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Sex Pheromone of the Baldcypress Leafroller (Lepidoptera: Tortricidae)

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ABSTRACT The baldcypress leafroller, *Archips goyerana* Kruse (Lepidoptera: Tortricidae), is a specialist on *Taxodium distichum* (L.) Richard and has caused serious defoliation in swamps of southeastern Louisiana, accelerating decline of baldcypress forests concurrently suffering from nutrient depletion, prolonged flooding, and saltwater intrusion. We investigated the composition of the sex pheromone of this species. Coupled gas chromatography–electroantennographic detection (GC-EAD) analyses indicated that male antennae were sensitive to four compounds [(Z)-11-tetradecenyl acetate (Z11-14:OAc), (*E*)-11-tetradecenyl acetate (*E*11-14:OAc), (Z)-9-tetradecenyl acetate (Z9-14:OAc), and (Z)-11-tetradecen-1-ol (Z11-14:OH)] present in female abdominal tip extracts in an approximately 100:1.5:0.6:10 ratio. In trapping trials performed in a cypress–tupelo swamp in southeastern Louisiana, moths were attracted to blends of these four components presented in approximately the female-produced ratios. Elimination of Z11-14:OH had no impact on moth response, whereas elimination of any of the three acetates strongly reduced or eliminated attraction. A blend in which the *E*11:Z11 ratio of 14:OAc was 5:100 was much less attractive than the same blend with the female produced ratio of 1.5:100. *A. goyerana* is closely related to the sympatric species *Archips argyrospilus* (Walker) with which it was previously synonymous. Our data revealed differences between the pheromone composition of *A. goyerana* and that reported for *A. argyrospilus*, which could account for the apparent absence of cross-attraction between these species. We conclude that a lure containing a 100:1.5:0.6 ratio of Z11-14:OAc, *E*11-14:OAc, and Z9-14:OAc has the potential to be used in traps to detect and measure *A. goyerana* populations and thereby monitor an important biotic factor contributing to the loss of coastal baldcypress forests.

KEY WORDS semiochemical, attractant, chemical ecology, mate location, wetland

Introduction

The baldcypress leafroller, *Archips goyerana* Kruse (Lepidoptera: Tortricidae), is a specialist on *Taxodium distichum* (L.) Richard and has caused extensive defoliation in Louisiana cypress forests experiencing the effects of environmental degradation (Goyer and Chambers 1996). It was initially detected in an outbreak that occurred in 1983 in and around the Atchafalaya Basin of southeastern Louisiana (Goyer and Lenhard 1988), and by 1993 it was causing defoliation within a 60,000-ha area stretching north to Baton Rouge, east to New Orleans, south to Terrebone Parish, and west to Point Coupee Parish (Goyer and Chambers 1996). In the last systematic survey conducted in 2006 (Goyer, R. A., unpublished data), 46,000 ha of mixed baldcypress forest in this region exhibited defoliation, with 32,000 ha having >50% foliage loss. This species has been collected in southeastern Louisiana and southwestern Mississippi, but not elsewhere in the distribution of baldcypress, which runs along the coastal plain from Delaware to Texas and inland north to Illinois. Repeated defoliation of Louisiana baldcypress has resulted in reductions in radial growth, crown dieback, and mortality, with the latter being largely restricted to smaller, understory trees (Goyer et al. 1990, Goyer and Chambers 1996). Damage by *A. goyerana* appears to be concentrated in forests affected by prolonged and intensive flooding attributable to sea level rise, land subsidence, and changes in hydrology caused by human activity (Goyer and Chambers 1996, Effler et al. 2006).

A. goyerana was initially identified as the fruittree leafroller, *A. argyrospilus* (Walker), whose range includes southern Louisiana but is known to use conifers as hosts only incidentally (Meeker and Goyer 1994). The two species are nearly indistinguishable morphologically (Kruse 2000). A study in which live females of each species were used as trap lures demonstrated that *A. goyerana* from Louisiana and *A. argyrospilus* from California were not cross-attractive and therefore differed in the composition of their sex pheromone

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(Goyer et al. 1995). Subsequently, a phylogenetic analysis of the *A. argyrospilus* species complex using cytochrome c oxidase subunit I haplotypes indicated that *A. goyerana* was monophyletic and that its sequence divergence from the rest of the complex was much greater than sequence divergence within the species (Kruse and Sperling 2001). These data along with evidence of differing host preferences and suitabilities precipitated publication of a formal description of *A. goyerana* as distinct from its sympatric sibling *A. argyrospilus* (Kruse 2000).

The purpose of this study was to determine the composition of the sex pheromone of *A. goyerana* and devise a lure for use in detection and population monitoring of this species. We used coupled gas chromatography–electroantennographic detection (GC-EAD) analysis of male antennae to isolate olfactory stimulants present in female pheromone gland extracts; these compounds were then identified and evaluated in differing combinations for their attractiveness to males in field trapping trials.

Materials and Methods

Female Abdominal Tip Extraction and Analysis. During the first 2 wk of May 2013 and 2014, pupae of *A. goyerana* were collected from low foliage of baldcypress growing along the banks of Blind River (30.10 N; 90.75 W) within Maurepas Swamp Wildlife Management Area and the shoreline of Lake Palourde (29.69 N, 91.11 W), both in southern Louisiana. Pupae were sexed by the morphology of the genital opening and then were housed individually in capped, vented plastic vials with a piece of moistened Kimwipe (Kimberly Clarke, Roswell, GA). Female vials were placed into an incubator with a photoperiod of 12:12 (L:D) h and coinciding 24°/21°C temperature cycle. For isolation of pheromone, abdominal tips were removed from adult females and extracted passively by steeping at room temperature for 15–30 min in a 100 -µl capacity conical vial containing 8–15 µl redistilled hexane per gland. Extractions occurred 2–3 d following eclosion and between the second and third hours of scotophase. Extracts were transferred to a clean vial and combined with an additional 10 µl of hexane rinsate from the extraction vial. Vials contained extracts of 2–6 females each, and were stored in a freezer at −60–−80°C. Initially male pupae were held in a refrigerator (~4°C for <3 wk) to delay eclosion until female extractions were completed. Afterwards, male pupae and emerged adults were maintained either in the incubator under the above conditions or kept on a bench-top exposed to an open window.

Gas chromatography–mass spectrometry (GC-MS) and GC-EAD analyses were performed with both a semi-polar phase HP-INNOwax (Agilent J&W, Santa Clara, CA; 60 m in length × 0.25 mm i.d. × 0.25 µm film) and a non-polar phase DB-5MS (Agilent J&W, 30 m in length × 0.25 mm i.d. × 0.25 µm film) column. The HP-INNOWax temperature program was 100°C for 1 min, then increased 6°C/min to 170°C and held for 6 min, then 5°C/min to 240°C and held for 10 min. The DB-5MS temperature program was 100°C for 1 min, and then 5°C/min to 250°C and held for 5 min. Approximately one female equivalent of extract was placed into a conical-tipped vial and concentrated passively to 2–3 µl prior to injection into the GC operating in splitless mode. GC-EAD analyses were performed using apparatus and methods described previously (Asaro et al. 2004). Antennal preparations consisted of a single antenna severed at both ends of the flagellum and mounted between two saline-filled $Ag/AgCl_2$ electrodes. The GC effluent was split 1:1 between the EAD and a flame-ionization detector (FID). Male moths used in GC-EAD analyses had eclosed in the previous four days.

Peaks in FID and total ion chromatogram traces were identified by comparing mass spectra and retention times to those of identified standards (from Bedoukian, Danbury, CT). Proportions among candidate pheromone components in extracts were calculated from peak integration area ratios of 82 amu single-ion chromatograms. These single ion chromatogram integration area ratios were adjusted with correction factors calculated by injecting standards in known proportions.

Synthetic Candidate Pheromone Components. Candidate pheromone components [(Z)-11-tetradecenyl acetate (Z11-14:OAc), (*E*)-11-tetradecenyl acetate (*E*11-14:OAc), (Z)-9-tetradecenyl acetate (Z9-14:OAc), and (Z)-11-tetradecen-1-ol (Z11-14:OH)] used to construct field lures were ≥95% pure according to the manufacturer's (Bedoukian) certificates of analysis. Each contained <1% of any of the other compounds as a contaminant except for Z11-14:OAc, which contained 5% *E*11-14:OAc, and *E*11-14:OAc, which contained 1.5% Z11-14:OAc. Contaminants other than these produced weak or no EAD responses. Preparative GC purification of the Bedoukian-supplied Z11-14:OAc was performed to reduce its *E*:Z ratio (5:100) to allow bioassay of lures with *E*11-14:OAc at and below its female-produced proportion to the Z isomer (1.5:100). The preparative GC was a Hewlett-Packard 5890 modified similarly as in Nojima et al. (2008). We injected 1.5 µl of a 20% (by volume) solution of Bedoukian Z11-14:OAc in hexane into this GC fitted with a megabore capillary column (HP-INNOWax, 30 m in length × 0.53 mm i.d. × 1 µm film thickness) and operating in splitless mode with the temperature program given above for the 0.25 mm i.d. HP-INNOWax column. Effluent eluting at the retention time of Z11-14:OAc was collected onto a dry ice-chilled, 20 cm length of deactivated 0.53 mm i.d. capillary column, and then extracted with 100 µl of hexane. Accumulated extracts from multiple GC runs were combined and evaporated under nitrogen to 2 ml. The *E*:Z ratio in this concentrate was less than 1:1000, as determined by GC, and the absolute concentration of Z11-14:OAc in hexane was estimated by analyzing an aliquot injected with a known quantity of Z9-14:OAc as an internal standard. Because of the small amounts of purified Z11-14:OAc generated by preparative GC, this material was used only in trapping trial 2.

Trapping Bioassays. Diamond-type sticky traps (Contech Inc., Victoria, British Columbia; part

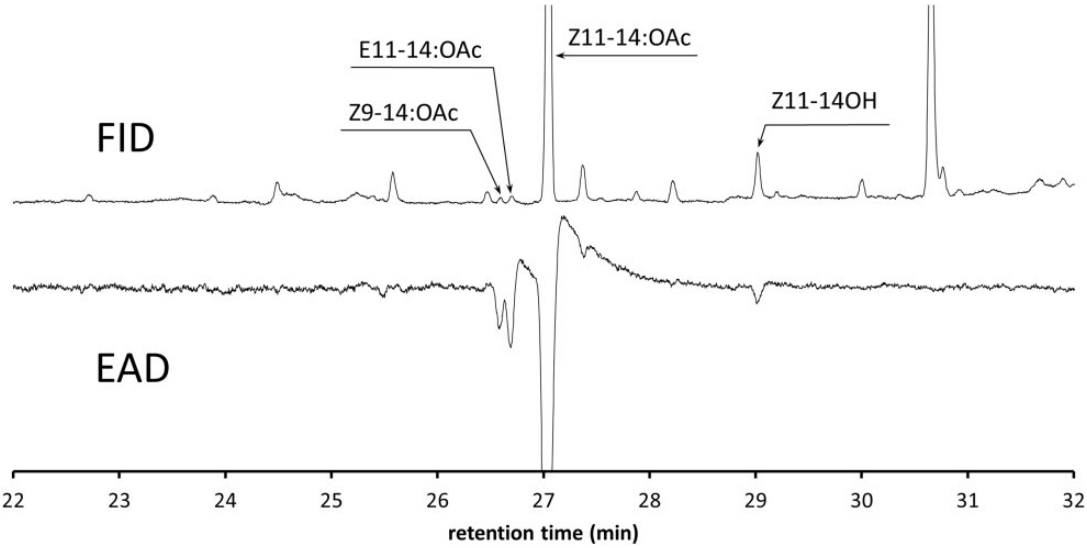

Fig. 1. Composite GC-EAD trace of runs with three different antennal preparations of male *A. goyerana*. The analyzed sample was a single insect equivalent of pooled hexane extract of female abdominal tips. FID peaks are labelled that consistently coincided with electrophysiological responses in male antennae. The average ratio among components Z11-14:OAc, *E*11-14:OAc, Z9-14:OAc, and Z11-14:OH detected in female abdominal tips was 100:1.5:0.6:10.

no. 100000178; deployed with bottom corners folded upward) were attached to low-hanging branches of baldcypress (or immediately adjacent branches of other trees) present along the shoreline of Blind River. These baldcypress were in clusters of three or more trees and nearly all had evidence of *A. goyerana* damage. Traps were in a single line following the river, positioned 1–2 m above the water surface, and spaced 30–100 m apart. Groups of consecutive traps equal in number to the treatments were considered complete blocks with treatments assigned randomly to traps within each block. Eight to nine complete blocks were deployed at one time and left in the field 5–7 d before trap recovery. Trap positions were re-used in successive tests. Lures consisted of red rubber septa (unextracted) to which 100 µl of hexane solution of candidate pheromone components were added. Final proportions of components used in lures were confirmed by GC-MS analysis. The solvent was allowed to evaporate completely prior to packaging of lures in foil bags for transport into the field. Lures were deployed within 2 d of preparation and inserted into the traps so that they rested against the inside bottom edge of the diamond; they were secured in place by the trap adhesive alone. Trapped moths were identified by size and wing scale pattern.

Trial 1 compared moth attraction to a four component blend of GC-EAD-identified candidate pheromone components (Z11-14:OAc, *E*11-14:OAc, Z9-14:OAc, and Z11-14:OH) either complete or with components removed. For this test, we utilized unpurified Z11-14:OAc (which contained 5% of the *E* isomer) as the only source of both *E* and Z11-14:OAc because this *E*:Z ratio somewhat exceeded that identified in female extracts (i.e., 5:100 vs 1.5:100). The remaining two candidate components (Z9-14:OAc and Z11-14:OH) were included in quantities that approximated their female-produced ratios to the predominant component Z11-14:OAc (i.e., 0.6:10:100). The quantities of each component added per lure were: 83 µg Z11-14:OAc, 4 µg *E*11-14:OAc (as contaminant), 0.51 µg Z9-14:OAc, and 8.5 µg Z11-14:OH. The combinations tested were 1) Z11-14:OAc, *E*11-14:OAc, Z9-14:OAc, and Z11-14:OH, 2) blend 1 less Z11-14:OH, 3) blend 1 less Z9-14:OAc, and 4) blend 1 less Z11-14:OAc and *E*11-14:OAc. The test was executed 30 April–7 May 2014.

Trial 2 tested the activity of *E*11-14:OAc within the four component blend. Combinations tested were 1) purified Z11-14:OAc (with <0.1% of the *E* isomer), Z9-14:OAc, and Z11-14:OH in approximately the female-produced ratios (100:0.6:10), 2) blend 1 plus *E*11-14:OAc at the female-produced *E*:Z ratio (i.e., 1.5:100; 0.70 µg *E*-isomer per lure), and 3) blend 1 with unpurified Z11-14:OAc (*E*:Z ratio 5:100; 1.8 µg *E*-isomer per lure) substituted for the purified material. The other quantities per lure were: 47 µg Z11-14:OAc, 0.30 µg Z9-14:OAc, and 5.2 µg Z11-14:OH. The test was executed 7–15 May 2014.

Trial 3 tested the activity of Z11-14:OAc (the predominant component) within the candidate pheromone blend. Z11-14:OH was eliminated from all lures as it failed to show activity in Trial 1. As in Trial 1, we utilized unpurified Z11-14:OAc (containing 5% of the *E* isomer) as the only source of the *E*-isomer in lure combinations that included the Z-isomer. The combinations tested were 1) Z11-14:OAc (83 µg/lure), *E*11-14:OAc (as contaminant; 4 µg per lure), and Z9-14:OAc (0.5 µg/lure), 2) *E*11-14:OAc (4 µg/lure) and Z9-14:OAc (0.5 µg/lure), and 3) blend 1 but with Z9-14:OAc at 1.7 µg per lure. Treatment 3 was intended to test whether increasing the quantity of Z9-14:OAc to

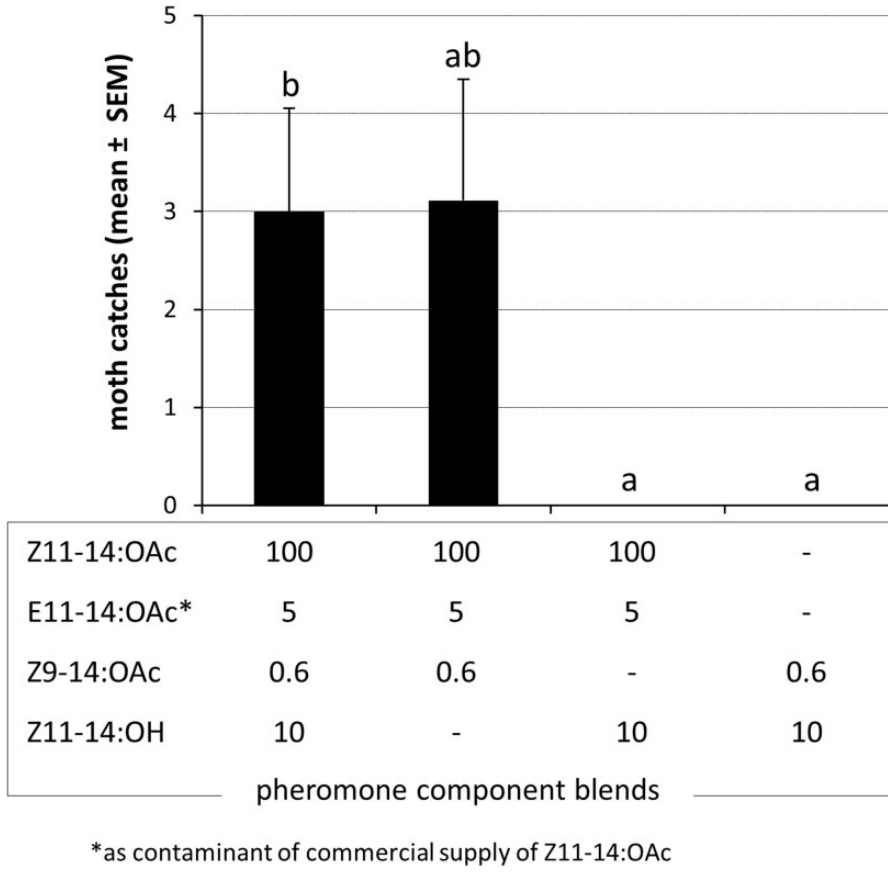

Fig. 2. Captures of male *A. goyerana* in adhesive traps baited with four female-produced, EAD-positive compounds presented either as a complete blend or with components removed. The mass proportion among compounds in the lure (a red rubber septum) is indicated in each column with 100 representing 83 μg. The ratios of minor components to the major component Z11-14OAc were identical to those produced by females except for *E*11-14:OAc, which was included in its proportion as contaminant in our commercially obtained supply of Z11-14OAc. Treatment means associated with the same letter did not differ significantly (see text for test description; $\alpha = 0.05$).

approximately match the *E*11-14:OAc to Z9-14:OAc ratio produced by females (i.e., a change from 5:0.6 to 5:2) might increase attraction to lures with the unnatural 5:100 *E*/Z ratio of the purchased Z11-14:OAc stock. The test was executed 15–20 May 2014.

Statistical Analysis. For all experiments catches of male moths were log-transformed as this normalized the residuals as determined by examination of residuals plots. Trials 2 and 3 were analyzed by analysis of variance (ANOVA; PROC GLM, SAS 9.3, Cary, NC) with model factors treatment and block, and then all pairwise comparisons were performed with a Tukey test ($\alpha = 0.05$). Two treatments in Trial 1 trapped no moths, and therefore these two treatments were dropped from the analysis and the ANOVA run as above to contrast the two treatments that did trap moths. This ANOVA provided estimated SEs that were then used for tests of whether catches by each of the two moth-catching treatments differed significantly from zero (ESTIMATE statement, SAS 9.3) with Bonferroni adjustment for experiment-wise error (i.e., *P*-values for *t*-tests were multiplied by six). A significant difference from zero was assumed to indicate a significant difference in catches from the zero-catching treatments (i.e., the zero-catch treatments were assumed to have a variance of zero).

Results

Female Abdominal Tip Extraction and Analysis. Extracts of abdominal tips of *A. goyerana* females contained four compounds (i.e., FID peaks) that in GC-EAD analyses elicited responses in multiple antennal preparations (i.e., in more than 5 of the 13 trials in which male antennae were exposed to a female extract). No other EAD deflections were both visibly greater than background noise levels and occurred more than twice at the same retention time. The recurring EAD deflections corresponded to FID peaks that were identified by mass spectral and retention time matches on two differing GC columns as Z11-14:OAc, *E*11-14:OAc, Z9-14:OAc, and Z11-14:OH (Fig. 1). Olfactory sensitivity to these compounds was confirmed

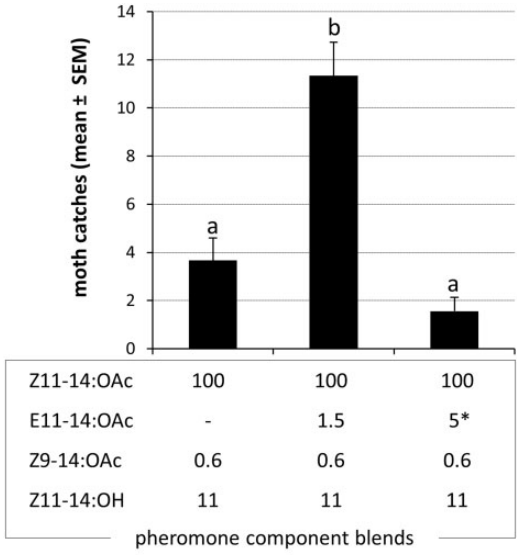

Fig. 3. Captures of male *A. goyerana* in adhesive traps baited uniformly with three female-produced, EAD-positive compounds and with a fourth, *E*11-14:OAc, either absent or present in one of two different proportions to the major component Z11-14:OAc. The mass ratios among compounds in each lure are indicated in each column with 100 representing 48 μg. The *E*/Z11-14:OAc ratio of 1.5:100 of the middle treatment represents the ratio produced by female moths, whereas 5:100 of the right-hand treatment was the ratio in our unpurified supply of commercially obtained Z11-14:OAc. The Z11-14OAc supply for the two left-hand treatments had been purified by preparative GC to remove the *E*-isomer. The ratios of both Z9-14:OAc and Z11-14:OH to Z11-14:OAc approximated those produced by females. Treatment means associated with the same letter did not differ significantly (Tukey test, log transformed data; $\alpha = 0.05$).

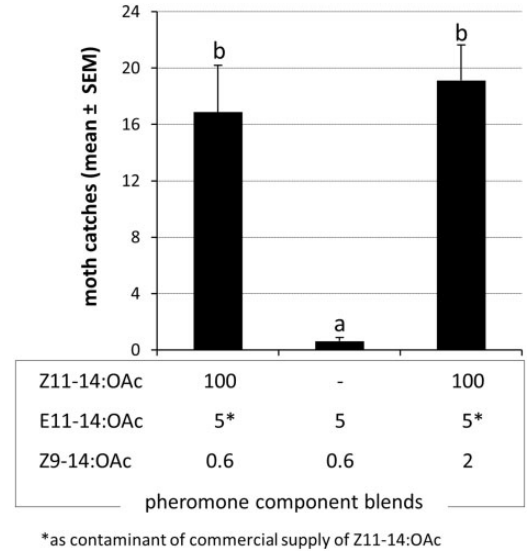

Fig. 4. Captures of male *A. goyerana* in adhesive traps baited with differing combinations of three female-produced, EAD-positive compounds. Z11-14:0H was eliminated from lure combinations in this test because of its apparent lack of activity in trapping Trial 1 (Fig. 2). The left-hand treatment included minor component Z9-14:OAc in its female-produced proportion to the major component Z11-14:OAc, whereas the right-hand treatment included Z9-14:OAc in its female-produced ratio to *E*11-14:OAc. The middle treatment tested removal of the major component Z11-14:OAc from the three component blend. Treatment means associated with the same letter did not differ significantly (Tukey test, log transformed data; $\alpha = 0.05$).

by means of GC-EAD analysis of a synthetic mixture of these four compounds in roughly equal concentrations, and we observed EAD deflections for all four synthetic compounds in at least three different antennal preparations. The EAD deflection voltage produced by the alcohol was conspicuously less than that produced by the acetates.

GC-MS analysis of four different samples composed each of 3-6 female abdominal tip extracts indicated a mean ratio among components Z11-14:OAc, *E*11-14:OAc, Z9-14:OAc, and Z11-14:OH of 100: 1.5 (1.1–1.9): 0.6 (0.3–0.7): 10 (4–17).

Trapping Bioassays. No females were trapped in any trial. In Trial 1, traps containing the blend of Z11-, *E*11-, and Z9-14:OAc, with or without Z11-14:OH, trapped a mean of approximately three males each, whereas lures that lacked Z9-14:OAc or both Z11- and *E*11-14:OAc trapped no moths (Fig. 2). The ANOVA with the zero-catching treatments dropped-out did not indicate a significant difference caused by removal of Z11-14:OH from the four component blend ($F = 0.07$; df = 1,8; $P = 0.79$), whereas removal of Z9-14:OAc or both Z11- and *E*11-14:OAc significantly reduced attraction (for both, $t = 3.53$; $P = 0.046$ after Bonferroni correction). In Trial 2, there was a significant treatment effect ($F = 22.2$; df = 2,16; $P < 0.001$). Traps with the four component lure containing the female-produced *E*11:Z11 ratio (1.5:100) of 14:OAc captured an average of approximately 11 moths, which was significantly more than traps with a somewhat higher ratio (5:100) or with *E*11-14:OAc absent (Fig. 3). These latter two treatments did not differ significantly. In Trial 3, there was also a significant treatment effect ($F = 84.5$; df = 2,14; $P < 0.001$). Removal of Z11-14:OAc from the trio of Z11-, *E*11-, and Z9-14:OAc (ratio of 100:5:0.6; mean ~17 moths per trap) significantly reduced attraction, whereas decreasing the *E*11:Z9 ratio of 14:OAc from 5:0.6 to 5:2 did not significantly alter attraction (Fig. 4).

Discussion

Our data indicate that *A. goyerana* females produce a pheromone consisting of at least three components, Z11-14:OAc, E11-14:OAc, and Z9-14:OAc, in the approximate proportion of 100:1.5:0.6. Elimination of any of the three components from lures significantly reduced male attraction. *A. goyerana* was first discovered in Louisiana baldcypress forests in 1983 (Goyer and Lenhard 1988) and initially was considered to be a host variant of *A. argyrospilus* (Goyer et al. 1990), a species that has been observed only rarely on conifers.

Phylogenetic analyses have confirmed that these two species are very closely related (Kruse and Sperling 2001). Extracts of female abdominal tips of *A. argyrospilus* contain the three pheromone components identified in *A. goyerana*, and all three compounds have been shown to influence attraction of *A. argyrospilus* males (Madsen et al. 1973, Roelofs et al. 1974, Cardé et al. 1977, Deland et al. 1993). We found a fourth compound, Z11-14:OH, in abdominal tip extracts of *A. goyerana* females that produced electrophysiological responses in male antennae but did not alter behavioral responses to the three-component blend. Z11-14:OH has likewise been identified in extracts of *A. argyrospilus* females and found to either enhance or reduce catches of males by attractive blends, and this response may vary geographically (Roelofs et al. 1974, Deland et al. 1993).

Despite sharing three pheromone components, *A. goyerana* and *A. argyrospilus* derived from populations in Louisiana and California, respectively, are apparently not cross-attractive (Goyer et al. 1995). One likely cause for the absence of cross-attraction is a disparity in the *E*/Z11-14:OAc ratio produced by these two species. We observed a ratio of 1–2:100 in *A. goyerana* females, whereas the ratios produced by *A. argyrospilus* sampled in British Columbia were found to be 64:100 and 67:100 (Roelofs et al. 1974, Deland et al. 1993). In addition, maximal attraction of *A. argyrospilus* is reported to occur at 43:100 and 67:100 in British Columbia and New York, respectively, and ratios below 12:100 were unattractive in New York (Roelofs et al. 1974, Cardé et al. 1977). In trapping trial 2, lures with an *E*/Z11-14:OAc ratio of 5:100 were significantly less attractive than lures with the *A. goyerana* female-produced ratio of 1.5:100, implying that the elevation of ratios of *E*/Z11-14:OAc above those produced by females reduced attraction of this species. The pheromone composition of *A. argyrospilus* in the sympatric zone with *A. goyerana* in Louisiana has not been investigated, and there is considerable regional variation in the pheromone of *A. argyrospilus* (Cardé et al. 1977, Kruse and Sperling 2001). However, if pheromone production and response of Louisiana *A. argyrospilus* resembles that of the New York or British Columbia populations, then this disparity in the *E*/Z11-14:OAc ratio could reduce or prevent cross attraction and provide a mechanism of reproductive isolation between sympatric populations of *A. argyrospilus* and *A. goyerana.* This hypothesis should be tested directly. Disparity in *E*/Z11-14:OAc ratios was proposed as a reproductive isolation mechanism between sympatric *A. argyrospilus* and *Archips mortuanus* Kearfoot in New York, as the latter species produced and was maximally attracted to lower ratios of *E*/Z11-14:OAc (Cardé et al. 1977).

The appearance of *A. goyerana* and its population outbreak during the 1980s and 1990s are likely a consequence of the weakening of defenses of baldcypress stressed by the more prolonged, extensive, and severe flooding of wetland forests of southern Louisiana during the past century (Souther and Shaffer 2000, Johnson et al. 2007). This flooding is due to land subsidence, sea level rise, and human activities (construction of levees, canals, and highway impoundments) that have changed the hydrology of these forests (Goyer and Chambers 1996). Furthermore, human-caused hydrological isolation of these forests from nutrient-rich Mississippi river sediments and resulting nutrient depletion is likely an additional stressing factor (Effler and Goyer 2006, Effler et al. 2006). Thus, the presence of *A. goyerana*, a species that was not noted prior to 1983, appears to be both a symptom and a causative factor of the general decline of wetland forests of Louisiana. Pheromone traps have been successfully used for monitoring population levels of and predicting outbreaks by tortricid forest pests (Grant 1991, Daterman et al. 2004, Nealis et al. 2010). Traps using the pheromone of *A. goyerana* may likewise be efficacious for monitoring population levels and potential range expansion of this insect, particularly when damage is below detectable levels and in areas that are difficult to access. Baldcypress frequently occur mixed with other species, and this can impede aerial surveys of defoliation caused by this insect. Baited traps may thus become valuable tools for detecting, evaluating, and monitoring an important factor in the decline of baldcypress forests.

Acknowledgments

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