,000 m^2 of phloem were quite likely to be colonized. At longer distances from the epicenter, however, even very large amounts of ash phloem

did not lead to a high probability of colonization. The apparent inclination of beetles to colonize nearby trees, particularly in areas where ash phloem was abundant, could reflect beetle response to a concentration of host volatiles or visual orientation toward ash foliage by beetles that must feed soon after emergence.

At the Shields site, where only a single cohort of adult beetles emerged from the nursery trees that initiated the infestation, the furthest gallery was 683 m from the origin. Overall, however, 93.6% of the galleries we recorded were within 450 m of the origin and if the single stressed, heavily infested tree is excluded, 73.3% of the galleries were within 450 m of the origin. At St. Joseph, dendrochronological evidence from the trees we sampled indicated that the trees colonized in 2001 or 2002 by beetles emerging from the infested nursery trees were located up to 535 m from the origin. Overall, 93.6% of the galleries found in the grid sampling were within 450 m of the origin. The most distant infested tree was 540 m from the origin and none of the trees in the 600–800 m radius were infested. Although extrapolating from these sites to other *A. planipennis* outlier sites should be done cautiously, the dispersal toward concentrations of ash phloem adjacent to or very near the origin of the Shields and St. Joseph infestations may be useful in developing delimitation survey plans.

While dispersing *A. planipennis* beetles likely respond to many factors, stressed ash trees appear to consistently affect host selection of ovipositing females. In Asia, *A. planipennis* appears to function as a secondary pest, colonizing only stressed or declining ash trees (CAS 1986, Yu 1992, Hou 1993, Xu 2003, Gao et al. 2004). At Shields, the tree that was visibly stressed and declining was 220 m from the origin but accounted for 62% all galleries recorded at the site. The relatively high density of larvae on this tree is consistent with results of other field studies that have shown stressed ash trees differ from healthy ash trees in volatile profiles and hyperspectral emissions (Bartels et al. 2007) and are consistently more attractive to *A. planipennis* (McCullough et al. 2009a,b).

The semivoltine (2 yr) life cycle of *A. planipennis* documented at Shields and St. Joseph has important implications for developing survey protocols, predicting population growth, and effectively managing *A. planipennis* infestations. The univoltine life cycle of *A. planipennis* was originally described in southeast Michigan in areas with relatively high densities of *A. planipennis.* Subsequent observations have confirmed that in trees with moderate to high *A. planipennis* densities, larvae typically feed in late summer and autumn, overwinter as fourth-instars or prepupae, then pupate and emerge as adults the following summer (Cappaert et al. 2005, Poland and McCullough 2006). In nearly all of the infested trees at Shields and St. Joseph, however, larvae required two years to complete development. Larval densities in these trees were typically low and galleries appeared to cause relatively little stress to the trees. In the seven healthy but infested trees at Shields, 77% of the larvae were overwintering as early instars and would have required another summer of feeding before emerging as adults in 2005. Similarly, in the St. Joseph trees, virtually all larvae that we encountered in our sampling developed or were developing over two years. In 2003, beetles emerged not only from the original point source (i.e., the nursery trees) but also from trees at the shopping center and at least three other trees detected in our grid samples. The notable exception to this pattern was the stressed, declining tree at the Shields site. Not only was this tree highly attractive to ovipositing adult beetles, the larvae on the tree developed much more rapidly than larvae on the other trees, where densities were much lower. Research in other newly infested sites have similarly shown prolonged larval development in healthy trees with low *A. planipennis* densities, while life cycles in trees with higher larval densities are predominately univoltine (Cappaert et al. 2005; Tluczek 2009; N.W.S. and D.G.M., unpublished data).

Ash trees at both the Shields and St. Joseph sites were present on a wide range of site conditions, including wooded, residential, agricultural, and urban areas. Although other overstory species were present at both sites, ash trees of all sizes were more abundant in forested areas than trees in urban or residential areas. Approximately 67 and 82% of the ash phloem at Shields and St. Joseph, respectively, was in wooded areas. Trees in grid cells classified as urban or residential, however, accounted for four and 11 of the 20 infested trees, respectively. This could simply reflect the higher likelihood of finding an infested tree in an urban or residential grid cell than in a forested area where numerous ash trees often occurred. However, the high proportion of infested trees in urban or residential areas may simply reflect the preference of adult *A. planipennis* beetles for the sunny conditions characteristic of open-grown landscape trees. Other studies have shown that *A. planipennis* beetles are more attracted to or more active on trees exposed to full sun compared with shaded or partially shaded trees (McCullough et al. 2009a,b).

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References Cited

Bartels, D., D. Williams, J. Ellenwood, and F. Sapio. 2007. Application of remote sensing technology for detection and mapping of hardwood tree species and emerald ash

borer-stressed ash trees, pp. 84–85. *In* V. Mastro, D. Lance, R. Reardon, and G. Parra [comps.], Proceedings, Emerald Ash Borer and Asian Longhorned Beetle Research and Technology Development Meeting, 29 October-2 November 2006, Cincinnati, OH. FHTET-2007–04. U.S. Department of Agriculture Forest Health Technology Enterprise Team, Morgantown, WV.

Batschelet, E. 1965. Statistical methods for the analysis of problems in animal orientation and certain biological rhythms. American Institute of Biological Sciences, Washington, DC.

[CAS] Chinese Academy of Science, Institute of Zoology. 1986. *Agrilus marcopoli* Obenberger, p. 445. *In* Editorial Committee [eds.], Agriculture Insects of China, Part I. China Agriculture Press, Beijing, China.

Cappaert, D. L., D. G. McCullough, T. M. Poland, and N. W. Siegert. 2005. Emerald ash borer in North America: a research and regulatory challenge. Am. Entomol. 51: 152–165.

Cronin, J. T., P. Turchin, J. L. Hayes, and C. A. Steiner. 1999. Area wide efficacy of a localized forest pest management practice. Environ. Entomol. 28: 496–504.

Crook, D. J., A. Khrimian, J. A. Francese, I. Fraser, T. M. Poland, A. J. Sawyer, and V. C. Mastro. 2008. Development of a host based semiochemical lure for trapping emerald ash borer *Agrilus planipennis* (Coleoptera: Buprestidae). Environ. Entomol. 37: 356–365.

EAB Information. 2009. Emerald ash borer. (http://www.emeraldashborer.info/).

Fraser, I., V. C. Mastro, and D. R. Lance. 2007a. Emerald ash borer dispersal: a release and recapture study, p. 42. *In* K. Gottschalk [ed.], Proceedings, 17th U.S. Department of Agriculture Interagency Research Forum on Gypsy Moth and Other Invasive Species, 10–13 January 2006, Annapolis, MD. Gen. Tech. Rep. NRS-P-10. U.S. Department of Agriculture Forest Service, Newtown Square, PA.

Fraser, I., V. C. Mastro, D. R. Lance, and D. Bopp. 2007b. Dispersal behavior of *Agrilus planipennis* (Fairmaire) (Coleoptera: Buprestidae): release-recapture studies, pp. 13–14. *In* V. Mastro, D. Lance, R. Reardon, and G. Parra [comps.], Proceedings, Emerald Ash Borer and Asian Longhorned Beetle Research and Technology Development Meeting, 29 October-2 November 2006, Cincinnati, OH. FHTET-2007–04. U.S. Department of Agriculture Forest Health Technology Enterprise Team, Morgantown, WV.

Gao, R. T., T. H. Zhao, H. P. Liu, L. S. Bauer, and T. R. Petrice. 2004. Studies on the investigation of *Agrilus marcopoli* Obenberger in China. Trans. China Pulp and Paper 19: 363–365.

Heinze, G. 2006. A comparative investigation of methods for logistic regression with separated or nearly separated data. Stat. Med. 25: 4216–4226.

Heinze, G., and M. Schemper. 2002. A solution to the problem of separation in logistic regression. Stat. Med. 21: 2409–2419.

Heinze, G., and M. Ploner. 2003. Fixing the nonconvergence bug in logistic regression with SPLUS and SAS. Comput. Methods Programs Biomed. 71: 181–187.

Hou, T. Q. 1993. *Agrilus marcopoli* Obenberger, p. 237. *In* Editorial Committee [eds.], Fauna of Shandong Forest Insect. China Forestry Publishing House, Beijing, China.

Liberman, A. M. 2005. How much more likely? The implications of odds ratios for probabilities. Am. J. Eval. 26: 253–266.

McCullough, D. G., and N. W. Siegert. 2007. Estimating potential emerald ash borer (*Agrilus planipennis* Fairmaire) populations using ash inventory data. J. Econ. Entomol. 100: 1577–1586.

McCullough, D. G., T. M. Poland, D. L. Cappaert, and A. C. Anulewicz. 2009a. Emerald ash borer (*Agrilus planipennis*) attraction to ash trees stressed by girdling, herbicide or wounding. Can. J. For. Res. 39: 1331–1345.

McCullough, D. G., T. M. Poland, A. C. Anulewicz, and D. L. Cappaert. 2009b. Emerald ash borer (Coleoptera: Buprestidae) attraction to stressed or baited ash trees. Environ. Entomol. 38: 1668–1679.

Mercader, R. J., N. W. Siegert, A. M. Liebhold, and D. G. McCullough. 2009. Emerald ash borer, *Agrilus planipennis*, dispersal in newly colonized sites. Ag. For. Entomol. 11: 421–424.

Narisu, J., A. Lockwood, and S. P. Schell. 1999. A novel mark-recapture technique and its application to monitoring the direction and distance of local movements of rangeland grasshoppers (Orthoptera: Acrididae) in the context of pest management. J. Appl. Ecol. 36: 604–617.

Poland, T. M., and D. G. McCullough. 2006. Emerald ash borer: invasion of the urban forest and the threat to North America's ash resource. J. Forestry 104: 118–124.

R Core Development Team. 2009. R: a language and environment for statistical computing. (http://www.R-project.org).

Rodriguez-Saona, C., T. M. Poland, J. R. Miller, L. L. Stelinski, G. G. Grant, P. de Groot, L. Buchan, and L. MacDonald. 2006. Behavioral and electrophysiological responses of the emerald ash borer, *Agrilus planipennis*, to induced volatiles of Manchurian ash, *Fraxinus mandshurica.* Chemoecology 16: 75–86.

Shigesada, N., and K. Kawasaki. 1997. Biological invasions: theory and practice. Oxford University Press, Oxford, United Kingdom.

Taylor, R.A.J., T. M. Poland, L. S. Bauer, K. N. Windell, and J. L. Kautz. 2007. Emerald ash borer flight estimates revised, pp. 10–12. *In* V. Mastro, D. Lance, R. Reardon, and G. Parra [comps.], Proceedings, Emerald Ash Borer and Asian Longhorned Beetle Research and Technology Development Meeting, 29 October-2 November 2006, Cincinnati, OH. FHTET-2007–04. U.S. Department of Agriculture Forest Health Technology Expertise Team, Morgantown, WV.

Tluczek, A. R. 2009. Influence of host vigor on larval distribution, development and mortality of *Agrilus planipennis* Fairmaire (Coleoptera: Buprestidae) in North America. M.S. thesis, Michigan State University, East Lansing, Michigan.

Vittinghoff, E., D. V. Glidden, S. C. Shiboski, and C. E. McCulloch. 2005. Regression methods in biostatistics: linear, logistic, survival, and repeated measures models. Springer, New York.

Xu, G. T. 2003. *Agrilus marcopoli* Obenberger, pp. 321–322. *In* G. T. Xu [ed.], Atlas of Ornamental Pests and Diseases. China Agriculture Press, Beijing, China.

Yu, C. M. 1992. *Agrilus marcopoli* Obenberger, pp. 400–401. *In* G. R. Xiao [ed.], Forest Insects of China, 2nd ed. China Forestry Publishing House, Beijing, China.

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