Comparison of Male and Female Emerald Ash Borer (Coleoptera: Buprestidae) Responses to Phoebe Oil and (Z)-3-Hexenol Lures in Light Green Prism Traps

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ABSTRACT We conducted trapping experiments for the emerald ash borer, *Agrilus planipennis* Fairmaire (Coleoptera: Buprestidae) in Michigan, USA, and Ontario, Canada, to compare unbaited light green sticky prism traps with traps baited with phoebe oil, (Z)-3-hexenol (Z3-6:OH), or blends of other green leaf volatiles (GLVs) with Z3-6:OH. Traps were placed in the lower canopy of ash trees (*Fraxinus* spp.). Catches with Z3-6:OH–baited traps showed a significant male bias and these traps caught significantly more males than the unbaited controls at both sites. They were also superior to phoebe oil-baited traps and those baited with GLV blends. Catches with phoebe oil showed a significant female bias but there was no difference in the number of females captured between traps baited with phoebe oil or Z3-6:OH lures. Catches were analyzed at regular time intervals to examine the response of *A. planipennis* to the lures over the course of the flight season. Z3-6:OH–baited traps consistently caught more males than the controls at each interval throughout the flight season. Catches of females with Z3-6:OH and phoebe oil were significantly better than the controls early in the flight season but declined to control levels by midseason. Our results suggest that Z3-6:OH–baited green traps placed in the ash canopy would be a superior lure for detecting and monitoring *A. planipennis* throughout the flight season.

KEY WORDS (Z)-3-hexenol, phoebe oil, green prism traps, ash canopy, monitoring

The emerald ash borer, *Agrilus planipennis* Fairmaire (Coleoptera: Buprestidae), an alien invasive pest of ash trees (*Fraxinus* spp), was discovered in Detroit, MI, and Windsor, ON, Ontario, in 2002 (Haack et al. 2002). *A. planipennis* has radiated rapidly across eastern and central North America from this discovery point and currently infests some 14 U.S. states and two Canadian provinces (USDA–APHIS 2010). It has killed millions of host trees as it propagates. The estimated projected cost of the resulting ash mortality in urban areas of the United States over the next decade is in the $10 billion range (Kovacs et al. 2010). Despite considerable progress in developing effective trap designs and lures (Crook and Mastro 2010, Grant et al. 2010), detection of infestations at their earliest stage is still difficult and remains a high research priority. As a consequence, efforts continue toward developing and improving detection tools, particularly colored sticky traps and host attractant lures, for areawide surveys (Francese et al. 2005; Crook et al. 2008, 2009; de Groot et al. 2008; Francese et al. 2008; Crook and Mastro 2010; Grant et al. 2010; Marshall et al. 2010; USDA–APHIS 2010).

Early studies of trap design demonstrated that generally more *A. planipennis* beetles were caught in purple traps than in traps of other colors (Francese et al. 2005, 2008). Hence, purple was adopted as the standard trap color for monitoring *A. planipennis* (USDA–APHIS 2008, 2010). More recently, unbaited painted green prism traps located in the ash canopy were found to be highly attractive to *A. planipennis,* particularly males (Crook et al. 2009). The ash canopy is a logical position for *A. planipennis* survey traps because adults feed on foliage for a week or more before mating and continue to feed on foliage for the remainder of their lives (Bauer et al. 2004). They also mate and engage in short range flights in the canopy and tend to rest there at night (Lance et al. 2007; Rodriguez-Saona et al. 2007; Lelito et al. 2007, 2008).

Two types of ash volatiles from different parts of the tree and different biosynthetic pathways are attractive to *A. planipennis.* At least six sesquiterpenes emitted by bark of stressed ash trees are active in gas chromatography-electroantennogram detection (GC-EAD) bioassays (Crook et al. 2008). Lures composed of manuka oil or phoebe oil, essential oils from nonhost trees in New Zealand and Brazil, respectively, are sources of many of these sesquiterpenes and at a re-

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lease rate of 50 mg/d are attractive to *A. planipennis* in purple traps, particularly in the ash canopy (Crook et al. 2008, Marshall et al. 2010). Purple prism traps baited with manuka oil were used operationally as the standard monitoring trap for national areawide surveys of *A. planipennis* in the United States in 2008 (USDA–APHIS 2008), and an 80:20 blend of manuka oil and phoebe oil at a release rate of 50 mg/d was used in the 2009 survey (USDA–APHIS 2009). (Z)-3-Hexenol (Z3-6:OH) and other green leaf volatiles (GLVs) that are characteristic volatiles emitted by ash foliage also are GC-EAD active and attractive to *A. planipennis* in both purple and green prism traps (Poland et al. 2006, 2007; Rodriguez-Saona et al. 2006; de Groot et al. 2008; Grant et al. 2010). Catches in Z3-6:OH–baited green traps (7.6–80 mg/d) at the lower edge of the ash canopy were superior to those in comparable manuka oil-baited traps (50 mg/d) (Grant et al. 2010). Both males and females are attracted by Z3-6:OH, but the sex ratio in both baited purple and baited green traps is biased significantly in favor of males (de Groot et al. 2008, Grant et al. 2010).

No comparison has been made between traps baited with Z3-6:OH lures and phoebe oil lures. Phoebe oil, which contains the additional GC-EAD–active sesquiterpene component 7-epi-sesquithujene that is not found in manuka oil was reported to be a more effective lure than manuka oil in purple traps at 1.5 m (Crook et al. 2008). A more recent study by Marshall et al. (2010) showed no difference between these lures in purple canopy traps. The main objective of our study was to compare Z3-6:OH lures against phoebe oil lures in light green prism traps in the lower ash canopy in Ontario, Canada, and Michigan, USA. Although Z3-6:OH is highly attractive to *A. planipennis*, ash foliage also produces many other GC-EAD–active GLVs with potential behavioral effects (Rodriguez-Saona et al. 2006, de Groot et al. 2008). In particular, a four-component GLV lure blend consisting of Z3-6:OH, (*E*)-2-hexenol, (*E*)-2-hexenal, and hexanal was as attractive as manuka oil in purple traps at 1.5 m (Poland et al. 2007, Crook et al. 2008). Thus, we included this four-component GLV lure in our tests and a binary GLV lure composed of the alcohols Z3-6:OH and (*E*)-2-hexenol (E2-6:OH) to compare with the Z3-6:OH and phoebe oil lures. Finally, we examined differences in the responses of male and female *A. planipennis* to these lures at regular intervals over the course of the flight season. Examination of seasonal changes in *A. planipennis* responsiveness to lures may reveal useful behavioral information that could lead to improvement in monitoring.

Materials and Methods

Field Tests. Experiments were carried out in Ontario and Michigan in 2009. The Ontario experiment was conducted near Port Lambton in a 3.8-ha green ash, *Fraxinus pennsylvanica* Marsh, plantation used previously in 2008 (Grant et al. 2010). It was established in 1987 with some 5,600 trees spaced 1.8 m apart in rows ≈2.4 m apart. The infestation was estimated to be in its third–fifth year and at a moderate population level in 2009. Trees showed symptoms of attack such as a thinning canopy, epicormic shoots, and exit holes. We used light green sticky prism traps (Synergy Semiochemicals, Burnaby, BC, Canada). To make them more manageable when deployed in the canopy, we reduced their size (36 by 61 cm) by removing a 15-cm strip from one edge so that each face of the three-sided trap measured 36 cm wide by 46 cm tall (Grant et al. 2010). Traps were hung in the bottom edge of the canopy from wooden hangers attached to the tree boles ≈3 m above ground. The 2009 areawide *A. planipennis* survey recommend that traps be place in the lower (>1.5 m) to midcanopy of ash trees (USDA–APHIS 2009). Traps were spaced 15–20 m apart. There were four lure treatments and a blank control, with eight replicates per treatment. The five treatments, detailed in Table 1, consisted of 1) Z3-6:OH alone; 2) Z3-6:OH combined with E2-6:OH; 3) Z3-6:OH combined with E2-6:OH, (*E*)-2-hexenal, and hexanal; 4) phoebe oil; and 5) blank control. Traps were baited on 9 June in a randomized complete block design. Beetles were collected from traps on 7 July, 21 July, and 5 August when the experiment was terminated. Lures were not changed during the test.

The Michigan experiment was conducted at Legg Park in Okemos, Ingham County. The presence of woodpecker attacks and some epicormic shoots indicated a moderate level of *A. planipennis* infestation. The 41.7-ha park comprised wooded and open areas and ≈1 km of frontage along the south bank of the Red Cedar River. Traps were set up along the edge of the wooded areas that consisted of mature green ash and mixed hardwoods, including some oak (*Quercus*) and maple (*Acer*) species. Mature trees within the stand were >30 cm in diameter at breast height (dbh) and 9–12 m tall. Smaller edge trees (≈15–30 cm dbh, 6–8 m tall) were selected for hanging traps; traps were suspended with string from a major limb as high as possible (average, ≈5 m high). Traps were clearly visible on the outer limbs of trees along the edge of the stand.

The traps and lures used in Michigan differed slightly from those used in Ontario. Light green sticky prism traps (Great Lakes IPM, Vestaburg, MI) were not modified and panel faces measured 36 cm wide by 60 cm tall. The lure treatments in Michigan were similar to those in Ontario; however, GLV treatments two and three inadvertently had double the release rate of the two alcohols (Table 1; Fig. 1). Traps were baited with 10 replicates of each treatment on 5 June in a randomized complete block design. Beetles were collected weekly until 5 August when the experiment was terminated. Lures were not changed during the experiment.

Adult *A. planipennis* removed from traps were transferred to individually labeled vials containing Histo-Clear II solvent (National Diagnostics, Atlanta, GA) to help remove trap glue. The Histo-Clear was later replaced with 70% alcohol when the vials were returned to the laboratory. Beetles were sexed by examination of their genitalia or by the presence or absence of the

Table 1. Lure compounds, releaser devices, and release rates used as trap baits for *A. planipennis*

Location, treatment	Lure	Releaser device	Release rate (mg/d[a])	Source[b]
Ontario 1	(Z)-3-Hexenol	2 bubble caps	7.6	Contech Inc.
2	(Z)-3-Hexenol	1 bubble cap	3.8	Contech Inc.
	(E)-2-Hexenol	1 bubble cap	3.8	
3	(Z)-3-Hexenol	1 bubble cap	3.8	Contech Inc.
	(E)-2-Hexenol	1 bubble cap	3.8	
	(E)-2-Hexenal	1 bubble cap	13.0	
	Hexanal	1 bubble cap	13.0	
4	Phoebe oil	1 pouch	50	Synergy Semiochemicals
5	Control	blank		
Michigan 1	(Z)-3-Hexenol	2 bubble caps	7.6	Contech Inc.
2	(Z)-3-Hexenol	2 bubble caps	7.6	Contech Inc.
	(E)-2-Hexenol	2 bubble caps	7.6	
3	(Z)-3-Hexenol	2 bubble caps	7.6	Contech Inc.
	(E)-2-Hexenol	2 bubble cap	7.6	
	(E)-2-Hexenal	1 bubble cap	13.0	
	Hexanal	1 bubble cap	13.0	
4	Phoebe oil	1 pouch	50	Synergy Semiochemicals
5	Control	Blank		

[a] GLV release rates obtained at 20°C. At 30°C, the release rate of two Z3-6:OH bubble caps would be 34 mg/d. Rates determined by Contech Inc., Delta BC, Canada.
[b] Contech Inc., Delta BC, Canada.

characteristic patch of long hairs found on the underside of the head and thorax of males (Rodriguez-Saona et al. 2007).

Statistical Analysis. Catches of males and females were analyzed separately for each test. Data were transformed by $\log(x + 1)$ or square root $(x + 0.5)$ to normalize data and were analyzed as a randomized complete block design. We used prior knowledge and formed a series of planned (a priori) comparisons (contrasts) of our treatments, as in previous studies (de Groot et al. 2008, Grant et al. 2010). Differences among treatments of a priori interest were analyzed by the five nonorthogonal contrasts (Sokal and Rohlf 1981) listed in Fig. 1. Because these were nonorthogonal contrasts, we set the significance level at $P = 0.01$ for $\alpha = 0.05$ by using the Holm–Sidak method to

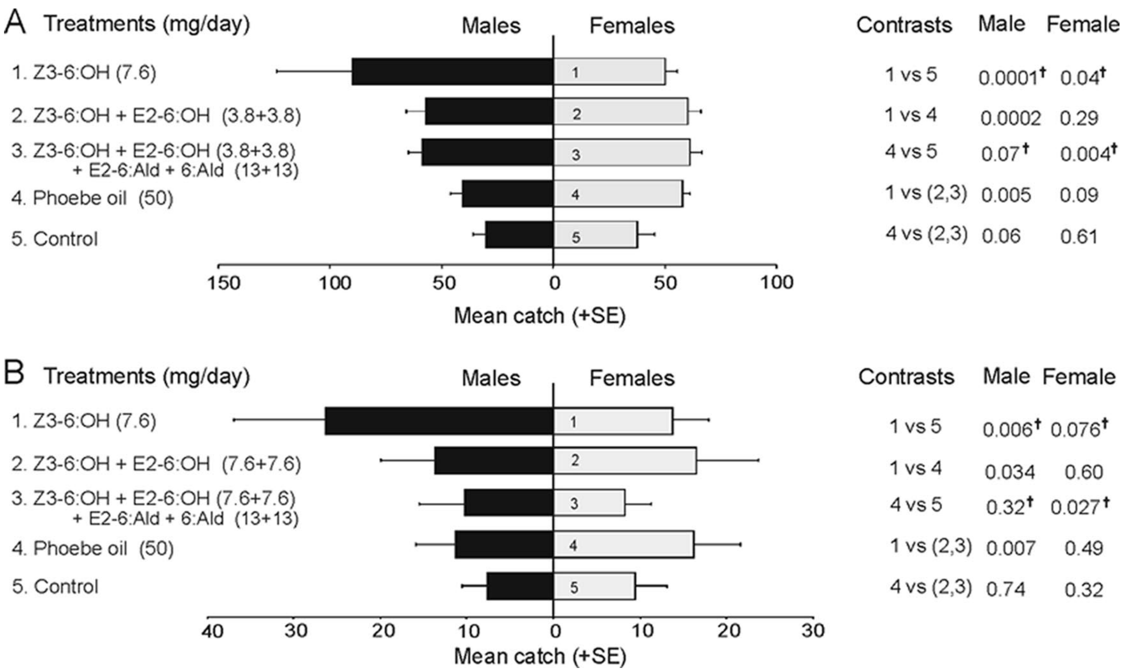

Fig. 1. Mean + SE catches of male and female *A. planipennis* in green prism traps baited with lure treatments 1–5 (see Table 1) in Ontario (A) and Michigan (B) in 2009. Data were analyzed by contrasts calculated independently for males and females. Contrasts are significant at $P \leq 0.01$ for all comparisons (see Materials and Methods). *P* values are two-tailed unless marked with the † symbol, indicating they are one-tailed. Abbreviations for chemicals are in the text.

Table 2. Ratio of male-to-female *A. planipennis* caught in light green traps baited with lures composed of host volatiles

Location, treatment[a]	Total catch	♂:♀ ratio	χ^{2b}	P
Ontario				
Z3-6:OH	1,121	1.79	89.1	<0.001
Z3-6:OH + E2-6OH	940	0.95	0.7	0.42
Z3-6:OH + E2-6:OH + E2:6:Ald + 6:Ald	960	0.96	0.4	0.53
Phoebe oil	788	0.71	23.1	<0.001
Control (blank)	542	0.79	6.9	0.009
Michigan				
Z3-6:OH	400	1.90	37.8	<0.001
Z3-6:OH + E2-6OH	302	0.82	2.8	0.10
Z3-6:OH + E2-6:OH + E2:6:Ald + 6:Ald	186	1.21	1.6	0.21
Phoebe oil	275	0.69	9.1	0.003
Control (blank)	172	0.79	2.2	0.15

[a] See Table 1 for abbreviations and ratios of lure components.
[b] Corrected for continuity; df = 1.

account for the number of nonindependent comparisons (Sokal and Rohlf 1981, Ruxton and Beauchamp 2008). Comparison of lure treatments with the control were one-sided tests, whereas comparisons of Z3-6:OH with phoebe oil or with the GLV blends were two-sided tests.

To compare how males and females responded to the Z3-6:OH and phoebe oil lures over the course of the flight season, we reanalyzed the total catch data for these two lures and the control, by using biweekly intervals for the Michigan data starting on 26 June. We used similar intervals for the Ontario data except that no reading was obtained for 26 June. The dates for intervals were chosen because they matched common dates when traps were visited and insects collected at the two sites. Catches by sex for each date and site were analyzed separately. Comparisons of lure treatments (i.e., Z3-6:OH versus control, phoebe oil versus control, and Z3-6:OH versus phoebe oil) were analyzed with contrasts. In this case, because there were only three comparisons we set $P = 0.017$ by using the Holm–Sidak method. All contrast analyses were carried out with Statistix 9 software (Analytical Software 2009).

Finally, sex ratios of the total trap catches were determined for each lure treatment. We used chi-square analysis on the VassarStats (2010) website to assess statistical significance of the observed sex ratios against a 1:1 male:female ratio ($P = 0.05$).

Results

Total Catches. Catches of *A. planipennis* in green prism traps hung in the ash canopy and baited with Z3-6:OH showed a strong male bias, whereas catches in the control traps showed a female bias (Table 2). The Z3-6:OH–baited traps caught 3.0- and 3.7-fold more males than the controls in Ontario and Michigan, respectively (Fig. 1A and B; contrasts 1 vs. 5). They also caught more males than phoebe oil in Ontario (contrast 1 vs. 4). Opposite to Z3-6:OH, catches with phoebe oil showed a significant female bias (Table 2), but there was no difference between Z3-6:OH and phoebe oil-baited traps for females at either site (contrasts 1 vs. 4). However, phoebe oil traps caught more females than the control traps in Ontario (contrast 4 vs. 5).

When catches of both sexes (i.e., total catches) were combined, Z3-6:OH–baited traps in Ontario caught more *A. planipennis* than phoebe oil traps ($P < 0.009$) and the controls ($P < 0.0001$), whereas phoebe oil catches were no better than the controls ($P = 0.024$). In Michigan, there were no differences in total catches among the treatments ($P > 0.01$).

Combining other GLVs with Z3-6:OH (i.e., the binary and four-component lure blends) substantially reduced catches of males compared with Z3-6:OH alone (contrasts 1 vs. 2, 3). There was no difference between these lures and phoebe oil (contrasts 4 vs. 2, 3). The sex ratios of the catches with these GLV blends did not differ from a 1:1 ratio (Table 2).

Catches at Biweekly Intervals. The pattern of *A. planipennis* catches by Z3-6:OH and phoebe oil lures at regular intervals over the flight season were similar in the two sites. The Z3-6:OH lure consistently provided significantly greater male catches than the controls for each date catches were counted during the entire flight season in both sites (Fig. 2A and B), and it provided numerically greater catches than phoebe oil for each trap reading, although these differences were generally not significant. The numbers of males caught in the phoebe oil-baited traps were also significant greater than in the controls throughout the trapping season for Ontario but not Michigan (Fig. 2A and B). These consistently greater male catches relative to the controls suggest that these lures retained their potency throughout the flight season. Catches of females with Z3-6:OH and phoebe oil were clearly greater than the controls in both sites but only in the early part of the flight season after which they declined to the level of the controls, particularly in Michigan.

Discussion

Development of an attractive combination of trap design and lure that provides consistent results is an important objective for development of an effective detection and monitoring tool for *A. planipennis.* Our results show that Z3-6:OH lures in light green prism traps placed in the lower edge of the canopy of ash trees were highly attractive to male *A. planipennis* and generally superior to traps baited with phoebe oil. Although phoebe oil in green canopy traps caught more females than males, there was little difference between it and Z3-6:OH for females. In a previous study comparing Z3-6:OH to manuka oil lures in green canopy traps, Z3-6:OH was the superior attractant for males, with no difference between the lures for females (Grant et al. 2010). As in the current study, males were attracted by Z3-6:OH lures over the entire flight season (G.G.G., unpublished data). Thus, Z3-6:OH–baited green traps have a strong, season-long effect on males in the ash canopy where adult *A.*

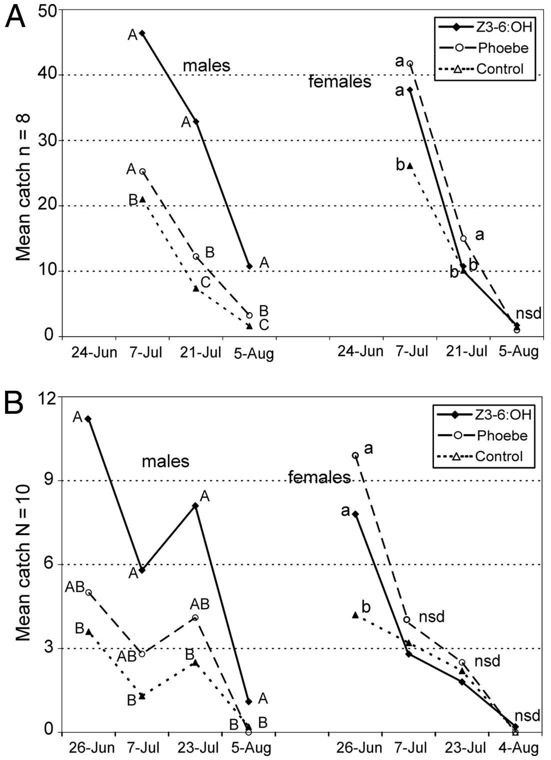

Fig. 2. Comparison of catches of male and female *A. planipennis* at regular intervals during the 2009 flight season in Ontario (A) and Michigan (B) in green prism traps baited with Z3-6:OH, phoebe oil, or blank control (data from Fig. 1). Dates selected to match comparable sampling intervals at both sites. No readings were available for 24 June in Ontario. Means were calculated independently for male and female catches and compared by contrast analysis. Means for each date marked with "nsd" or with the same letter (uppercase for males, lowercase for females) are not significantly different at $P > 0.017$ (error bars are omitted for visual clarity).

planipennis spend most of their time feeding on foliage, engaging in short flights, or mating.

Electroretinogram studies of the spectral sensitivity of *A. planipennis* showed that they are sensitive to light in the green range, with males having peak sensitivity between 540 and 560 nm and females having peak sensitivity at 540 nm (Crook et al. 2009). These peaks correspond to a 540-nm peak reflectance for sticky prism traps painted light green and a 545–555-nm reflectance peak for foliage of green ash. As a result, Crook et al. (2009) hypothesized that *A. planipennis* were attracted to green canopy traps because they provide a foliage-type visual stimulus that elicits food or host seeking behavior. Their unbaited green traps, particularly the dark green traps, positioned at mid-canopy preferentially caught male *A. planipennis.* In contrast, catches of *A. planipennis* in our unbaited light green traps, placed at the lower edge of the ash canopy, were biased in favor of females in both Ontario and Michigan. Hence, the behavioral effects of the Z3-6:OH lures on males observed in our study were caused substantially by the lures themselves and not the color of the traps. Indeed, Z3-6:OH lures in purple traps (at 1.5 m) are also preferentially attractive to males (de Groot et al. 2008, Grant et al. 2010). The strong behavioral effect of this lure on males is consistent with electroantennogram and GC-EAD bioassays that have shown that Z3-6:OH elicits an unusually large antennal response from males in contrast to that of females, and was by far the most stimulating of all the host foliage GLVs (Rodriguez-Saona et al. 2006, de Groot et al. 2008). de Groot et al. (2008) suggested that, in addition to any role foliage GLVs might play in host attraction, Z3-6:OH itself may provide an important sexual cue in conjunction with other chemical or visual stimuli to aid males in finding females.

Combining other EAD-active GLVs (E2-6:OH, E2-6:Ald, and 6:Ald) with Z3-6:OH did not enhance catches of either male or female *A. planipennis* in our study or in similar previous studies (de Groot et al. 2008, Grant et al. 2010). Thus, although the four-component GLV lure is attractive to *A. planipennis* in purple traps at 1.5 m (Poland et al. 2007, Crook et al. 2008), it was not as effective in green canopy traps as Z3-6:OH alone.

In summary, Z3-6:OH lures in light green prism traps placed in the lower ash canopy are superior to these traps baited with sesquiterpene-based lures (i.e., phoebe oil in this study and manuka oil in Grant et al. (2010)) and should be an effective tool for detection and monitoring *A. planipennis* infestations throughout the flight season. Recently, Marshall et al. (2010) reported that purple prism traps hung in the ash canopy and baited with manuka oil were significantly more attractive to *A. planipennis* than manuka oil-baited light green traps or unbaited green traps in the canopy (sex ratios of catches were not provided). Our previous study showed that Z3-6:OH–baited light green canopy traps hung in the ash canopy caught significantly more *A. planipennis* males than manuka oil-baited green traps (Grant et al. 2010). Thus, a comparison of Z3-6:OH–baited green traps in the ash canopy (possibly at lower and mid-canopy levels) with manuka oil-baited purple traps at the same levels should be pursued to evaluate their relative efficacy for males and females. If the two types of baited traps preferentially target different sexes, which seems likely because unbaited purple traps preferentially attract females (Francese et al. 2008, Crook et al. 2009), it may be advantageous to deploy both of these lure–trap combinations for detecting *A. planipennis* infestations. Operationally, however, this approach would be less convenient than an approach using a single combination of lure type and trap color. It is worth noting that manuka oil and phoebe oil are natural oils produced by steam distillation of nonhost trees; they vary in availability and in composition from batch to batch, and are relatively expensive. Z3-6:OH, however, has several advantages as a lure (Grant et al. 2010): it is a single, stable, and inexpensive compound that is readily available in high purity from many commercial sources. Thus a consistent standardized Z3-6:OH lure for detection and monitoring can be established easily. The most recent study of trap color has indicated that a dark green trap in the canopy is more attractive to *A. planipennis* males than the light green trap (Crook et al. 2009). Adding Z3-6:OH lures to a dark green trap may further improve trap sensitivity for *A. planipennis.*

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