Influence of Host Stress on Emerald Ash Borer (Coleoptera: Buprestidae) Adult Density, Development, and Distribution in *Fraxinus pennsylvanica* Trees

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ABSTRACT Emerald ash borer, *Agrilus planipennis* Fairmaire (Coleoptera: Buprestidae), a phloem-feeding beetle native to East Asia, was first discovered in southeast Michigan and Essex County, Ontario, in June 2002 and has since killed millions of ash (*Fraxinus* spp.) trees in North America. Initial studies in southeast Michigan indicated that the life cycle of *A. planipennis* was univoltine but more recent observations indicated some larvae feed for two summers, resulting in a 2-yr life cycle. Understanding factors that affect *A. planipennis* attraction to and development on host trees could improve detection and predictions of its population dynamics. We assessed adult *A. planipennis* attraction and larval density, distribution, and development rates in 2006 and 2007 on pole-sized green ash (*Fraxinus pennsylvanica* Marshall) trees that were girdled, exposed to the stress-elicitor methyl jasmonate, or left untreated. The study was conducted in a homogenous plantation with low levels of infestation. Overall, adult captures increased fivefold and four times as many larvae were recorded in 2007 compared with 2006. In both years, girdled trees captured significantly more adult *A. planipennis*, had higher larval densities, and larvae developed faster than on untreated control trees or trees exposed to methyl jasmonate. In 2006, larvae feeding below the girdle developed significantly faster than larvae feeding above the girdle. Adult *A. planipennis* captures, larval density and development did not differ significantly between untreated trees and trees exposed to methyl jasmonate in either year.

KEY WORDS Invasive forest pest, green ash, phloem- and wood-boring insect, girdled trees, methyl jasmonate

Emerald ash borer, *Agrilus planipennis* Fairmaire (Coleoptera: Buprestidae), a phloem-feeding beetle native to Asia, was identified as the cause of widespread ash (*Fraxinus* spp.) decline and mortality in southeastern Michigan and Essex County, Ontario in July 2002. As of August 2010, populations have been found in at least 14 additional states and the province of Quebec (EAB.info 2010). To date, *A. planipennis* has colonized and killed tens of millions of trees representing five ash species native to the upper Midwest and host trials suggest additional *Fraxinus* spp. may be threatened (Anulewicz et al. 2006, 2008). Discrete and localized outlier populations, initiated by inadvertent transport of infested ash nursery trees, logs, or firewood, are likely to continue to be discovered as public awareness increases and detection efforts continue.

Initial studies conducted in heavily infested sites in southeast Michigan indicated that the life cycle of *A. planipennis* was univoltine (Cappaert et al. 2005). Adults oviposited during the summer, larvae fed from late summer to fall, then overwintered as fourth instars or, more commonly, as prepupal larvae. Pupation occurred in spring and adults emerged in early summer.

More recent observations, however, indicated that at least some larvae overwinter as early instars, feed during a second summer, overwinter as prepupae, and emerge the following summer, resulting in a 2-yr life cycle. For example, in newly established infestations where *A. planipennis* density was low, >80% of larvae overwintered as early instars and would have required a second year for development (Cappaert et al. 2005, Siegert et al. 2010). In one of the new infestations, however, nearly all larvae on a tree stressed by a previous injury overwintered as fourth instars or prepupae and would have developed in a single year (Siegert et al. 2010).

Prolonged larval development, if common, would strongly influence *A. planipennis* population dynamics and rate of spread, especially in outlier sites (Mercader et al. 2010). A 2-yr life cycle also has implications for survey protocols and *A. planipennis* management in outlier sites. Moreover, if larval development is consistently delayed in healthy trees but not in stressed trees, mechanisms contributing to resistance in native ash trees could perhaps be identified and enhanced.

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Table 1. Mean (±SE) diam. at DBH, ht, surface area sampled, and no. of trees by canopy exposure class for green ash (*F. pennsylvanica*) trees by stress treatment in 2006 and 2007

	Control	Methyl jasmonate	Girdled	Control	Methyl jasmonate	Girdled
		2006			2007	
No. trees	30	30	30	30	30	30
DBH (cm)	12.2 ± 0.6	12.4 ± 0.4	12.3 ± 0.5	12.1 ± 0.5	12.7 ± 0.7	13.0 ± 0.5
Tree ht (m)	11.1 ± 0.3	10.8 ± 0.3	10.6 ± 0.3	10.7 ± 0.3	10.5 ± 0.4	10.9 ± 0.3
Exposed surface area (m^2)	2.4 ± 0.1	2.4 ± 0.2	2.3 ± 0.2	2.6 ± 0.2	3.2 ± 0.4	3.1 ± 0.3
Phloem thickness (mm)[a]	—	—	—	2.4 ± 0.6	2.5 ± 0.7	2.5 ± 0.5
No. of trees by canopy exposure						
Class 1	16	18	19	9	8	9
Class 2	3	4	4	7	8	11
Class 3	10	7	7	9	9	10
Class 4	1	1	0	5	5	0

No variables differed significantly among stress treatments ($P > 0.05$). Canopy exposure class 1 indicated full sun exposure, 2 indicated shading on one side, 3 indicated shading on two or three sides, and 4 indicated the tree was fully shaded.

[a] Mean (±SE) phloem thickness was measured in 2007 only.

Our primary objective in this 2-yr study was to evaluate adult *A. planipennis* attraction to as well as larval density and development on relatively homogeneous ash trees subjected to different stress treatments. In 2006 and again in 2007, trees were girdled, exposed to methyl jasmonate, or left as untreated controls. Girdled trees have been repeatedly shown to be highly attractive to *A. planipennis* (McCullough et al. 2009a,b). Methyl jasmonate, a volatile derivative of jasmonic acid, elicited stress responses in several plant species (Gols et al. 2003, Rodriguez-Saona and Thaler 2005) and adult *A. planipennis* were attracted to volatile compounds produced by ash seedlings exposed to methyl jasmonate (Poland et al. 2011, Rogriguez-Saona et al. 2006). We compared adult beetle captures on sticky bands affixed to the trunk of each tree during the summer. Trees were felled and debarked each winter to quantify larval density, developmental stage and within-tree distribution.

Materials and Methods

Study Site. This study was conducted in a well-stocked plantation of green ash (*F. pennsylvanica*) trees established in 1980 in the Rose Lake State Wildlife Research area, Clinton County, MI. The plantation was organized into 54 rows of 10 trees each, spaced at 1.5 m. Occasional trees were missing, but 363 ash trees were present with an average (±SE) Diameter at breast height (DBH) of 10.8 ± 0.20 cm. Trees in the plantation were visually surveyed in fall 2005 and there was no evidence of *A. planipennis* infestation. Trees were intensively examined again in spring 2006 and 11 trees with one to three *A. planipennis* exit holes on the bole were identified. These trees were felled and debarked from the base to the point where the upper leader was ≈4 cm in diameter. Larval density was standardized per meter square of exposed phloem. Woody material from these trees was removed from the site at least 3 wk before *A. planipennis* emergence began.

In May 2006, 10 blocks of nine trees each (total of 90 trees) were established. Trees were assigned to blocks based on their proximity to each other within the plantation but were separated from each other by at least one nonstudy tree in each direction, ensuring there was no overlap or contact between canopies of our study trees. DBH (1.3 m above ground) of all study trees was measured in May 2006 (Table 1).

Three trees within each block were randomly assigned to be girdled, exposed to the stress-elicitor methyl jasmonate, or left as untreated controls (30 trees per treatment). Trees were girdled by removing a 20 cm-wide band of outer bark and phloem, 0.85 m to 1.0 m aboveground, on 10 May. To expose trees to methyl jasmonate, a line with 20 bubble caps spaced 20 cm apart was suspended through the canopy on 17 May, using a Big Shot Line Launcher (WesSpur Tree Equipment, Bellingham, WA). Each bubble cap contained 150 μl of methyl jasmonate with a release rate (per bubblecap) of 0.38 mg per day, as determined in the laboratory at 20°C (Contech Enterprises, Inc., Delta, BC).

Study trees were qualitatively ranked from 1 to 4 based on the amount of canopy exposure to sun. A score of one indicated an open grown tree exposed to full sun, two indicated that the tree was shaded on one side, three indicated that the tree was shaded on two or three sides, and four indicated that the tree was fully shaded by adjacent trees.

Adult *A. planipennis* Capture. A 30 cm-wide band of plastic wrap was wrapped tightly around the trunk of each tree, 1.3 to 1.6 m aboveground. Tanglefoot (The Tanglefoot Company, Grand Rapids, MI) was applied to each band in May and reapplied in early July to ensure that the sticky bands remained effective. Adult *A. planipennis* were collected from sticky bands weekly from 21 June until 16 August 2006. Adults were soaked in 70% ethanol to dissolve the Tanglefoot, then sex was determined by examining beetles under a stereoscope. Surface area of the sticky bands on the relatively homogeneous trees was 0.12 m^2. Number of beetles captured per tree was used for analyses. Accumulated degree-days (base 10C) corresponding to dates of peak *A. planipennis* capture were acquired from the Michigan Agricultural Weather Network (MAWN) station located at East Lansing, MI, ≈10 km from the study site.

***A. planipennis* Larval Development.** From December 2006 through March 2007, trees were felled and debarked to quantify larval density and development. Trees in each block were felled within a few days of each other. Once trees were felled, height was measured, then each tree was bucked into 1 m long logs, up to at least 8 m aboveground or until the diameter of the main leader was ≈4 cm.

Logs were returned to the lab and carefully debarked with drawknives and chisels to expose *A. planipennis* larvae and galleries. Length and diameter at the midpoint of each log were measured and exposed surface area calculated. Number and life stage of *A. planipennis* larvae were recorded and density was standardized per meter square of exposed surface area for each tree. One control tree and one methyl jasmonate tree were not measured accurately; larval density was therefore not estimated on these trees. Developmental instars were determined by head capsule width (Cappaert et al. 2005). Larvae overwintering as first, second, or third instars were assumed to require another summer of feeding, and were recorded as 2-yr larvae following Cappaert et al. (2005). Larvae overwintering as fourth instars or prepupae would have emerged as adults the following summer and were recorded as 1-yr larvae. Larvae that began feeding in 2005 were distinguished from larvae representing progeny of adults that were active in 2006 based on gallery appearance and the presence of earlywood overlaid on the portion of the gallery excavated in 2005. These larvae were recorded but excluded from density, distribution, and development analyses. Maximum width and length of an intact gallery excavated by a 2006 prepupal larva were measured on the upper, middle, and lower section of each log.

The study was repeated in 2007 with a few modifications. Ten blocks of nine trees were again selected using the same parameters as in 2006 (total of 90 trees). Trees were girdled on 10 May 2007. A line with 10 methyl jasmonate bubble caps spaced 20 cm apart was suspended through the canopy of trees assigned to the methyl jasmonate treatment on 25 May. A second line, also with ten methyl jasmonate bubble caps, was suspended on 25 June. This ensured emission levels were sustained over the summer but the total amount of methyl jasmonate was equal to that released in 2006. Sticky bands were checked for *A. planipennis* adults weekly from 29 May until 29 August 2007.

Blocks of trees were felled, sectioned, and debarked from late October 2007 through February 2008. Larvae that began feeding in 2006 were again distinguished from larvae that began feeding in 2007. As in 2006, larvae remaining from the 2006 cohort were not included in analyses. In addition to variables recorded in 2006, phloem thickness was measured on opposing sides of the cut ends of each log using a caliper and averaged for each log.

Statistical Analysis. Four response variables, including number of captured *A. planipennis* adults, larval density, the proportion of larvae that developed in 1 yr, and horizontal gallery dimensions were evaluated for the 2006 and 2007 larvae. Data were tested for normality using the Shapiro-Wilk test (Shapiro and Wilk 1965) and residual plots. Number of captured adults, larval density, and horizontal gallery dimensions were $\text{Log}_{10}(x + 1)$ transformed to meet assumptions of normality. Proportion of larvae that developed in 1 yr required no transformation. All response variables were analyzed using the GLIMMIX procedure for mixed models in SAS statistical software (PROC GLIMMIX; SAS Institute 2003). Treatment effect (control, methyl jasmonate, or girdled), canopy exposure, and height aboveground (1 m increments) were treated as fixed effects in our analysis. Block and block × treatment were used as random factors. Differences among treatment means were tested as unplanned comparisons using the Tukey-Kramer least significance means test, sometimes called the honestly significant difference (HSD) test (Ott and Longnecker 2001). Multiple comparison tests were applied only when overall effects were significant ($P < 0.05$). Differences in larval density and development above and below the girdle on girdled trees were evaluated using a *t*-test. The relationship between larval density and the number of beetles captured on sticky bands was analyzed using a general linear model with $\text{Log}_{10}(x + 1)$ transformed data (PROC GLM, SAS institute 2003).

Results

2006 Study. While *A. planipennis* was present at the site before our study began, densities were very low and no trees exhibited external symptoms of infestation such as woodpecker attacks, canopy decline, or epicormic sprouts. The 11 trees removed from the site in spring 2006 before our study began had a mean (±SE) larval density of 12.8 ± 7.2 larvae per meter square. No more than three exit holes left by previously emerged *A. planipennis* adults were present on any of the trees.

Trees used for our study were relatively homogeneous in terms of size and exposure to sunlight (Table 1). Neither tree height ($F = 0.83$; df = 2, 18; $P = 0.45$) nor DBH ($F = 0.08$; df = 2, 18; $P = 0.92$) differed significantly among trees assigned to the three stress treatments (Table 1). Exposure to sunlight was also fairly consistent. Few trees were fully shaded and the canopy of most trees was either fully or partially exposed to sun (Table 1). Canopy exposure did not vary among trees in different stress treatments ($F = 0.80$; df = 2, 85; $P = 0.59$).

A total of 81 *A. planipennis* adults were captured on sticky bands on the 90 trees in 2006. Peak captures occurred during the first and third weeks of July, when 27.4 and 26.2%, respectively, of the total beetles were captured (Fig. 1A), corresponding to an accumulation of 1060 and 1380 DD_{10C} (Michigan State University Michigan Automated Weather Network [MSU MAWN] 2010), respectively. Heavy rain on 11 July and cloudy conditions (MSU MAWN 2010) may have slowed beetle activity during the second week of July.

Significantly more *A. planipennis* adults were captured on girdled trees than trees in other treatments

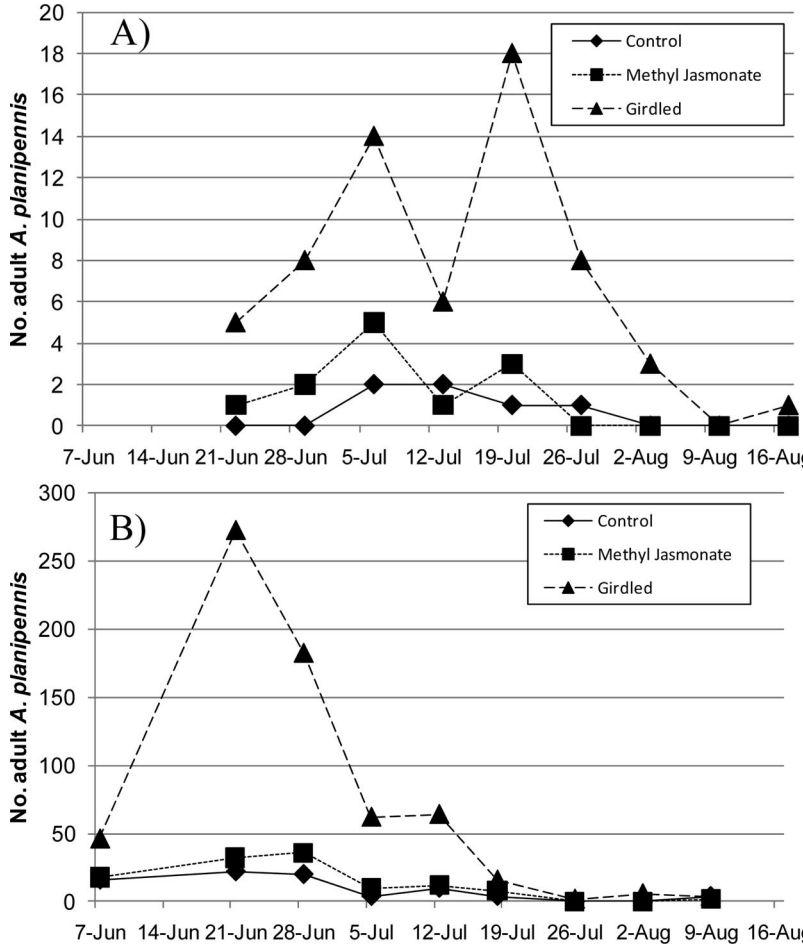

Fig. 1. Number of adult *A. planipennis* captured on sticky bands (area of 0.075 m^2) over time by treatment in (A) 2006 and (B) 2007. Beetles were collected from sticky bands from 22 June to 16 August in 2006 and from 7 June to 9 August in 2007. ($N = 30$ trees per treatment each year).

($F = 23.70$; df = 2, 18; $P < 0.001$). At least one beetle was captured on 5, 9, and 24 of the control, methyl jasmonate, and girdled trees, respectively. There was no significant difference between the number of adults captured on control and methyl jasmonate trees. On average (±SE), 0.2 ± 0.1, 0.4 ± 0.1, and 2.1 ± 0.5 beetles were captured on control, methyl jasmonate, and girdled trees, respectively. Total numbers of beetles captured per tree ranged from 0 to 2, 0–3, and 0–13 adults per tree for control, methyl jasmonate and girdled trees, respectively. Of the total beetles captured, 79.1% were female. Adult capture did not vary among canopy exposure classes ($F = 2.69$; df = 3, 57; $P = 0.055$).

A total of 4,621 *A. planipennis* larvae were recorded when the 90 trees were debarked. An additional 81 larvae that began feeding in 2005 were also identified (27, 42, and 12 larvae on control, methyl jasmonate, and girdled trees, respectively). An average (±SE) of 2.34 ± 0.89 m^2 of phloem was exposed per tree (total of 207.9 m^2). Overall, the mean density of the 2006 cohort of *A. planipennis* larvae was 34.5 ± 5.8 larvae per meter square and total numbers of larvae per tree ranged from 0 to 514.

Oviposition by *A. planipennis* adults was concentrated on girdled trees. Larval density (±SE) averaged 3.7 ± 0.9, 6.7 ± 4.4, and 71.1 ± 10.9 larvae per meter square on control, methyl jasmonate, and girdled trees, respectively. At least one larva was found on 24, 21, and 30 of the control, methyl jasmonate, and girdled trees, respectively. Larval density was significantly higher on girdled trees than on trees treated with methyl jasmonate or untreated control trees ($F = 85.02$; df = 2,18; $P < 0.001$) (Fig. 2), but did not differ between control trees or methyl jasmonate trees. Few larval cadavers were encountered when trees were debarked, but woodpecker predation of prepupal larvae and intraspecific competition on some heavily infested girdled trees resulted in mortality of ≈24% of the 2006 larvae (Tluzcek 2009).

Larval density varied by height on girdled trees only ($F = 10.46$; df = 7, 644; $P < 0.001$). This pattern was driven by the significantly higher densities of larvae found between 2–4 m above ground compared with

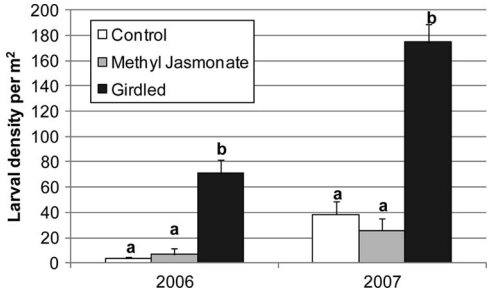

Fig. 2. Mean (±SE) density of *A. planipennis* larvae per meter square on untreated control trees, trees exposed to methyl jasmonate, and girdled trees in 2006 and 2007. Within years, means with the same letter are not significantly different (Tukey's HSD test; $P < 0.05$). (2006: $N = 29$ control and methyl jasmonate trees; $N = 30$ girdled trees. 2007: $N = 30$ trees per treatment).

densities in logs at least 6 m above ground (Table 2). In addition, densities of larvae were lower below the girdle than above the girdle ($t = 2.19$; df = 59; $P = 0.032$). Larval density was not affected by the interaction between height and treatment ($F = 1.48$; df = 14, 647; $P = 0.115$) nor did density differ among trees with different levels of canopy exposure ($F = 2.55$; df = 3, 54; $P = 0.066$).

A significant linear relationship between larval density and adults captured ($F = 59.64$; df = 1, 87; $P < 0.001$) (Fig. 3A) was observed. Approximately 54 larvae were recorded for each adult *A. planipennis* captured on the sticky bands. The relationship was strongly influenced, however, by two girdled trees that captured 8 and 14 beetles during the summer (Fig. 3A). For trees that captured 0–5 beetles, larval density was highly variable. On trees that captured zero adults, larval density ranged from 0 to 178 larvae per meter square. Larval densities on trees that captured 1–5 adults ranged from 0.2 to 195.7 larvae per meter square.

Overall, an average (±SE) of 28.1 ± 3.2% of the 2006 larvae were overwintering as fourth instars or prepupae and would have completed a 1-yr life cycle. A significantly greater proportion of larvae reached the

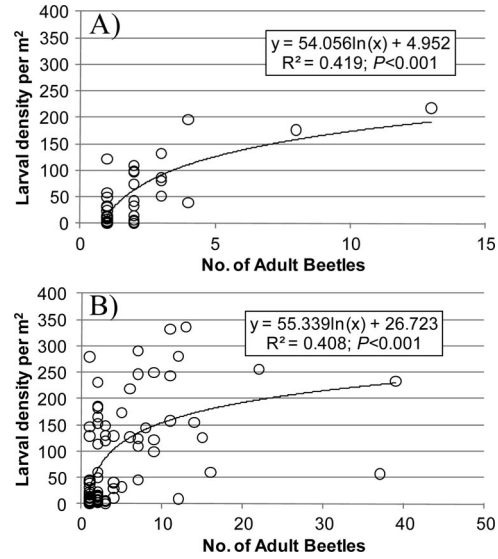

Fig. 3. $\text{Log}_{10}(x + 1)$ relationship between *A. planipennis* larvae per meter square and total adult capture on sticky bands on trees in (A) 2006 ($N = 88$ trees) and (B) 2007 ($N = 90$ trees).

fourth instar or prepupal stage on girdled trees than on control and methyl jasmonate trees ($F = 19.95$; df = 2, 18; $P < 0.001$), but there was no significant difference in larval development between control and methyl jasmonate trees. On average, 16.0 ± 3.8%, 12.1 ± 4.2%, and 49.0 ± 4.3% of larvae were fourth instars or prepupae on control, methyl jasmonate, and girdled trees, respectively.

On the girdled trees, significantly more larvae feeding below the girdle had reached the fourth instar or were prepupae compared with larvae feeding above the girdle ($F = 40.16$; df = 3, 27; $P < 0.001$) (Fig. 4). Less than one-third of the larvae feeding above the girdle were fourth instars or prepupae, while >75% of larvae feeding below the girdle were either fourth instars or prepupae (Fig. 4). Larval development did not vary among canopy exposure levels ($F = 1.80$; df = 3, 42; $P = 0.162$).

Table 2. Mean (±SE) *A. planipennis* larval density (m^2) in *F. pennsylvanica* trees by ht above ground and stress treatment in 2006 and 2007. Total no. of debarked logs from the trunk and primary branches at each ht is shown in parentheses

Ht (m)	Control (N)	Methyl jasmonate (N)	Girdled (N)	Control (N)	Methyl jasmonate (N)	Girdled (N)
		2006			2007	
0–1	1.1 ± 0.64a (31)	1.3 ± 1.06a (31)	47.93 ± 8.25ab (31)	22.1 ± 11.25b (30)	17.8 ± 10.59ab (30)	130.4 ± 14.38b (34)
1–2	1.2 ± 0.67a (32)	4.8 ± 3.78a (31)	49.93 ± 10.19ab (31)	26.9 ± 9.73b (30)	15.0 ± 6.98ab (30)	92.6 ± 8.4b (33)
2–3	4.4 ± 1.72a (33)	8.5 ± 5.01a (33)	93.47 ± 16.17a (31)	50.9 ± 13.73a (31)	32.6 ± 14.93a (32)	265.7 ± 20.93a (36)
3–4	5.9 ± 1.58a (34)	11.3 ± 6.24a (38)	87.33 ± 13.86a (32)	49.1 ± 13.23a (30)	39.1 ± 11.59a (34)	246.1 ± 23.22ab (40)
4–5	5.1 ± 1.35a (36)	2.7 ± 0.68a (44)	71.89 ± 14.21ab (36)	39.5 ± 10.56ab (38)	28.5 ± 6.68a (42)	211.9 ± 24.31ab (47)
5–6	2.1 ± 0.74a (28)	1.6 ± 0.57a (30)	52.78 ± 17.33abc (27)	22.4 ± 5.39ab (45)	15.5 ± 3.51ab (46)	160.1 ± 20.12b (52)
6–7	1.5 ± 0.65a (20)	0.3 ± 0.23a (23)	32.21 ± 9.26bc (28)	14.3 ± 3.96b (46)	8.4 ± 2.38b (52)	95.5 ± 14.21bc (48)
7–8	1.8 ± 1.27a (9)	0.0 ± 0.00a (9)	14.67 ± 7.09c (18)	8.4 ± 2.15b (37)	4.8 ± 1.65b (32)	66.5 ± 11.71c (37)

Means for different heights within the same treatment with the same letter (a, b, and c) were not significantly different (Tukey HSD test; $P < 0.05$). The girdle was located between ht 0–1 and 1–2 m.

[a] Number of logs per ht differed from the total no. of trees when trees had split trunks and when few logs near the tree top were >4 cm in diam.

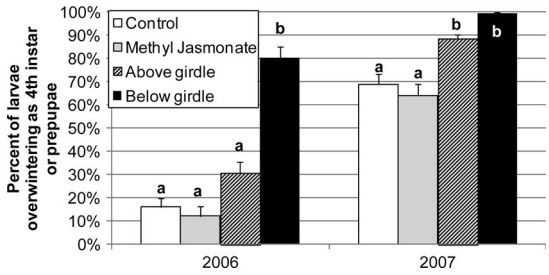

Fig. 4. Mean (±SE) percentage of *A. planipennis* larvae that overwintered as fourth instars or prepupae on untreated control trees, trees exposed to methyl jasmonate, and above and below the girdle on girdled trees in 2006 and 2007. Within years, means with the same letter are not significantly different (Tukey's HSD test; $P < 0.05$) ($N = 30$ trees per treatment each year).

There were also obvious differences in the extent and pattern of galleries made by larvae feeding below the girdle compared with larvae feeding above the girdle and on nongirdled trees. Overall, dimensions of galleries made by larvae that reached the prepupal stage on the 90 trees averaged (±SE) 3.8 ± 0.2 cm in horizontal distance and 7.8 ± 0.4 cm in vertical distance. Gallery width did not vary by treatment ($F = 1.96$; df = 2, 11; $P = 0.187$) or canopy exposure ($F = 1.04$; df = 3, 21; $P = 0.395$). However, on girdled trees, galleries extended significantly further horizontally when larvae fed below the girdle than above the girdle ($F = 52.74$; df = 3, 57; $P = 0.001$) (Fig. 5). Similarly, length of galleries was greater below the girdle than above, with mean lengths of 13.7 ± 1.1 cm and 6.9 ± 0.2 cm, respectively. If the galleries below the girdle are excluded, the dimensions of galleries made by larvae overwintering as prepupae on all treatments averaged (±SE) 2.9 ± 0.2 cm in horizontal distance and 6.7 ± 0.2 cm in vertical distance.

2007 Study. As in 2006, trees used in 2007 were similar in size and growing condition. Tree height ($F = 0.49$; df = 2, 18; $P = 0.62$), DBH ($F = 0.64$; df = 2, 18; $P = 0.54$), bark thickness ($F = 0.82$; df = 2, 16; $P = 0.46$), and canopy exposure score did not vary significantly among trees assigned to the three treatments.

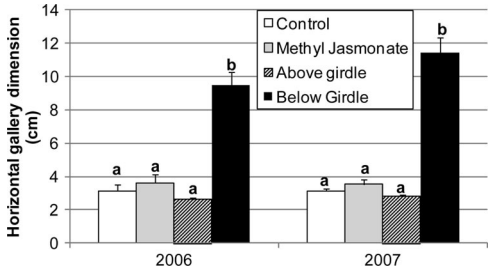

Fig. 5. Mean (±SE) width of *A. planipennis* prepupal galleries on control and methyl jasmonate trees, and above and below the girdle on girdled trees in 2006 and 2007. Within years, means with the same letter are not significantly different (Tukey's HSD test; $P < 0.05$) ($N = 30$ trees per treatment each year).

Numbers of trees in each of the four canopy exposure classes also did not differ significantly among treatments ($F = 0.80$; df = 2, 85; $P = 0.45$) (Table 1).

A total of 426 *A. planipennis* adults were captured on the sticky bands in 2007, representing a fivefold increase over adult captures in 2006. Although sticky bands were in place by 10 May, no beetles were captured until June. Captures peaked in mid June when 36% of all beetles were captured (Fig. 1B), which corresponded to 920 accumulated degree-days$_{10c}$ (MSU MAWN 2010). More than half (63%) of the *A. planipennis* adults were captured in June, compared with 34% in July and 3% in August (Fig. 1B). Overall, 55.8% of adult beetles captured on sticky bands were female.

Significantly more *A. planipennis* adults were captured on girdled trees than on other trees ($F = 52.63$; df = 2, 18; $P < 0.001$), while captures did not differ between control and methyl jasmonate trees. At least one beetle was captured on 20, 21, and 30 of the control, methyl jasmonate, and girdled trees, respectively. On average, 1.3 ± 0.2, 2.0 ± 0.4, and 10.9 ± 2.0 adults were captured on control, methyl jasmonate, and girdled trees, respectively. Counts ranged from 0 to 7, 0–12, and 2–39 adults per tree for control, methyl jasmonate, and girdled trees, respectively. Number of adults captured did not vary by canopy exposure class ($F = 1.48$; df = 4, 56; $P = 0.222$).

A total of 18,891 larvae were recorded on the 90 trees that were debarked in 2007, representing a fourfold increase in larval abundance from 2006. An additional 710 larvae that began feeding in 2006 were also present (349, 162, and 199 larvae on control, methyl jasmonate, and girdled trees, respectively). An average of 2.9 ± 0.18 m^2 of phloem was exposed per tree (total of 263.9 m^2). The number of 2007 larvae per tree ranged from 0 to 1862. Overall, the mean density of the 2007 *A. planipennis* larvae was 79.6 ± 9.8 larvae per meter square. At least one 2007 larva was feeding on 29, 29, and 30 of the control, methyl jasmonate, and girdled trees, respectively.

Larval density was significantly higher on girdled trees than on other trees ($F = 30.87$; df = 2, 18; $P < 0.001$) (Fig. 2), while differences between control and methyl jasmonate trees were not significant. Larval density averaged 38.4 ± 10.4, 25.8 ± 9.7, and 174.5 ± 14.3 larvae per meter square on control, methyl jasmonate, and girdled trees, respectively. Nearly all phloem on girdled trees was consumed by *A. planipennis* larvae in 2007. Approximately 33% of larvae on girdled and on nongirdled trees had died by the time trees were felled and debarked during the 2007–2008 winter. Mortality was caused primarily by a combination of woodpecker predation and intraspecific competition (Tluczek 2009). Larval density did not vary significantly above and below the girdle ($t = 0.65$; df = 58; $P = 0.519$) (Table. 2) nor among trees assigned to different canopy exposure classes ($F = 1.08$; df = 6, 50; $P = 0.386$).

Densities of 2007 *A. planipennis* larvae were significantly lower on logs collected from the base and tops of trees compared with other sections ($F = 26.09$; df =

7, 859; $P < 0.001$) (Table 2). Average larval densities were highest 2–4 m aboveground although differences among logs from different heights were not consistently significant (Table 2). No significant interaction between stress treatment and tree height was observed for larval density ($F = 1.34$, df = 14, 859; $P = 0.178$).

As in 2006, a significant linear relationship existed between the number of adults captured on sticky bands during the summer and larval density ($F = 66.40$; df = 1, 89; $P < 0.001$) (Fig. 3B). Roughly 55 larvae were recorded for each adult *A. planipennis* captured on a sticky band, a ratio similar to that observed in 2006. The relationship between larval densities and adult captures on individual trees, however, was again variable. Larval densities ranged from 0 to 279 larvae per meter square on trees that captured 0–5 adult *A. planipennis* (Fig. 3B).

Overall, 88.7% of larvae that began feeding in 2007 were overwintering as fourth instars or prepupal larvae and would have emerged in 2008. A significantly higher proportion of larvae would have developed in 1-yr on girdled trees than on control and methyl jasmonate trees ($F = 18.07$; df = 2, 18; $P < 0.001$), while development rates did not differ between control and methyl jasmonate trees. On average, 69.0 ± 4.2%, 64.1 ± 4.8%, and 91.3 ± 3.4% of larvae overwintered as fourth instars or prepupae on control, methyl jasmonate, and girdled trees, respectively. In contrast to 2006, girdled trees were heavily colonized in 2007 and development rates of larvae below and above the girdle did not differ ($t = 1.92$; df = 27; $P = 0.244$) (Fig. 4). Canopy exposure class did not significantly affect larval development ($F = 2.24$; df = 4, 54; $P = 0.077$).

Galleries formed by 2007 larvae that reached the prepupal stage averaged 3.5 ± 0.1 cm in horizontal distance and 8.6 ± 0.3 cm in vertical distance. As in 2006, larvae that developed below the girdle on girdled trees had galleries that extended significantly further horizontally than larvae above the girdle ($F = 78.92$; df = 3, 27; $P < 0.001$). Horizontal dimensions of galleries did not differ for larvae that developed on control and methyl jasmonate trees, and above the girdle on girdled trees (Fig. 5). Similarly, vertical dimensions of galleries were greater below the girdle than above, averaging 15.5 ± 1.5 cm and 7.3 ± 0.1 cm, respectively. There was no significant difference in the vertical dimensions of galleries among larvae that developed on control and methyl jasmonate trees, and above the girdle on girdled trees. If the galleries below the girdle are excluded, the dimensions of galleries made by larvae overwintering as prepupae on all treatments averaged (±SE) 3.2 ± 0.1 cm in horizontal distance and 8.3 ± 0.3 cm in vertical distance.

Discussion

Despite the similarity of trees in the plantation, adult *A. planipennis* were strongly attracted to girdled trees in both 2006 and 2007. Even in 2006, when *A. planipennis* density was very low, at least one adult beetle was captured on 80% of the girdled trees and every girdled trees had larvae. In comparison, only 17 and 30% of the control trees and methyl jasmonate trees, respectively, captured an adult beetle and we found no evidence of larvae on 20–30% of these trees in fall 2006. Differences in larval density among treatments were also pronounced in both years. In 2006, larval density on girdled trees was 10–18 fold higher than on other trees and the average larval density on girdled trees would be considered moderate to high (McCullough and Siegert 2007). In 2007, when the *A. planipennis* population had increased substantially, larval density remained 4.5–7 fold higher on girdled trees than on the nongirdled trees.

Other field studies with native *Agrilus* beetles have similarly documented a strong attraction to stressed or girdled trees. Native buprestids including two-lined chestnut borer, *Agrilus bilineatus* (Weber), (Haack and Benjamin 1982, Dunn et al. 1986), bronze birch borer, *Agrilus anxius* Gory (Barter 1957), and flatheaded borer, *Agrilus burkei* Fisher (Svihra and Koehler 1993) were attracted to declining oak (*Quercus* sp.), birch (*Betula* sp.), and alder (*Alnus* sp.), respectively. *A. bilineatus* adults were captured at seven times the rate on girdled oaks compared with controls and larval densities were significantly higher on stressed oak trees than on healthy trees (Haack and Benjamin 1982). A meta-analysis showed that higher densities of buprestid larvae were generally associated with trees stressed by drought (Koricheva and Larsson 1998).

In its native range in Asia, *A. planipennis* attacks stressed or dying ash trees (Akiyama and Ohmomo 2000, Williams et al. 2005). In North American studies, girdled trees attracted significantly more adult *A. planipennis* and had higher larval densities than nongirdled trees as well as trees that were wounded, treated with herbicide, or exposed to methyl jasmonate (McCullough et al. 2009a,b). Preferential attraction of *A. planipennis* beetles to girdled or severely stressed trees likely results from changes in host volatiles (Crook et al. 2008, de Groot et al. 2008, Poland et al. 2011) and perhaps hyperspectral reflectance of foliage (Bartels et al. 2008).

Abundance of *A. planipennis* within sites can increase markedly from one year to the next. Despite the destruction of all larvae on the 90 trees that were felled and debarked during the 2006 winter, approximately five times as many adult beetles were captured on sticky bands in 2007 as in 2006 and the total number of larvae we recorded increased by more than fourfold. Anulewicz et al. (2007) counted *A. planipennis* exit holes on landscape trees in four sites for 3 yr and reported number of exit holes increased by two- to fourfold annually. Captures of *A. planipennis* on sticky bands increased by sixfold in a 2-yr study conducted in four sites (McCullough et al. 2009b).

Availability of ash phloem limits the number of *A. planipennis* that can be produced in a given tree or site. McCullough and Siegert (2007) reported that on average, 105 *A. planipennis* beetles per meter square can potentially be produced on green ash and white ash (*F. americana*) trees (DBH ≥13 cm). In 2007, average

larval density on girdled trees in our site substantially exceeded this level and nearly all phloem from the base to the top of the trees was consumed on heavily infested trees. Larval mortality on these trees, however, was relatively high and <66% of the larvae on girdled trees would likely have emerged as adults in 2008. In contrast, larval densities on the untreated control and methyl jasmonate trees remained at low or moderate levels in 2007. There was little evidence of canopy decline or other symptoms on the control and methyl jasmonate trees and considerable amounts of healthy phloem would have been available for *A. planipennis* larvae the following year.

Exposure to methyl jasmonate had no detectable effect on adult *A. planipennis* capture rates, larval density, development, or distribution in either year of our study. We originally hypothesized that sustained release of methyl jasmonate within the canopy would induce stress responses in the trees, similar to those associated with girdling or other physical stress. Methyl jasmonate exposure activated the jasmonic pathway, resulting in altered volatile emissions and other stress responses in plants ranging from cotton (Rodriguez-Saona et al. 2001) to young conifers (Hudgins and Franceschi 2004). In laboratory trials with ash seedlings, exposure to methyl jasmonate altered foliar volatile profiles and adult *A. planipennis* were attracted to the volatile compounds produced by those seedlings (Poland et al. 2006, Rodriguez-Saona et al. 2006).

In field studies with ash trees, however, there has been little evidence of induced responses resulting from exposure to methyl jasmonate (McCullough et al. 2009b). The quantity of methyl jasmonate released within the tree canopies in our study may have been too low to elicit stress responses or trees may be less sensitive to methyl jasmonate than seedlings (Cippolini and Redmann 1999, Henery et al. 2008). Alternatively, the trees in this study may have been too large or mature to be affected by methyl jasmonate. In the herbaceous plant *Catharanthus roseus* L. G. Don, exposure to methyl jasmonate increased synthesis of protective alkaloids in seedlings but not in mature plants (Aerts et al. 1994).

Adult *A. planipennis* emergence and activity appear relatively consistent with respect to temperature, but larval development rates differed between years and among treatments in our site. Degree day accumulations corresponding with the onset and peak of adult *A. planipennis* captures in our study were similar in both years to those reported for numerous other sites and years in studies conducted in Michigan (McCullough et al. 2009a,b, Poland et al. 2011). Larvae, however, generally developed faster on girdled trees than on nongirded trees. In 2006, >80% of the larvae on the lightly infested control and methyl jasmonate trees overwintered as early instars and would have required a second year to complete development. Overall, the proportion of larvae that overwintered as fourth instars or prepupae, consistent with a 1-yr life cycle, increased by fivefold from 2006 to 2007, corresponding to the similar increase in *A. planipennis* density. Other North American studies have reported high proportions of *A. planipennis* overwintered as early instars in low density sites, while most larvae in sites with moderate to heavy infestations overwinter as fourth instars or prepupae and emerge the following year (Cappaert et al. 2005, Siegert et al. 2010).

The difference in larval development rates between girdled trees and the nongirdled control and methyl jasmonate trees was largely driven by the larvae feeding below the girdle in 2006. Most of the 2006 larvae (70%) feeding above the girdle in 2006 overwintered as early instars while 80% of larvae below the girdle overwintered as fourth instars or prepupae. The difference in development rate cannot be explained solely by differences in density; larval density was actually lower below the girdle than above the girdle. Galleries below the girdle were also notably longer, extended further horizontally and were less likely to be excavated in the serpentine pattern characteristic of galleries on lightly infested trees. Galleries of larvae feeding above the girdle, in contrast, usually displayed the distinct serpentine pattern and were similar in size to galleries on the control and methyl jasmonate trees. In 2007, however, when larval densities on girdled trees were very high, nearly all phloem was consumed, and trees were visibly stressed by midsummer, most larvae would have completed a 1-yr life cycle.

Although *A. planipennis* larvae exhibited both univoltine and 2-yr life cycles in our site, climate can also influence larval development rates. In China, larvae reportedly required at least 150 frost-free days for feeding (Wie et al. 2007). Larvae needed 2 yr to develop in the northern province of Heilongjiang 45.45 °N (Yu 1992), 1 yr to develop in the more southerly Liaoning Province 41.8 °N (Zhao et al. 2005), and either 1 or 2 yr to develop in the transitional area of Jilin Province (Wie et al. 2007). Our study site, located at 42.7 °N, corresponds to the transitional area in China where larvae take 1–2 yr to develop. To date, development of *A. planipennis* has not been shown to vary with climate or latitude in North America but as populations expand, climate may play a more significant role on larval development.

Development of the native *A. anxius* in North America similarly varies with latitude and host condition. Larvae required at least 2 yr to develop in New Brunswick and Quebec, 1 yr in Connecticut and New York (Barter 1957) and 1–2 yr in Minnesota and Maine, depending on host vigor (Anderson 1944, Nash et al. 1951). Even in northern locations, however, *A. anxius* larvae could develop in 1 yr on plant tissue that was fairly moribund, including girdled trees that had been attacked repeatedly (Barter 1957). Larvae able to survive on healthy birch trees, in contrast, required at least 2 yr for development (Barter 1957). Collectively, these reports and our results suggest girdling or high densities of galleries may interrupt transport of one or more nutrient or defensive compounds in the phloem that act to slow or inhibit development of *A. planipennis* and related buprestid larvae. Additional research to identify such compounds could help to elucidate potential mechanisms of host resistance.

Operational programs typically use pole-sized trees (10–20 cm DBH) like those in our plantation for *A. planipennis* detection surveys (e.g., Flint 2005, Harrison 2005, SLAMEAB.info 2010). Average larval densities were generally highest on logs that were 2–5 m above ground, although distribution in 2006 varied significantly only on girdled trees. Debarking this portion of the trunk may be most efficient for locating larvae on pole-sized trees in sites with low *A. planipennis* density. This should be welcomed by survey crews, given that the base of the trunk typically has thick bark that is difficult to remove, while numerous small branches in the upper canopy also increase the difficult of debarking. On larger trees, *A. planipennis* typically colonize the upper canopy before galleries are present on the trunk (Cappaert et al. 2005). Large trees are seldom used for operational surveys because of costs and logistical difficulties. Our results also indicate debarking trees to find larvae is critical if girdled trees are used for *A. planipennis* detection or monitoring. Sticky bands, which cover only a small fraction of the surface area of a tree, captured zero beetles on six of the 30 girdled trees in 2006, but all girdled trees were infested, with larval densities as high as 178 larvae per meter square. Other studies with girdled trap trees have similarly reported that sticky bands sometimes fail to capture adult beetles even on trees found to be heavily colonized when debarked (McCullough et al. 2009a,b).

Previous research has shown that buprestids, including *A. planipennis,* are attracted to and more likely to oviposit on trees exposed to sun or growing in open areas than on shaded trees (McCullough et al. 2009a,b). Wermelinger et al. (2007) found that *Anthaxia nitidula* (Linné), *Agrilus olivicolor* Kiesenwetter, *Agrilus viridus* (L), *Agrilus convexicollis* Redtenbacher, and *Agrilus laticollis* Kiesenwetter preferred to colonize trees along edges than trees in the interior of forests. In our plantation, however, at least part of the canopy of most trees was exposed to sunlight and canopy exposure did not affect either adult beetle captures or larval density.

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