Attraction of the emerald ash borer to ash trees stressed by girdling, herbicide treatment, or wounding

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Abstract: New infestations of emerald ash borer, *Agrilus planipennis* Fairmaire, an invasive pest native to Asia, are difficult to detect until densities build and symptoms appear on affected ash (*Fraxinus* spp). We compared the attraction of *A. planipennis* to ash trees stressed by girdling (bark and phloem removed from a 15 cm wide band around the tree (2003–2005)), vertical wounding (same area of bark and phloem removed in a vertical strip (2004)), herbicide treatment (Pathway applied with a Hypo-Hatchet tree injector (2003) or basal bark application of Garlon 4 (2004, 2005)), exposure to the volatile stress elicitor methyl jasmonate (2005), or left untreated (2003–2005). The number and density of captured adults and density of larvae were recorded for 24, 18, and 18 replicates of each treatment at four, three, and five sites in 2003, 2004, and 2005, respectively. Girdled trees generally captured more adult *A. planipennis* and consistently had higher larval densities than untreated trees, and at most sites, than trees stressed by other treatments. Differential attraction to girdled trees was more pronounced at sites with lower densities of *A. planipennis*. Rates of capture of adults and densities of larvae were higher on trees in full or nearly full sun than on shaded trees. Girdled trees could be a useful tool for use in operational programs to detect or manage localized *A. planipennis* infestations.

Résumé : Les nouvelles infestations de l'agrile du frêne, *Agrilus planipennis* Fairmaire, un ravageur invasif, indigène de l'Asie, sont difficiles à détecter jusqu'à ce que la densité de l'insecte augmente et que les symptômes apparaissent sur les frênes (*Fraxinus* spp.) infestés. Nous avons comparé l'attirance d'*A. planipennis* pour des tiges de frêne stressées par une annélation (bande d'écorce et de phloème de 15 cm enlevée autour de la tige de 2003 à 2005; une blessure verticale (bande verticale d'écorce et de phloème enlevée sur une surface équivalente (2004)); l'application d'un herbicide (Pathway appliqué avec une hachette injectrice (2003)); l'application de Garlon sur l'écorce à la base du tronc (2004–2005)); l'exposition au jasmonate de méthyle, un éliciteur de stress volatil (2005) et pour des tiges non traitées (2003 à 2005). Le nombre et la densité des adultes capturés ainsi que la densité des larves ont été notés pour 24, 18 et 18 répétitions de chaque traitement à quatre, trois et cinq endroits respectivement en 2003, 2004 et 2005. Les tiges annelées ont permis de capturer généralement plus d'*A. planipennis* adultes et avaient une densité de larves constamment plus élevée que les tiges non traitées et, à la plupart des endroits, que les arbres stressés par les autres traitements. L'attirance pour les tiges annelées était plus prononcée aux endroits où la densité d'*A. planipennis* était plus faible. Les captures d'adultes et la densité des larves étaient plus élevées sur les arbres exposés au plein soleil ou presque que sur les arbres ombragés. Des arbres annelés pourraient être un outil utile dans les programmes opérationnels pour détecter ou gérer les infestations localisées d'*A. planipennis*

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Introduction

The emerald ash borer, *Agrilus planipennis* Fairmaire (Coleoptera: Buprestidae), a phloem-feeding beetle native to Asia, was identified in July 2002 as the cause of widespread ash (*Fraxinus* spp.) decline and mortality in southeastern Michigan, USA, and Essex County, Ontario, Canada. *Agrilus planipennis* was not generally considered to be a significant forest pest in its native range (Chinese Academy of Science Institute of Zoology 1986; Yu 1992; Gao et al. 2004) and little was known about it at the time of its discovery.

Adult *A. planipennis* feed on small patches of ash foliage throughout their life-span, which may last 3–6 weeks (Bauer et al. 2004). After at least 2 weeks of foliage feeding, females lay individual eggs in bark cracks and crevices, typically from late June through early August. Eggs hatch in 1–2 weeks. Larvae feed in serpentine galleries in the phloem of the branches and trunk until late fall. Most *A. planipennis* complete four instars, then overwinter as prepupal larvae in the outer sapwood or in thick bark (Cappaert et al. 2005). When *A. planipennis* density is high, canopy dieback can progress rapidly and even large trees may succumb after 3

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or more years of heavy infestation (Poland and McCullough 2006).

Tens of millions of ash trees have been killed by *A. planipennis* in Michigan as of late 2008. Established populations continue to expand, and additional infestations, most initiated by inadvertent transport of infested ash firewood, logs, and nursery trees, have been found in at least nine additional states and two Canadian provinces (www.emeraldashborer.info 2008).

Methods to detect newly established *A. planipennis* infestations were identified as a critical research need when this invasive pest was first discovered. Accurate and efficient survey methods are also needed to delimit localized, outlier infestations and to monitor the effectiveness of management activities implemented to slow population growth or expansion. Developing effective survey methods, however, remains problematic. *Agrilus planipennis*, like other phloem-feeding buprestids, does not appear to utilize long-range sex or attraction pheromones. When *A. planipennis* was discovered, no traps, lures or other survey methods were available for operational use.

In 2002 and 2003, regulatory agencies relied largely on visual surveys of ash trees to delimit the core *A. planipennis* infestation in southeastern Michigan (Poland and McCullough 2006). Survey crews progressed systematically, using external symptoms such as canopy dieback, epicormic sprouts, signs of woodpecker attacks, and D-shaped exit holes left by emerging beetles to identify infested trees. Visual surveys of high-risk areas such as sawmills and campgrounds, along with regulatory trace-backs of ash nursery stock originating in southeastern Michigan, were successfully employed to identify some outlier populations. Scientists and many regulatory officials were concerned, however, that low-density infestations were not being detected.

Locating newly infested trees and trees with low densities of *A. planipennis* is exceptionally difficult because these trees do not exhibit the external symptoms that characterize heavily infested trees. On large trees the upper portions of the trunk or canopy branches are generally colonized first (Cappaert et al. 2005), making it difficult to find D-shaped exit holes, often the first sign of infestation. In addition, some *A. planipennis* larvae require 2 years for development. In China, 2-year development occurs only in the northern part of the *A. planipennis* range (Yu 1992) but in North America, 2- and 1-year larval development can occur in the same location and even on the same trees. The underlying cause of this extended development is not known, but it appears to be most common in newly infested trees (Siegert et al. 2007; Tluczek et al. 2008), exacerbating detection and survey problems.

Although *A. planipennis* has colonized and killed healthy trees as well as stressed trees in North America, we hypothesized that beetles are preferentially attracted to stressed trees for oviposition, maturation feeding, or both. Several phloem-feeding *Agrilus* species, including the native *A. anxius* Gory and *A. bilineatus* (Weber), are secondary pests that colonize stressed or declining host trees (Anderson 1944; Haack and Benjamin 1982), and *A. planipennis* appears to function similarly in Asia (Yu 1992; Gao et al. 2004). Our objective was to assess the attraction of *A. planipennis* to stressed, wounded, and healthy ash trees.

Methods

In May 2003 we selected 18 apparently healthy ash trees at each of four sites in southeastern Michigan (72 trees in total) and measured diameter at breast height (DBH) (1.3 m above ground) of each study tree. At the Kensington Golf Course (KGC) (Livingston County) site, open-grown green ash (*Fraxinus pennsylvanica* Marsh.) trees (DBH = 29.7 ± 1.7 cm; mean ± SE) were located in an unmowed area between the golf course and a highway easement. The Ann Arbor airport (AAA) (Washtenaw County) site (DBH = 5.1 ± 0.2 cm) was an abandoned nursery with green ash planted in rows roughly 10 m apart in an open field. Ash trees within or near these two sites were generally healthy and few had visible *A. planipennis* exit holes or signs of woodpecker attacks, indicating that *A. planipennis* populations were likely to be at low to moderate densities. At the Kensington Maintenance Woodlot area (KMW) (Livingston County) site, white ash (*F. americana* L.) trees (DBH = 16.6 ± 0.8 cm) were growing in a closed-canopy woodlot with an overstory that included black cherry (*Prunus serotina* Ehrh.) and oaks (*Quercus* spp.). The Maybury State Park (MSP) (Wayne County) site was composed of open-grown white ash trees (DBH = 14.9 ± 0.99 cm) growing in fields, along the edge of wooded areas, and within a closed-canopy stand that included red maple (*Acer rubrum* L.) and oaks. Several ash trees growing in or near these sites had thinning canopies, numerous signs of woodpecker attacks, or D-shaped exit holes, suggesting moderate to high densities of *A. planipennis*. Trees at the KGC site were significantly larger than those at the KMW and MSP sites, which in turn were significantly larger than those at the AAA site (analysis of variance (ANOVA), $F_{[3,63]} = 91.85$; $P < 0.0001$; see Statistical methods below).

At each site, trees were assigned to blocks on the basis of size, location, and growing conditions. There was roughly 8–10 m between trees within blocks. Within each block, trees were randomly assigned to be girdled, treated with herbicide, or left as untreated controls. Average tree size did not vary significantly among treatments at individual sites except the KMW site ($F_{[2,15]} = 5.4$, $P = 0.02$), where girdled trees were slightly larger (DBH = 19.5 ± 1.2 cm) than control (15.4 ± 1.2 cm) or herbicide-treated trees (14.9 ± 0.9 cm).

Treatments were applied on 27 May 2003. To girdle trees we used a small chainsaw to carefully cut through the bark and phloem around the circumference of the trunk, roughly 85 cm above ground. A second cut was made 15 cm higher and bark and phloem between the two radial cuts were removed with the saw. Care was taken to minimize injury or removal of xylem during the girdling. A Hypo-Hatchet tree injector (Forestry Suppliers, Inc., Jackson, Mississippi) was used to apply Pathway herbicide (5.4% picloram + 20.9% D-amine). Trees were frilled with the Hypo-Hatchet, which injects approximately 1 mL of formulated herbicide per cut every 2–3 cm around the circumference of the tree, 1 m above ground.

We also evaluated the attractiveness of freshly cut ash logs. Cut trees or logs are attractive to several species of bark and wood-boring beetles and have been used for survey and management purposes (McCullough and Sadof 1998; MacLauchlan et al. 2003). If effective, trap logs would be more efficient than girdled trees for use in large-scale *A. planipennis* surveys. Green and white ash logs, each 2 m long and 10–15 cm in diameter, were cut on 20–22 May at Michigan State University's W.K. Kellogg Forest (Kalamazoo County), an area well beyond the *A. planipennis* infestation. Similar-sized black ash (*Fraxinus nigra* Marsh.) logs were cut on 28 May from Kensington Park, roughly 5 km from the nearest study site. Although *A. planipennis* populations were present in other areas of this large (15 000 km^2) park, there was no sign of infestation in any of the black ash trees we used for this and related studies. The cut ends of each log were dipped in paraffin wax to reduce desiccation. Logs were transported to the study sites and one log of each species was randomly assigned to each existing block of three trees. Logs were set vertically on the ground and wired to t-posts for support. Logs were interspersed among the trees in each block but were at least 7–10 m from any of the study trees. Black ash logs were not used at the AAA site because of the limited availability of suitable black ash trees.

On 27 May a band of plastic shrink wrap, approximately 25 cm wide, was wrapped tightly around the trunk of each tree and log and covered with Tanglefoot. The lower edge of the band was 1.35 m above ground. The area of sticky bands on the trap trees was 1360 ± 80 cm^2 (mean ± SE). Sticky bands were checked weekly from 26 June through 22 August and the number of adult *A. planipennis* trapped in the Tanglefoot was recorded. Beetles were removed from all bands each week and returned to the laboratory, where species identity was confirmed. Bands were removed in mid-August. The density of adults captured on each tree or trap log was standardized as the number per 1400 cm^2, the approximate area of each sticky band.

Canopy dieback was visually estimated in June after leaf expansion and in late summer before leaf senescence. The percentage of the canopy that was dead was recorded to the nearest 10% on each occasion by two experienced people. When estimates differed, the mean of the two estimates was recorded. At the AAA site, where trees were ≤ 6 cm in diameter, one girdled tree and one tree frilled with the Hypo-Hatchet broke in late June during a storm. Two more girdled trees broke in early July. The broken trees were eliminated from the study.

The density of *A. planipennis* larvae was determined by sampling areas of the trunk and canopy of each tree beginning in mid-September and continuing through the fall. Using chisels and drawknives, we excavated bark windows, each at least 1200 cm^2, to expose *A. planipennis* larvae and galleries. Two bark windows were located on opposite sides of the trunk of all trees, 1–1.5 m above ground. Between 4 and 10 additional bark windows, depending on tree size, were sampled on the main leader and large branches in the canopy, which we accessed with ladders and by climbing. An effort was made to distribute the bark windows throughout the canopy to ensure that samples were representative of the density of *A. planipennis* in the tree. A total of 1.8–7.6 m^2 of phloem was exposed on each tree. We recorded the area and number of larvae for each bark window. Larval density (number/m^2) in exposed phloem was calculated for each tree. The black, green, and white ash logs were transported to the MSU campus in late August, measured, and totally debarked to determine larval density. Larval density on the ash trap logs at the AAA site was not recorded. The logs had desiccated, owing to exposure at the site, and were too dry to debark effectively to locate larvae.

In 2004 we selected and measured DBH of 24 white ash trees at each of three sites in Washtenaw County, Michigan (72 trees in total). DBH was 38.2 ± 1.9 cm (mean ± SE) at the M14 site (near Highway M14), 32.4 ± 1.4 cm at the County Farm Park (CFP) site, and 38.2 ± 1.9 cm at the St. Joseph (STJ) site. Trees at the M14 site were significantly larger than those at the CFP site, while the trees at the STJ site were intermediate in size ($F_{[2,65]} = 3.15$; $P = 0.04$). All three sites were well-stocked, closed-canopy woodlots with a mix of white ash, oaks, maple, and other hardwoods. We expected *A. planipennis* densities to be low to moderate at the sites, based on the lack of canopy dieback, signs of woodpecker attacks, or other obvious evidence of infestation. There was at least 7.5–10 m between any of the trees used in our study.

Trees at each site were randomly assigned to one of four treatments: girdling, vertical wounding, herbicide treatment, or untreated control. Trees were girdled using a drawknife and chisel to remove bark and phloem from a 15 cm wide area that encircled the trunk from 0.85 to 1.0 m above ground. On trees assigned to the wounding treatment, we used chisels to remove bark and phloem from a 15 cm wide vertical strip that began 1 m above ground. The length of the vertical wound was equivalent to the circumference of the trunk. This ensured that the area of bark removed on the vertically wounded trees was the same as the area that would have been removed if the trees had been girdled. Trees were wounded or girdled on 17–20 May. Trees assigned to the herbicide treatment were treated on 26 May with a basal bark application of Garlon 4 (60.45% triclopyr butoxyethylester; Dow AgroSciences, Indianapolis, Indiana) mixed in diesel fuel, following label directions. This herbicide was expected to have a more pronounced effect on treated trees than Pathfinder, the herbicide used in 2003.

As in 2003, a 25 cm wide band of plastic shrink wrap was wrapped tightly around the trunk of each tree, with the lower edge 1.35 m above ground, and coated with Tanglefoot. The area of the sticky bands was 2560 ± 60 cm^2 (mean ± SE). The sticky bands were checked weekly from 9 June through 5 August, all *A. planipennis* were removed and returned to the laboratory, and species identity was confirmed. The density of adults captured on each tree was standardized as the number per 2600 cm^2, the approximate area of the sticky bands. Canopy dieback was estimated visually to the nearest 10% in mid-July, before most current-year *A. planipennis* larvae began feeding.

Sampling to assess larval density began in mid-September and continued through December. All trees were felled and 6–12 sample areas were marked at 1 m intervals along the trunk and on large branches (>6 cm diameter) in the canopy. Sample areas ranged in size from 1200 to 1500 cm^2 and a total of 0.72–1.8 m^2 of bark and phloem was peeled per tree. The density of *A. planipennis* larvae was standardized as the number per square metre for each tree, as before.

In May 2005 we established a total of 18 blocks, each consisting of four trees of similar sizes, at four sites (72 trees in total). At the M52 site (near Highway M52) in Livingston County, open-grown green ash trees were abundant in the median of a major interstate highway (I-96) and the cloverleaf area bounded by the highway on- and off-ramps. We selected five blocks of trees at the M52 site (DBH 23.8 ± 1.2 cm; mean ± SE). Additional green ash trees were selected in an area near Pierce Lake in Washtenaw County. We set up three blocks at Pierce Lake West (PLW) (DBH 14.6 ± 0.8 cm) in an area bounded by the rough, untended area bordering a golf course, a highway easement, and a dense wooded area. Five blocks of trees (DBH 14.3 ± 0.8 cm) were selected at Pierce Lake East (PLE) in an area with scattered trees in fields and wooded areas. Ash was abundant at both PLE and PLW, along with cottonwood (*Populus deltoides*) and other hardwoods. At the Dexter–Huron (DEX) MetroPark in Washtenaw County, we selected five blocks of white ash trees (DBH 13.7 ± 0.8 cm) growing in a wooded area. Trees at the M52 site were larger than trees at the PLE, PLW, and DEX sites ($F_{[3,68]} = 26.63$; $P < 0.0001$).

Trees in each block were randomly assigned to one of four treatments: control, girdling, herbicide treatment, or exposure to methyl jasmonate (MeJa). Trees were girdled from 31 May to 2 June using a drawknife and chisel, following the same procedures as in 2004. Trees assigned to the herbicide treatment were treated with a basal bark application of Garlon 4 mixed with diesel oil from 31 May to 2 June. Because many Garlon-treated trees died relatively quickly in 2004, we applied half the dose by treating only half of the circumference of the tree with the basal bark spray (two opposing sides of the trunk). Jasmonic acid, a ubiquitous signaling molecule in plants, is a key elicitor of production of volatiles in plants (Hopke et al. 1994; Boland et al. 1998). Exogenous application of jasmonic acid, or its volatile derivative MeJa, can trigger volatile production by plants in response to herbivore feeding (Rodriguez-Saona et al. 2001; Gols et al. 2003). Ten bubble caps, each with 150 μL of MeJa, were attached to a line, approximately 30 cm apart. The release rate was 0.38 mg/day, determined in the laboratory at 20 °C (Phero Tech Inc., Delta, British Columbia). The line with the bubble caps was suspended across the middle portion of the tree canopy using a slingshot on 9 June. The bubble caps remained in the canopy until trees were felled in the fall. DBH did not vary significantly among treatments at any of the sites.

In previous years our observations suggested that adult *A. planipennis* were more active or more abundant on trees growing in sunny conditions than on shaded trees. In 2005 the relative exposure of each tree to sun was visually estimated and ranked from 1 to 4: (1) open-grown and fully exposed to sun, (2) partially open and exposed to sun on at least one side; (3) fully shaded, and (4) superdominant. Superdominant referred to trees growing in well-stocked stands where the trunk was shaded but most or all of the branches and leaves extended above the canopy of surrounding trees and were exposed to sun. All trees at the M52 field site were open-grown (rank 1). Two canopy-closure categories were represented at the DEX site: superdominant trees (rank 4) and partially open trees (rank 2). The superdominant trees (DBH 15.4 ± 1.0 cm; mean ± SE) were significantly larger than the partially open trees (DBH 11.7 ± 0.9 cm) included in the study ($F_{[1,18]} = 6.23$, $P = 0.02$). At both the PLE and PLW sites, the trees in our study represented all four canopy-closure categories, and DBH did not vary significantly among canopy-closure categories at either of these sites.

On 9 June, a sticky band (25 cm wide band of plastic wrap coated with Tanglefoot) was wrapped around each tree trunk with the lower edge 1.35 m above ground, as in previous years. The area of each sticky band was 1400 ± 50 cm^2 (mean ± SE). In addition, we randomly selected half of the blocks at each site for additional traps. On these trees we used ladders to place a second sticky band (25 cm wide) on the trunk 4–5 m above ground. Two purple plastic panels, each 30 cm by 30 cm and coated with clear Pest-Stick on both sides, were suspended on opposite sides of the tree in the mid to upper canopy using a slingshot and line. The panels could be raised and lowered each week with the line. The standard-height (low) sticky bands were checked weekly, while the high sticky bands and panels were checked at 2-week intervals throughout the summer. All *A. planipennis* were removed, returned to the laboratory, and examined to confirm identification as in previous years. The density of adults captured on each sticky band and on canopy traps was standardized to the mean area of the sticky band (number of adults per 1400 cm^2).

Canopy dieback was estimated visually to the nearest 10% on at least two or three blocks of trees at each site on 12 September 2005. At that time, oviposition was complete, larval feeding was advanced and larvae were still active, and leaves had not yet senesced.

Statistical analysis

Data from all experiments were tested for normality using the univariate procedure and transformed as necessary to meet the requirements of normality and homoscedasticity. DBH values were compared among sites and treatments at each site in 2003, 2004, and 2005 by one-way ANOVA (PROC GLM) with either site or treatment as the main effect. The density of adult *A. planipennis* captured on sticky bands or traps (standardized per mean sticky band area) and larval density (number/m^2) were log-transformed ($x + 1$) to satisfy assumptions of normality and homoscedasticity. Similarly, estimates of percent canopy dieback were arcsine square-root transformed for analysis. For each site, transformed data for the standardized density of *A. planipennis* adults, larval density, and canopy dieback were analyzed by two-way ANOVA (PROC GLM) to evaluate the effects of treatment and block. When ANOVA was significant, means were compared using the Ryan–Einot–Gabriel–Welsch (REGW) multiple comparison procedure which controls the maximum experimentwise error rate.

In 2003, data for all sites combined were analyzed by three-way ANOVA (PROC GLM) with main effects for site, block, and treatment. In 2004, data were analyzed by two-way ANOVA (PROC GLM) with main effects for site and treatment (blocking was not needed, given the homogeneous conditions within each site). In 2005, for all sites combined, adult *A. planipennis* density on low sticky bands, high sticky bands, and canopy traps, and larval density and percent canopy dieback were analyzed by three-way ANOVA (PROC GLM) with main effects for site, block, and treatment. A two-way ANOVA (PROC GLM) was used to analyze the effects of treatment and block on density of adult *A. planipennis* on low sticky bands, high sticky bands, and canopy traps, and on larval density and percent canopy dieback for each site.

Potential effects of shading and canopy exposure to sun were also assessed in 2005. For all sites combined and each site separately, DBH values were compared among canopy-exposure classes using one-way ANOVA. Because tree diameter did not vary among treatments at any site or at all sites combined, but did vary significantly among canopy-exposure classes, DBH was included as a covariate in analyses with canopy closure. For all sites combined, transformed data for standardized density of adult *A. planipennis* captured on low sticky bands, high sticky bands, and canopy traps, and for larval density, were compared among canopy-closure categories using analysis of covariance (PROC GLM) with main effect for canopy-closure category and DBH as a covariate. Means were compared using the LS means procedure. The ratios of beetle density on canopy traps to beetle density on low sticky bands were compared among canopy-closure categories using one-way ANOVA followed by the REGW test.

In each year the standardized density of adults captured on sticky bands was compared with the larval density in each tree by linear regression analysis (PROC REG) for all sites by treatment and for all treatments combined. Since larval densities were extremely low on the trap logs used in 2003, they were not included in the analysis.

Results

In 2003 we captured a total of 2863 *A. planipennis* on sticky bands on the 72 trees at the four sites between mid-June and early August. Catch peaked during the first week of July, when 1142 beetles were captured (Fig. 1). Cumulative degree-days in southeastern Michigan were 1005 (base 50 °F = 10 °C) on 9 July 2003 (Michigan State University Michigan Automated Weather Network 2008). Roughly 70% of the beetles were captured at the MSP site, while 18% and 9% were captured at the KMW and KGC sites, respectively. Few beetles (<2% of the total) were captured on the small trees at the AAA site.

Overall, for all sites combined, the density of adult *A. planipennis* captured on sticky bands was significantly higher on girdled trees than on untreated trees or logs, while the density of adults captured on herbicide-treated trees did not differ significantly from densities in the other treatments (Fig. 2A). Within sites, the density of captured beetles varied significantly among treatments at every site except AAA (Table 1). The girdled trees at the MSP site captured a significantly higher density of adult *A. planipennis* than the untreated ash trees or the black, white, or green ash trap logs, while the density of adults on herbicide-treated trees was not significantly different from densities on girdled trees or white ash trap logs (Table 1). At the KGC site the density of adult *A. planipennis* captured was significantly higher on the girdled or herbicide-treated ash trees than on the untreated trees or all of the trap logs. At the KMW site the density of adult *A. planipennis* captured was significantly higher on all the ash trees than on the trap logs.

Patterns in the relative density of *A. planipennis* larvae were similar to those for adults captured and varied significantly among treatments. Overall, for the four sites combined, larval densities were significantly higher in girdled or herbicide-treated ash trees than in untreated trees (Fig. 2B). Black, green, and white ash trap logs, which were completely debarked, had very few *A. planipennis* larvae (Fig. 2B). Scolytids and cerambycids colonized several of the trap logs but were never observed in debarked areas on the ash trees.

Both the MSP and KMW sites had relatively high densities of *A. planipennis* larvae. At the MSP site, larval density was nearly three times greater in the girdled or herbicide-treated trees than in the untreated trees (Table 1). At the KMW site in particular, virtually all phloem in the ash trees, including the untreated trees, was consumed by *A. planipennis* larvae, obscuring any possible treatment effect. At the KGC site, where few trees had any obvious symptoms of infestation, larval density was significantly higher in girdled trees than in herbicide-treated or untreated trees (Table 1). At the AAA site, within-treatment variability was relatively high, largely because three girdled trees and one herbicide-treated tree broke during the summer. Larval densities in the girdled and herbicide-treated trees, however, were significantly higher than in the untreated ash trees.

Larval density was positively correlated with the standardized density of adults captured on sticky bands on the trap trees. For all sites and treatments combined, there was a significant linear relationship between larval density (y) and standardized adult density (x) ($y = 0.62\ (\pm 0.1)x + 43.3\ (\pm 8.1)$, $R^2 = 0.35$, $P < 0.0001$). Similarly, there was a positive linear relationship between larval density and standardized adult density for each treatment (control trees: $y = 1.63\ (\pm 0.3)x + 15.4\ (\pm 9.2)$, $R^2 = 0.58$, $P < 0.0001$; girdled trees: $y = 0.41\ (\pm 0.1)x + 57.2\ (\pm 13.6)$, $R^2 = 0.39$, $P = 0.002$; herbicide-treated trees: $y = 1.28\ (\pm 0.4)x + 36.2\ (\pm 17.8)$, $R^2 = 0.39$, $P = 0.002$).

Overall, for all sites combined, canopy dieback was relatively low in mid-June and did not vary significantly among treatments: 14.5 ± 3.5% (mean ± SE) on the untreated trees, 19.1 ± 4.4% on the girdled trees, and 28.2 ± 5.7% on the herbicide-treated trees. In late July, foliage on some stressed trees began to yellow or appeared wilted, while we could observe no discernible change in the condition of other trees. Average canopy dieback of the girdled (23 ± 5.0%) and herbicide-treated trees (31 ± 6.4%) in late July was significantly higher than on the control trees (9 ± 2.9%) ($F_{[2,69]} = 5.18$; $P = 0.008$). None of the girdled or herbicide-treated trees had died by the time leaves dropped in fall 2003.

We did not capture nearly as many adult *A. planipennis* at the densely wooded M14, CFP, and STJ sites used in the 2004 study as in 2003. A total of 396 beetles were collected from sticky bands on the 72 trees in 2004. Captures of *A. planipennis* peaked in late June and early July at all sites (Fig. 3). The highest weekly total occurred from 23 to 30 June, when we collected 126 beetles, 32% of the total capture. Cumulative degree-days (base 50 °F = 10 °C) in

Fig. 1. Numbers of adult *A. planipennis* captured on green or white ash trap trees or black, green, or white ash trap logs over time in 2003 at the Ann Arbor Airport (AAA), Kensington Golf Course (KGC), Kensington Maintenance Woodlot (KMW), and Maybury State Park (MSP) sites.

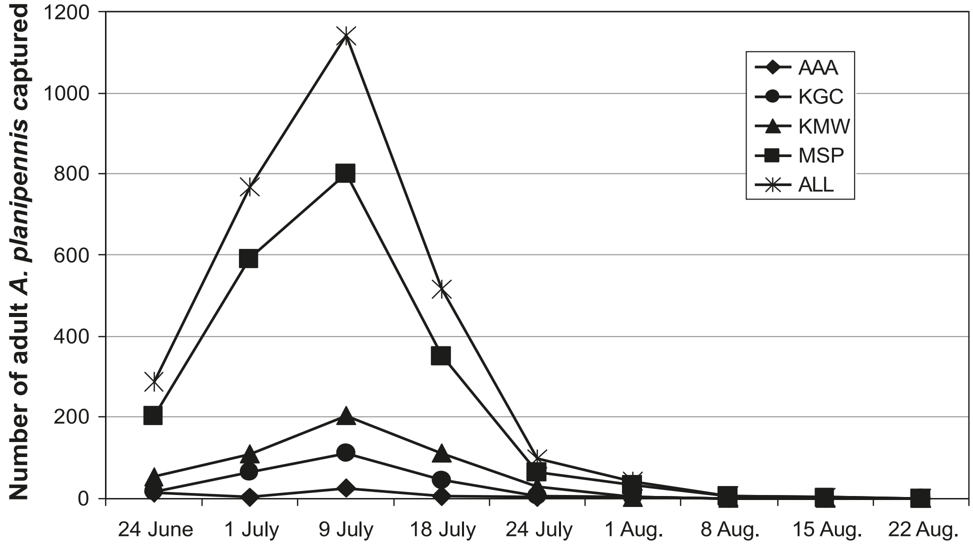
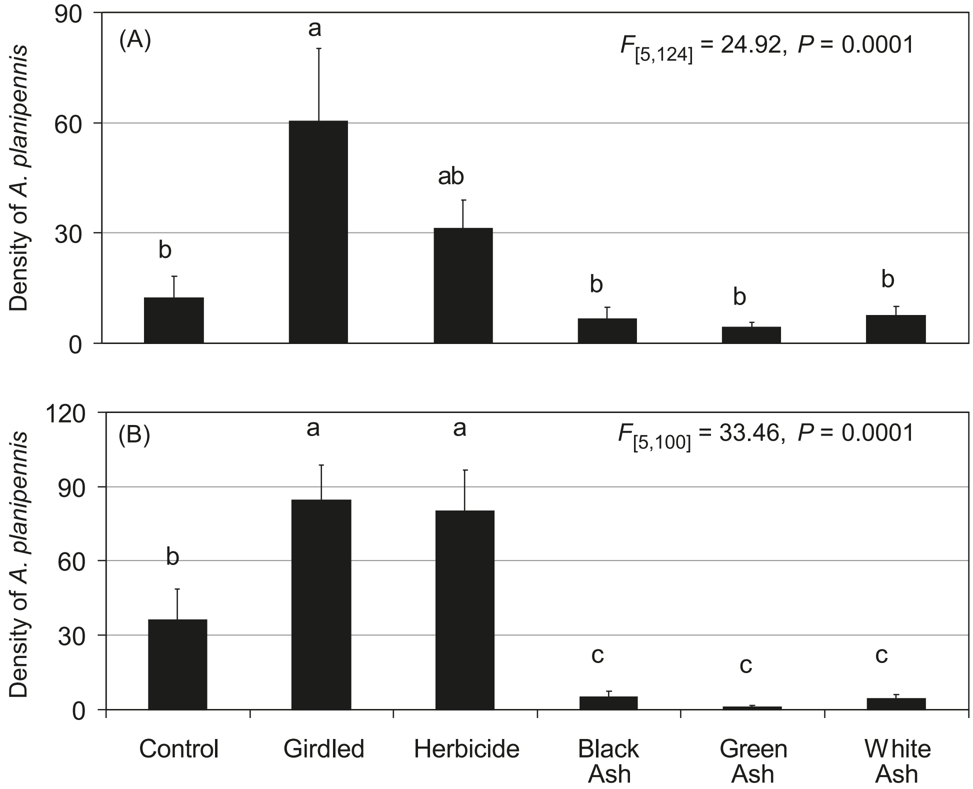


Fig. 2. Densities (mean + SE) of adult *A. planipennis* captured (number/1400 cm^2 sticky band) (A) and larval density (number/m^2) (B) on healthy, girdled, or herbicide-treated green or white ash trap trees and on black, green, or white ash trap logs in 2003 (N = 24). The same letter above a bar indicates that values are not significantly different.



southeastern Michigan were 925 on 30 June 2004 (Michigan State University Michigan Automated Weather Network 2008). Beetle activity dropped sharply in mid-July, after which only 10% of the beetles were captured (Fig. 3).

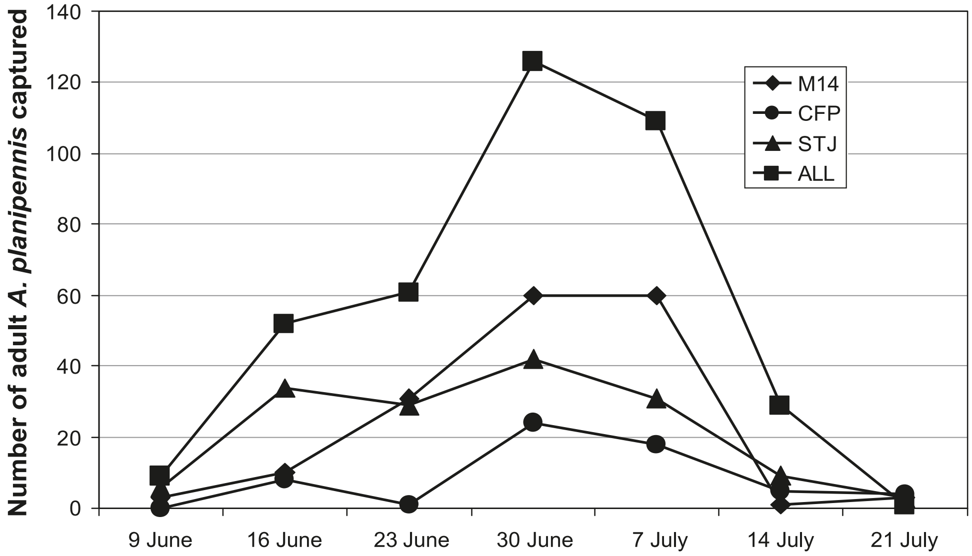
Overall, there was a tendency for more *A. planipennis* to be captured on the stressed or wounded trees than on the untreated ash trees. For all sites combined, the untreated control trees captured the fewest beetles, but variability within treatments was substantial. The density of captured *A. planipennis* was significantly higher on the herbicide-treated trees than on the untreated trees, while adult density on the girdled and wounded trees did not differ significantly from that on either the herbicide-treated or untreated trees (Fig. 4A). Differences among treatments were not signifi-

Table 1. Density of adult *A. planipennis* captured (number/1400 cm^2 sticky band) and density of larvae (number/m^2) on healthy, girdled, and herbicide-treated ash trap trees and on ash trap logs in 2003 at the Ann Arbor Airport (AAA; green ash), Kensington Golf Course (KGC; green ash), Kensington Maintenance Woodlot (KMW; white ash), and Maybury State Park (MSP; white ash) sites in southeastern Michigan.

Treatment	AAA (*N* = 6)	KGC (*N* = 6)	KMW (*N* = 6)	MSP (*N* = 6)
Adult density				
Trees				
Control	0±0a	1.8±0.8b	15.5±3.8a	32.1±20.5c
Girdle	5.0±1.7a	14.2±5.6a	28.0±5.5a	194.3±48.3a
Herbicide	5.6±2.8a	7.5±1.8a	30.9±8.9a	81.5±14.3ab
Logs				
Black ash		1.2±0.1b	1.5±0.5b	17.3±8.1c
Green ash	1.8±1.0a	0.2±0.1b	2.3±0.5b	12.8±4.4c
White ash	1.5±0.4a	0.2±0.06b	3.8±1.2b	24.8±5.6bc
ANOVA: *F*; df; *P*	2.21; 4,20; 0.1	15.9; 5,25; 0.0001	29.3; 5,25; 0.0001	8.05; 5,25; 0.0001
Larval density				
Trees				
Control	5.8±2.4b	4.2±4.2bc	75.6±23.6a	54.5±36.2b
Girdle	53.0±23.6a	31.3±4.6a	93.5±18.7a	146.3±30.6a
Herbicide	57.7±15.7a	5.4±1.7b	107.0±34.1a	133.9±32.6a
Logs				
Black ash		0.46±0.46bc	2.8±1.5b	10.3±4.9bc
Green ash		0±0c	2.4±1.7b	0±0c
White ash		0.8±0.3bc	7.2±3.1b	3.6±3.0bc
ANOVA: *F*; df; *P*	4.2; 2,8; 0.056	12.97; 5,17; 0.0001	13.02; 5,25; 0.0001	14.83; 5,23; 0.0001

Note: Values are given as the mean ± SE. Values within a column and life stage followed by the same letter are not significantly different from each other (REGW multiple comparison test on log-transformed ($x + 1$) data, $P > 0.05$).

Fig. 3. Numbers of adult *A. planipennis* captured on white ash trap trees over time in 2004 at the M14, County Farm Park (CFP), and St. Joseph Hospital (STJ) sites.



cant within all sites (Table 2). At the M14 site we captured a total of 182 beetles over the course of the summer but there were no significant differences among treatments (Table 2). At the CFP and STJ sites we captured a total of 60 and 154 beetles, respectively. At both sites the densities of adult *A. planipennis* captured on the girdled and herbicide-treated trees were similar (Table 2), but only the herbicide-treated trees differed significantly from the untreated and wounded trees. When we felled and sampled trees at the 2004 sites, densities of *A. planipennis* larvae were higher at the M14 and STJ sites than we expected, based on the relatively low densities of adult beetles captured at all sites. Overall, larval densities were 7.8 ± 2.25/m^2 (mean ± SE) at CFP, 33.2 ± 6.04/m^2 at M14, and 47.7 ±12.23/m^2 at STJ. Larval densities across all sites were significantly higher in the girdled trees than in the herbicide-treated or untreated

Fig. 4. Densities (mean + SE) of adult *A. planipennis* (number/2600 cm^2 sticky band) (A) and larval density (number/m^2) (B) on healthy, girdled, herbicide-treated, or wounded white ash trap trees in 2004 (N = 18). The same letter above a bar indicates that values are not significantly different.

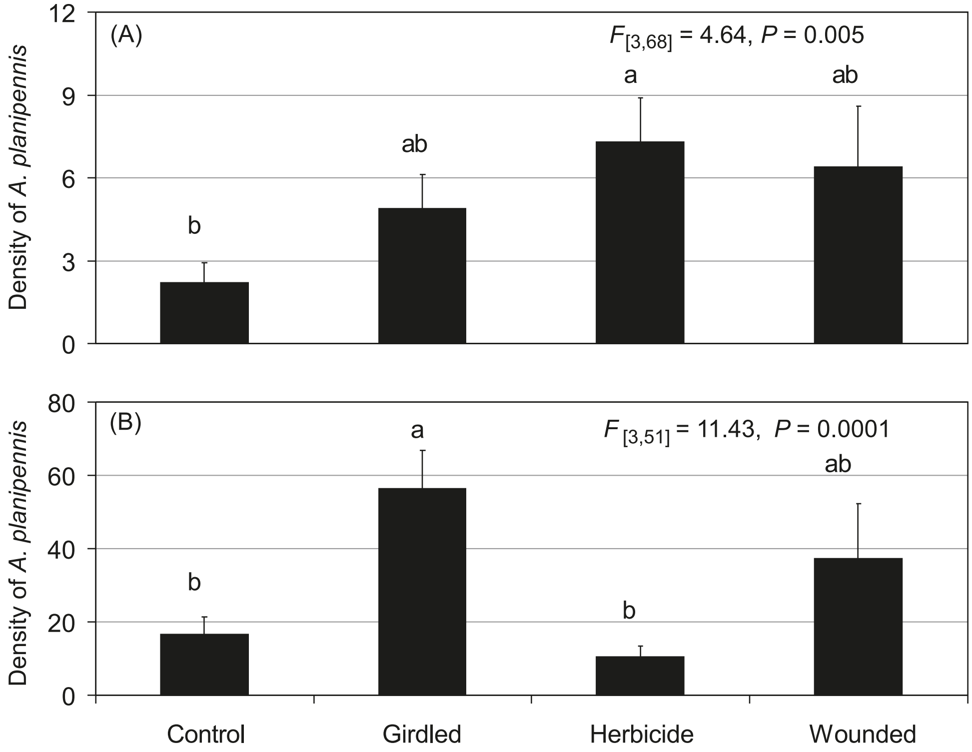


Table 2. Densities of adult *A. planipennis* captured (number/2600 cm^2 sticky band) and larval density (number/m^2) on healthy, girdled, herbicide-treated, or wounded white ash trap trees in 2004 at the M14 (near Highway M14), County Farm Park (CFP), and St. Joseph Hospital (STJ) sites in southeastern Michigan.

Treatment	M14 (N = 6)	CFP (N = 6)	STJ (N = 6)
Adult density			
Control	4.5±1.7a	0.3±0.2b	1.7±0.8b
Girdled	6.1±2.1a	3.7±2.6ab	5.4±0.9ab
Herbicide	4.2±1.0a	4.3±0.8a	13.5±3.4a
Wounded	12.3±4.8a	0.9±0.6b	5.0±3.7b
ANOVA: F; df; P	0.94; 3,20; 0.4	4.05; 3,22; 0.02	5.43; 3,20; 0.007
Larval density			
Control	21.4±8.8a	0.74±0.74b	23.6±7.5b
Girdled	43.1±7.8a	22.6±10.3a	99.4±15.2a
Herbicide	13.0±5.7a	4.33±3.02ab	10.0±3.7b
Wounded	53.1±19.4a	3.0±1.5b	60.5±44.6ab
ANOVA: F; df; P	3.06; 3,19; 0.05	7.13; 3,11; 0.006	6.41; 3,15; 0.005

Note: Values are given as the mean ± SE. Values within a column and life stage followed by the same letter are not significantly different from each other (REGW multiple comparison test on log-transformed (x + 1) data, $P > 0.05$).

trees. Larval density in the wounded trees did not differ significantly from densities in the other treatments (Fig. 4B). Differences among treatments within sites varied (Table 2). At the M14 site, larval density was highly variable and there were no significant differences among treatments. At the CFP and STJ sites, the girdled trees had significantly higher larval densities than the untreated trees (Table 2). Larval densities in the wounded and untreated trees did not differ at any site and densities were significantly lower than in the girdled trees at the CFP site. The herbicide-treated trees had significantly lower larval densities than the girdled trees at the STJ site but not at the CFP site (Table 2).

For all sites and all treatments combined, there was a significant linear relationship between larval density (y) and standardized adult density on sticky bands (x) (y = 2.38 (±0.66)x + 16.2 (±6.2), R^2 = 0.19, P = 0.0007). Similarly, there was a positive linear relationship between larval density and adults captured for the control trees and wounded trees (control trees: $y = 4.06\ (\pm1.0)x + 6.14\ (\pm4.4)$, $R^2 = 0.52$, $P = 0.002$; wounded trees: $y = 4.3\ (\pm0.91)x + 5.22\ (\pm1.4)$, $R^2 = 0.65$, $P = 0.0005$). The relationship between larval density and adults captured was not significant for the girdled trees ($R^2 = 0.01$, $P = 0.7$) or herbicide-treated trees ($R^2 = 0.04$, $P = 0.5$).

Some trees treated with herbicide (Garlon 4) began to fade and die by mid to late June and several trees were completely dead by mid-July, a period that corresponds to high oviposition activity by *A. planipennis*. By the end of July, all herbicide-treated trees had died. In contrast, the vertical wounding and even the girdling had little discernible effect on foliage or tree condition. For all sites combined, percent canopy dieback in mid-July was significantly higher in the herbicide-treated trees (56.7 ± 3.9%) than in the untreated control trees (14.9 ± 2.9%), girdled trees (14.8 ± 2.4%), or wounded trees (12.8 ± 2.1%) ($F_{[3,70]} = 44.3$, $P = 0.0001$).

We captured a total of 1901 beetles on the 72 trees included in our 2005 study. The low sticky bands, placed at the standard height of 85 cm to 1.0 m above ground on all trees, collected 65% (1229 beetles) of the total collection. Half the blocks (36 trees) also had high sticky bands (3–4 m above ground) and two small purple panel traps suspended in the canopy. In these trees the low bands captured 745 beetles (53%), the high bands captured 298 beetles (21%), and the small panel traps captured 374 beetles (26%).

Adult *A. planipennis* activity peaked in late June at all sites in 2005, as in other years (Fig. 5). Beetle capture on the low sticky bands, the high bands, and the small panel traps followed similar patterns over the summer (Fig. 6). Our highest catch occurred during the week of 24–30 June, when 458 beetles were captured. Cumulative degree-days (base 50 °F = 10 °C) were 1002 on 30 June 2005 (Michigan State University Michigan Automated Weather Network 2008). Thunderstorms and heavy rains that occurred between 4 and 7 July (National Oceanic and Atmospheric Administration 2005) may have interfered with *A. planipennis* flight the following week, and also could have washed some captured beetles off the traps. In total, 194 beetles were captured between 30 June and 7 July, while 299 beetles were captured the following week (7–14 July) (Fig. 5). The number of beetles on the traps then steadily declined at all sites.

Across all sites the density of adult *A. planipennis* captured on the standard-height (low) sticky bands was significantly higher in the girdled trees than in the untreated trees or trees exposed to MeJa, while adult density in the herbicide-treated trees did not differ significantly from that in the girdled trees or trees exposed to MeJA (Fig. 7A). The density of adults captured in the untreated control trees was significantly lower than in any of the treated trees. At the M52 (near Highway 52) and PLW sites, adult density tended to be higher in the treated trees than in the untreated control trees, but variability was high and there were no significant differences among treatments (Table 3). At the PLE and DEX sites, the density of *A. planipennis* captured was significantly higher in the girdled and herbicide-treated trees than in the control trees; adult density in the trees treated with MeJa did not differ from the density in the control trees at the PLE site or from in that in any other treatment at the DEX site (Table 3).

In general, the densities of *A. planipennis* beetles captured on the high sticky bands and small panel traps in the canopy were lower than on the standard-height (low) sticky bands, but the patterns of beetle response to the treatments were similar. For all sites combined, the density of *A. planipennis* captured on the high sticky bands was significantly higher on the girdled trees than on the untreated controls, while the densities of adults caught on the herbicide-treated trees or the trees exposed to MeJa did not differ from densities on the girdled or untreated trees (Fig. 7B). The pattern of *A. planipennis* capture on the small panel traps was similar, but differences among treatments were not significant (Fig. 7C). The pattern of *A. planipennis* response to stress treatments at individual sites were also similar for the high sticky bands and canopy traps, but differences among treatments within sites were generally not significant (data not shown).

The density of *A. planipennis* larvae across all sites was two to three times higher in the girdled trees than in any of the other trees. Across all sites, larval density was significantly higher in the girdled trees than in other trees, but there was little difference among the other three treatments (Fig. 7D). The overall density of *A. planipennis* larvae in untreated trees was relatively low at all sites except M52. At the M52 and PLW sites, larval densities tended to be higher on the girdled trees than in other treatments, but differences were not significant because of variability and relatively low sample size (Table 3). At the PLE and DEX sites, larval density was significantly higher in the girdled trees than in all other trees. Larval density in herbicide-treated trees was significantly higher than in the MeJa-treated trees or control trees at the PLE site but not at the DEX site (Table 3).

For all sites and all treatments combined, there was a significant linear relationship between larval density (y) and standardized adult density on the sticky bands (x) ($y = 1.37\ (\pm0.4)x + 13.62\ (\pm5.7)$, $R^2 = 0.43$, $P < 0.0001$). Similarly, there was a positive linear relationship between larval density and standardized adult density for the control trees ($y = 7.1\ (\pm0.4)x - 2.98\ (\pm3.1)$, $R^2 = 0.95$, $P < 0.0001$) girdled trees ($y = 0.95\ (\pm0.4)x + 46.8\ (\pm18.0)$, $R^2 = 0.24$, $P = 0.03$), and MeJa-treated trees ($y = 1.35\ (\pm0.13)x + 3.83\ (\pm4.7)$, $R^2 = 0.87$, $P < 0.0001$), but not for the herbicide-treated trees ($R^2 = 0.07$, $P = 0.25$).

By mid-September, most of the herbicide-treated trees had died and the girdled trees were displaying significant signs of decline, whereas the MeJa-treated and control trees had little dieback. For all sites combined, percent canopy dieback was significantly higher in the herbicide-treated trees (96.7 ± 2.1%; mean ± SE) than in the girdled trees (48.0 ± 13.9%), which in turn was significantly higher than in the MeJa-treated trees (6.7 ± 3.3%) or untreated control trees (6.25 ± 1.6%) ($F_{[3,21]} = 45.56$; $P < 0.0001$).

We assessed effects of exposure to sun in 2005, when trees ranged from open-grown trees exposed to sun throughout the day to shaded trees in dense woodlots with little exposure to direct sunlight. Because canopy-closure category was weakly but significantly correlated with DBH ($R^2 = 0.54$, $P < 0.0001$), we included DBH as a covariate in models comparing the densities of captured adult *A. planipennis* and of larvae by canopy-exposure category. There were no

Fig. 5. Numbers of adult *A. planipennis* captured on green or white ash trap trees over time in 2005 at the M52, Pierce Lake East (PLE), Pierce Lake West (PLW), and Dexter Huron Metropark (DEX) sites.

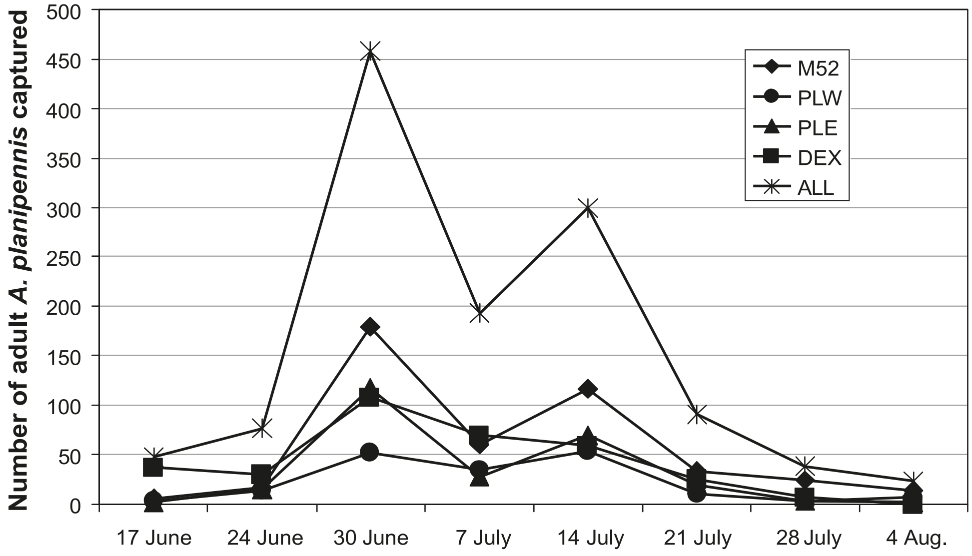
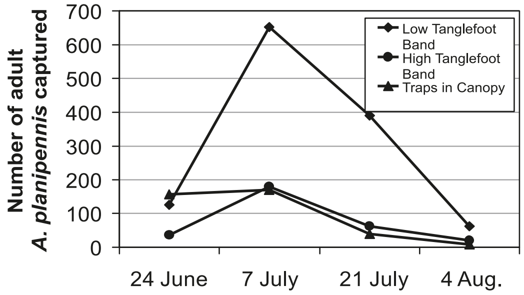


Fig. 6. Numbers of adult *A. planipennis* captured over time in 2005 on the low and high sticky bands and canopy traps on green or white ash trap trees.



significant differences in density of adult beetles captured among trees grouped by 5 cm diameter classes on the standard-height (low) sticky bands ($F_{[3,68]}$ = 1.21; P = 0.3), the high sticky bands ($F_{[3,40]}$ = 1.74; P = 0.2), or the small panel traps in the canopy ($F_{[3,35]}$ = 1.54; P = 0.22).

The density of *A. planipennis* adults captured on the standard-height (low) sticky bands was significantly lower in shaded trees growing in a closed-canopy setting than in open-grown trees and superdominant trees, which had shaded trunks but fully exposed crowns that extended above the canopy. Adult captures in trees partially exposed to sun did not differ from those in open-grown, superdominant, or closed-canopy trees (Fig. 8A). Responses were similar for the high sticky bands, but differences among tree-exposure categories were not significant (Fig. 8B).

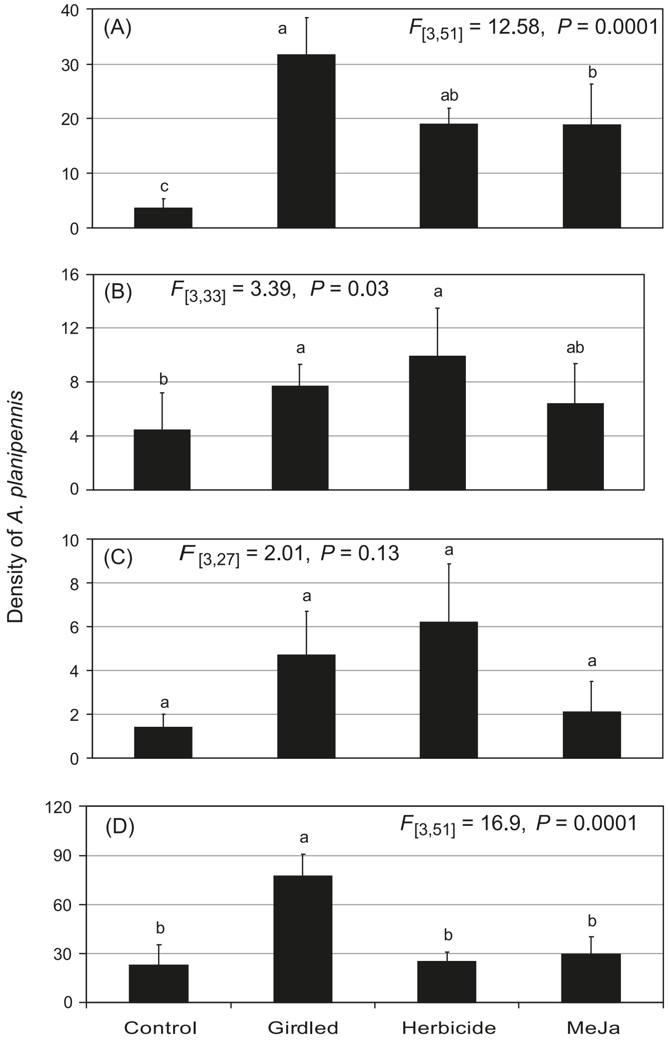
In contrast, the small purple panels suspended in tree canopies yielded a somewhat different pattern. The density of adult *A. planipennis* captured on the panel traps in superdominant trees was significantly higher than in either open-grown or shaded trees, while beetle density on panels in trees partially exposed to sun did not differ from that in the other exposure categories (Fig. 8C). Differences in beetle capture between the low sticky bands and panel traps were more pronounced in superdominant trees than in open-grown, shaded, or partially exposed trees. For example, the ratio of beetle density on canopy traps to that on low sticky bands was 0.89 ± 0.3 (mean ± SE) in superdominant trees compared with 0.10 ± 0.04, 0.33 ± 0.1, and 0.18 ± 0.18 in open-grown, partially exposed, and shaded trees, respectively ($F_{[3,24]}$ = 3.81; P = 0.02).

Female *A. planipennis* appeared to preferentially oviposit on trees in sunny conditions. Larval density was significantly higher in the superdominant and open-grown trees than in the shaded trees, while larval density in the trees partially exposed to sun did not differ from densities in superdominant, open-grown, or shaded trees (Fig. 8D). Larval density varied among trees grouped by 5 cm diameter class but there was no consistent pattern. Trees that were 20–25 cm in DBH had higher larval densities than trees <15 cm in DBH, while larval densities in trees with DBHs of 15–20 or >25 cm did not differ from densities in the other diameter classes ($F_{[3,68]}$ = 3.65, P = 0.02).

Discussion

Adult *A. planipennis* were active throughout the summer in all 3 years, but activity consistently peaked during a 1- to 2-week period in midsummer. At least a few *A. planipennis* beetles were captured on the sticky bands by early to mid-June, but the greatest number of beetles were captured in late June or early July each year. Cumulative degree-days corresponding to the period of peak *A. planipennis* activity were generally similar in each year. By late July, beetle captures dropped sharply, although low numbers of beetles continued to be captured through mid-August, when the bands were removed. In laboratory conditions, *A. planipennis* must feed on foliage for at least 4–7 days before mating, and females require an additional 1–2 weeks of feeding before oviposition begins. Assuming that *A. planipennis* exhibits similar behavior in the field, we surmise that most beetles were relatively young and feeding on foliage throughout much of June, while most oviposition probably occurred in July.

Fig. 7. Densities (mean + SE) of adult *A. planipennis* (number/1400 cm^2) captured on low sticky bands (A), high sticky bands (B), and canopy traps (C), and larval density (number/m^2), on healthy, girdled, herbicide-treated, or MeJa-treated green or white ash trap trees in 2005 (N = 18). The same letter above a bar indicates that values are not significantly different.



We anticipated that *A. planipennis* would be preferentially attracted to stressed ash trees because in its native range it behaves as a secondary pest (Chinese Academy of Science Institute of Zoology 1986; Yu 1992; Gao et al. 2004). Two economically important *Agrilus* species native to North America, *A. bilineatus* and *A. anxius,* similarly colonize oaks (*Quercus* spp.) and birches (*Betula* spp.), respectively, but only when the trees are stressed by drought, injury, or other factors (Anderson 1944; Haack and Benjamin 1982; Dunn et al. 1987; Katovich et al. 2001). Adult *A. bilineatus* appear to be attracted to ethanol or other volatiles produced by stressed oaks (Dunn 1985; Dunn et al. 1986), and sticky bands on girdled oaks were previously used to capture adult beetles (Haack and Benjamin 1982). In paper birch (*Betula papyrifera*) trees, drought stress substantially reduced the wound periderm (callus) response that enables trees to resist feeding by *A. anxius* larvae (Herms 1991).

In our studies, girdled ash trees were generally more attractive to *A. planipennis* than untreated ash trees. Our girdling method, which involved removing a 15 cm wide band of outer bark and phloem, obviously disrupted nutrient translocation. Because we avoided or minimized injury or damage to xylem vessels in the outer sapwood, girdling presumably had little effect on water relations, or tree vigor would have declined more rapidly. None of the trees girdled in our studies died during summer or fall, except for three small trees at the AAA site in 2003 that snapped off during a storm. Crown thinning and yellowing of leaves were noticeable in late summer on some trees, which likely reflected stress from the girdling injury combined with effects of *A. planipennis* feeding. Using hyperspectral imagery, Bartels et al. (2007) found that ash stressed by girdling could be differentiated from nongirdled ash 2 months after the girdling event.

Other treatments used to stress ash trees were less effective than girdling in attracting *A. planipennis*. Some adult *A. planipennis* were captured on sticky bands on the logs used in the 2003 study, especially at the heavily infested MSP site, but there were almost no *A. planipennis* larvae or galleries on the logs at any site (Table 1). The relative probability of beetles being captured on the sticky bands was presumably greater on the 2 m long logs than on trees, simply because on logs, the band covered a greater proportion of the surface area available for landing. In other studies, *A. planipennis* have developed to late-instar larvae on logs that were smaller than those used in this study (Anulewicz et al. 2006, 2008), which suggests that beetles largely ignored the logs for oviposition.

The herbicide (Pathway) applied with the Hypo-Hatchet in 2003 did not appear to severely affect the vigor of most trees. Except for the small trees at the AAA site, there was generally little visible evidence of decline until late summer, when foliage on some herbicide-treated trees began to yellow. Full-range spectrometer analysis of leaf signatures in the visible spectrum to shortwave infrared, however, did distinguish between herbicide-treated and healthy ash trees (Bartels 2005). When we debarked herbicide-treated trees in the fall, we typically found a long, diamond-shaped area of dead tissue associated with each injection point. There was ample wound periderm tissue along the margins of the affected areas, but the remaining vascular tissue appeared to be healthy and functional. Ash trees are highly sectorial (Tanis et al. 2007) and appeared to readily compartmentalize the injury caused by herbicide.

The effects of Garlon 4, the herbicide applied in 2004 and 2005, were much more pronounced than those of Pathway, the herbicide used in 2003. In 2003, none of the Pathway-treated trees died, while in 2004 and 2005, nearly all of the Garlon 4-treated trees were severely declining or dead when most *A. planipennis* oviposition likely occurred. Our efforts in 2005 to reduce the level of stress imposed by the herbicide by treating only half the circumference of the trees were not consistently successful. On many trees, canopy decline progressed nearly as rapidly as in 2004. The generally low larval densities in the herbicide-treated trees in 2004 and 2005 could reflect little oviposition or poor survival of neonate larvae on the dying trees. Given that *A. planipennis* larvae can successfully develop to late instars on cut logs

Table 3. Densities of adult *A. planipennis* captured (number/1400 cm^2 sticky band) and larval density (number/m^2) on healthy, girdled, herbicide-treated, or MeJa-treated ash trap trees in 2005 at the M52 (near Highway M52; green ash), Pierce Lake West (PLW; green ash), Pierce Lake East (PLE; green ash), and Dexter Huron Metropark (DEX; white ash) sites in southeastern Michigan.

Treatment	M52 (*N* = 5)	PLW (*N* = 3)	PLE (*N* = 5)	DEX (*N* = 6)
Adult density				
Control	8.7±5.8a	3.3±1.7a	0.3±0.3b	2.1±0.8b
Girdled	24.8±9.8a	26.2±21.0a	42.8±17.5a	30.6±12.4a
Herbicide-treated	22.0±9.7a	9.0±1.9a	19.9±3.9a	20.5±3.5a
MeJa-treated	19.6±7.9a	40.5±29.4a	0.6±0.4b	23.2±13.5ab
ANOVA: *F*; df; *P*	1.22; 3,12; 0.3	0.79; 3,6; 0.5	15.78; 3,12; 0.0002	5.38; 3,12; 0.01
Larval density				
Control	62.5±42.1a	19.0±12.1a	1.3±0.8c	7.0±2.8b
Girdled	94.7±44.5a	81.5±34.4a	62.9±8.3a	70.9±16.5a
Herbicide-treated	42.9±13.9a	21.8±6.2a	27.5±12.3b	7.3±4.5b
MeJa-treated	40.3±20.9a	53.6±45.5a	0.6±0.5c	32.8±21.5b
ANOVA: *F*; df; *P*	1.55; 3,12; 0;25	1.43; 3,16; 0.32	34.11; 3,12; 0.0001	10.89; 3,12; 0.001

Note: Values are given as the mean ± SE. Values within a column and life stage followed by the same letter are not significantly different from each other (REGW multiple comparison test on log-transformed ($x + 1$) data, $P > 0.05$).

(Anulewicz et al. 2006, 2008), it appears most likely that adult females laid few eggs on the herbicide-treated trees.

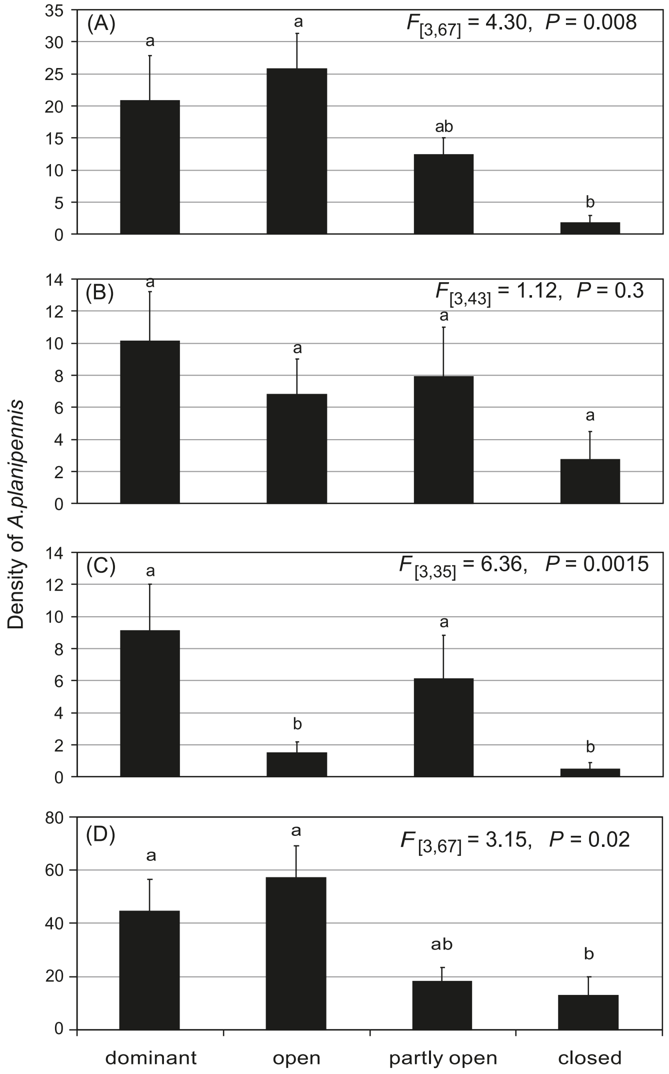
The relative attractiveness of trees subjected to vertical wounding in our 2004 study varied considerably. The vertical wound and the standard, horizontal girdling removed similar amounts of bark and phloem from trees, and volatiles were presumably emitted from the exposed tissue of trees affected by either treatment. The physiological effects on nutrient translocation, however, were likely more pronounced on the girdled trees than on the wounded trees. Wounding did not strongly affect beetle capture, and the substantial within-treatment and site-related variability indicates that wounded trees were not consistently attractive to ovipositing beetles. The different abilities of trees to compartmentalize or otherwise recover from the vertical wound could have affected volatile emissions or other factors related to *A. planipennis* host selection. The results do indicate, however, that stress imposed by girdling, rather than exposure of tissue as a result of wounding, had the strongest influence on host selection by *A. planipennis*.

MeJa emitted by bubble caps suspended in the canopy of trees in 2005 appeared to have little effect on tree condition or host selection by *A. planipennis*. Profiles of volatiles emitted by ash seedlings exposed to MeJa differed from those of healthy plants, and the emission of several compounds that was enhanced by damage caused by adult *A. planipennis* was also enhanced by MeJa exposure (Rodriguez-Saona et al. 2006). However, we found no evidence that *A. planipennis* preferentially oviposited on MeJa-exposed trees. Exposure rates may need to be much greater than those that we used in our field study to enhance production of volatiles, or older trees and seedlings may react differently to MeJa exposure.

The results from our studies suggest that girdling trees can be an effective tool for *A. planipennis* detection or survey activities, particularly if they are debarked during fall or winter to locate larval galleries. Securing sticky bands or other traps to girdled trees may be advantageous in that a *A. planipennis* infestation can be detected during summer, several weeks before trees would be debarked. In our experience, however, sticky bands needed to be checked at 1- to 2-week intervals to ensure that beetles were not lost. Occasionally, the Tanglefoot on some bands had to be reapplied because of high temperatures or heavy rains. In an operational survey program, weekly or biweekly trap checks are unlikely to be practical. Moreover, sticky bands or other traps are unnecessary if survey crews intend to fell and debark trees to look for larval galleries. We found that adult captures on sticky bands were significantly correlated with larval density at nearly all sites over the 3 years. In most cases, the slope of the equation relating larval density (y) to adult density (x) (standardized per mean area of sticky bands) was >1 and the intercept was positive, indicating that larval densities were higher and increased at a higher rate than adult captures. Thus, there was a higher probability of finding larval galleries within the debarked area than of capturing an adult on the standardized sticky band area. The notable exception was herbicide-treated trees, where the relationship was not significant in either 2004 or 2005. This reflects the deteriorating condition of the Garlon 4-treated trees, which attracted adult beetles early in the summer, but were dying or dead by the time that beetles were ovipositing in July. The relationship between adult density and larval density was not as strong for the girdled trees as it was for the control, MeJa-exposed, and wounded trees. In some cases, larval density was so high in the girdled trees that the phloem was completely consumed. While an unlimited number of adults could be captured on girdled trees, larval density was constrained by the amount of phloem available (McCullough and Siegert 2007).

Most trees at our 2004 and 2005 sites had no visible symptoms of *A. planipennis* infestation, and often, only a few adult beetles were captured on the relatively small sticky bands. When these trees were felled and large sample areas were debarked, however, larvae and galleries were readily apparent. In part, this simply reflects the fact that individual adult females may lay several eggs on the same tree. Female *A. planipennis* reared in the laboratory typically lay 30–60 eggs over their life-span, though they are capable

Fig. 8. Densities (mean + SE) of adult *A. planipennis* (number/1400 cm^2) captured on standard-height (low) sticky bands (A), high sticky bands (B), and canopy traps (C), and larval density (number/m^2), on green or white ash trap trees by canopy-exposure category in 2005 ($N = 13$ superdominant trees, 30 open-grown trees, 21 partially open-grown trees, and 8 closed-canopy trees). The same letter above a bar indicates that values are not significantly different.



of laying more than 200 eggs if they survive for >5 weeks (Lyons et al. 2004). In addition, the sticky bands covered only a small proportion of the trunk of a tree, while female beetles could oviposit anywhere on the trunk or large branches. In operational survey programs in Michigan, Ohio, and Indiana, girdled trees were used in *A. planipennis* detection surveys in 2004–2007. When the girdled trees were debarked, dozens of previously unknown infestations were identified (e.g., Flint 2005; Rauscher 2006; Hunt 2007).

While *A. planipennis* preferred to colonize trees stressed by girdling or, in some cases, herbicide treatment or wounding, there are problems that may limit the use of stressed trees in large-scale detection or survey programs. Debarking trees is labor-intensive and suitable detection trees may not be readily available in areas of interest. In addition, the radius and intensity of attraction of stressed trees to *A. planipennis* are not known. The attraction radius of a girdled ash tree is likely to be strongly influenced by site-specific factors, including the density and distribution of *A. planipennis* and the abundance and distribution of healthy and declining ash trees. The relative attractiveness of a girdled ash tree growing in the midst of heavily infested and (or) declining ash trees, for example, is presumably different than that of a girdled ash tree surrounded by healthy ash trees or even nonhost trees. We found that at sites with low *A. planipennis* densities, where external symptoms of infestation were rare or absent, the differences in larval density between stressed and untreated trees were more pronounced than at sites with high densities. At two sites in 2003 (KMW and MSP) and the M52 site in 2005, signs of woodpecker attack and bark cracks were present and many ash trees in the vicinity exhibited some canopy dieback. When we debarked our study trees in the fall, the density of *A. planipennis* larvae was so high in the stressed trees that virtually all phloem had been consumed. Even in the untreated trees, larval densities were often high enough to cause substantial canopy dieback. Although the stressed trees had higher larval densities than the untreated trees at all sites, differences among treatments were obscured because of the overall heavy infestation, even on the untreated trees.

Girdled ash trees could presumably be employed as part of an integrated strategy to reduce *A. planipennis* density or manage localized infestations. For example, girdled ash trees could effectively function as trap trees if they are destroyed after *A. planipennis* oviposition but before the larvae complete development. Other options include attracting beetles to girdled trees treated with insecticide or away from an area of concern. Trap trees have been used in various strategies for managing several bark beetles and woodborers (Bentz 2000; Wermelinger 2004; Borden 1989). The effectiveness of such strategies against *A. planipennis* needs to be assessed at sites with varying levels of beetle populations and densities of ash.

We hypothesized that open-grown trees exposed to full sun would be more attractive to *A. planipennis* than trees growing in shaded settings, such as a densely stocked woodlot, based on our 2004 data and behavioral observations in the field (e.g., Yu 1992; Rodriguez-Saona et al. 2007). We endeavored to assess this behavior in 2005, when trees at our sites represented a wide range of growing conditions and sun exposure. In making our qualitative estimates of sun exposure, we distinguished between ash trees at wooded sites, where trees were almost completely shaded, and superdominant trees, where most foliage extended above the canopy and was exposed to full sun but the trunk and lower branches were shaded. As expected, the density of adult *A. planipennis* captured and the density of larvae were positively related to sun exposure. On superdominant trees with shaded trunks but exposed crowns, beetles were still more likely to be in the sun, as demonstrated by the relatively high rate of beetle capture on the small panel traps suspended in the canopy. In open-grown trees that were fully exposed to sunlight, more *A. planipennis* were captured on the low sticky bands and fewer on the small panel traps in the canopy. These results indicate that girdled trees or traps for *A. planipennis* will be more effective in sunny locations than in shaded or partially shaded locations.

Past and ongoing research indicates that *A. planipennis* relies on host-plant volatiles to locate host trees and to distinguish between stressed and healthy ash trees. Bark volatiles from girdled ash trees had elevated levels of antennally active sesquiterpenes compared with ungirdled ash trees (Crook et al. 2008), and traps baited with lures containing the antennally active sesquiterpenes captured significantly more *A. planipennis* than unbaited traps. At our field sites, stressed and untreated ash trees of similar sizes were growing within 10 m of each other and *A. planipennis* clearly distinguished between the stressed and healthy trees when ovipositing. Efforts to enhance the efficacy of *A. planipennis* traps and lures would be facilitated by focusing on the consistent differences in the volatile compounds that are emitted by stressed and healthy ash trees.

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