

Mating Disruption of Citrus Leafminer Mediated by a Noncompetitive Mechanism at a Remarkably Low Pheromone Release Rate

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Abstract The citrus leafminer, *Phyllocnistis citrella* Stainton (Lepidoptera: Gracillariidae), is a worldwide pest of citrus. A season-long investigation was conducted that evaluated mating disruption for this pest. Effective disruption of the male *P. citrella* orientation to pheromone traps (98%) and reduced flush infestation by larvae was achieved for 221 d with two deployments of a 3:1 blend of (*Z,Z,E*)-7,11,13-hexadecatrienal/(*Z,Z*)-7,11-hexadecadienal at a remarkably low rate of 1.5 g active ingredient (AI)/ha per deployment. To gain insight into the mechanism that mediates the disruption of *P. citrella*, male moth catch was quantified in replicated plots of citrus treated with varying densities of pheromone dispensers. The densities of septum dispensers compared were: 0 (0/ha, 0.0 g AI/ha), 0.2 (one every fifth tree or 35/ha, 0.05 g AI/ha), 1 (215/ha, 0.29 g AI/ha), and 5 per tree (1,100/ha, 1.5 g AI/ha). Profile analysis by previously published mathematical methods matched predictions of noncompetitive mating disruption. Behavioral observations of male *P. citrella* in the field revealed that males did not approach mating disruption dispensers in any of the dispenser density treatments. The current report presents the first set of profile analyses combined with direct behavioral observations consistent with previously published theoretical predictions for a noncompetitive mechanism of mating disruption. The results suggest that disruption of *P. citrella*

should be effective even at high population densities given the density-independent nature of disruption for this species and the remarkably low rate of pheromone per hectare required for efficacy.

Keywords *Phyllocnistis citrella* · Mating disruption mechanisms · Desensitization · Camouflage · Competitive attraction · Citrus

Introduction

The citrus leafminer, *Phyllocnistis citrella* Stainton (Lepidoptera: Gracillariidae), originated from India (Stainton 1856) and is a major citrus pest throughout the world (Heppner 1993). It was first recorded in Florida in 1993 (Heppner 1993) and since has spread throughout the US Gulf Coast as well as to California (Gill 1999) and Hawaii (Nagamine and Heu 2003). Although this species infests all varieties of citrus, as well as other Rutaceae and certain ornamental plants, grapefruit, tangerine, and pumello are the preferred hosts (Legaspi and French 2003).

Mated female *P. citrella* oviposit on host leaves, and emerging larvae tunnel within young leaves to feed. Infestations greater than 16% leaf area damage reduce yield on “Tahiti” lime (Peña et al. 2000). Control of the leafminer with chemical sprays is often ineffective in Florida because of the prolonged and sporadic leaf flush (immature leaves as described by Hall and Albrigo 2007) influenced by frequent rain and the fact that larvae are concealed within feeding galleries. Consequently, to be effective, sprays need to be applied biweekly (Peña et al. 2002; Rogers and Stelinski, unpublished data).

The association of *P. citrella* with citrus bacterial canker, *Xanthomonas axonopodis* pv. *citri*, a major disease affect-

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ing citrus, is of greater importance than its impact as an herbivore. Infection by *X. axonopodis* results in defoliation, premature fruit drop, and general decline in tree quality (Graham et al. 2004). Although this disease is spread primarily by wind-driven rain, the serpentine-feeding galleries of *P. citrella* are easily colonized by the bacterium, and the resulting canker lesions generally are larger and more infectious than those formed without the benefit of *P. citrella* leaf injury (Graham et al. 2004; Gottwald et al. 2007).

In Japan, (Z,Z)-7,11-hexadecadienal (Z7Z11-16Ald) was reported as the behaviorally active sex pheromone (Mafi et al. 2005). Brazilian and US populations of *P. citrella* produce a 30:10:1 mixture of (Z,Z,E)-7,11,13-hexadecatrienal (Z7Z11E13-16Ald), Z7Z11-16Ald, and (Z)-7-hexadecenal (Leal et al. 2006; Moreira et al. 2006). However, a 3:1 blend of Z7Z11E13-16Ald/Z7Z11-16Ald is sufficient for eliciting the full complement of male sexual behaviors (Leal et al. 2006; Moreira et al. 2006) and is now being exploited in management programs for this pest (Lapointe et al. 2006; Stelinski and Rogers 2008).

Recently, two mathematical transformations of moth catch *versus* dispenser density data were developed to differentiate between competitive and noncompetitive mechanisms of mating disruption (Miller et al. 2006a,b). Competitive disruption occurs when males are attracted to the source of synthetic pheromone, while noncompetitive mechanisms, such as camouflage or sensory desensitization, by definition, do not require attraction to the synthetic pheromone source (Miller et al. 2006a). If competitive attraction occurs, then plotting 1 over male visitation rate to a given attractant source against dispenser density (on the *Y*- and *X*-axes, respectively, Miller–Gut plot) yields a straight line with a positive slope, while plotting male visitation rate to a given attractant source against dispenser density \times visitation rate (Miller–de Lame plot) results in a straight line with a negative slope (Miller et al. 2006a). In contrast, noncompetitive attraction predicts a characteristically concave Miller–Gut plot, as well as a recurved Miller–de Lame plot (Miller et al. 2006a). Post hoc analyses of 13 published mating disruption trials across a range of moth species were consistent with the hypothesis that competitive attraction is the mechanism that explains the majority of cases (Miller et al. 2006b).

The first objective of the current investigation was to evaluate the potential of using mating disruption as a management tactic for *P. citrella* in Florida citrus. The second was to gain insight into the behavioral mechanisms that underlie disruption of this species, which may help facilitate development of robust and economical management of *P. citrella* with pheromones. In addition, the current study was designed to test directly the predictions recently outlined by Miller et al. (2006a) by developing moth catch *versus* dispenser density profiles while concurrently observing moth behavior in the field.

Methods and Materials

Field plots The experiment was conducted in an 8-yr-old 10.2-ha orange grove (*Citrus sinensis* [L.] var. “Valencia”) in Clermont, FL, USA. Trees were planted on a 3 \times 6-m spacing, and the average canopy height was 4 m. The grove was managed by the University of Florida according to commercial pruning, irrigation, herbicide, and fungicide management practices but without the input of insecticides.

Dispenser Density Treatments and Experimental Design Disruption trials were conducted by comparing four application densities of red rubber septa (The West Company, Lionville, PA, USA): 0 (0/ha, 0.0 g active ingredient [AI]/ha), 0.2 (one every fifth tree or 35/ha, 0.05 g AI/ha), 1 (215/ha, 0.29 g AI/ha), and 5 (1,100/ha, 1.5 g AI/ha) per tree loaded with 1.0 mg of Z7Z11E13-16Ald and 0.33 mg of Z7Z11-16Ald (ISCA Technologies, Riverside, CA, USA). Pheromone components were greater than or equal to 98% pure by gas chromatographic analysis. The experiment was arranged as a randomized complete block design with five replicates, each consisted of a 30-tree (0.14 ha) plot of five rows of six trees. Replicate plots were separated by 40 m, and blocks of treatments were separated by 50 m. Rubber septum dispensers were affixed to foliage via metal paper clips on the edge of tree canopies approximately 2.0 m above ground level, which is the location of greatest male *P. citrella* activity within trees approximately 4 m tall (Stelinski and Rogers 2008). Treatments were applied on 4 April 2007 and renewed on 15 June 2007 so that the experiment could be conducted throughout the *P. citrella* seasonal flight.

Oriental Disruption Measurements Disruption of male *P. citrella* orientation was quantified by using two pheromone traps (LPD Scenturion Guardpost, Suterra, Bend, OR, USA) deployed within each replicate plot. One trap was placed in the central tree of each plot and the second on the inside border row two trees from the plot edge. All traps were baited with a single red rubber septum lure loaded with 0.1 mg of Z7Z11E13-16Ald and 0.03 mg of Z7Z11-16Ald as this has been shown to be highly effective for trapping male *P. citrella* in Florida (Stelinski and Rogers 2008). Monitoring traps were hung at least 1.0 m from the nearest mating disruption dispenser, at approximately 1.5–2 m above ground level in the midcanopy (Stelinski and Rogers 2008). Pheromone lures were replaced a total of four times or approximately every 7.5 wk throughout the season based on known longevity of attractiveness (Lapointe and Leal 2007). Moths captured in traps were counted and removed weekly.

Flush Infestation Damage to newly flushed leaves was assessed weekly 15 April through 28 October, 2007, except during the weeks of 16 July, 6 and 13 August, 10 and 17

September, and 15 October because of insufficient new flush on those dates. Twenty shoots, ten from the midcanopy (2.5 m) and ten from the lower canopy (1.0 m), were inspected at random from 20 trees per replicate block (2,000 flush samples per treatment), and the number of shoots per tree containing live mining *P. citrella* larvae was recorded.

Field Observations Male *P. citrella* behavior was studied in the field to test the prediction that male moths approach mating disruption dispensers in pheromone-treated plots, as other studies have reported male moths of various species orienting to, closely approaching, and even touching pheromone dispensers of a wide range of release rates in the field (Stelinski et al. 2004; Epstein et al. 2006). Observations of dispensers in tree canopies were conducted for approximately 2 hr each night between 21:00 and 23:00 hours, the period of greatest male *P. citrella* response (Stelinski and Rogers 2008), on eight nights between 24 August and 13 September and on five subsequent nights between 27 September and October 11. An observer rotated among plots conducting 20 min observational bouts per treatment such that multiple treatments were observed on a given night. The order of observations across treatments was randomized nightly.

In addition, male moth orientation to pheromone traps (as described above) was observed for 2-hr periods on four separate nights (14–22 September 2007) in control plots to verify that male *P. citrella* could be observed orienting to an attractive point source in the field. The number of moths observed orienting to such traps, as well as the number caught in traps under observation, was assessed. During the observations of both dispensers and traps, data were dictated into a hand-held microcassette audio recorder by an investigator standing 0.75 m from the pheromone source under observation. Observations after dusk employed night-vision goggles (Rigel, Model 3250, DeWitt, IA, USA) as described by Stelinski et al. (2004).

Profile Analyses Moth catch vs. dispenser density data were analyzed according to the profile analyses developed by Miller et al. (2006a,b). In addition to examining the untransformed data, two types of transformations were performed on male catch vs. dispenser density data: (1) 1 over male catch per trap per night on the y -axis was plotted against dispenser density on the x -axis (Miller–Gut plot), and (2) male catch per trap per night on the y -axis was plotted against dispenser density \times visitation rate on the x -axis (Miller–de Lame plot).

Trapping Evaluation of Pheromone Dispensers An experiment was conducted to compare the lure dose used to monitor the effect of disruption treatments (0.1 mg of Z7Z11E13-16Ald and 0.03 mg of Z7Z11-16Ald) with the dose used to induce mating disruption (1.0 mg of Z7Z11E13-16Ald and

0.33 mg of Z7Z11-16Ald). The objective was to determine whether the release rate of the pheromone from the mating disruption dispensers was attractive to *P. citrella* in pheromone-free air over the course of the mating disruption study. This test was conducted on 13 April through 1 November, 2007 in 4.0 ha of untreated plots of “Valencia” oranges. Fresh lures were installed every 7.5 wk into plastic delta traps. Unbaited delta traps were included as a negative control treatment. The experiment was arranged in a randomized complete block with five replicates. Traps, hung approximately 1.5–2 m above ground level in the upper third of the tree canopy, were spaced approximately 40 m apart within replicates, and replicate blocks were spaced by 60–70 m. Moths captured in traps were counted and removed weekly, at which time the position of traps was rotated.

Statistical Analyses For orientational disruption and trapping studies, data were transformed to $\ln(x+1)$ (which normalized the distributions) and then subjected to analysis of variance (ANOVA). Flush injury data were arcsine transformed prior to ANOVA. When significant ANOVAs were identified, differences among means were separated by using the least significant difference (LSD) test (SAS Institute 2000). In all cases, the significance level was $\alpha < 0.05$. Percent disruption was calculated as $1 - [(\text{mean moth catch per trap in the pheromone-treated block} / \text{mean moth catch per trap in the control block})] \times 100$.

Results

Moth Catches and Leaf Infestation Preliminary analysis revealed no significant difference in moth catch between traps placed at the centers and borders of plots. Thus, data from the two traps per plot were combined for subsequent analyses. Fewer ($F=29.3$, $df=3$, 16 , $P<0.001$) male *P. citrella* were captured in traps in plots treated with 1,100 dispensers per hectare (five dispensers per tree) than in any other treatment (Fig. 1a). This highest dispenser density treatment resulted in 98% disruption of moth catch in traps relative to untreated control plots over the season. There also was a significant reduction in male catch in traps placed in plots treated with 215 dispensers per hectare (69% disruption) compared with plots treated with 35 dispensers per hectare and untreated control plots; however, there was no difference in male catch between the latter two treatments (Fig. 1a).

There was a trend of declining infestation with increasing dispenser density with a significant reduction ($F=12.1$, $df=3$, 16 , $P<0.01$) in infestation of flush by both the 1,100- and 215-dispensers-per-hectare treatments relative to untreated plots (Fig. 1b), and the lowest infestation occurred

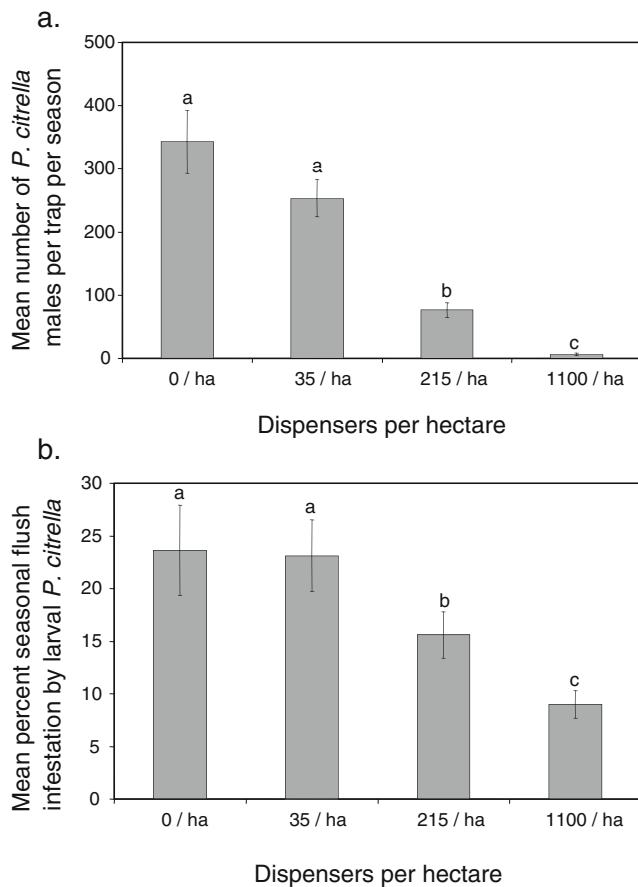


Fig. 1 Mean captures of male *Phyllocnistis citrella* in lure-baited delta traps in plots containing various densities of red septum dispensers of a 3:1 blend of Z7Z11E13-16Ald and Z7Z11-16Ald (**a**), Mean percent flush infestation by *P. citrella* larvae (**b**). Means followed by the same letter are not significantly different (AVOVA followed by LSD test at $\alpha < 0.05$)

in plots treated with 1,100 dispensers per hectare. Flush infestation in plots treated with 35 dispensers per hectare was not significantly different from control plots.

Field Observations No male *P. citrella* were observed orienting to rubber septum disruption dispensers in any of the treatments during 26 hr of observation. In contrast, in control plots, 17.0 ± 2.1 (mean \pm SE) males per night ($N=4$ nights) were observed orienting to baited monitoring traps, and 11.6 ± 0.9 males were captured.

Profile Analysis The untransformed plots of dispenser density (Fig. 2a), as well as both secondary transformation plots (Fig. 2b,c), were consistent with the predictions of mating disruption by a noncompetitive mechanism. The untransformed plot was initially linear (Fig. 2a), the Miller–Gut plot was concave (Fig. 2b), and the Miller–de Lame plot was re-curved (Fig. 2c). This set of traits is diagnostic of a noncompetitive mating disruption mechanism (Miller et al. 2006a).

Trapping Evaluation of Pheromone Dispensers In plots not under pheromone disruption, the number of male *P. citrella* captured per night in traps baited with the lower-loading monitoring lures (261.4 ± 18.2 , $X \pm \text{SEM}$) was significantly greater ($F=15.7$, $df=2, 8$, $P < 0.01$) than the number captured with those baited with higher-dose mating disruption dispensers (179.3 ± 16.9). Traps baited with both lure dosages captured significantly more moths over the course of the season than blank negative control traps (0.03 ± 0.01).

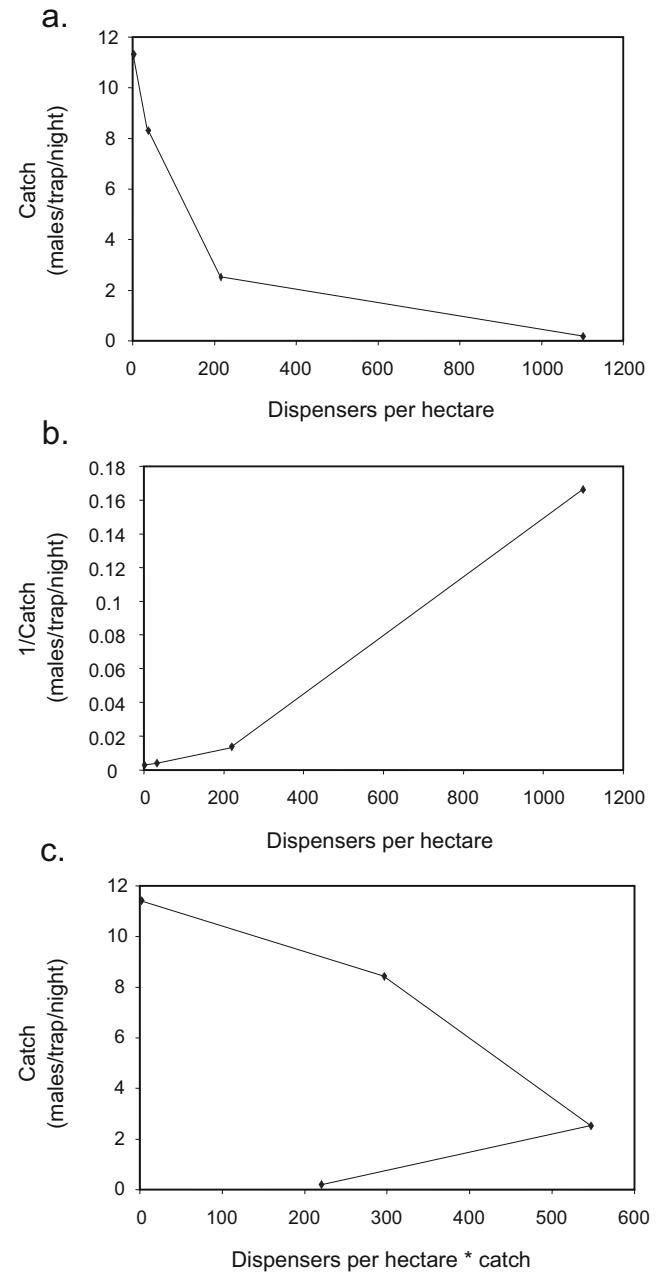


Fig. 2 Untransformed (**a**), Miller–Gut (**b**), and Miller–de Lame (**c**) plots of the disruption profile varying pheromone dispenser density for disruption of *P. citrella*

Discussion

Nearly complete disruption of *P. citrella* orientation to female-proxy-monitoring traps was achieved for 221 d with only two deployments of just 1.5 g AI/ha each. This would be sufficient for the season-long disruption of *P. citrella* males in Florida. Furthermore, nearly 70% disruption was achieved with only a 0.25-g/ha rate. The pheromone rate per hectare required for the disruption of *P. citrella* was well below 75–300 g of pheromone per hectare required for effective disruption of other species such as the Oriental fruit moth, *Grapholita molesta* (Rice and Kirsch 1990), the European grape moth, *Eupoecilia ambiguella* (Charmillot et al. 1987), the grape berry moth, *Paralobesia viteana* (Trimble et al. 1991), and the codling moth, *Cydia pomonella* (Howell et al. 1992). Ten grams of pheromone per hectare is one of the lowest effective rates for disruption of pink bollworm, *Pectinophora gossypiella*, when applied every 23 weeks as a microencapsulated sprayable formulation (Critchley et al. 1984). Short (2–3 wk) residual activity is characteristic of sprayable formulations in general (Gut et al. 2004). Effective disruption at a relatively low deployment rate (10 g of pheromone per hectare) was also achieved for a different leafmining species, the tomato pinworm (*Keiferia lycopersicella*; Jenkins et al. 1990). Thus, the low amount of pheromone required for effective season-long disruption of *P. citrella* is unique among moth species investigated to date and may be characteristic of Gracillariids and Gelechiids.

One of the objectives of this investigation was to test directly the predictions of Miller et al. (2006a,b) by conducting a disruption experiment where male moth catch in pheromone monitoring traps was quantified in plots with varying dispenser densities to differentiate between competitive and noncompetitive attraction. Furthermore, the outcomes of the theoretical predictions were compared with behavioral data collected directly in the field, thus providing evidence for a noncompetitive mechanism of disruption for *P. citrella* (Fig. 2a–c). As predicted, males did not approach mating disruption dispensers in any of the dispenser density treatments. Furthermore, we confirmed that male *P. citrella* could be observed orienting to attractive pheromone dispensers in plots not treated with pheromone. In addition, our trapping study confirmed that the dosage of pheromone loaded into the dispensers used as the mating disruption treatment attracts male *P. citrella* in control plots. These findings present a dilemma—how does a noncompetitive disruption profile arise from deployment of dispensers that, in a trapping study, were attractive? We speculate that the release rate of pheromone from the “disruptive dispensers” was well above normal but insufficient to preclude brief attraction events when such dispensers were sparse and hence rarely encountered. However, when these higher-dosage dispensers were packed together promoting numerous plume encoun-

ters, males enveloped in them for prolonged periods became desensitized and ceased plume following, or discrete plumes were enveloped within a miasma of background pheromone precluding orientation to an individual point source. Cessation of attraction under high dispenser density was supported both by the profile analysis and the failure to observe males arriving at dispensers in the disruption trials. Had attraction been a required first step mediating disruption of all males under these conditions, some males should have been observed approaching dispensers in pheromone-treated plots, and the profiles should have reflected competitive attraction. It appears that the disruption in this study was occurring mainly at some distance from the dispensers.

This reasoning raises the question of over what area each dispenser exerted a given effect. An examination of Fig. 2a reveals that approximately 100 dispensers per hectare were required to reduce male catch by 50% (11.5 to 5.7 males per trap per night). Since 1 ha=10,000 m², each dispenser can be calculated to have halved catch across approximately 100 m² of citrus grove (10,000 m² per 100 dispensers). If each dispenser had released all of its 1.33 mg of pheromone over the 14 weeks it was deployed, the average release rate per dispenser per hour would be 0.6 µg/hr, and the corresponding specific area for 1/2 trap suppression per microgram pheromone per hour would be 167 m². We suspect that this value underestimates pheromone specific activity for this study, because it is likely that pheromone load was not completely exhausted over the 14 wk of deployment, given that catch in traps was still being suppressed when the dispensers were replaced on 15 June. Nevertheless, this specific activity value for *P. citrella* pheromone is 40-fold higher than the 4 m/ µg pheromone/hr calculated to halve male catch of Oriental fruit moth based on the noncompetitive disruption profiles reported by Miller et al. (2006b).

Mating disruption could be an important contribution to *P. citrella* management programs in the USA and elsewhere. Spray programs for leafminers in citrus are often ineffective, require biweekly application given continual growth of new flush, and are detrimental to natural enemy populations of *P. citrella* and other citrus pests (Peña et al. 2002). In the current study, new flush infestation by larval *P. citrella* was reduced by more than half in the highest pheromone rate treatment, despite the small size of study plots (0.14 ha). It is well known that disruption outcomes are better in larger plots (see reviews by Gut et al. 2004; Witzgall et al. 2008), and thus, the current data suggest that the disruption of *P. citrella* should be effective on a larger scale. Furthermore, the control of this species by mating disruption should be density independent given the noncompetitive mechanism (Miller et al. 2006a,b). This bodes well for the development of commercial formulations that are economically feasible in the face of high *P. citrella* populations in Florida (Lapointe et al. 2006; Stelinski and Rogers 2008).

The primary challenge to developing a commercially viable mating disruption formulation for *P. citrella* is the complexity of the pheromone chemistry (Leal et al. 2006; Moreira et al. 2006), which currently renders the cost of synthesis economically prohibitive from a management perspective. Fortunately, little pheromone is required for effective disruption, and even lower rates of pheromone may prove effective for integrated programs that combine pheromone and reduced insecticide input. However, opportunities also exist to improve the economic feasibility of this pheromone technology if a less expensive synthesis protocol could be developed. In addition, even though it has been proven that a 3:1 blend of Z7Z11E13-16Ald/Z7Z11-16Ald is required for the attraction of *P. citrella* to traps (Leal et al. 2006; Moreira et al. 2006), the evidence for a noncompetitive mechanism of disruption, such as desensitization or camouflage, suggests that the diene or triene components alone might yield effective disruption. Indeed, Z7Z11-16Ald alone has been shown to effectively disrupt communication of *P. citrella* in Japan (Mafi et al. 2005). Finally, the large acreage of citrus in Florida will demand mechanical application for economic feasibility; therefore, long-lasting formulations amendable to mechanical application should be explored (Stelinski et al. 2007).

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