

Emerald Ash Borer (*Agrilus planipennis*) Density and Canopy Dieback in Three North American Ash Species

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Abstract. Emerald ash borer (*Agrilus planipennis* Fairmaire) (Coleoptera: Buprestidae), a phloem-feeding insect native to Asia, was identified in 2002 as the cause of widespread ash (*Fraxinus*) mortality in southeast Michigan, U.S. and Windsor, Ontario, Canada. Little information about *A. planipennis* is available from its native range and it was not known whether this invasive pest would exhibit a preference for a particular North American ash species. We monitored *A. planipennis* density and canopy condition on green ash (*F. pennsylvanica*) and white ash (*F. americana*) street trees in four neighborhoods and on white and blue ash (*F. quadrangulata*) trees in two woodlots in southeast Michigan. Green ash street trees had significantly more canopy dieback and higher *A. planipennis* densities than white ash trees growing in the same neighborhood. Density increased by two- to fourfold in both species over a 3-year period. Canopy dieback increased linearly from 2002 to 2005 as *A. planipennis* density increased ($R^2 = 0.70$). In each of the woodlots, *A. planipennis* densities were significantly higher on white ash trees than blue ash trees. Woodpecker predation occurred in all sites and accounted for 35% of the *A. planipennis* that developed on trees we surveyed. Results indicate that surveys for *A. planipennis* detection in areas with multiple ash species should focus on the relatively preferred species.

Key Words. Blue ash; emerald ash borer; *Fraxinus*; green ash; host preference; insect survey; invasive pest; white ash; woodpecker.

The emerald ash borer (*Agrilus planipennis* Fairmaire), an invasive buprestid, was identified in July 2002 as the cause of widespread ash (*Fraxinus*) mortality in southeast Michigan, U.S. and Windsor, Ontario, Canada (Cappaert et al. 2005c). Dozens of additional infestations have been found since 2003 in other areas of Michigan, Ohio, Indiana, Illinois, and Maryland (www.emeraldashborer.info 2006). *Agrilus planipennis* is native to China, Korea, and other Asian countries (Yu 1992) but is not a major pest in its native range (Akiyama and Ohmomo 2000). It was likely introduced into North America through solid wood packing material (Cappaert et al. 2005c; Poland and McCullough 2006).

In southeast Michigan, *A. planipennis* adult emergence begins in mid to late May (Brown-Rytlewski and Wilson 2005; Cappaert et al. 2005c). On emergence, beetles feed on ash foliage for 5 to 7 days before mating and another 5 to 7 days before females begin oviposition (Bauer et al. 2004; Lyons et al. 2004). Individual adult beetles live for 3 to 6 weeks and adult activity peaks from late June to early July (Cappaert et al. 2005c). Eggs laid in July and August hatch in ≈ 2 weeks (Lyons et al. 2004). Larvae feed on phloem for several weeks, often scoring the outer sapwood (McCullough and Katovich 2004; www.emeraldashborer.info 2006). Most *A. planipennis* overwinter as prepupal larvae in shallow chambers excavated

in the outer sapwood or in the bark of thick-barked trees. Recent evidence has shown that some larvae overwinter as early instars and complete their feeding during the second summer. The underlying cause of this extended development is not understood, but it seems to be most common in healthy trees with low densities of *A. planipennis* (Cappaert et al. 2005c). Woodpecker predation of prepupal larvae is common in many sites and occurs mostly during winter and early spring (Cappaert et al. 2005b; Lindell et al., unpublished data). Pupation begins in late April or May and adults emerge roughly 2 weeks later, leaving distinctive D-shaped exit holes, 3 to 4 mm (0.12 to 0.16 in) in diameter (McCullough and Katovich 2004).

In North America, *A. planipennis* is aggressively attacking healthy, as well as stressed, ash trees. An estimated 20 million ash trees in southeast Michigan alone were dead or dying by late 2006. This invasive pest could potentially spread throughout North America through natural dispersal by adult beetles and artificial spread caused by humans moving infested ash material. In the United States, there are at least 16 native species of *Fraxinus* (Harlow et al. 1991) and more than 8 billion ash trees on forest land (FIA 2006). At least 800 million ash trees occur on timberlands in Michigan, including green ash (*F. pennsylvanica*), white ash (*F. americana*), black

ash (*F. nigra*), and blue ash (*F. quadrangulata*) (Barnes and Wagner 1981; FIA 2006). In natural forests, *A. planipennis* could substantially alter biodiversity and stand dynamics (MacFarland and Meyer 2005). Ash trees, particularly green ash and white ash, are also commonly planted in many urban areas of the United States (Ottman and Kielbaso 1976; Giedraitis and Kielbaso 1982; Poland and McCullough 2006).

Given the extensive damage that *A. planipennis* has caused to date, an important question is whether *A. planipennis* preferentially feeds or oviposits on certain North American species of *Fraxinus*. Understanding the preference hierarchy and underlying mechanisms of *A. planipennis* attraction among *Fraxinus* species will increase our ability to accurately assess stand susceptibility to this pest based on species composition. It is also important for developing survey, detection, and management options and predicting spread and impact of *A. planipennis* throughout North America.

To assess host preference, we quantified the density of *A. planipennis* exit holes and woodpecker attacks at four sites with green and white ash street trees and at two woodlots where white and blue ash trees co-occurred. We also monitored canopy dieback and changes in exit hole and woodpecker attack densities over time.

MATERIALS AND METHODS

Study Sites

Study sites were selected based on four criteria. Each site had to have two species of similarly sized ash trees that were untreated, growing in close proximity under similar site conditions, and presumably exposed to similar levels of *A. planipennis* pressure. Permission to survey trees was acquired from the respective property owners. Trees included in our surveys ranged from 4 to 38 cm (1.6 to 15.2 in) in diameter at breast height (dbh) (Table 1).

Green versus White Ash Street Trees

In 2003, we sampled green and white ash street trees at two sites (Table 1). At the first site, Butzel School in Detroit, Wayne County, Michigan, eight small green ash and eight small white ash trees were growing around the perimeter of the school yard. At the second site on Larned Boulevard, also in Detroit, there were 11 green ash trees on the east side of the street and 11 white ash trees in the grassy median (Table 1). In 2004, we also surveyed seven green ash and seven white ash trees growing in the grass strip between the sidewalk and the street in the Windemere neighborhood in Ann Arbor, Washtenaw County, Michigan (Table 1). The fourth site, surveyed during the 2005 season only, included eight green ash and nine white ash trees growing within 30 m (99 ft) of one another near the Lakeside Terraces condominium complex in Sterling Heights, Macomb County, Michigan (Table 1).

White versus Blue Ash Woodlot Trees

In 2004, we located two woodlots that had established *A. planipennis* populations and included white and blue ash trees growing in close proximity. In Superior Township, Washtenaw County, Michigan, white and blue ash trees ranged from 17 to 32 cm (6.8 to 12.8 in) in dbh and trees were growing 6 to 24 m (19.8 to 79.2 ft) apart (Table 1). In a woodlot in Plymouth Township, Wayne County, Michigan, trees ranged from 11 to 35 cm (4.4 to 14 in) in dbh and trees were growing 3 to 7 m (9.9 to 23.1 ft) apart (Table 1). Trees in both woodlots were surveyed in 2004 and trees were evaluated in Superior Township, again in 2005.

Sampling and Data Collection

Green versus White Ash Street Trees

For each tree, visual estimates of canopy dieback were made annually in late summer, when damage from the current year larvae had become apparent. The cumulative number of

Table 1. Number of trees (n) and mean (\pm SE) diameter at breast height (dbh) for green and white ash trees at four residential sites and blue and white ash trees at two woodlots.

Site	Green ash ^z		White ash ^z		Survey year(s)
	n	dbh (cm/in)	n	dbh (cm/in)	
Butzel	8	8.1 \pm 1.2/3.2 \pm 0.5	8	4.2 \pm 0.2/1.7 \pm 0.1	2003, 2004, 2005
Larned	11	18.0 \pm 0.5/7.1 \pm 0.2	11	23.3 \pm 0.7/9.2 \pm 0.3	2003, 2004, 2005
Windemere	7	27.7 \pm 2.5/10.9 \pm 1.0	7	23.3 \pm 1.3/9.2 \pm 0.5	2004, 2005
Lakeside	8	32.0 \pm 5.3/12.6 \pm 2.1	9	33.0 \pm 4.7/13.0 \pm 1.9	2005
		Blue ash ^y		White ash ^y	
Superior Twp.	5	20.1 \pm 3.9/7.9 \pm 1.5	4	20.6 \pm 2.4/8.1 \pm 0.9	2004
Plymouth Twp.	5	22.2 \pm 3.7/8.7 \pm 1.5	5	24.2 \pm 4.6/9.5 \pm 1.8	2004
Superior Twp.	4	21.2 \pm 2.4/8.3 \pm 0.9	4	23.4 \pm 4.0/9.2 \pm 1.6	2005

^zThe same trees were resurveyed each year.

^yTrees were felled for sampling and new trees were selected each year.

D-shaped exit holes made by emerging *A. planipennis* adults and woodpecker attacks were counted in the fall, after adult beetle emergence was complete. Woodpeckers primarily prey on prepupae, which have completed their feeding and would otherwise have a high probability of emerging as adults (Cappaert et al. 2005b, 2005c; Lindell et al. unpublished data). The sum of adult exit holes and woodpecker attacks, therefore, represented the cumulative number of *A. planipennis* larvae that developed in the area surveyed on each tree.

Exit holes and woodpecker attacks were counted on the entire trunk or branch circumference in four areas of each tree: at 1.5 and 3 m (4.95 and 9.9 ft) aboveground, at the base of the lowest first order branch, and 1 m (3.3 ft) out on that branch. Areas above 1.5 m (4.95 ft) were accessed using a ladder. On each tree, an area of $\approx 0.26 \text{ m}^2$ ($\approx 2.81 \text{ ft}^2$) was inspected at 1.5 m (4.95 ft) aboveground and 0.13 m^2 (1.40 ft^2) was examined on the other three sample areas {average total area of $0.65 (\pm 0.01 \text{ standard error [SE]}) \text{ m}^2$ [$7.0 (\pm 0.11 \text{ SE}) \text{ ft}^2$] per tree}. At the Butzel site, 11 trees were less than 5 cm (2 in) in dbh, so the entire stem and all branches of each tree were examined. On average, we inspected $0.52 (\pm 0.03 \text{ SE}) \text{ m}^2$ [$5.60 (\pm 0.32 \text{ SE}) \text{ ft}^2$] on each of the small trees. Percentage of the canopy that was dead, number of *A. planipennis* exit holes, and number of woodpecker attacks on *A. planipennis* prepupal larvae was recorded for each area inspected on each tree. Mean *A. planipennis* density per tree was calculated by summing the total number of *A. planipennis* exit holes and woodpecker attacks and dividing by the total area sampled in the tree. In 2003, canopy dieback was recorded on 12 August and *A. planipennis* exit holes and woodpecker attacks were counted between 12 August and 11 October.

Survey methods were modified in 2004 because related research showed that initial attacks by *A. planipennis* were more common in the upper canopy than on the trunk (Cappaert et al. 2005a). Therefore, on all trees greater than 5 cm (2 in) in dbh, tree climbers inspected four to six areas between 1.5 and 8.5 m (4.95 and 28.1 ft) aboveground on each tree. On average, the total area examined on each tree was $1.04 (\pm 0.07 \text{ SE}) \text{ m}^2$ [$11.19 (\pm 0.75 \text{ SE}) \text{ ft}^2$]. Small trees [dbh < 5 cm (2 in)] were completely surveyed as before. With the exception of the sample area at 1.5 m (4.95 ft) aboveground, sample areas were randomly selected each year and may or may not have overlapped with areas sampled the previous year. Counts of exit holes and woodpecker attacks in 2004 were collected on 6 August at Butzel and Larned and on 9 August at Windemere. Canopy dieback was estimated at the three sites on 13 September. In July 2004, however, four green ash trees at Larned and two green ash and one white ash tree at Butzel were felled and removed from the survey sites by the respective municipalities. Canopy dieback for these seven trees was recorded as 100% in the subsequent year's survey.

Seven additional dead trees were removed in 2005, including one green ash and two white ash trees at Butzel and two green ash and two white ash trees at Windemere. The two white ash trees at Windemere were felled after dieback estimates were made but before exit hole and woodpecker attack data could be collected. Dieback for these five trees, therefore, was recorded as 100% in 2005. Dieback estimates were made on 16 September 2005 at all sites, except Lakeside where leaves began falling before estimates of dieback could be made. Exit holes and woodpecker attacks on the remaining 25 green ash and 30 white ash (55 trees total) were counted on 12 October at Butzel and Windemere, 19 October at Lakeside, and 19 and 21 October 2005 at Larned. Data collected from 25 green ash and 26 white ash trees (51 trees total) at Larned and Butzel in 2003 and at Windemere in 2004 were used to assess the relationship between canopy dieback and *A. planipennis* density.

White versus Blue Ash Woodlot Trees

On 2 March 2004, two white ash and three blue ash trees were surveyed by climbers in the Superior Township woodlot. Seven to 11 areas on the main stem and branches between 1.5 and 15 m (4.95 and 49.5 ft) aboveground were examined per tree and *A. planipennis* exit holes and woodpecker attacks were recorded for each area. An average of $2.9 (\pm 0.22 \text{ SE}) \text{ m}^2$ [$31.2 (\pm 2.37 \text{ SE}) \text{ ft}^2$] per tree was inspected. On 28 May 2004, before the onset of *A. planipennis* adult emergence, two additional white ash and two blue ash trees were felled. Four to eight intervals between 1.5 and 15 m (4.95 and 49.5 ft) aboveground were inspected on each tree. An average of $0.8 (\pm 0.09 \text{ SE}) \text{ m}^2$ [$8.6 (\pm 0.97 \text{ SE}) \text{ ft}^2$] per tree was examined. Trees that were felled were debarked and the percentage of phloem surface area covered by *A. planipennis* galleries was estimated. The total number of exit holes and woodpecker attacks were summed and divided by the total area sampled for each tree. There was no significant difference between counts of *A. planipennis* density recorded by tree climbers and counts recorded after trees were felled ($S = 26.0$; $df = 1,7$; $P = 0.09$). Because of the difficulty of accurately estimating dieback on tall, closed-canopy woodlot trees, dieback was not estimated for the woodlot trees.

On 20 January 2005, we felled five white ash and five blue ash trees in the Plymouth Township woodlot. Five to 16 trunk and branch sections between 1.5 and 17 m (4.95 and 56.1 ft) aboveground were removed from each tree and transported to the laboratory for inspection and debarking. Average area sampled per tree was $1.4 (\pm 0.21 \text{ SE}) \text{ m}^2$ [$15.1 (\pm 2.26 \text{ SE}) \text{ ft}^2$]. Number of *A. planipennis* exit holes, woodpecker attacks, and percentage of phloem surface area covered by galleries was recorded.

On 21 November and 2 December 2005, another four white ash and four blue ash trees in the Superior Township woodlot were felled and inspected using methods from the

2004 Plymouth Township survey. Five to eight sections were taken from each tree between 1.5 and 21.5 m (4.95 and 71 ft) aboveground with an average sample area of 1.1 (± 0.10 SE) m^2 [11.8 (± 1.1 SE) ft^2] per tree.

Statistical Analysis

All data were tested for normality using the Shapiro-Wilk test (Shapiro and Wilk 1965) and residual plots. Data were not normally distributed after transformations. Therefore, the nonparametric Wilcoxon rank sum test (Ott and Longnecker 2001) was used to determine if the mean number of *A. planipennis* exit holes and woodpecker attack density, percentage of phloem surface area covered by galleries, and percentage of canopy dieback differed significantly between species at each site.

Counts of *A. planipennis* exit holes and woodpecker attacks and canopy dieback data from Larned and Butzel in 2003 and Windemere in 2004 were pooled and tested for normality. Data were normally distributed and simple linear regression was used to determine if canopy dieback was a significant predictor of *A. planipennis* exit hole and woodpecker attack densities. All analyses were conducted at the $P < 0.05$ level of significance using SAS statistical software (SAS Institute 2003).

RESULTS

Green versus White Ash Street Trees

At the Butzel site where trees were small, canopy dieback of green ash trees was, on average, 13% to 20% higher than canopy dieback of white ash trees during the 3-year period, but differences were not significant in 2003 ($S = 83.5$; $df = 1,14$; $P > 0.0532$), 2004 ($S = 79.0$; $df = 1,14$; $P > 0.13$), or 2005 ($S = 73.0$; $df = 1,14$; $P > 0.31$) (Figure 1A). Average canopy dieback for green ash and white ash trees increased 32% and 25%, respectively, from 2003 to 2004, and 13% and 18%, respectively, from 2004 to 2005 (Figure 1A). In 2004, canopy dieback, excluding the three dead green ash and one dead white ash trees that were removed, averaged 43% (± 10.2 SE) for green ash and 30% (± 18.2 SE) for white ash. In 2005, canopy dieback (excluding the dead trees) averaged 53% (± 11.4 SE) for green ash and 29% (± 18.5 SE) for white ash.

Green ash trees at Butzel had an average of 17 to 39 more exit holes and woodpecker attacks per m^2 (2 to 4 per ft^2) than white ash trees throughout the study, but differences were not significant in 2003 ($S = 80.0$; $df = 1,14$; $P > 0.11$), 2004 ($S = 47.0$; $df = 1,11$; $P > 0.27$), or 2005 ($S = 33.0$; $df = 1,8$; $P > 0.15$) (Figure 1B). Exit hole and woodpecker attack densities in green ash more than tripled from 2003 to 2004 and increased fivefold in white ash (Figure 1B). Densities remained relatively consistent from 2004 to 2005 (Figure 1B). Average exit hole density ranged from 21 to 78 exit

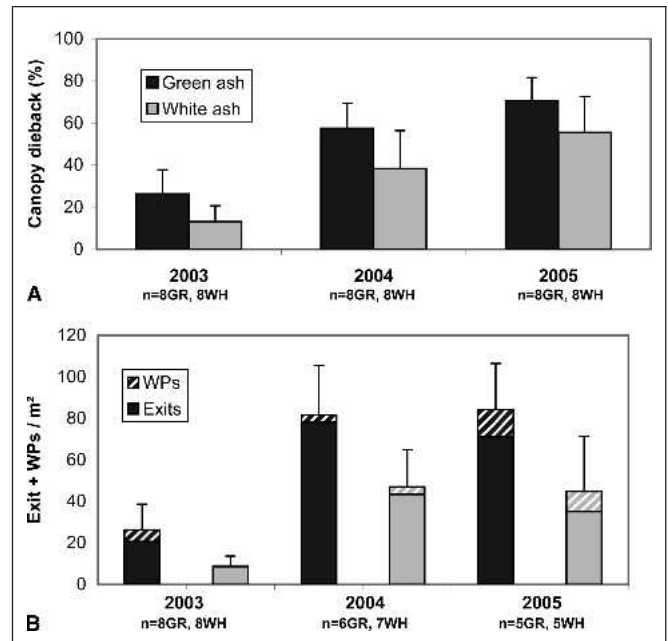


Figure 1. (A) Mean (\pm SE) percent canopy dieback and (B) mean (\pm SE) number of *Agilus planipennis* exits holes (exits) and woodpecker attacks (WPs) per meter squared for the small green (GR) and white (WH) ash trees at Butzel in 2003, 2004, and 2005. Three dead green ash and three dead white ash trees were removed in 2004 and 2005. Means for canopy dieback include removed trees as having 100% dieback. Means within years were not significantly different between species (Wilcoxon rank sum test; $P > 0.05$).

holes/ m^2 (2 to 7 per ft^2) in green ash and 9 to 43 exit holes/ m^2 (1 to 4 per ft^2) in white ash from 2003 to 2005. Woodpecker attacks were found on both branches and trunks of green and white ash trees. Average woodpecker attack density ranged from 4 to 13 woodpecker attacks/ m^2 (0.3 to 1.2 per ft^2) in green ash and 0 to 10 (0 to 1 per ft^2) in white ash over the 3-year period. On average, by 2005, woodpeckers had preyed on 21% of the *A. planipennis* in these trees.

At Larned, green ash trees had significantly more canopy dieback than white ash trees in 2003 ($S = 182.0$; $df = 1,20$; $P < 0.0001$), 2004 ($S = 187.0$; $df = 1,20$; $P < 0.0001$), and 2005 ($S = 181.5$; $df = 1,20$; $P < 0.0001$) (Figure 2A). Dieback increased approximately 25% each year for both species and green ash trees averaged 49% to 69% more dieback than white ash trees (Figure 2A). In 2004, canopy dieback was 100% on six of the seven remaining green ash trees and only 10% of the canopy was alive on the other tree. By 2005, all green ash trees in the survey were dead.

Green ash trees at Larned had 1.5 to four times as many *A. planipennis* exit holes and woodpecker attacks per m^2 as white ash trees throughout the study. Exit hole and woodpecker attack densities were significantly greater in green ash

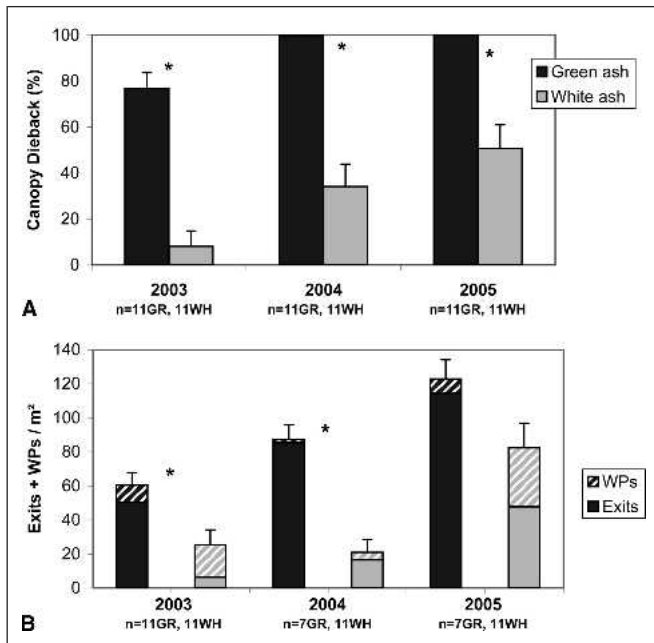


Figure 2. (A) Mean (\pm SE) percent canopy dieback and (B) mean (\pm SE) number of *Agrilus planipennis* exits holes (exits) and woodpecker attacks (WPs) per meter squared for green (GR) and white (WH) ash trees at Larned in 2003, 2004, and 2005. Four dead green ash trees were removed in 2004. Means for canopy dieback include removed trees as having 100% dieback. *Significant differences between green and white ash trees (Wilcoxon rank sum test; $P < 0.05$).

than in white ash in 2003 and 2004 ($S = 169.0$; $df = 1,20$; $P = 0.002$ and $S = 101.0$; $df = 1,16$; $P < 0.0004$, respectively), but differences were marginally insignificant in 2005 ($S = 85.0$; $df = 1,16$; $P = 0.0521$) (Figure 2B). Exit hole and woodpecker attack densities in green ash increased by 45% from 2003 to 2004 and by 41% from 2004 to 2005. Densities in white ash did not change dramatically from 2003 to 2004, but nearly quadrupled from 2004 to 2005 (Figure 2B). Average exit hole density ranged from 50 to 114 exit holes/m² (5 to 11 per ft²) in green ash and 6 to 48 exits holes/m² (0.5 to 4.5 per ft²) in white ash from 2003 to 2005. Average woodpecker attack density ranged from 2 to 10 woodpecker attacks/m² (0.2 to 1 per ft²) in green ash and 4 to 35 woodpecks/m² (0.4 to 3 per ft²) in white ash. By 2005, all trees surveyed at the Larned site had woodpecks and, on average, woodpeckers preyed on 34% of the *A. planipennis* in these trees.

At Windemere, green ash trees had significantly more canopy dieback than white ash trees in both 2004 ($S = 77.0$; $df = 1,12$; $P < 0.0003$) and 2005 ($S = 77.0$; $df = 1,12$; $P < 0.0003$) (Figure 3A). Green ash trees were at or near 100% dieback both years, whereas average dieback in white ash trees increased more than 45% from 2004 to 2005. In

2005, two green ash trees were removed in midsummer and all of the five remaining green ash trees were dead by September.

In 2004, green ash trees at Windemere had significantly more *A. planipennis* exit holes and woodpecker attacks per m² than white ash trees ($S = 66.0$; $df = 1,12$; $P = 0.0487$) (Figure 3B). In 2005, however, white ash trees had significantly greater exit hole and woodpecker densities than the remaining dead or dying green ash ($S = 17.0$; $df = 1,8$; $P = 0.0159$). One white ash tree in 2005 with a recorded density of 229 exit holes and woodpecker attacks per meter squared (21 per ft²) was considered an outlier and removed from the data set. The data were reanalyzed and white ash trees still had significantly more exits holes and woodpecker attacks per meter squared than green ash trees ($S = 28.0$; $df = 1,7$; $P = 0.0317$) (Figure 3B). Average exit hole density from 2003 to 2005 ranged from 44 to 76 exit holes/m² (4 to 7 per ft²) on green ash and 32 to 93 exit holes/m² (3 to 9 per ft²) on white ash. Average woodpecker attack density ranged from 6 to 14 woodpecker attacks/m² (0.6 to 1.3 per ft²) on

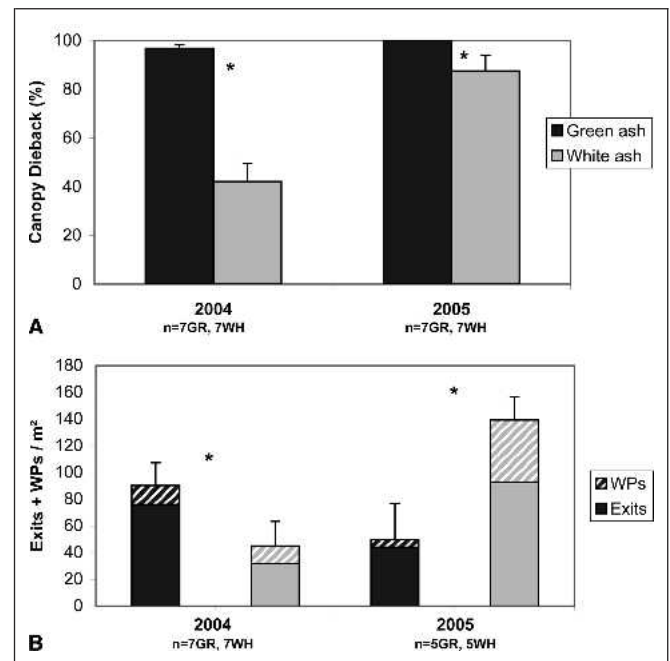


Figure 3. (A) Mean (\pm SE) percent canopy dieback and (B) mean (\pm SE) number of *Agrilus planipennis* exits holes (exits) and woodpecker attacks (WPs) per meter squared for green (GR) and white (WH) ash trees at Windemere in 2004 and 2005. Two dead green ash trees were removed in 2005. Means for canopy dieback include removed trees as having 100% dieback. One outlier for exits and woodpecks per meter squared was removed from the 2005 white ash tree data set. *Significant differences between green and white ash trees (Wilcoxon rank sum test; $P < 0.05$).

green ash and 13 to 46 woodpecker attacks/m² (1.2 to 4 per ft²) on white ash over the 3-year period. By 2005, all Windemere trees had woodpecker attacks and, on average, woodpeckers preyed on 27% of the *A. planipennis* in these trees.

Green ash trees at Lakeside, surveyed in 2005, had significantly more exit holes and woodpecks per meter squared than white ash trees with an average of 22.8 (±6.86 SE) per meter squared [2.1 (±0.64 SE) per ft²] for green ash and 5.9 (±1.02 SE) per meter squared [0.6 (±0.09 SE) per ft²] for white ash (S = 94.0; df = 1,15; P = 0.0180). On green ash trees, 56% of the average total density was comprised of exit holes, whereas woodpeckers attacked the remaining 44% of the *A. planipennis*. On white ash trees, exit holes made up 29% of the average total density and woodpecker attacks made up 71% of *A. planipennis* density.

Overall, using the Butzel, Larned, and Windemere data, canopy dieback increased as the density of *A. planipennis* exit holes and woodpecker attacks increased. A positive and significant linear relationship existed between these two variables for green ash, for white ash, and the two species combined (Figure 4). In general, if dieback was less than 30%, fewer than 30 exit holes and woodpecker attacks per meter squared (3 per ft²) were found. If dieback was less than 50%, the density of exit holes and woodpecker attacks ranged from 30 to 60 per m² (3 to 6 per ft²) (Figure 4). Two dead trees had densities as low as 37 to 50 exit holes and woodpecker attacks per meter squared (3 to 5 per ft²). Overall, on trees with more than 90% dieback, the density of exit holes and woodpecker attacks ranged from 60 to 155 per m² (6 to 14 per ft²) (Figure 4).

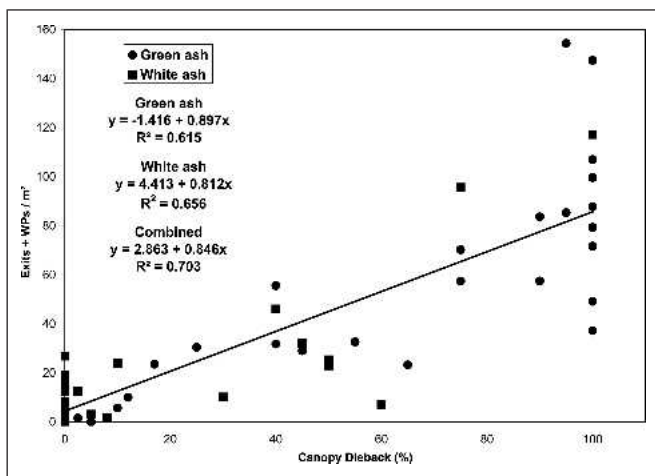


Figure 4. Percent canopy dieback and number of *Agrilus planipennis* exit holes (exits) and woodpecker attacks (WPs) per meter squared for 25 green ash and 24 white ash trees (49 trees total) surveyed at three residential sites in 2003 and 2004.

White versus Blue Ash Woodlot Trees

The white ash trees in both woodlots were heavily infested and declining or dying, whereas blue ash trees of similar size had much lower exit hole and woodpecker attack densities. In 2004, white ash trees in the Plymouth Township woodlot had significantly more *A. planipennis* exit holes and woodpecker attacks per meter squared than blue ash trees with an average of 80.1 (±20.65 SE) per m² [7.4 (±1.92 SE) per ft²] for white ash and 11.5 (±7.83 SE) per m² [1.1 (±0.73 SE) per ft²] for blue ash (S = 16.0; df = 1,8; P = 0.0079). Exit holes and woodpecker attacks were found on branches and trunks of both species. Exit holes comprised 70% and 61% of the average total *A. planipennis* density in white ash and blue ash trees, respectively, whereas woodpecker attacks accounted for 30% and 39% of the *A. planipennis* in white and blue ash, respectively. Percentage of phloem surface area covered by *A. planipennis* larval galleries ranged from 0% to 100% in white ash, with an average of 39% (±10.9 SE), and from 0% to 40% in blue ash, with an average of 8% (±5.7 SE). Significantly more phloem area was covered by galleries in white ash than in blue ash (S = 18.0; df = 1,8; P = 0.0278).

Similarly, in the Superior Township woodlot, white ash trees had significantly more exit holes and woodpecker attacks per meter squared than blue ash in 2004 (S = 30.0; df = 1,7; P = 0.0079) and 2005 (S = 10; df = 1,6; P = 0.0143) (Figure 5). There was a significant increase in the density of exit holes and woodpecker attacks from 2004 to 2005 for the white ash trees in the Superior Township woodlot (S = 26.0; df = 1,6; P = 0.0143), but not for the blue

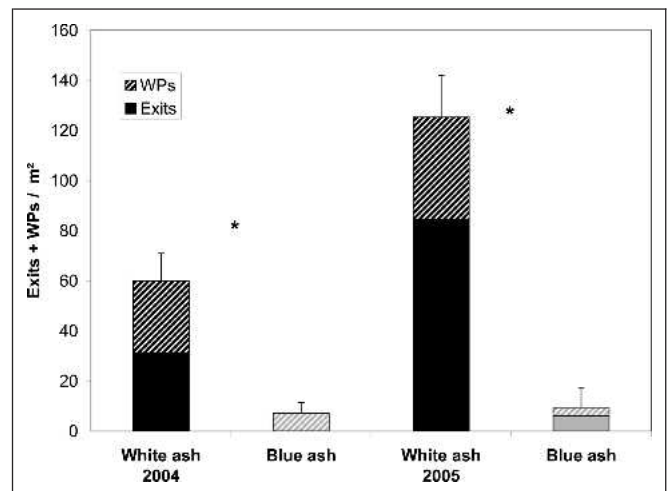


Figure 5. Mean (±SE) number of *Agrilus planipennis* exit holes (exits) and woodpecker attacks (WPs) per meter squared for white and blue ash trees at Superior Township in 2004 and 2005. *Significant differences between white and blue ash trees (Wilcoxon rank sum test; P < 0.05).

ash trees ($S = 22.0$; $df = 1,7$; $P > 0.36$) (Figure 5). For the two trees of each species that were felled and debarked in 2004, the percentage of phloem surface area covered by galleries ranged from 25% to 100% in white ash, with an average of 67% (± 5.9 SE), and from 0% to 40% in blue ash, with an average of 15% (± 7.6 SE). In 2005, percentage of phloem covered by galleries ranged from 0% to 100% in white ash, with an average of 73% (± 8.1 SE), and from 0% to 30% in blue ash, with an average of 7% (± 5.0 SE). The percentage of phloem covered by galleries did not differ significantly between species in 2004 ($S = 7.0$; $df = 1,2$; $P > 0.17$), but were significant in 2005 ($S = 10.0$; $df = 1,6$; $P = 0.0143$). Callous tissue grew around the edge of many of the galleries on blue ash trees, but we observed little evidence of callous tissue on white ash trees.

The overall frequency and extent of woodpecker predation was notable; more than 86% of the green, white, and blue ash trees included in our surveys had at least one woodpecker attack. The percentage of *A. planipennis* killed by woodpeckers on urban street trees ranged from 0% to 100%, with an average of 33% (± 5.8 SE). This predation rate was greater for woodlot trees, where woodpecker attacks killed 0% to 100% of the *A. planipennis*, with an average mortality of 48% (± 6.6 SE).

DISCUSSION

One of the key questions our study addressed was whether *A. planipennis* exhibits a host preference hierarchy among the predominant ash species native to Michigan. We determined that *A. planipennis* densities were consistently higher in green ash trees than in white ash trees growing in the same residential sites. Our counts represented the cumulative density of larvae that successfully completed their feeding and either emerged as adults or were preyed on by woodpeckers as prepupae. Our data also illustrate the progression of the *A. planipennis* infestation in sites monitored for multiple years. In the residential sites, *A. planipennis* densities in white ash increased from year to year as available phloem in green ash declined.

The only exception to this trend was at Windemere in 2005, where, on average, white ash trees had significantly higher exit hole and woodpecker attack densities than green ash both before and after the removal of the outlier point. Unlike the other sites that had fairly equal numbers of each species in the surrounding area, Windemere was unique in that the street trees were predominantly white ash with an occasional green ash tree in the midst of white ash trees. Singer (1983) noted that insects may not use their most highly preferred host if they encounter another acceptable host first. The reduced density of exit holes and woodpecker attacks in the green ash from 2004 to 2005 at Windemere [40 exit holes and woodpecker attacks per meter squared (4 per ft²)] also reflected the removal of two dead green ash trees in 2005.

Average *A. planipennis* densities would have been substantially greater if the dead trees had been retained in our annual surveys. Similarly, *A. planipennis* densities in trees at the Larned site would likely have been higher in 2005 if four dead trees had not been removed in 2004. At the Butzel site, where most trees were less than 5 cm (2 in) dbh, average *A. planipennis* densities were consistently higher in green ash than white ash trees, but differences between species were not significant. Because the trees were small, only a limited amount of phloem was available for *A. planipennis* at this site, probably obscuring some interspecific differences.

Agrilus planipennis clearly preferred white ash trees over blue ash trees in both woodlots we surveyed. When our survey began in 2004, numerous white ash trees in the two woodlots were declining or had been killed by *A. planipennis*, whereas nearby blue ash trees were just becoming infested. Blue ash trees may have also been less suitable hosts for developing larvae. We noted that callous tissue often grew on the edges or over the top of larval galleries on blue ash trees but was rarely associated with galleries on white or green ash trees. It was also evident that most larvae would have taken 2 years to develop on the blue ash trees. Future studies are needed to address potential differences among ash species in their phloem chemistry, attraction to ovipositing beetles, and initial resistance to *A. planipennis* larval feeding.

Canopy dieback caused by *A. planipennis* was consistently more pronounced in green ash trees than white ash trees at all residential sites in all years. Similar patterns have been observed in other infested areas. For example, in a residential site in Washtenaw County, Michigan, dieback on green ash trees averaged 60% compared with less than 10% dieback for white ash trees of the same age (McCullough et al. 2005). As expected, we found an increasing proportion of the canopy died each year, because the density of *A. planipennis* larvae escalated and the proportion of intact phloem declined.

Although canopy dieback, an external symptom of infestation, is not necessarily a direct measure of larval density, we did find a significant correlation between canopy dieback and the density of *A. planipennis* exit holes and woodpecker attacks. Linear models derived to describe this relationship were nearly identical for green ash and white ash trees, indicating that in both species, a 10% increase in dieback was associated with eight or nine more *A. planipennis* per meter squared (≈ 1 per ft²).

Ash trees and other ring-porous hardwoods are generally more vulnerable to injury caused by phloem-feeding insects or wilt diseases than diffuse-porous hardwoods or conifers (Haack and Benjamin 1982; Kozłowski and Pallardy 1997). In the 14 dead green ash and 19 dead white ash trees we sampled in the residential and woodlot sites, the maximum number of *A. planipennis* per meter squared that were able to develop on a single tree was ≈ 107 (± 10.8 SE) per meter squared [10 (± 1.0 SE) per ft²] for green ash and 109 (± 10.6

SE) per meter squared [$10 (\pm 1.0 \text{ SE})$ per ft^2] for white ash. McCullough and Siegert (2007) sampled 71 green and white ash trees killed by *A. planipennis* and reported that, on average, roughly 89 to 105 *A. planipennis* could develop per meter squared (8 to 10 per ft^2).

At least six trees we surveyed had more than 50% dieback but less than 40 *A. planipennis* exits or woodpecker attacks per millimeter squared (4 per ft^2). Although not all surveyed trees were debarked, a similar pattern was observed in other sites. If tree trunks become heavily infested before phloem in the canopy is exhausted, trees will succumb at lower *A. planipennis* densities than might otherwise be expected (McCullough and Siegert 2007). We also observed a few trees with extensive dieback that had virtually no exit holes or woodpecker attacks. Once these trees were debarked, it was apparent that nearly 100% of the phloem had been consumed, but virtually all larvae died as second or third instars because of intraspecific competition. The negative y-intercept derived for our green ash model likely reflected trees that exhibited some canopy dieback but few or no *A. planipennis* exit holes or woodpecker attacks.

Smitley et al. (2006) reported a significant correlation ($R^2 = 0.59$) between canopy dieback and density of *A. planipennis* exit holes in a survey of ash trees growing near highway exits in southeast Michigan. They counted exit holes visible on the tree trunks but did not examine branches in the canopy, which are usually colonized by *A. planipennis* before the trunk becomes infested (Cappaert et al. 2005c). A scatterplot of their data suggests that they observed a lower density of exit holes relative to canopy dieback than we observed, probably because they did not attempt to assess *A. planipennis* emergence in the canopy. For example, Smitley et al. (2006) recorded almost no exit holes in trees with 30% or less dieback. In contrast, we found up to 30 exit holes and woodpecker attacks per meter squared (3 per ft^2) in trees with 30% or less dieback.

Woodpeckers can play an important role in regulating populations of phloem-feeding or wood-boring beetle larvae (Anderson 1944; Nash et al. 1951; Barter 1957; Akers and Nielsen 1990; Fayt et al. 2005) and appear to be an important natural enemy of *A. planipennis* in North America (Cappaert et al. 2005b; Fuester and Schaefer 2006; Marshall et al. 2006; Strazanac 2006). Woodpeckers are known to feed on native buprestids such as *A. anxius* (bronze birch borer) with predation rates reportedly ranging from very low to 50% of *A. anxius* larvae (Anderson 1944; Nash et al. 1951; Barter 1957; Akers and Nielsen 1990). Overall, woodpecker attacks accounted for an average of 35% of the *A. planipennis* in the trees we surveyed. Other native natural enemies of *A. planipennis* in Michigan appear to be much less effective. Bauer et al. (2006) reported less than 2% of larvae were infected with pathogenic fungi, and less than 1% of larvae and 0.5% of eggs were killed by parasitoids. Even in its native range in

China, less than 7% of *A. planipennis* larvae, on average, were killed by hymenopteran parasitoids (Liu et al. 2003). Woodpeckers were present at all of the sites we surveyed and attacks were noted on trees with relatively low, moderate, and high *A. planipennis* densities. At least three species of woodpeckers have been observed preying on *A. planipennis* in Michigan (Lindell et al. unpublished data), but little is known about their functional or numerical responses to this invasive pest. More research is warranted to address woodpecker behavior and habitat use and effects of woodpecker predation on *A. planipennis* dynamics.

The observational data reported here provide a framework for future studies that will be needed to identify mechanisms that underlie differential host preference by *A. planipennis*. There are clearly differences in host susceptibility or vulnerability between North American ash species and Asian ash species, which have a long coevolutionary history with *A. planipennis*. In an experimental plot established in southeast Michigan in 2003, for example, European and North American ash species sustained more *A. planipennis* attacks and higher mortality than Manchurian ash, a species native to Asia (Herms et al. 2005). Liu et al. (2003) reported that in the 1960s, when a plantation of North American white ash was established in China, an outbreak of *A. planipennis* erupted and all of the trees were killed.

Within North America, numerous factors are likely to affect *A. planipennis* host selection and should not be considered mutually exclusive. Several studies have shown that although *A. planipennis* is capable of attacking healthy trees in North America, it prefers trees stressed by girdling or other biotic or abiotic agents (McCullough et al. 2005, 2006; Poland et al. 2006). This is consistent with observations made by Liu et al. (2003) who noted that in its native range, *A. planipennis* appears to function as a secondary pest, typically attacking stressed trees. *Agrilus* species native to North America such as *A. bilineatus* and *A. anxius* exhibit an analogous pattern, similarly typically attacking only hosts that are severely stressed by drought, defoliation, disease or injury (Anderson et al. 1944; Ball and Simmons 1980; Cote and Allen 1980; Dunn et al. 1986; Muzika et al. 2000; Herms 2002).

In addition, native *Agrilus* species and *A. planipennis* demonstrate an ovipositional preference for rough-barked portions of trees (Barter 1957; Loerch and Cameron 1984; Anulewicz 2006). Many varieties of green ash have rough, flaky bark even as young trees, whereas most varieties of white ash produce relatively smooth bark until they reach maturity. Blue ash trees, however, were less preferred or less suitable hosts than either green or white ash despite their rough textured bark. Host selection by *A. planipennis* is also likely affected by secondary compounds in ash leaves, bark, or phloem encountered by beetles as they feed on foliage or search for oviposition sites (Haack and Slansky 1986). Poland et al. (2006) found that traps baited with a blend of

volatiles isolated from ash leaves captured significantly more *A. planipennis* than traps with individual compounds. Similarly, Crook et al. (2006) reported that sesquiterpenes isolated from ash bark elicited consistently strong antennal responses from *A. planipennis* adults.

Results from this study can be used to more thoroughly assess the susceptibility of both urban and forest trees based on species composition and to increase efficiency in developing survey, detection, and management options. In areas where two or more ash species occur, newly established or low-density populations of *A. planipennis* are more likely to be detected by focusing survey efforts on the preferred ash species (i.e., green ash). Additional research to evaluate interactions between *A. planipennis* and ash species may also identify traits that could be augmented or propagated to enhance resistance of North American trees to this invasive pest.

Acknowledgments. We thank Elizabeth Grisham, Robert McDonald, Sarah Smith, and Christopher Pell from Michigan State University (MSU) for their invaluable assistance in the field. We also thank Dr. Therese Poland (USDA Forest Service) and Dr. Bert Cregg (MSU) for their advice and support. We appreciate the cooperation provided by Dan Kurkowski, City of Detroit; Paul Bairley and Kay Sicheneder, City of Ann Arbor; Jan and Michael David BenDor, and Cynthia Shake for providing trees for survey. Funding for this project was provided by the USDA Agricultural Research Service, USDA Forest Service, Northeastern Area Forest Health Protection, and MSU's Project GREEN.

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- Résumé.** L'agrire du frêne (*Agrilus planipennis* Fairmaire) (coléoptère de la famille des Buprestidacées), un insecte originaire d'Asie qui s'alimente du phloème, a été identifié en 2002 comme la cause de la mortalité à grande échelle du frêne dans le Sud-est du Michigan et la région de Windsor en Ontario. Peu d'informations sur *A. planipennis* est disponible quant à son milieu d'origine et on ne sait pas non plus si cet insecte invasif va démontrer une préférence pour une espèce particulière de frêne indigène de l'Amérique du Nord. Nous avons suivi la densité de *A. planipennis* ainsi que la condition du couvert arboré du frêne de Pennsylvanie (*Fraxinus pennsylvanica*) et du frêne d'Amérique (*F. americana*) en arbres de rues au sein de quatre quartiers ainsi que du frêne d'Amérique et du frêne bleu (*F. quadrangulata*) dans deux boisés du Sud-est du Michigan. Les frênes de Pennsylvanie de rues avaient une mortalité de cime significativement plus élevée ainsi que des densités en *A. planipennis* aussi plus élevées par rapport aux frênes d'Amérique dans les mêmes quartiers. La densité augmentait de 2 à 4 fois chez ces deux espèces après trois ans. La mortalité du couvert arboré augmentait de manière linéaire de 2002 à 2005 avec l'augmentation de la densité en *A. planipennis* ($R^2 = 0,70$). Dans chacun des boisés, les densités en *A. planipennis* étaient significativement plus élevées chez le frêne d'Amérique que le frêne bleu. La prédation par les pics était présente sur tous les sites et comptait pour 35% des arbres étudiés où *A. planipennis* s'était développé. Les résultats indiquent que les inventaires pour la détection de *A. planipennis* dans les zones où plusieurs espèces de frênes sont présentes devraient se faire en fonction des préférences de l'insecte.
- Zusammenfassung.** Der Eschenbohrer (*Agrilus planipennis* Fairmaire), ein aus Asien stammendes Insekt, welches Phloem frisst, wurde 2002 als die Ursache von einem weitverbreiteten Eschensterben in Südwest-Michigan und Windsor, Ontario identifiziert. Es ist wenig Information über den Bohrer und sein natürliches Wirtsspektrum erhältlich und es ist nicht bekannt, ob dieses Schadinsekt eine Vorliebe für bestimmte amerikanische Eschen hat. Wir beobachteten die Populationsdichte des Insekts und den Zustand der Belaubung von Grünen und Weißen Eschen als Straßenbäume in vier Gemein-

den und auf Weißer und Blauer Esche an zwei Waldstandorten in Südost-Michigan. Die Grünen Eschen hatten wesentlich mehr Absterberscheinungen in der Krone und größere Schädlingspopulationen als die Weißen Eschen in der Nachbarschaft. Die Populationsstärke stieg um das zwei- bis vierfache bei beiden Arten in einer dreijährigen Periode. Das Kronenabsterben stieg linear von 2002 bis 2005, als die Populationen anstiegen ($R^2 = 0,70$). An den beiden Waldstandorten waren die Populationen auf den Weißen Eschen wesentlich höher als auf den Blauen Eschen. Spechte griffen an allen Standorten in das Geschehen ein und vertilgten 35 % der beobachteten Schadinsekten. Die Ergebnisse zeigen, dass Untersuchungen zum Vorkommen von *A. planipennis* in Gegenden mit vielen Eschenarten sich auf die bevorzugten Eschen konzentrieren sollten.

Resumen. El barrenador esmeralda del fresno (*Agrilus planipennis* Fairmaire) (Coleoptera: Buprestidae), un insecto que se alimenta del floema, nativo de Asia, fue identificado en 2002 como la causa de la mortalidad del fresno (*Fraxinus*) en el sureste de Michigan y Windsor, Ontario. Hay poca información disponible acerca de *A.*

planipennis en su rango nativo y no se conocía si esta plaga invasiva prefería una especie de fresno Norte americano en particular. Se monitoreó la condición de la copa y la densidad de *A. planipennis* en fresno verde (*F. pennsylvanica*) y fresno blanco (*F. americana*) en árboles de la calle en cuatro vecindarios y en fresno blanco y azul (*F. quadrangulata*) en dos lotes arbolados en el sureste de Michigan. Los árboles de fresno verde tuvieron significativamente más muerte regresiva de la copa y más alta densidad de *A. planipennis* que los fresnos blancos creciendo en el mismo vecindario. La densidad incrementó de 2 a 4 veces en ambas especies en un período de tres años. La muerte regresiva incrementó linealmente de 2002 a 2005 a medida que la densidad de *A. planipennis* incrementó ($R^2 = 0.70$). En cada uno de los lotes arbolados, las densidades de *A. planipennis* fueron significativamente más altas en fresnos blancos que en azules. La depredación del pájaro carpintero ocurrió en todos los sitios y contabilizó por 35% de *A. planipennis* desarrollado en los árboles que sobrevivieron. Los resultados indican que las encuestas para la detección de *A. planipennis* en áreas con múltiples especies de fresno deberán enfocarse a especies preferidas, relativamente.