Emerald Ash Borer (Coleoptera: Buprestidae) Attraction to Stressed or Baited Ash Trees

DEBORAH G. McCULLOUGH,[1,2,3] THERESE M. POLAND,[4]
ANDREA C. ANULEWICZ,[1] AND DAVID CAPPAERT[1]

Environ. Entomol. 38(6): 1668–1679 (2009)

ABSTRACT Emerald ash borer, *Agrilus planipennis* Fairmaire (Coleoptera: Buprestidae), has killed millions of ash (*Fraxinus* sp.) trees in North America since its discovery in Michigan in 2002. Efficient methods to detect low-density *A. planipennis* populations remain a critical priority for regulatory and resource management agencies. We compared the density of adult *A. planipennis* captured on sticky bands and larval density among ash trees that were girdled for 1 or 2 yr, wounded, exposed to the stress-elicitor methyl jasmonate, baited with Manuka oil lures, or left untreated. Studies were conducted at four sites in 2006 and 2007, where *A. planipennis* densities on untreated trees ranged from very low to moderate. In 2006, 1-yr girdled trees captured significantly more adult *A. planipennis* and had higher larval densities than untreated control trees or trees treated with methyl jasmonate or Manuka oil. Open-grown trees captured significantly more *A. planipennis* beetles than partially or fully shaded trees. In 2007, *A. planipennis* population levels and captures of adult *A. planipennis* were substantially higher than in 2006. The density of adults captured on sticky bands did not differ significantly among canopy exposure classes or treatments in 2007. Larval density was significantly higher in untreated, wounded, and 1-yr girdled trees (girdled in 2007) than in 2-yr girdled trees (girdled in 2006), where most phloem was consumed by *A. planipennis* larvae the previous year. A total of 36 trees (32 in 2006, 4 in 2007) caught no beetles, but 16 of those trees (13 in 2006, 3 in 2007) had *A. planipennis* larvae. In 2006, there was a positive linear relationship between the density of adults captured on sticky bands and larval density in trees. Our results show that freshly girdled and open grown trees were most attractive to *A. planipennis*, especially at low-density sites. If girdled trees are used for *A. planipennis* detection or survey, debarking trees to locate larval galleries is crucial.

KEY WORDS trap tree, detection methods, methyl jasmonate, Manuka oil, girdled trees

Since its discovery in 2002, emerald ash borer (*Agrilus planipennis* Fairmaire) (Coleoptera: Buprestidae), a native of Asia, has killed tens of millions of ash (*Fraxinus*) trees in Michigan, at least 12 additional states, and two Canadian provinces (www.emeraldashborer.info 2009). Adult *A. planipennis* beetles, typically active from May through August in Michigan, feed on ash foliage throughout their life span, but cause little damage. Individual eggs are laid in bark cracks or under flaps of outer bark in July or August and hatch within 2 wk. Larvae feed in serpentine galleries in the phloem and cambium, often scoring the outer sapwood. Galleries disrupt the vascular system of the tree, leading to canopy dieback and eventually tree mortality (Cappaert et al. 2005).

Effective methods to detect, delineate, and monitor low-density populations of this phloem-feeding beetle remain a critical priority for regulatory and resource management agencies. Visual surveys were initially used by regulatory agencies, but it became apparent by 2004 that they were not effective because newly infested trees with low *A. planipennis* densities had virtually no external symptoms (Poland and McCullough 2006).

Studies of *A. planipennis* and related *Agrilus* sp. have shown that girdling a potential host tree by removing a band of bark and phloem around the circumference of the trunk stresses the tree, making it highly attractive to adult *Agrilus* beetles (Haack and Benjamin 1982; Poland et al. 2004, 2005; Francese et al. 2006; Fraser et al. 2006; McCullough et al. 2009). Sticky bands or traps on girdled trees are sometimes used to capture adult *A. planipennis* beetles, but more commonly, girdled trees are felled then debarked to determine whether larvae are present (McCullough et al. 2009). Although girdled trap trees are an effective method to detect low-density populations of *A. planipennis,* locating suitable trees can be difficult, and felling and debarking trap trees to locate larvae is expensive and laborious.

[1] Department of Entomology, Michigan State University, 243 Natural Science, East Circle Dr., East Lansing, MI 48824.
[2] Department of Forestry, Michigan State University, 243 Natural Science, East Circle Dr., East Lansing, MI 48824.
[3] Corresponding author, e-mail: mccullo6@msu.edu.
[4] USDA Forest Service, Northern Research Station, 1470 S. Harrison Rd., East Lansing, MI 48823.

Alternative options for *A. planipennis* detection could include enhancing the attraction of adult *A. planipennis* to ash trees without requiring destruction of the trees. Blends of volatile compounds associated with ash leaves or bark can elicit a positive response by adult *A. planipennis* (Poland et al. 2006, Crook et al. 2008, de Groot et al. 2008). Manuka oil, a commercially available steam distillate from the New Zealand tea tree, *Leptospermum scoparium* J.R. and G. Forst (Myrtaceae), contains four of the six antenally active volatile sesquiterpenes found in ash bark (Crook at al. 2008). Previous tests indicated Manuka oil lures may attract *A. planipennis* adults to a tree or trap (Crook et al. 2008, but see Tluczek 2009). Exposure to methyl jasmonate (MeJA), a volatile derivative of the stress-eliciting hormone jasmonic acid (Hopke et al. 1994; Boland et al. 1998), could also be a means to enhance *A. planipennis* attraction to trap trees. In laboratory tests, adult *A. planipennis* were attracted to foliar volatiles emitted by ash seedlings exposed to MeJA or subjected to *A. planipennis* larval feeding (Rodriguez-Saona et al. 2006).

In 2006, we evaluated *A. planipennis* attraction to ash trees in four sites. Trees were either stressed by girdling, exposed to MeJa, baited with Manuka oil lures, or left untreated. We recorded adult *A. planipennis* capture rates on all trees and debarked half the trees during the winter to quantify *A. planipennis* larval density. In 2007, the remaining trees were used to compare *A. planipennis* attraction to trees girdled in 2006 (2-yr girdle), trees girdled in 2007 (1-yr girdle), trees with a vertical wound, and untreated trees.

Materials and Methods

Study Sites

Study sites were selected based on the extent of canopy dieback, evidence of woodpecker predation on *A. planipennis*, and observations of adult beetle activity to ensure that *A. planipennis* density ranged from very low to moderate to relatively high among sites. A total of 40 blocks, each consisting of four ash trees, were established across four sites using a randomized complete block design ($n = 160$ trees total; Table 1). Trees within blocks were similar in size, growing conditions, and exposure to sun. There was ≈8–10 m between trees within blocks. Ten blocks of green ash (*F. pennsylvanica* Marsh; Oleaceae) trees were established in a wooded area with a low-density *A. planipennis* population in the Shiawassee River State Game Area, in St. Charles, Saginaw Co., MI. Eight blocks of green ash trees were selected in a woodlot with a moderate density of *A. planipennis* in Grand Blanc, Genesee Co., MI. Fourteen blocks of white ash (*F. americana* L.) trees were established in a wooded area at Seven Lakes State Park in Holly, Oakland Co., MI, also with a moderate density of *A. planipennis.* Eight blocks of green ash trees were selected in the cloverleaf rights-of-way in the intersection of Interstate 96 and Michigan State Road 59 (M-59 in Webberville, Ingham Co., MI). This site had a high density of *A. planipennis.* Trees at the four sites ranged from 7.9 to 26.9 cm in diameter at breast height (dbh; Table 1).

Table 1. Number of trees (*n*), mean ± SE tree DBH, and mean ± SE canopy exposure ranking for ash trees at four study sites in mid-Michigan

Site	*n*	DBH (cm)	2006 canopy exposure rank[a]	2007 canopy exposure rank
Grand Blanc	32	12.5 ± 0.3	2.9 ± 0.2ab	2.6 ± 0.2abc
Seven Lakes	56	13.3 ± 0.4	2.2 ± 0.1c	2.3 ± 0.2c
Shiawassee	40	13.6 ± 0.5	3.5 ± 0.2a	3.5 ± 0.3a
Webberville	32	18.9 ± 0.7	1.9 ± 0.2c	2.3 ± 0.1bc

Within columns, means followed by the same letter are not significantly different (Kruskal-Wallis test and nonparametric multiple comparisons procedure; $P < 0.05$).

[a] Canopy exposure rankings: 1, all sides open; 2, dominant/above canopy; 3, two to three sides open; 4, one side/edge open; 5, closed/all sides shaded.

Exposure of each individual tree to sun or shade was visually assessed and ranked in midsummer, when leaves were fully expanded. Trees were ranked as (1) completely open-grown and exposed to full sunlight (open); (2) super-dominant with canopies that extended above surrounding trees (dominant); (3) growing partially in the open with two or three sides exposed to sunlight (partly open); (4) growing along the edge of a wooded area with only a single side exposed (partly closed) or (5) shaded trees in a closed-canopy (closed; Table 1).

2006. Trees within blocks were randomly assigned to be treated by girdling, exposure to MeJa, baited with Manuka oil lures, or left as a control. To girdle trees, we used drawknives and chisels to remove the outer bark and phloem from a 15-cm-wide band around the circumference of the trunk between 85 and 100 cm above ground. Care was taken to avoid injury to the outer sapwood. Trees were girdled on 17 and 19 May 2006.

To expose trees to MeJa, we tied 10 bubble caps, each containing 150 μl of MeJa, to a line at 30-cm intervals and suspended two lines of bubble caps within the mid- to upper canopy of trees using a Big Shot Launcher (WesSpur Tree Equipment, Bellingham, WA). The MeJa release rate from the bubble caps was 0.38 mg/d as determined in the laboratory at 20°C (Phero Tech International; now Contech Enterprises, Delta, British Columbia, Canada). The MeJa bubble caps were placed into trees on 7 and 8 June 2006. The Manuka oil treatment consisted of attaching clusters of five 0.4-ml polyethylene snap cap tubes (Fisher, Pittsburgh, PA), each filled with 400 μl of Manuka oil (Coast Manuka Type A; East Cape Chemotype Manuka; Coast Biologicals, Manukau City, Aukland, New Zealand) to the trunk of trees. The release rate of Manuka oil from individual tubes was 2 mg/d (determined in the laboratory at 20°C). On 6 and 7 June 2006, we attached three evenly spaced clusters of tubes around the trunk, between 0.8 and 2 m above ground (15 tubes total per tree, total release rate of 30 mg/d). An additional 15 tubes filled with

Manuka oil were similarly attached to the trees on 27 and 28 June 2006 to ensure the continued presence of Manuka oil volatiles during *A. planipennis* oviposition. Manuka oil tubes were removed from all trees in autumn.

On 6 and 7 June, sticky bands, ≈30 cm wide and consisting of clear, plastic stretch wrap covered with Tanglefoot, were placed around the circumference of the trunk of each tree at 1.5 m above ground. The mean ± SE area of sticky bands on the trap trees was 1,338 ± 27 cm^2. Bands were checked weekly from 22 June to 17 August 2006. *A. planipennis* adults were removed, transported to the Forest Entomology Laboratory at Michigan State University, and frozen until they could be examined. During the fall, beetles from the sticky bands were soaked in 70% EtOH for a minimum of 4 wk to remove Tanglefoot and examined under a microscope to determine sex. Density of adults captured on each tree was standardized as the number of adults per 1,340 cm^2, the approximate area of the sticky bands. The proportion of female beetles captured in sticky bands was used for analysis only when a total of five or more beetles were captured in a given week.

Between 15 November and 15 December, trees in one half of the blocks at each site were felled and debarked to assess larval densities (20 of the original 40 blocks were felled). After each tree was felled, four to eight sample areas, depending on the size of the tree, were delineated on the trunk and the leader or major branches in the canopy. Sample areas were at least 160 cm^2; total area sampled per tree ranged from 0.3 m^2 on the smallest trees (8–9 cm dbh) to 1.4 m^2 on larger trees (>25 cm dbh). Each sample area was intensively examined, and *A. planipennis* exit holes and woodpecker attacks were counted and marked. The bark was carefully peeled down to the sapwood, and the exposed area was measured. Number and stage of *A. planipennis* larvae in each sample area were recorded. Larval density was standardized by determining the total number of larvae per square meter of area exposed on each tree.

2007. The remaining 20 blocks of trees from 2006 were used for the 2007 experiment. Trees used as controls in 2006 were again used as untreated controls in 2007. Trees that had been treated with Manuka oil or MeJa did not differ in the density of adults captured or larval density from control trees (see Results); therefore, they were assigned to new treatments. Because the Manuka oil and MeJa were removed in autumn 2006, there were no remaining or interacting effects of these treatments in 2007. Trees that had Manuka oil lures in 2006 were girdled on 17 May 2007, using the same methods as in the previous year. Trees girdled in 2006 were again included in our study, to compare *A. planipennis* attraction between the newly girdled trees (1-yr girdled trees) and 2-yr girdled trees. Trees that were exposed to MeJa in 2006 were assigned to be stressed by wounding in 2007. Trees were wounded on 17 May 2007 by removing a 15-cm-wide vertical strip of bark and phloem along the trunk with a drawknife and chisel, taking care to avoid injury to the outer sapwood. The lower edge of the wound was at 85 cm above ground, and the vertical length of the wound was equal to the circumference of the tree at breast height. This ensured that the vertical wound resulted in removal of the same area of bark and phloem as a horizontal girdle but affected only a portion of the trunk and phloem. Sticky bands were again applied to each tree on 17 May 2007, using the same methods as in 2006. Mean area of sticky bands was 1,372 ± 38 cm^2. Bands were checked and beetles were removed from Tanglefoot weekly between 22 May and 23 August 2007. Beetles were cleaned and sex determined, as described for 2006. Density of adults captured on each sticky band and on canopy traps was standardized to the mean sticky band area (number of adults per 1,370 cm^2). Between 9 October 2007 and 10 January 2008, trees at all four sites were felled and debarked to determine larval density, using methods described above.

Statistical Analysis

All variables were tested for normality using the Shapiro-Wilk test (Shapiro and Wilk 1965) and residual plots. Adult catch, larval densities, and adult catch by canopy exposure rank were normalized by $\ln(x + 1)$ transformations (Ott and Longnecker 2001). Differences among sites and treatments were tested as unplanned comparisons and multiple comparison tests were applied only when overall analysis of variance (ANOVA) was significant ($P < 0.05$). ANOVAs were performed to determine significant effects of site, treatment, and site × treatment interaction using SAS statistical software (PROC GLM; SAS Institute 2003). When significant differences occurred, the Tukey-Kramer least significant means test was used to evaluate species and site differences (Ott and Longnecker 2001). Adult capture rates and larval densities were normalized by $\ln(x + 1)$ transformations for linear regression analysis (Ott and Longnecker 2001).

Some variables, including effects of canopy exposure ranking, larval densities, and proportion of captured beetles that were female, could not be normalized by transformations. For non-normal variables, nonparametric ANOVAs (Friedmans' F statistic; Kruskal-Wallis H statistic) were applied to assess differences among sites, treatments, and canopy exposure rankings (Kruskal and Wallis 1952, PROC NPAR1WAY; SAS Institute 2003). When results were significant, nonparametric multiple comparisons were used to identify differences among variables (Zar 1984). All analyses were conducted at the $P < 0.05$ level of significance.

Results

2006. A total of 2,363 *A. planipennis* beetles were captured in sticky bands throughout the flight season, with peak catch occurring the week of 5 July 2006 (Fig. 1). Number of beetles captured on individual trees ranged from 0 to 230 beetles and averaged 14.8 ± 2.3

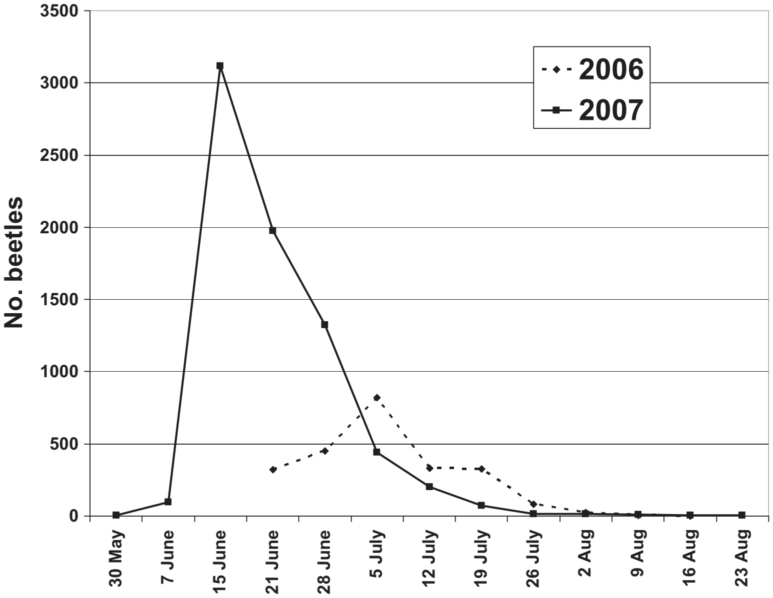

Fig. 1. Total number of adult *A. planipennis* captured per week on sticky bands on *Fraxinus* trees at four sites in central Michigan during the 2006 ($N = 160$) and 2007 ($N = 80$) flight seasons.

(SE) beetles. The number of adult *A. planipennis* caught per tree differed significantly among sites ($F = 38.67$; df = 3,156; $P < 0.0001$; Fig. 2). Trees at Webberville caught an average of 38.4 ± 8.7 beetles per tree, significantly more than trees at Seven Lakes (13.9 ± 2.8) and Grand Blanc (9.2 ± 2.5), whereas trees at Seven Lakes and Grand Blanc caught significantly more beetles than trees at Shiawassee (1.6 ± 0.4; Fig. 2). A total of 32 trees, 22 of which were at Shiawassee, caught no beetles.

The density of *A. planipennis* beetles captured was significantly higher on girdled trees than any of the other trees ($F = 14.23$; df = 3,159; $P < 0.0001$; Fig. 3a). Overall, the density of *A. planipennis* beetles on girdled trees averaged 28.3 ± 5.9 beetles/1,340 cm^2, which was significantly higher than the number of beetles captured on trees with Manuka oil lures (10.3 ± 2.2), exposed to MeJa (6.3 ± 1.8), or left as untreated controls (8.6 ± 3.3). The interaction between the main effects of site and treatment was not significant ($F = 0.74$; df = 9,159; $P = 0.67$).

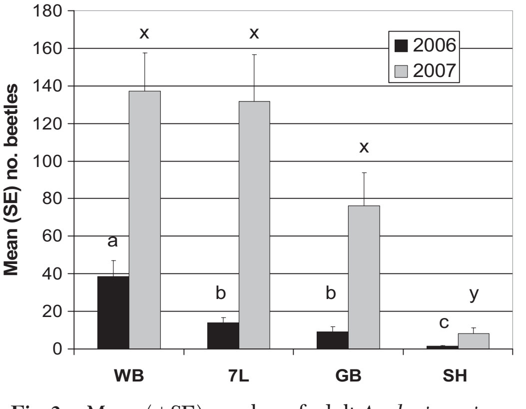

Fig. 2. Mean (±SE) number of adult *A. planipennis* captured on sticky bands per tree at four sites, Webbervile (WB; $N = 32$ in 2006, 16 in 2007), Seven Lakes (7L; $N = 56, 28$), Grand Blanc (GB; $N = 40, 20$), and Shiawassee (SH; $N = 32, 16$), in central Michigan in 2006 and 2007. Within each year, means with the same letter are not significantly different (Kruskal-Wallis test and nonparametric multiple comparisons procedure; $P < 0.05$).

Overall, canopy exposure rankings did not differ significantly among treatments ($F = 0.25$; df = 3,159; $P = 0.86$), indicating that a similar distribution of trees of each canopy exposure ranking were represented among treatments. Trees that were open-grown and fully exposed to sunlight (rank 1) caught a significantly higher density of beetles than trees exposed to less sunlight ($F = 8.12$; df = 4,159; $P < 0.0001$; Fig. 4a). Trees with two to three sides exposed to sunlight (rank 3) caught a significantly higher density of beetles than edge trees with one exposed side or shaded trees (ranks 4 and 5, respectively; Fig. 4a). Super-canopy (dominant) trees, those with shaded trunks but with canopies extending above surrounding trees and exposed to sun (rank 2), were intermediate (Fig. 4a). More than 90% of all beetles were captured on trees with at least two to three sides exposed to sunlight (ranks 1, 2, and 3), which represented only 67% or 107 of the 160 trees in 2006. The interaction of canopy exposure and treatment was not significant ($F = 1.43$; df = 12,159; $P = 0.16$).

Across all sites, nearly 53% of the *A. planipennis* beetles captured on the sticky bands were female. Proportion of beetles that were female ranged from 50% on girdled trees to 59% on control trees and differences among treatments were not significant

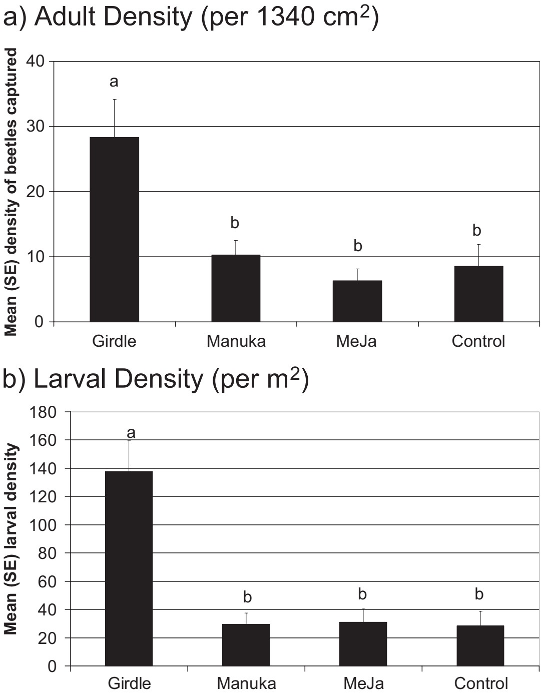

Fig. 3. Mean density (±SE) of *A. planipennis* (a) adult beetles (per 1,340-cm^2 sticky band) and (b) larval density (per m^2 of phloem after debarking) in untreated ash trees or trees treated by girdling, manuka oil or methyl jasmonate (MeJa) at four sites in central Michigan in 2006 (N = 20). Means with the same letter are not significantly different [Tukey-Kramer multiple comparisons on data transformed by ln(x + 1); $P < 0.05$].

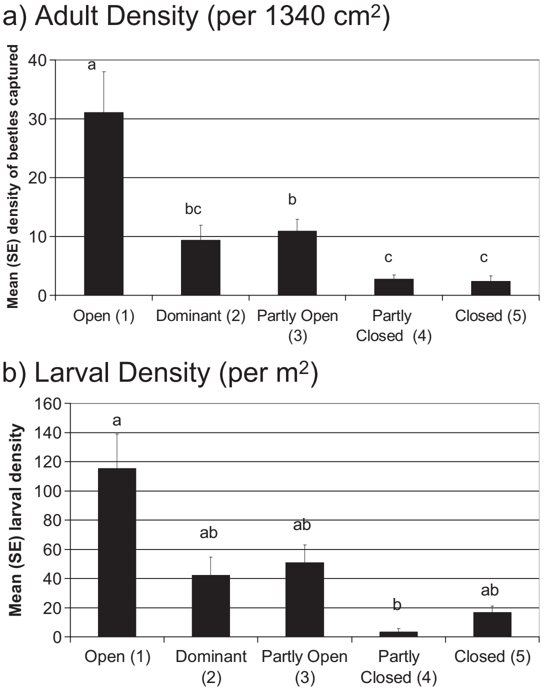

Fig. 4. Mean density (±SE) of *A. planipennis* (a) adult beetles (per 1,340-cm^2 sticky band) and (b) larval density (per m^2 of phloem after debarking) in ash trees by canopy exposure ranking: (1) open-grown and fully exposed (N = 36), (2) super-dominant, extending above canopy (N = 53), (3) two to three sides open (N = 18), (4) edge tree exposed on one side (N = 15), and (5) closed canopy and fully shaded (N = 38) at four sites in central Michigan in 2006. Within each year, means with the same letter are not significantly different [Tukey-Kramer multiple comparisons on data transformed by ln(x + 1); $P < 0.05$].

(H = 6.39; df = 3,123; P = 0.09). Female beetles comprised 34–68% of the total weekly capture throughout the summer (Fig. 5). The highest proportion of females was captured the week of 21 June and the lowest during the week of 19 July 2006 (Fig. 5). Super-canopy trees (rank 2) captured significantly higher proportions of female beetles (76 ± 5.0%) than trees fully exposed to sunlight (rank 1; 56 ± 10.0%; H = 13.70; df = 4,122; P = 0.0083). Trees with canopy exposure ranks of 3, 4, and 5 were intermediate (69 ± 4.0, 50 ± 13.0, and 73 ± 12.0%, respectively). The interaction between treatment and canopy exposure ranking was not significant (Friedmans' F = 0.55; df = 12,118; P = 0.88).

When trees were felled, we examined and subsequently debarked a total of 46.2 m^2 of phloem, averaging 0.58 ± 0.03 m^2 of phloem per tree. We found a total of 3,038 larvae or prepupal larvae, 213 successful woodpecker attacks on larvae and 16 *A. planipennis* exit holes left by previously emerged adult beetles. Prepupae that had completed their feeding and moved into overwintering chambers comprised 74% of the larvae. Of the remaining larvae, 12% were fourth instars, 8% were third instars, and <3% were overwintering as second or first instars. Dead larvae were occasionally observed, but >97% of the larvae were alive when trees were sampled. Thirteen trees of the 32 trees that captured no adults during the summer had been colonized, with larval densities ranging from 1.3 to 79.4 larvae/m^2.

Trees at Webberville had significantly more *A. planipennis* larvae per square meter (131.3 ± 23.9) than trees at all other sites, whereas trees at Seven Lakes had higher densities (61.2 ± 13.9) than trees at Grand Blanc (24.4 ± 9.7) and Shiawassee (16.9 ± 5.4; F = 18.2; df = 3,76; $P < 0.0001$). Larval density on trees at Grand Blanc and Shiawassee did not differ significantly. Girdled trees had significantly more larvae per square meter than trees with Manuka oil lures, exposed to MeJA, or left as untreated controls (F = 14.66; df = 3,76; $P < 0.0001$; Fig. 3b). Overall, larval density was more than four times higher on girdled trees than on the other trees, which all had similar densities of larvae. The interaction between the main effects of site and treatment was not significant (F = 0.47, df = 9,76; P = 0.89).

Trees fully exposed to sunlight had an average of 115.3 ± 23.6 larvae/m^2, whereas all other trees had an average of 3–54 larvae/m^2 (Fig. 4b). Significantly more larvae per square meter were found on trees

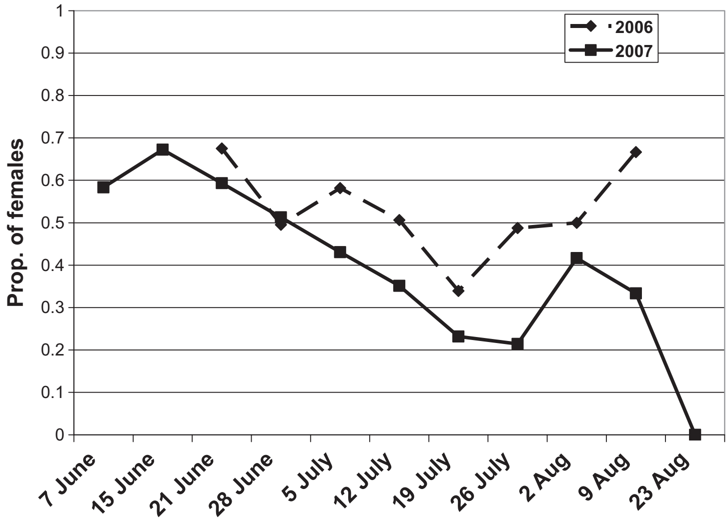

Fig. 5. Proportion of female *A. planipennis* beetles captured on sticky bands of all trees at four sites in central Michigan during the field season in 2006 ($N = 160$) and 2007 ($N = 80$). Proportions calculated only for weeks when a total of five or more beetles were captured in sticky bands.

with canopies fully exposed to sunlight (rank 1) than on trees with less than one side exposed (rank 4; $H = 15.7$; df = 4,75; $P = 0.0034$). Super-canopy trees, trees with two to three sides exposed, and shaded trees were intermediate (ranks 2, 3, and 5; Fig. 4b). The interaction between canopy exposure and treatment was not significant ($H = 0.47$; df = 11,75; $P = 0.31$).

Overall in 2006, *A. planipennis* larval density increased as the density of adults captured on sticky bands increased. A positive linear relationship existed between these two variables transformed by $\ln(x + 1)$ for all treatments combined ($n = 79$; $R^2 = 0.40$; $P < 0.0001$; Fig. 6) and when only girdled trees were analyzed ($n = 19$; $R^2 = 0.67$; $P < 0.0001$; Fig. 7a). There was no significant relationship when only untreated control trees were analyzed ($n = 19$; $R^2 = 0.05$; $P = 0.35$; Fig. 7b).

2007. A total of 7,269 *A. planipennis* beetles were captured in sticky bands throughout the flight season. Beetle captures peaked the week of 15 June 2007 (Fig. 1). Individual trees captured between 0 and 555 beetles, with an overall mean of 90.9 ± 11.6 beetles per tree, which is >6 times higher than the mean number captured per tree in 2006. At the Shiawassee site, an

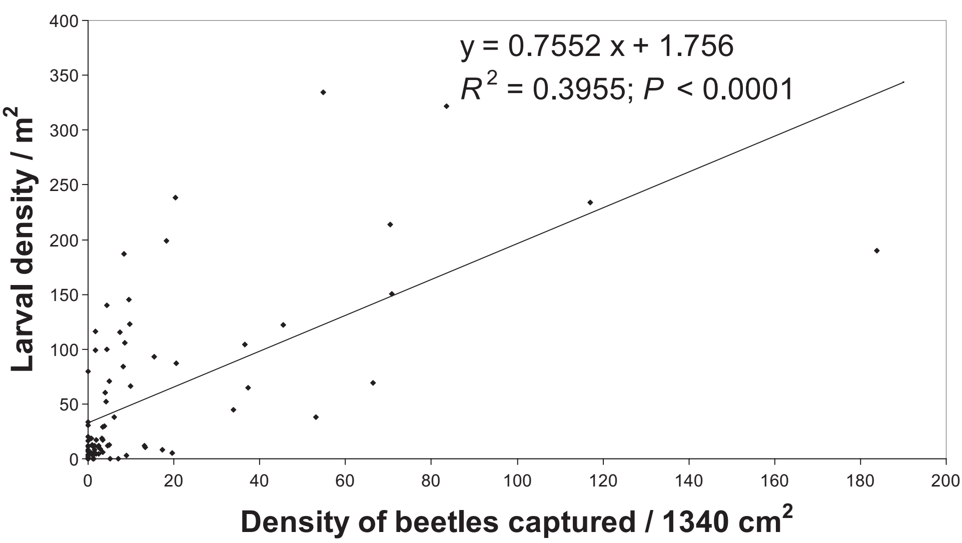

Fig. 6. Linear relationship between the density of adult *A. planipennis* captured per 1,340-cm^2 sticky band and larvae per square meter of phloem after debarking for all ash trees ($N = 79$ total) at four sites in central Michigan in 2006. Variables were $\ln(x + 1)$ transformed for regression analysis.

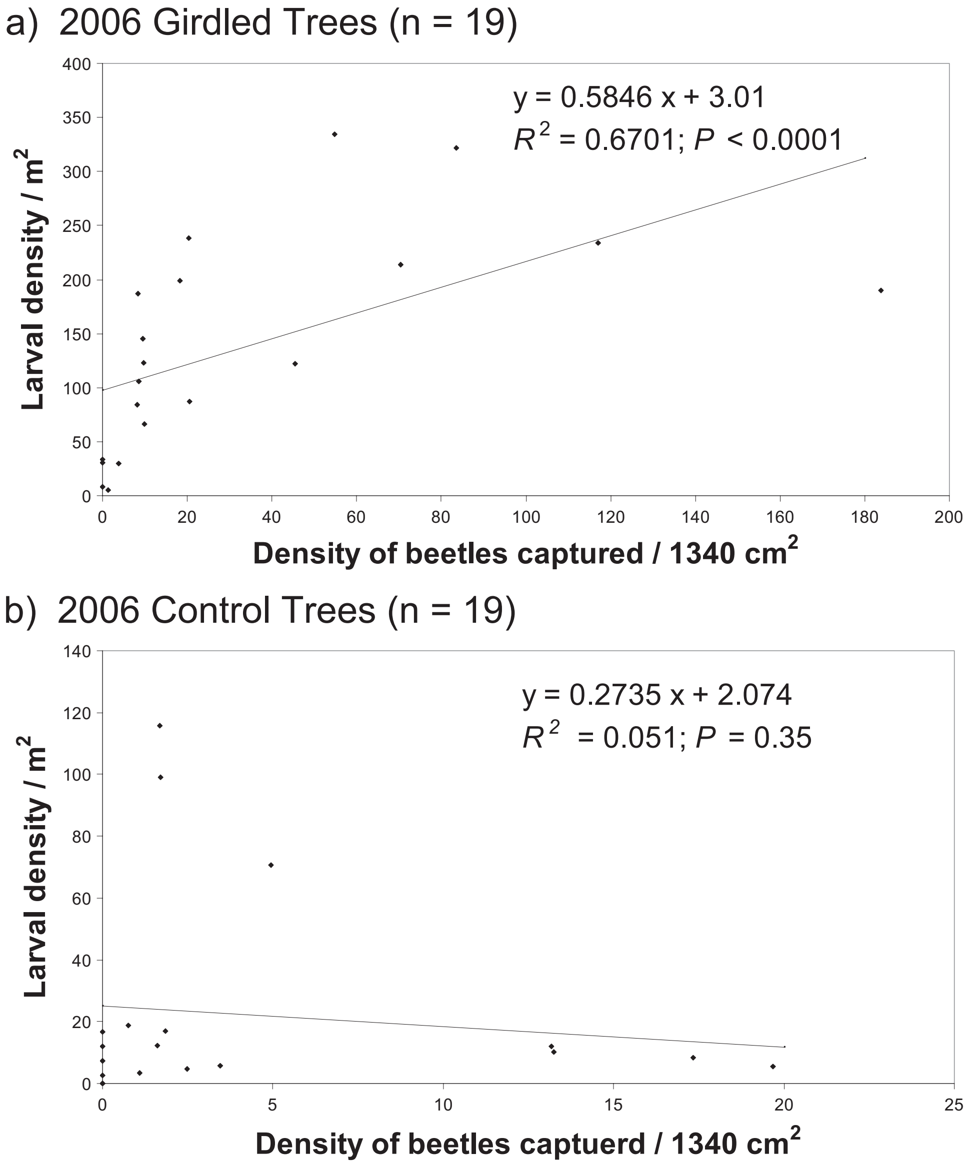

Fig. 7. Linear relationship between the density of adult *A. planipennis* captured per 1,340-cm^2 sticky band and larvae per square meter of phloem after debarking for (a) girdled ash trees ($N = 19$ trees) and (b) control trees ($N = 19$ trees) at four sites in 2006. Variables were $\ln(x + 1)$ transformed for regression analysis.

average of 8.1 ± 3.2 beetles were captured per tree, and four trees captured no beetles (Fig. 2). Trees at the Webberville, Seven Lakes, and Grand Blanc sites captured an average of 137.3 ± 20.2, 131.8 ± 24.7, and 76.3 ± 17.5 beetles per tree, respectively. Beetle capture did not differ significantly among these three sites, but all had significantly higher capture rates than the trees at the Shiawassee site ($F = 49.02$; df = 3, 76; $P < 0.0001$; Fig. 2).

One-year girdled trees (girdled in spring 2007) captured an average of 129.4 ± 32.9 beetles/1,370 cm^2 average sticky band area, which was 2.24 times as many beetles as 2-yr girdled trees (girdled in spring 2006), which captured an average density of 57.9 ± 13.9 beetles (Fig. 8a). Wounded and control trees were intermediate, with mean densities of 91.2 ± 23.4 and 77.0 ± 17.3 per average sticky band area, respectively. Differences among treatments were not significant ($F = 2.3$; df = 3,78; $P = 0.09$; Fig. 8a), nor was the interaction between site and treatment ($F = 0.4$; df = 9,78; $P = 0.93$).

Canopy exposure did not differ significantly among treatments in 2007 ($F = 0.01$; df = 3,75; $P = 0.99$), indicating that the distribution of trees of each canopy exposure ranking was similar among treatments. Open-grown trees (rank 1) caught a significantly

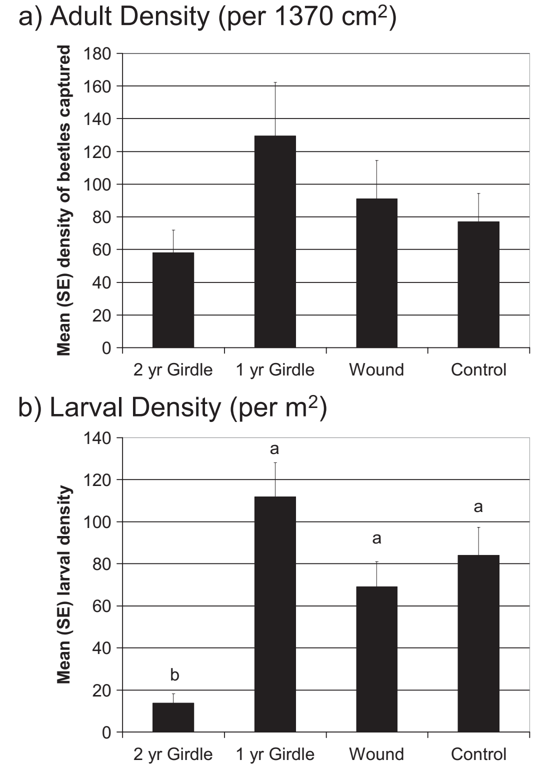

Fig. 8. Mean density (±SE) of *A. planipennis* (a) adult beetles (per 1,370-cm^2 sticky band) and (b) larval density (per m^2 of phloem after debarking) in untreated ash trees or trees girdled in 2006 (2-yr girdle), girdled in 2007 (1-yr girdle), or wounded at four sites in central Michigan in 2007 ($N = 10$). Means with the same letter are not significantly different [Tukey-Kramer multiple comparisons on data transformed by $\ln(x + 1)$; $P < 0.05$].

higher density of beetles on sticky bands than edge trees with one exposed side or shaded trees (ranks 4 and 5, respectively; $F = 6.58$; df = 4,75; $P < 0.0001$; Fig. 9a). Super-canopy (dominant) trees and trees with two to three sides exposed (ranks 2 and 3) were intermediate. There was no significant interaction between treatment and canopy exposure ($F = 1.2$; df = 12,75; $P = 0.31$).

Approximately 59% of the *A. planipennis* beetles captured in 2007 were female. Over the course of the flight season, the proportion of captured female beetles ranged from 55% on 1-yr girdled trees to 63% on 2-yr girdled trees. Proportion of female beetles captured on trees did not differ significantly among treatments ($H = 5.60$; df = 3,72; $P = 0.13$) nor among canopy exposure ranks ($H = 4.25$; df = 4,71; $P = 0.37$). The interaction between treatment and canopy exposure ranking was not significant (Friedmans' $F = 0.48$; df = 11,67; $P = 0.91$).

The highest proportion of females was captured the week of 15 June (67% of the total 4,878 beetles that week) and the lowest proportion was captured the week of 23 August (0% of the 5 total beetles captured; Fig. 5).

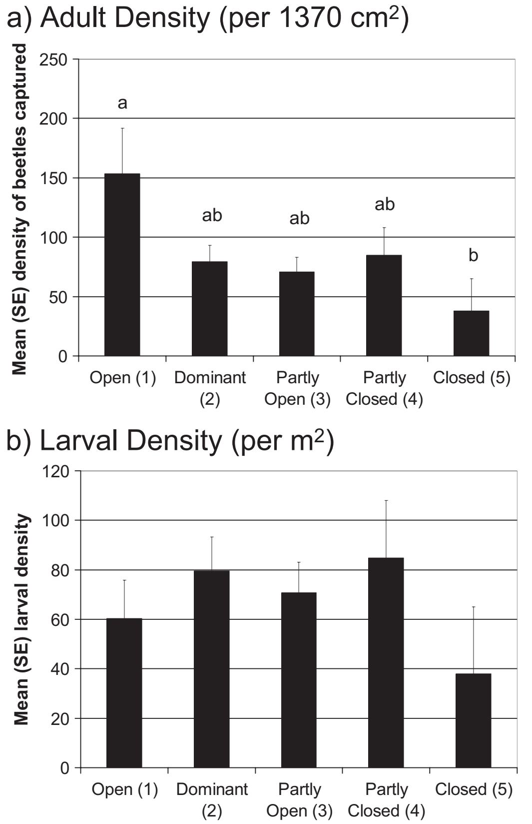

Fig. 9. Mean density (±SE) of *A. planipennis* (a) adult beetles (per 1,370-cm^2 sticky band) and (b) larval density (per m^2 of phloem after debarking) by canopy exposure ranking: (1) open-grown and fully exposed ($N = 17$), (2) super-dominant, extending above canopy ($N = 25$), (3) two to three sides open ($N = 12$), (4) edge tree exposed on one side ($N = 6$), and (5) closed canopy and fully shaded ($N = 20$) at four sites in central Michigan in 2007. Means with the same letter are not significantly different (Kruskal-Wallis test and nonparametric multiple comparisons procedure; $P < 0.05$).

A total of 42.2 m^2 of phloem was examined and subsequently debarked, with a mean of 0.53 ± 0.01 m^2 of phloem per tree. We found a total of 2,409 *A. planipennis* larvae or prepupae and 876 woodpecker attacks. More than 90% of the larvae were prepupae, 5% were fourth instars, and <1% were third instars or younger. Larval mortality was <3%. Three of the four trees that captured no beetles during the summer were infested with current-year larvae, with densities ranging from 1.6 to 13.5 larvae/m^2. An additional 1,146 *A. planipennis* exit holes left by emerged beetles were recorded; 611 of the exit holes were on 2-yr girdled trees compared with 233 on 1-yr girdled trees.

Trees at Grand Blanc had twice as many larvae per square meter (99.6 ± 21.1) as trees at Shiawassee (44.1 ± 11.4). Trees at Seven Lakes and Webberville were intermediate with 78.2 ± 12.7 and 64.2 ± 11.5, respectively. Differences in larval densities among sites were not significant ($F = 1.4$, df = 3,75; $P = 0.35$).

One-year girdled, wounded, and control trees had significantly more larvae per square meter than the severely declining 2-yr girdled trees ($F = 14.42$; df = 3,75; $P < 0.0001$; Fig. 3b). On average, larval density on 2-yr girdled trees was three to five times lower than on the other trees. The interaction between site and treatment was not significant ($F = 1.2$; df = 9,75; $P = 0.31$).

Differences in larval densities among canopy exposure rankings were not significant ($H = 4.83$; df = 5,75; $P = 0.44$). Average larval densities ranged from 37.9 ± 27.2 on completely shaded trees (rank 5) to 60.3 ± 15.5 and 86.0 ± 23.4 larvae/m^2 on open-grown (rank 1) and edge trees (rank 4), respectively (Fig. 4b).

In 2007, a weak, positive linear relationship existed between larval density and density of adults captured per mean sticky band area when data from all treatments were analyzed together ($n = 77$; $R^2 = 0.12$; $P = 0.0024$) and when data from control trees were analyzed ($n = 20$; $R^2 = 0.34$; $P = 0.007$). There was no significant linear relationship when data from 1-yr girdled trees ($n = 18$; $R^2 = 0.06$; $P = 0.29$) or 2-yr girdled trees ($n = 18$; $R^2 = 0.014$; $P = 0.64$) were analyzed separately.

Discussion

Adult *A. planipennis* captures on sticky bands peaked the week of 5 July in 2006, corresponding roughly to 1,055–1,065 accumulated degree-days (base 50°F = 10°C; MSU MAWN 2008). In related studies conducted from 2003 to 2005, *A. planipennis* beetle captures on sticky bands similarly peaked in late June or early July, corresponding to ≈925–1,005 accumulated degree-days base 50°F (McCullough et al. 2009). In 2007, however, beetle captures at our sites peaked in mid-June, 3 wk earlier than in 2006 and corresponding to only 759–780 accumulated degree-days base 50°F (MSU MAWN 2008). The earlier emergence of adult beetles in 2007 could have resulted from increased larval development rates corresponding to higher larval density. In low-density *A. planipennis* populations, larvae often require 2 yr to complete development, but at higher densities, most larvae develop in a single year (Cappaert et al. 2005, Tluczek 2009). When we debarked our 2007 trees, nearly 90% of the larvae were overwintering as late instars or prepupae, but pupation and development of adults in spring could have been accelerated in response to high densities. Further study is needed to determine how *A. planipennis* development and emergence can vary with density.

Number of adult *A. planipennis* beetles captured on sticky bands increased six-fold from 2006 to 2007 (Figs. 1 and 2). More than three times as many beetles were captured on the sticky bands in 2007 (7,269 beetles), when we had 80 trees in our study, than in 2006 (2,363 beetles) when we had 160 trees. Ash trees were abundant at all of our sites, and the trees used in our study comprised only a small proportion of the ash trees available for *A. planipennis* colonization. Therefore, the substantial increase in beetle capture reflects increased *A. planipennis* density rather than a lack of available host trees. Within sites, the greatest increase occurred at Grand Blanc, where beetle captures increased seven-fold from 2006 to 2007 (Fig. 2). Differences between beetle captures in 2006 and 2007 were pronounced for trees in all treatments except the trees girdled in 2006 and retained as 2-yr girdled trees in 2007. The density of beetles captured were 11.6–15.6 times higher on 1-yr girdled, wounded, and control trees in 2007 than on the same trees in 2006, whereas beetle captures decreased by 40% on the 2-yr girdled trees (Figs. 3a and 8a).

The notable increase in *A. planipennis* abundance was also apparent when trees were felled and debarked in autumn. The density of exit holes left by adult *A. planipennis* that had emerged either in or before the year of dissection increased from 0.3/m^2 in 2006 to 27.1/m^2 in 2007. With the exception of the 2-yr girdled trees, larval density was two to five times higher in 2007 than in 2006. On the untreated control trees, larval density was ≈2.5 times higher in 2007 than in 2006 (Figs. 3b and 8b).

Differences in *A. planipennis* attraction between girdled trees and nongirdled trees were most apparent in 2006, when population densities were generally low or moderate at our sites (Fig. 3). In 2006, a total of 3,251 larvae, including 213 late instars killed by woodpeckers (6.5%), were recorded in our samples. Overall, larval density on the girdled trees in 2006 was approximately six times higher than on the control, Manuka oil-baited, or MeJa trees (Fig. 3b). Larval density was so high on most of the girdled trees in 2006, however, that relatively little phloem remained for the 2007 larvae. Previous research has shown that, on average, roughly 105 *A. planipennis* beetles can complete development and emerge as adults from 1 m^2 of phloem on trees ≥13 cm dbh (McCullough and Siegert 2007). Densities of *A. planipennis* larvae on girdled trees at all sites except Shiawassee approached these levels in 2006, and it was apparent that much of the phloem had already been consumed when trees were sampled that winter. In 2007, we recorded a total of 3,285 *A. planipennis* larvae, including 876 (26.7%) late instars killed by woodpeckers. The 2-yr girdled trees, where most of the phloem had been consumed by the 2006 larvae, averaged fewer than 20 *A. planipennis* larvae/m^2 compared with the other trees that averaged 69–112 larvae/m^2 (Fig. 8b).

Although the 1-yr girdled trees in this and other studies were consistently more attractive to *A. planipennis* beetles than untreated ash trees, the extent of this difference varied with *A. planipennis* density (McCullough et al. 2009). Host selection by *A. planipennis* beetles seems to be strongly influenced by volatile compounds, and beetles in laboratory tests responded positively to foliar volatiles emitted by stressed ash seedlings (Rodriguez-Saona et al. 2006). As *A. planipennis* densities increase, the injury caused by feeding larvae disrupts nutrient and water transport, stressing trees in a manner similar to girdling. In areas where *A. planipennis* is present at moderate to high densities, beetles are presumably exposed to stress-related volatiles from many trees and suitable feeding or oviposition sites become limited. We observed this pattern in 2007 in three sites, when differences in the density of adults captured between girdled trees and trees in other treatments were obscured by the generally high density of *A. planipennis* (Fig. 8a). External symptoms of infestation, including canopy dieback, epicormic sprouts, and bark cracks, became increasingly apparent in all these areas, however, and there would be little reason to use girdled trees or other detection or survey tools in these settings.

Much of our interest in evaluating 2-yr girdled trees and the MeJa exposure, Manuka oil lures, and wounding treatment arose from difficulties associated with large-scale use of girdled trees for *A. planipennis* detection. Regulatory agencies in several states established systematic grids of girdled ash trees from 2004 to 2007 (Flint 2005, Hunt 2007, Rauscher 2006), which led to the identification of dozens of previously unknown, low-density *A. planipennis* infestations. For these surveys, crews typically girdled trees in late fall or spring and felled and debarked the trees the following winter. In a few cases, two trees at a given location were girdled; one tree would be felled and debarked during the winter and the other would be debarked the following year. Using girdled trees for *A. planipennis* detection in large operational programs, however, requires survey crews to find suitable and accessible trees each year. In addition, the attraction radius of girdled trees is unknown, and as our 2007 data showed, differential attraction of girdled trees can be strongly influenced by the abundance and condition of other ash trees in the vicinity. We had initially expected that one or more of the alternative treatments we evaluated could provide a means to use individual trees for *A. planipennis* surveys in multiple years and perhaps indefinitely in the case of MeJa and Manuka oil. None of the treatments we evaluated, other than the 1-yr girdled trees, however, consistently increased the density of *A. planipennis* captured or larval density compared with untreated controls (Figs. 3 and 8).

Our results showed that, if girdled trees are used for *A. planipennis* detection or survey programs, debarking trees to locate larval galleries is crucial. In our 2006 and 2007 studies, sticky bands on 36 trees caught no beetles during the summer and had few or no external symptoms of infestation. Sixteen of these trees, however, were colonized by *A. planipennis,* with larval densities ranging from 1 to 80 larvae/m^2. Similarly, in an operational *A. planipennis* survey conducted by the Michigan Department of Agriculture in 2004, ≈44% of the positive (infested) trees had larvae but no adult beetles were captured on sticky bands (M. Philip, Michigan Department of Agriculture, unpublished data). This is not surprising given that sticky bands typically cover only a small portion of the trunk, whereas beetles can oviposit on nearly all of the trunk and branches. It does indicate, however, that, whereas sticky bands or other traps may be relatively simple to monitor compared with debarking trees, they can generate false negatives, leading to an unwarranted sense of security and delaying early detection of infested sites.

The lack of *A. planipennis* response to trees exposed to MeJa in 2006 was disappointing. Exposure to MeJa, which activates the jasmonic acid pathway, generated stress responses in plants ranging from cotton (Rodriguez-Saona et al. 2001, Rodriguez-Saona and Thaler 2005) to conifer saplings (Martin et al. 2003, Hudgins and Franceschi 2004). In laboratory studies, volatile profiles of ash seedlings exposed to MeJa were altered in a manner similar to physical injury associated with insect feeding, and treated seedlings were more attractive to adult beetles than healthy seedlings (Rodriguez-Saona et al. 2006). We found no effect of the MeJa on *A. planipennis* adult capture or larval density. Tluczek (2009) also exposed pole-sized ash trees to MeJa in 2006 and 2007, using methods similar to our study, but found no effect of the compound on *A. planipennis* adult capture, larval density, or larval development rate. The amount of MeJa released by the bubble caps in the canopy of our trees may have been inadequate to elicit a detectable stress response. In addition, younger plants are more inducible with MeJa than older plants (Cipollini and Redman 1999), and trees may be less likely to respond to MeJa than seedlings.

Manuka oil lures have been previously evaluated in field trials, and in one study, they increased *A. planipennis* attraction to purple panel traps (Crook et al. 2006). Thousands of purple panel traps baited with Manuka oil baits were subsequently deployed by USDA–APHIS and state regulatory agencies in 2008 for *A. planipennis* detection. In other field trials, however, purple "double decker" traps (with purple panels at two levels) baited with Manuka oil captured significantly fewer *A. planipennis* adults than traps baited with a lure comprised of ash foliar volatiles (Poland and McCullough 2007) or traps baited with both the foliar lure and Manuka oil (McCullough et al. 2008). Similarly, in this study, we found no effect of Manuka oil lures on *A. planipennis* attraction to trap trees. Volatiles emitted by the lures could have been overwhelmed by volatiles emitted by the study trees or surrounding ash trees. Additional research to evaluate efficacy of Manuka oil as an *A. planipennis* attractant in areas with abundant ash trees, particularly when stressed ash are present, is needed.

Regulatory officials in Canada and some local or state personnel in the United States have used wounded ash trees, similar to those evaluated in our study, for *A. planipennis* detection. Our data from 2007, along with results of a similar trial in 2004 (McCullough et al. 2009), however, indicated that freshly wounded trees were not substantially more attractive than unwounded trees. Observations from this and earlier studies (McCullough et al. 2006, 2009) indicated ash trees, which are highly sectorial (Tanis 2008), readily compartmentalize wounds, and both phloem and xylem will subsequently grow over the affected area. Therefore, wounded trees would be unlikely to become more attractive to *A. planipennis* in the second year.

Survey crews in some states have occasionally used 2-yr girdled trees for *A. planipennis* detection, largely to reduce labor and travel costs. The 2-yr girdled trees in our study were decidedly stressed in 2007, as might be expected, although 13 of the 20 trees were still alive at the end of the summer. We expected that *A. planipennis* adults would be highly attracted to the declining trees in 2007. Although adult capture did not differ significantly among treatments in 2007, overall, the 2-yr girdled trees captured less than one half as many beetles as the 1-yr girdled trees (Fig. 8a). Ovipositing beetles may avoid severely declining trees, either because foliage becomes less suitable for adult feeding or because little live phloem will be available for larval development. In a previous study, beetles similarly avoided herbicide-treated ash trees that declined severely or died during the summer (McCullough et al. 2009). We also noted that the 2-yr girdled trees were drier and more difficult to debark than any of the other trees. Although girdling two trees in a location may seem to be efficient, the reduction in travel costs may be offset by reduced efficacy of the 2-yr girdled trees.

Trees that were open-grown, super-dominant, or had at least two to three sides of the canopy exposed to sunlight were much more likely to be colonized by *A. planipennis* than trees growing along the edge of a wooded area or shaded trees (Figs. 4 and 9). Previous studies have noted the preference of *A. planipennis* for sunny conditions (Francese et al. 2006; McCullough et al. 2006, 2009). Other buprestids, including native *Agrilus* species, exhibit similar behavior (Barter 1957, Carlson and Knight 1969). For *A. planipennis* detection or monitoring, girdled trap trees or artificial traps are more likely to be effective if they are positioned in sunny areas than in shady or partially shaded areas.

We initially hypothesized that male beetles might emerge and be captured in sticky bands earlier in the summer than female beetles and that female beetles would account for a higher proportion of the captured beetles if they spent more time or were more likely to land on tree trunks than male beetles. We could discern no consistent pattern, however, in the proportion of females captured throughout the summer. In both years, females comprised roughly 60–70% of the beetles captured in early June, the first week that our bands were on trees. Relatively few beetles were captured late in the season, but of those captured, females represented anywhere from 20 to 70% of the beetles. Results indicate that the trees were similarly attractive to male and female *A. planipennis* beetles throughout the flight season.

Acknowledgments

We thank J. Baker, T. Dell, S. Bloomer, J. Wieferich, K. Chambers, B. McDonald, A. Tluczek, C. Limback, B. Schmitt, E. Burkett, and S. Smith (MSU) and A. Wroblewski, T. Ciaramitaro, and S. Burr (USDA Forest Service), who assisted with implementing treatments, monitoring sticky bands, and debarking trees in 2006–2008. Cooperation from the Michigan Department of Agriculture, the city of Grand Blanc, the Michigan Department of Natural Resources, and the Michigan Department of Transportation is gratefully acknowledged. Comments provided by R. Mercader and D. Pureswaran helped to improve this manuscript. Funding for this project was provided by the USDA Forest Service, NA FHP.

References Cited

Barter, G. W. 1957. Studies of the bronze birch borer, *Agrilus anxius* Gory, in New Brunswick. Can. Entomol. 89: 12–36.

Boland, W., J. Hopke, and J. Piel. 1998. Induction of plant volatile biosynthesis by jasmonates, pp. 255–269. *In* P. Schreier, M. Herderich, H.-U. Humpf, and W. Schwab (eds.), Natural product analysis. Vieweg, Wiesbaden, Germany.

Cappaert, D., 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.

Carlson, R. W., and F. B. Knight. 1969. Biology, taxonomy, and evolution of four sympatric *Agrilus* beetles. Contrib. Am. Entomol. Inst. 4: 1–105.

Cipollini, D. F., Jr., and A. M. Redman. 1999. Age dependent effects of jasmonic acid treatment and wind exposure on foliar oxidase and insect resistance in tomato. J. Chem. Ecol. 25: 271–181.

Crook, D., A. Khrimian, J. A. Francese, I. Fraser, T. M. Poland, and V. C. Mastro. 2006. Chemical ecology of the emerald ash borer, pp. 79. *In* V. Mastro, D. Lance, R. Reardon, and G. Parra (compilers), Emerald ash borer research and technology development meeting, 26–27 September 2005, Pittsburgh, PA. U.S. Department of Agriculture, Morgantown, WV.

Crook, D., A. Khrimian, I. Fraser, J. A. Francese, T. M. Poland, 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.

de Groot, P., G. G. Grant, T. M. Poland, R. Scharbach, L. Buchan, R. W. Nott, L. MacDonald, and D. Pitt. 2008. Electrophysiological response and attraction of emerald ash borer to green leaf volatiles (GLVs) emitted by host foliage. J. Chem. Ecol. 34: 1170–1179.

Flint, T. 2005. Michigan's emerald ash borer response project, p. 6. *In* V. Mastro and R. Reardon (compilers), Emerald ash borer research and technology development meeting, 5–6 October 2004, Romulus, MI. U.S. Department of Agriculture, Morgantown, WV.

Francese, J. A., J. B. Oliver, I. Fraser, N. Youssef, D. R. Lance, D. J. Crook, and V. C. Mastro. 2006. Effects of trap design and placement on capture of emerald ash borer, *Agrilus planipennis*, pp. 57–58. *In* V. Mastro, D. Lance, R. Reardon, and G. Parra (compilers), Emerald ash borer research and technology development meeting, 26–27 September 2005, Pittsburgh, PA. U.S. Department of Agriculture, Morgantown, WV.

Fraser, I., J. A. Francese, D. R. Lance, D. J. Crook, J. B. Oliver, N. Youssef, and V. C. Mastro. 2006. Effects of tree wounding and banding on emerald ash borer capture, pp. 59–60. *In* V. Mastro, D. Lance, R. Reardon, and G. Parra (compilers), Emerald ash borer research and technology development meeting, 26–27 September 2005, Pittsburgh, PA. U.S. Department of Agriculture, Morgantown, WV.

Haack, R. A., and D. M. Benjamin. 1982. The biology and ecology of the twolined chestnut borer, *Agrilus bilineatus*

(Coleoptera: Buprestidae), on oaks, *Quercus* spp., in Wisconsin. Can. Entomol. 114: 385–396.

Hopke, J., J. Donath, S. Blechert, and W. Boland. 1994. Herbivore-induced volatiles: the emission of acyclic homoterpenes from leaves of *Phaseolus lunatus* and *Zea mays* can be triggered by a β-glucosidase and jasmonic acid. FEBS. Lett. 352: 146–150.

Hudgins, J. W., and V. R. Franceschi. 2004. Methyl-jasmonate induced ethylene production is responsible for conifer phloem defense responses and reprogramming of stem cambial zone for traumatic resin duct formation. Plant Physiol. 135: 2134–2149.

Hunt, L. 2007. Emerald ash borer state update: Ohio, p. 2. *In* V. Mastro, D. Lance, R. Reardon, and G. Parra (compilers), Emerald ash borer research and Asian longhorned beetle research and development review meeting, 20 October to 2 November 2006, Cincinnati, OH. U.S. Department of Agriculture, Morgantown, WV.

Kruskal, W. H., and W. A. Wallis. 1952. Use of ranks in one-criterion variance analysis. J. Am. Stat. Assoc. 47: 583–621.

Martin, D. M., J. Gershenzon, and J. Bohlmann. 2003. Induction of volatile terpene biosynthesis and diurnal emission by methyl jasmonate in foliage of Norway spruce. Plant Physiol. 132: 1586–1599.

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, and D. Cappaert. 2006. Attraction of emerald ash borer to trap trees: effects of stress agents and trap height, pp. 61–62. *In* V. Mastro, D. Lance, R. Reardon, and G. Parra (compilers), Emerald ash borer research and technology development meeting, 26–27 September 2005, Pittsburgh, PA. U.S. Department of Agriculture, Morgantown, WV.

McCullough, D. G., T. M. Poland, A. C. Anulewicz, and D. L. Cappaert. 2008. Double-deckers and towers: emerald ash borer traps in 2007, pp. 73–75. *In* V. Mastro, D. Lance, R. Reardon, and G. Parra (compilers), Emerald ash borer research and technology development meeting, 23–24 October 2007, Pittsburgh, PA. U.S. Department of Agriculture, Morgantown, WV.

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

[MSU MAWN] Michigan State University Michigan Automated Weather Network. 2008. Michigan automated weather network. (http://www.agweather.geo.msu.edu/mawn/station.asp?id=msu&rt=0).

Ott, R. L., and M. Longnecker. 2001. An introduction to statistical methods and data analysis. Duxbury Thomson Learning, Pacific Grove, CA.

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

Poland, T. M., and D. M. McCullough. 2007. Evaluation of a multicomponent trap for emerald ash borer incorporating color, silhouette, height, texture, and ash leaf and bark volatiles, pp. 74–76. *In* V. Mastro, D. Lance, R. Reardon, and G. Parra (compilers), Emerald ash borer research and technology development meeting, 29 October to 2 November 2006, Cincinnati, OH. U.S. Department of Agriculture, Morgantown, WV.

Poland, T. M., P. de Groot, G. Grant, L. MacDonald, and D. G. McCullough. 2004. Developing attractants and trapping techniques for the emerald ash borer, pp. 15–16. *In* V. Mastro and R. Reardon (compilers), Emerald ash borer research and technology development meeting, 30 September to 1 October 2003, Port Huron, MI. U.S. Department of Agriculture, Morgantown, WV.

Poland, T. M., D. G. McCullough, P. de Groot, G. Grant, and D. Cappaert. 2005. Progress toward developing trapping techniques for the emerald ash borer, pp. 53–54. *In* V. Mastro and R. Reardon (compilers), Emerald ash borer research and technology development meeting, 5–6 October 2004, Romulus, MI. U.S. Department of Agriculture, Morgantown, WV.

Poland, T. M., C. Rodriguez-Saona, G. Grant, L. Buchan, P. D. Groot, J. Miller, D.G. McCullough. 2006. Trapping and detection of emerald ash borer: identification of stress-induced volatiles and test of attraction in the lab and field, pp. 64–65. *In* V. Mastro, D. Lance, R. Reardon, and G. Parra (compilers), Emerald ash borer research and technology development meeting, 26–27 September 2005, Pittsburgh, PA. U.S. Department of Agriculture, Morgantown, WV.

Rauscher, K. 2006. The 2005 Michigan emerald ash borer response: an update, p. 1. *In* V. Mastro, R. Reardon, and G. Parra (compilers), Emerald ash borer research and technology development meeting, 26–27 September 2005, Pittsburgh, PA. U.S. Department of Agriculture, Morgantown, WV.

Rodriguez-Saona, C., and J. S. Thaler. 2005. The jasmonate pathway alters herbivore feeding behaviour: consequences for plant defenses. Entomol. Exp. Appl. 115: 125–134.

Rodriguez-Saona, C., S. J. Crafts-Brandner, P. W. Paré, and T. J. Henneberry. 2001. Exogenous methyl jasmonate induces volatile emissions in cotton plants. J. Chem. Ecol. 27: 679–694.

Rodriguez-Saona, C., T. M. Poland, J. R. Miller, L. L. Stelinski, L.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.

SAS Institute. 2003. PROC user's manual, version 9.1. SAS Institute, Cary, NC.

Shapiro, S. S., and M. B. Wilk. 1965. An analysis of variance test for normality. Biometrika 52: 591–599.

Tanis, S. 2008. Distribution of trunk-injected ^{14}C imidacloprid in *Fraxinus* and *Acer* trees: a test of the sectored flow hypothesis. MS thesis, Michigan State University, East Lansing, MI.

Tluczek, A. R. 2009. Larval distribution, development and mortality of *Agrilus planipennis* Fairmaire (Coleoptera: Buprestidae) in North America as influenced by host vigor. MS thesis, Department of Entomology, Michigan State University, East Lansing, MI.

Zar, J. H. 1984. Biostatistical analysis. Prentice Hall, Englewood Cliffs, NJ.

Received 13 March 2009; accepted 18 July 2009.