Captures of two leafroller moth species (Lepidoptera: Tortricidae) in traps baited with varying dosages of pheromone lures or commercial mating-disruption dispensers in untreated and pheromone-treated orchard plots

L.L. Stelinski,[1,2] J.R. Miller, L.J. Gut

Department of Entomology, Michigan State University, East Lansing, Michigan 48824,
United States of America

Abstract—A 2-year study conducted in 0.6-ha apple (*Malus domestica* Borkh.) blocks examined the effects of treatment with pheromone rope dispensers on captures of the obliquebanded leafroller, *Choristoneura rosaceana* (Harris, 1841), and the redbanded leafroller, *Argyrotaenia velutinana* (Walker, 1863), in traps baited with varying dosages of pheromone lures or Isomate®-OBLR/PLR Plus pheromone rope dispensers. In untreated blocks, captures of male *A. velutinana* were high and did not differ among (*i*) traps baited with a standard lure loading used to monitor this pest, (*ii*) lure loadings 10 and 100 times the standard loading, and (*iii*) traps baited with an Isomate-OBLR/PLR Plus pheromone rope dispenser. In pheromone-treated blocks, captures of *A. velutinana* in traps were reduced 94%–99% for all loadings tested (up to 1000 times the standard loading). The results for *C. rosaceana* were different. In untreated blocks in 2002, traps baited with 10 or 30 standard lures captured significantly more *C. rosaceana* than traps baited with a single standard lure; however, in 2003, traps baited with the standard lure loading captured significantly more moths than traps baited with 100 and 1000 times the standard loading. Also, traps baited with Isomate-OBLR/PLR Plus pheromone rope dispensers captured significantly fewer *C. rosaceana* than traps with standard lures in untreated blocks. In pheromone-treated blocks, traps baited with standard monitoring lures and lures with higher loadings (10 and 1000 times the standard) captured equivalent numbers of *C. rosaceana*; the capture of moths was reduced by only 50%–71%. We conclude that Isomate-OBLR/PLR Plus pheromone rope dispensers deployed in Michigan, United States of America, are effective in disrupting orientation of *A. velutinana*; however, they are not very effective for *C. rosaceana*. In addition, increasing lure loading above that of 1× monitoring lures (rubber septa or membrane type) does not appear to reliably increase the effectiveness of monitoring of males of either leafroller species in orchards where pheromone ropes are deployed at recommended densities.

Résumé—Une étude de 2 ans dans des parcelles de 0,6 ha de pommeraies (*Malus domestica* Borkh.) a permis d'évaluer les effets d'un traitement avec des diffuseurs de phéromone en corde sur les captures de la tordeuse à bandes obliques, *Choristoneura rosaceana* (Harris, 1841), et de la tordeuse à bandes rouges, *Argyrotaenia velutinana* (Walker, 1863), dans des pièges munis de doses diverses d'appâts de phéromone ou de diffuseurs en corde de la phéromone Isomate®-OBLR/PLR Plus. Dans les parcelles non traitées, les captures d'*A. velutinana* mâles sont élevées et elles ne varient pas entre (*i*) les pièges munis d'un appât couramment utilisé pour surveiller le ravageur, (*ii*) les pièges chargés de 10 et 100 fois l'appât standard et (*iii*) les pièges munis d'un diffuseur en corde d'Isomate-OBLR/PLR Plus. Dans les parcelles traitées à la phéromone, les captures ont été réduites de 94 % – 96 % pour toutes les doses utilisées, y compris une dose de 1000 fois la dose standard. Les résultats chez *C. rosaceana* sont différents. En 2002, dans les parcelles non traitées, les pièges garnis de 10 ou 30 appâts standard ont capturé significativement plus de *C. rosaceana* que les pièges avec un seul appât. En 2003, cependant, les pièges munis de la dose standard ont capturé significativement plus de papillons que les pièges garnis de doses 100 ou 1000 fois la dose standard. De plus, dans les parcelles non traitées, les pièges munis de diffuseurs de la

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phéromone Isomate-OBLR/PLR Plus ont capturé significativement moins de *C. roseaceana* que les pièges munis d'appâts standard. Dans les parcelles traitées à la phéromone, les pièges munis d'appâts standard de surveillance et les pièges garnis de doses 10 et 1000 fois la valeur standard ont capturé des nombres équivalents de *C. rosaceana*; les captures de papillons ont été réduites de seulement 50 % – 71 %. Nous concluons que les cordes garnies de phéromone Isomate-OBLR/PLR Plus perturbent effectivement l'orientation d'*A. velutinana*, mais pas celle de *C. rosaceana*. De plus, l'augmentation des doses des appâts (avec septum de caoutchouc ou membrane) au-dessus de la valeur standard (1×) pour l'observation ne semble pas augmenter de façon fiable l'efficacité de la surveillance des mâles chez ni l'une ni l'autre des espèces de tordeuses dans les vergers où on a posé des cordes de phéromone aux densités recommandées.

[Traduit par la Rédaction]

Introduction

The obliquebanded leafroller, *Choristoneura rosaceana* (Harris, 1841) (Lepidoptera: Tortricidae), is native to North America and is widely distributed from British Columbia to Nova Scotia and south to Florida (Chapman *et al.* 1968). *Choristoneura rosaceana* has an extremely wide host range; however, the preferred hosts are woody plants including Rosaceae species. *Choristoneura rosaceana* is an important pest of pome fruits in North America. The redbanded leafroller, *Argyrotaenia velutinana* (Walker, 1863) (Lepidoptera: Tortricidae), is sympatric with *C. rosaceana* and native to temperate eastern North America (Chapman 1973). This species also has a broad host range. It feeds on leaves of diverse plant species except conifers. The larvae feed on many unrelated plants, including most common fruits, vegetables, weeds, flowers, ornamentals, and shrubs (Hull *et al.* 1995). *Argyrotaenia velutinana* prefers apples over other fruits and commonly occurs in the apple-growing areas of the midwestern and eastern United States and eastern and western Canada (Howitt 1993; Hull *et al.* 1995).

The pheromone blends of *C. rosaceana* and *A. velutinana* have the same major components: (*Z*)-11-tetradecenyl acetate (*Z*11-14:Ac) and (*E*)-11-tetradecenyl acetate (*E*11-14:Ac) in a ratio of 98:2 for *C. rosaceana* and 93:7 for *A. velutinana* (Roelofs and Arn 1968; Roelofs and Tette 1970; Roelofs *et al.* 1975; Cardé and Roelofs 1977; Hill and Roelofs 1979). Efforts to disrupt mating of *A. velutinana* using synthetic pheromones have been judged successful (Novak *et al.* 1978; Roelofs and Novak 1981; Cardé and Minks 1995). In contrast, less successful mating disruption has been documented for *C. rosaceana* in New York using single-pheromone-component dispensers (Reissig *et al.* 1978) as well as more complex three-component blends (Agnello *et al.* 1996; Lawson *et al.* 1996).

We continue to investigate the reasons underlying differences in susceptibility to mating disruption between these two sympatric leafroller species. Recent studies with leafroller moths revealed species-specific expression and duration of long-lasting peripheral adaptation following exposure to pheromone dispensers used in mating disruption (Stelinski *et al.* 2003*a*, 2003*b*). This adaptation was expressed in *C. rosaceana* caged within a few centimetres of pheromone dispensers but was not present in *A. velutinana*. Furthermore, in behavioral studies in a flight tunnel, *C. rosaceana* became more responsive to low-release lures containing an attractive synthetic blend of pheromone components 24 h after brief exposure to pheromone, whereas *A. velutinana* became more responsive to high-release, off-blend rope dispensers 24 h after brief exposure to pheromone (Stelinski *et al.* 2004*a*).

The objectives of the current study were to (*i*) determine the effectiveness of Isomate®-OBLR/PLR Plus rope dispensers for disrupting orientation of *A. velutinana* and *C. rosaceana* to synthetically baited pheromone traps in Michigan, (*ii*) compare lure dosage versus moth capture relationships for both species in pheromone-treated and untreated orchards to identify possible lure loadings that may permit monitoring of male activity of both species in pheromone-treated orchards, and (*iii*) investigate the attractiveness of Isomate-OBLR/PLR Plus pheromone rope dispensers deployed in delta-style monitoring traps relative to monitoring lures releasing highly attractive synthetic blends of pheromone.

Materials and methods

General methods for field study

This experiment was carried out at the Trevor Nichols Research Complex of Michigan State University in Fennville, Michigan, during the summers of 2002 and 2003. Experiments were conducted within plots of 12- and 18-year-old apple (*Malus domestica* Borkh.) trees (*M. domestica* 'Rome' and 'Delicious', respectively), both with canopy heights of approximately 2–3 m. Trees were planted 3 m apart within rows and 6 m apart between rows. Pheromone-treated plots were established at the beginning of the season by applying Isomate-OBLR/PLR Plus pheromone rope dispensers (Pacific Biocontrol Co., Vancouver, Washington) containing 274 mg of pheromone (93.4% Z11-14:Ac, 5.1% E11-14:Ac, and 1.5% (Z)-9-tetradecenyl acetate (Z9-14:Ac)). Ropes were applied at a density of 500 dispensers/ha.

In 2002, the monitoring lures (1×) used for *A. velutinana* were red rubber septa (The West Company, Linville, Pennsylvania) loaded with 0.93 mg of Z11-14:Ac, 0.07 mg of E11-14:Ac, and 2.0 mg of dodecyl acetate (12:Ac) (Roelofs *et al.* 1975; Cardé and Roelofs 1977). For *C. rosaceana*, identical rubber septa were loaded with 0.485 mg of Z11-14:Ac, 0.015 mg of E11-14:Ac, and 0.026 mg of (Z)-11-tetradecen-1-ol (Z11-14:OH) (Hill and Roelofs 1979). Pheromone blend solutions were prepared in HPLC-grade hexane and stored at –8 °C. All pheromone lures were deployed in Scenturion Guardpost LPD traps (delta-style trap with 20 cm × 19 cm sticky trapping surface, Suterra, Bend, Oregon).

2002 tests

The experimental design was a split-plot. Either orientational disruption using rope dispensers at the density described above or no disruption was applied to whole plots (0.6 ha) at random. There were three replicates of the two whole-plot factors applied to 0.6-ha apple blocks (*i.e.*, three whole plots were treated with pheromone and three were not treated). Each whole plot contained five levels of the subplot factor. These levels were different loadings of the optimally attractive blends of each species' pheromone, achieved by varying the number of rubber septum lures placed inside traps. The subplot factor levels were (1) unbaited traps (control), (2) traps baited with one rubber septum containing 1/10 of the standard (1×) loading described above, (3) traps baited with 1 standard (1×) rubber septum, (4) traps baited with 10 standard (1×) rubber septa, and (5) traps baited with 30 standard (1×) rubber septa. Four subsamples (traps) of each of the five subplot levels (lure loadings) were placed in each whole plot. Rubber septa were affixed to the roofs of traps by pinning them to the traps' plastic surface. In cases where multiple septa were affixed to traps, septa were tightly clustered (in direct contact with each other) in rows of 10. Neither the area of the sticky trapping surface nor the trap openings were affected by the presence of rubber septa. Although pheromone dispenser surface area differed between traps containing 1, 10, and 30 rubber septa, the large-scale structure of pheromone plumes emanating from such traps was likely similar because the overall size of the trap, rather than that of the pheromone dispenser within the trap, determines the large-scale structure of the plume released from the odor source (Murlis *et al.* 1992).

All traps were hung in trees approximately 1.5–2 m above ground in the upper third of the tree canopy. Species-specific traps within whole plots were spaced 20 m apart (five traps per 120 m long row of trees). Trap placement for each species was alternated between rows, resulting in at least 12 m between traps for *C. rosaceana* and *A. velutinana*. Five rows were used for each species within each plot. Pairs of pheromone-treated and untreated whole plots were separated by at least 85 m. Moths captured in traps were counted and removed twice weekly. Lures were replaced at the onset of each moth generation.

2003 tests

As in 2002, the experiment was arranged in a split-plot design with presence or absence of pheromone disruption using rope dispensers as the whole-plot factor and lure loading in pheromone traps as the subplot factor. Pheromone treatment was randomly applied to whole plots. Each whole plot contained six levels of the subplot factor. The subplot factor levels included four loadings of the optimally attractive pheromone blends of each species, as described previously, in decadal steps ranging from 1× to 1000×. The final two subplot levels were unbaited traps (control) and traps baited with a single Isomate-OBLR/PLR Plus rope.

There were four replicates of the two whole-plot factors applied to 0.6-ha apple blocks (*i.e.*, four whole plots were treated with pheromone and four were not treated). One set of each of the six subplot levels was placed in each whole plot.

We elected to test higher loadings in 2003 because it appeared that maximal captures were not achieved with the highest dosages tested in 2002 (see Fig. 1). The 1× monitoring lures for *A. velutinana* were plastic membrane lures loaded with 0.93 mg of Z11-14:Ac, 0.07 mg of *E*11-14:Ac, and 2.0 mg of 12:Ac (BioLure, Suterra). The 1× membrane lures for *C. rosaceana* were loaded with 0.485 mg of Z11-14:Ac, 0.015 mg of *E*11-14:Ac, and 0.026 mg of Z11-14:OH. For the 10× and 100× treatments, the amounts of the various pheromone components were multiplied appropriately and loaded into lures. These lures were custom manufactured by Suterra. All pheromone lures were deployed in the traps described above; the 1000× treatment was achieved by placing ten 100× lures in a single trap. All lures were affixed to the roofs of traps with adhesive tape. We elected to use membrane lures in 2003 rather than vary the numbers of rubber septa in traps, as was done in 2002, to achieve higher loadings and to minimize the effects of volume changes of the pheromone-release apparatus on the dispersion pattern of the pheromone plume.

All traps were hung in trees approximately 1.5–2 m above ground in the upper third of the tree canopy. Traps within whole plots were spaced at least 20 m apart as described above. Traps were checked twice per week, at which point all moths were counted and removed. Lures were replaced at the onset of each moth generation.

Data analysis

Comparisons of mean moth captures in traps between loading of pheromone in lures were made with a split-plot analysis of variance and Fisher's protected least significant difference multiple comparison procedure (SAS Institute Inc. 2000). Because no males were attracted to unbaited (control) traps, these data were excluded from the analysis. Data were square-root transformed $((x + 0.5)^{1/2})$ before analysis. In all cases, the significance level was $\alpha < 0.05$.

Results

2002 field trials for *C. rosaceana* using rubber septum lures

There was a significant effect of both the whole-plot factor (application of ropes) ($F_{1,29} = 10.1$, $P < 0.05$) and the subplot factor (lure dosage) ($F_{4,29} = 58.1$, $P < 0.001$) on captures of *C. rosaceana*. In addition, there was a significant interaction between the application of pheromone disruption ropes and lure dosage in traps on captures of *C. rosaceana* ($F_{4,29} = 4.6$, $P < 0.001$).

Within the subplot factor, significantly more male *C. rosaceana* were captured in traps baited with 0.1×, 1×, 10×, and 30× lure dosages under no pheromone disruption than under disruption (Fig. 1A).

Within the whole-plot factor, significantly more male *C. rosaceana* were captured in traps baited with 10× or 30× lure dosages than in traps baited with 0.1× or 1× dosages, with or without pheromone disruption (Fig. 1A). Significantly more male *C. rosaceana* were captured in traps baited with 1× lures than in traps baited with 0.1× lures in both untreated and pheromone-treated plots (Fig. 1A).
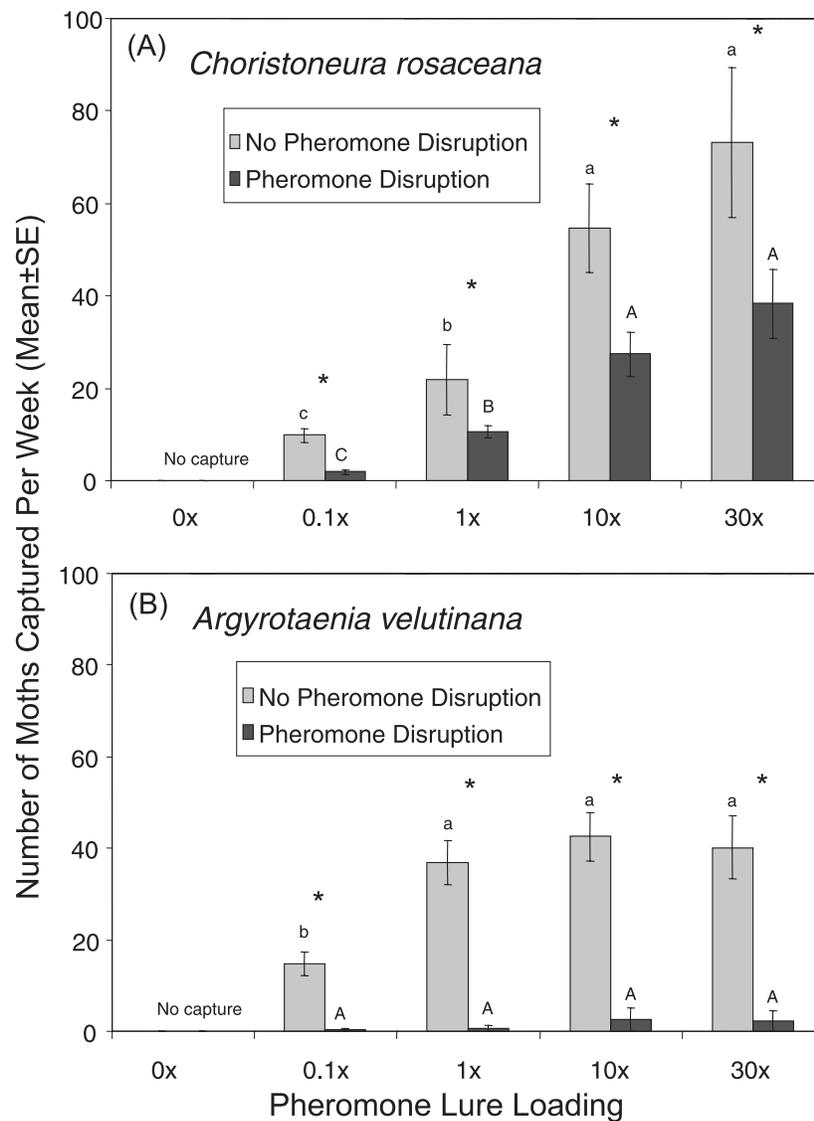
2002 field trials for *A. velutinana* using rubber septum lures

There was a significant effect of both the whole-plot factor (application of ropes) ($F_{1,23} = 82.7$, $P < 0.001$) and the subplot factor (lure dosage) ($F_{3,23} = 5.9$, $P < 0.001$) on captures of *A. velutinana*. In addition, there was a significant interaction between application of pheromone disruption ropes and lure dosage in traps on captures of *A. velutinana* ($F_{3,23} = 4.4$, $P < 0.01$).

Within the subplot factor, significantly more male *A. velutinana* were captured in traps baited with 0.1×, 1×, 10×, and 30× lure dosages under no pheromone disruption than under disruption (Fig. 1B).

Within the whole-plot factor, there were no differences between numbers of male *A. velutinana* captured in traps baited with 1×, 10×, or 30× loadings under no pheromone disruption (Fig. 1B). However, traps with 1×, 10×, or 30× loadings captured significantly more *A. velutinana* than traps baited with the 0.1× dosage in the untreated plots (Fig. 1B). Very few *A. velutinana* were captured with any of the lure loadings under disruption treatment, and

Fig. 1. (A) Captures of male *Choristoneura rosaceana* in pheromone traps baited at various loadings using rubber septum dispensers in untreated plots (light bars) and in pheromone-treated plots (dark bars). Within the subplot factor (pheromone lure loading), pairs of means marked with an asterisk are significantly different, reflecting a significant effect of the application of pheromone treatment. Within the whole-plot factor (pheromone disruption application), means not marked by a letter of the same case (lowercase letters for no pheromone disruption and capitals for pheromone disruption) are significantly different, reflecting a significant effect of lure loading. There was a significant interaction between pheromone treatment and lure loading. (B) Captures of male *Argyrotaenia velutinana* in pheromone traps baited at various loadings using rubber septum dispensers in untreated plots (light bars) and in pheromone-treated plots (dark bars). Within the subplot factor (pheromone lure loading), pairs of means marked with an asterisk are significantly different, reflecting a significant effect of the application of pheromone treatment. Within the whole-plot factor (pheromone disruption application), means not marked by a letter of the same case (lowercase letters for no pheromone disruption and capitals for pheromone disruption) are significantly different, reflecting a significant effect of lure loading. There was a significant interaction between pheromone treatment and lure loading.

lure dosage had no significant effect on captures of *A. velutinana* in pheromone-treated plots (Fig. 1B).

2003 field trials for *C. rosaceana* using membrane lures

There was a significant effect of both the whole-plot factor (application of ropes) ($F_{1,39}$ = 20.0, $P < 0.01$) and the subplot factor (lure dosage) ($F_{4,39}$ = 3.7, $P < 0.05$) on captures of *C. rosaceana*. However, the interaction between the application of pheromone disruption ropes and lure dosage in traps on captures of *C. rosaceana* was not significant ($F_{4,39}$ = 1.47, $P = 0.21$).

Within the subplot factor, significantly more male *C. rosaceana* were captured in traps baited with 1×, 10×, 100×, and 1000× lure dosages and with ropes under no pheromone disruption than under disruption (Fig. 2A).

Within the whole-plot factor, significantly more male *C. rosaceana* were captured in traps baited with 1× lures than in traps baited with 100× or 1000× lures or with ropes in plots not treated with pheromone (Fig. 2A). Also, there were no differences in captures of *C. rosaceana* between traps baited with 10×, 100×, or 1000× lure dosages or with ropes in untreated plots (Fig. 2A). Under pheromone disruption, significantly more *C. rosaceana* were captured in traps baited with 1× or 1000× lure dosages than in traps baited with ropes (Fig. 2A). Also, there were no differences in captures of *C. rosaceana* between traps baited with 10× or 100× lure dosages or with ropes under pheromone disruption (Fig. 2A).

2003 field trials for *A. velutinana* using membrane lures

There was a significant effect of the whole-plot factor (application of ropes) ($F_{1,39}$ = 17.7, $P < 0.01$) on captures of *A. velutinana* but no significant effect of the subplot factor (lure dosage) ($F_{4,39}$ = 1.8, $P = 0.12$). In addition, the interaction between the application of pheromone disruption ropes and lure dosage in traps on captures of *A. velutinana* was not significant ($F_{4,39}$ = 1.5, $P = 0.19$).

Within the subplot factor, significantly more male *A. velutinana* were captured in traps baited with 1×, 10×, 100×, and 1000× lure dosages and with ropes under no pheromone disruption than under disruption (Fig. 2B).

Within the whole-plot factor, significantly more *A. velutinana* were captured in traps baited with 1× lure dosages than in traps baited with 1000× lure dosages in plots not treated with pheromone (Fig. 2B). There were no differences in captures of *A. velutinana* between traps baited with 1×, 10×, or 100× lures or with ropes in plots with no pheromone disruption (Fig. 2B). Very few *A. velutinana* were captured with any of the lure loadings under pheromone disruption, and lure dosage had no significant effect on captures of *A. velutinana* in pheromone-treated plots (Fig. 2B).

Discussion

Application of pheromone dispensers (Isomate-OBLR/PLR Plus, 500 dispensers/ha) releasing primarily Z11-14:Ac and containing a small amount (approximately 1.5%) of a pheromone antagonist of *C. rosaceana*, Z9-14:Ac, (Evenden *et al.* 1999*c*) significantly decreased captures of both *C. rosaceana* and *A. velutinana* in pheromone traps relative to those in untreated plots. However, this pheromone treatment caused greater disruption of orientation to pheromone-baited traps for *A. velutinana* than for *C. rosaceana* over a wide range of lure loadings. For *C. rosaceana*, orientation to traps baited with 1× rubber septum and membrane lures containing an optimally attractive blend was disrupted only 52% and 71% for the 2002 and 2003 seasons, respectively. In contrast, disruption of orientation for *A. velutinana* to attractive 1× rubber septum and membrane lures was 98% and 94% for the 2002 and 2003 seasons, respectively. These results agree with those of Roelofs and Novak (1981), who also found that *A. velutinana* was easier to disrupt than *C. rosaceana* when only the main component of their pheromone blends (Z11-14:Ac) was used. However, greater levels of disruption (88%–96%) have been achieved for *C. rosaceana* using dispensers containing a 93:7 ratio of Z11-14:Ac and E11-14:Ac without the antagonist Z9-14:Ac (Deland *et al.* 1994). Addition of this antagonist to currently marketed Isomate rope dispensers for leafrollers may explain the reduced level of disruption for *C. rosaceana* reported in this study relative to that reported by Deland *et al.* (1994), particularly if false-plume-following to ropes was an important operating mechanism. Although reduction in the numbers of males trapped at synthetic pheromone sources cannot be reliably used as the sole indicator that pheromone treatment prevents males from finding virgin

Fig. 2. (A) Captures of male *Choristoneura rosaceana* in pheromone traps baited at various loadings using membrane dispensers in untreated plots (light bars) and in pheromone-treated plots (dark bars). Within the subplot factor (pheromone lure loading), pairs of means marked with an asterisk are significantly different, reflecting a significant effect of the application of pheromone treatment. Within the whole-plot factor (pheromone disruption application), means not marked by a letter of the same case (lowercase letters for no pheromone disruption and capitals for pheromone disruption) are significantly different, reflecting a significant effect of lure loading. The interaction between pheromone treatment and lure loading was not significant. (B) Captures of male *Argyrotaenia velutinana* in pheromone traps baited at various loadings using membrane dispensers in untreated plots (light bars) and in pheromone-treated plots (dark bars). Within the subplot factor (pheromone lure loading), pairs of means marked with an asterisk are significantly different, reflecting a significant effect of the application of pheromone treatment. Within the whole-plot factor (pheromone disruption application), means not marked by a letter of the same case (lowercase letters for no pheromone disruption and capitals for pheromone disruption) are significantly different. The interaction between pheromone treatment and lure loading was not significant.
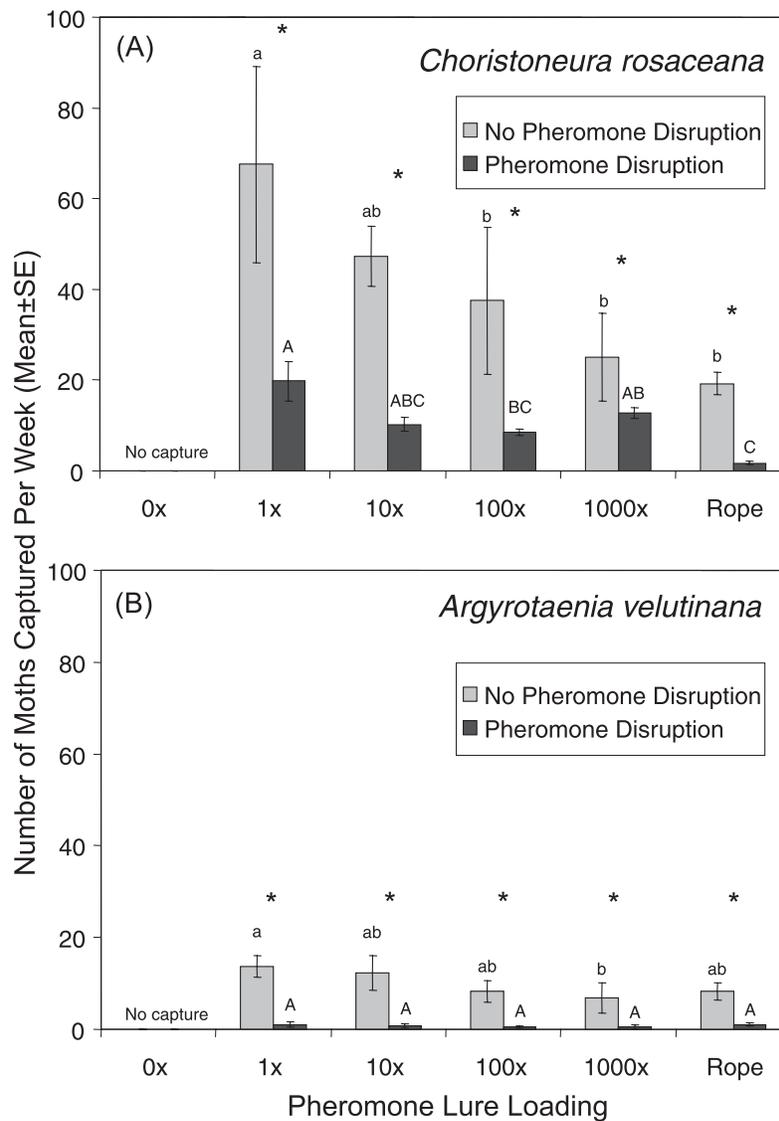
females (Agnello *et al.* 1996), a substantial difference in percent disruption of orientation to pheromone-baited traps between these two species suggests that *A. velutinana* should be easier to control with Isomate-OBLR/PLR dispensers than *C. rosaceana*.

Argyrotaenia velutinana responded to very high loadings (up to 1000× in membrane lures) of its three-component pheromone blend. In addition, it is notable that captures of *A. velutinana* in traps baited with high-release pheromone ropes equaled captures in traps baited with the three-component lures shown to be highly attractive to *A. velutinana* (Cardé and Roelofs 1977). In associated studies, we found that approximately 50% of unexposed *A. velutinana* and >80% of *A. velutinana* pre-exposed to pheromone oriented to such ropes in a wind tunnel (Stelinski *et al.* 2004*a*) and we observed numerous feral *A. velutinana* orienting to these ropes in the field (Stelinski *et al.* 2004*b*). Linn *et al.* (1985) showed that *A. velutinana* in a wind tunnel were most responsive (75%–100% responding) to the full seven-component blend of this species compared with less complete blends, especially at the lowest loadings tested (3 and 10 µg/septum), which still elicited a response in approximately 75% of the moths. However, significant responses (approximately 75% to >80%) were also elicited by the incomplete 92:8 *Z*11-14:Ac–*E*11-14:Ac mixture when presented at higher loadings of 100 and 300 µg/septum. Thus, Isomate-OBLR/PLR Plus ropes attract *A. velutinana* males despite releasing pheromone having a suboptimally attractive *Z*11-14:Ac/*E*11-14:Ac ratio and lacking other minor components of the pheromone blend. Perhaps the high pheromone loading and corresponding high release rate from such dispensers accounts for their marked attractiveness to *A. velutinana* (Roelofs 1978).

In contrast to the results for *A. velutinana*, significantly more *C. rosaceana* were captured in traps baited with lures containing 0.526 mg (1× rubber septum or membrane lure) of a blend optimally attractive for this species than in traps baited with single Isomate-OBLR/PLR Plus pheromone ropes or with 100× lure loadings. In addition, significantly fewer *C. rosaceana* (approximately 25%) responded to ropes compared with *A. velutinana* in a wind tunnel (Stelinski *et al.* 2004*a*). Although we have observed numerous feral *C. rosaceana* approaching within 100 cm of Isomate-OBLR/PLR

ropes in orchard plots (Stelinski *et al.* 2004*b*), it is possible that the presence of *Z*9-14:Ac, a pheromone antagonist, in these ropes resulted in fewer captures of *C. rosaceana* in rope-baited traps relative to lure-baited traps. However, increasing the lure loading of an optimally attractive blend lacking the antagonist also decreased captures of *C. rosaceana* in the field (Fig. 2A), while the responses of *A. velutinana* remained equivalent over a wide range of high loadings (Fig. 2B). Overall, our results are similar to earlier work by Klun and Robinson (1972) showing that *A. velutinana* was equally responsive to traps baited with only its major pheromone component (Z11-14:Ac) over a wide range of loadings in olive oil (3.5–3000 µg). Those authors also found that *C. rosaceana*'s responsiveness to lures reached an upper limit at a loading of 896 µg of *Z*11-14:Ac and that captures in traps significantly decreased as loadings were increased up to 3000 µg. Our data obtained with increasing doses of three-component blends corroborate the same dose–response trends observed for *A. velutinana* and *C. rosaceana* by Klun and Robinson (1972), who varied only the major pheromone component of each species, *Z*11-14:Ac.

We observed contrasting lure dosage versus moth capture relationships for *C. rosaceana* under no pheromone disruption in 2002 versus 2003 (Figs. 1A, 2A). It is likely that we documented the upward trend of the dosage versus capture relationship in 2002 at the lower lure dosages tested while the downward trend was documented in 2003 when much higher lure dosages were tested. Both upward and downward trends of such a histogram can be found in Figure 1 of Klun and Robinson (1972), where captures of *C. rosaceana* in traps increased to a maximum at loadings of 896 µg of *Z*11-14:Ac/lure and then decreased beyond that loading. As mentioned previously, there appears to be an upper lure-loading limit for *C. rosaceana* above which captures of moths in traps are reduced. The methodological switch from varying numbers of equally loaded rubber septa in 2002 to varying loading by increasing the release rate of pheromone in single membrane-type lures in 2003 may also account for the discrepancy in captures between years. However, our results suggest that maximum captures of *C. rosaceana* using a three-component blend occur between 1× (membrane lure) and 30× (rubber septa) of the standard 0.526-

mg loading of the attractive three-component blend.

Collectively, these results indicate that *A. velutinana* and *C. rosaceana* respond differently to varying quantities of their pheromone emitted from lures. *Argyrotaenia velutinana* appears to have a higher response threshold (*i.e.*, is less sensitive) than *C. rosaceana*. Electrophysiological studies (Stelinski *et al.* 2003*a*) have shown that the peripheral receptors of *C. rosaceana* exhibit a long-lasting adaptation following prolonged exposure to the species' own pheromone components, whereas those of *A. velutinana* do not; however, it is unclear whether these species-specific patterns of long-lasting receptor adaptation contributed to the differing behavioral responses to lures in the field. As documented by Stelinski *et al.* (2004*b*), feral *C. rosaceana* and *A. velutinana* males are attracted to and closely approach (within 0–100 cm) Isomate-OBLR/PLR dispensers. Furthermore, laboratory-reared males of both species approach such dispensers in a 2.4 m long wind tunnel (Stelinski *et al.* 2004*a*). However, feral males of both species do not remain in close proximity (within 10 cm) to Isomate-OBLR/PLR dispensers in the field long enough (males leave within 10 s) to receive the required pheromone pre-exposure dosage necessary to induce long-lasting adaptation as quantified by Stelinski *et al.* (2003*b*). These results suggest that long-lasting adaptation may not be a contributing factor to the species-specific differences in susceptibility to mating disruption.

In addition to long-lasting adaptation, instantaneous reductions of peripheral sensitivity may influence moth behavior as they approach sources of concentrated pheromone. Kuenen and Baker (1981) documented instantaneous antennal adaptation using electroantennograms for moths continuously exposed to pheromone in the laboratory. However, no long-term effects were found after removal from pheromone. Interestingly, some tortricid moths are known to orient along the edges of concentrated pheromone plumes or walls of pheromone in wind tunnels (Kennedy *et al.* 1981; Willis and Baker 1984). Such moths effectively modulate their exposure dosage while being attracted to the source of concentrated plumes. Therefore, the antennal exposure to pheromone of moths following the edge of concentrated pheromone plumes may be discontinuous and less severe than that achieved under constant laboratory exposures. Systematic studies of the similarities

or differences in short-term or instantaneous adaptation (Stelinski *et al.* 2003*a*) between *C. rosaceana* and *A. velutinana* have not yet been conducted and may contribute to our understanding of the behavioral differences documented in this study.

Significantly more codling moths, *Cydia pomonella* (L., 1758) (Lepidoptera: Tortricidae), were captured in traps baited with 10-mg lures of codlemone ((*E*,*E*)-8,10-dodecadien-1-ol) than in traps baited with 1-mg lures of codlemone under mating disruption using pheromone ropes applied at recommended densities for that species (Charmillot 1990; Barrett 1995; Judd *et al.* 1996). If a mating disruption treatment raises the response threshold of male moths via adaptation of peripheral receptors or habituation of the central nervous system (Vickers and Rothchild 1991), then it is conceivable that high-release lures should be more attractive than low-release lures under conditions of mating disruption. However, we did not obtain this outcome for either leafroller species in this study, in contrast to results documented for *C. pomonella* (Charmillot 1990; Barrett 1995). The ineffectiveness of high-load lures for trapping leafrollers under mating disruption was most dramatic for *A. velutinana*, for which captures in traps baited with every lure dosage tested were nearly completely abrogated (Figs. 1B, 2B). For *C. rosaceana* in 2002, traps baited with 10 or 30 1× rubber septum lures did capture more moths than a trap baited with a single 1× rubber septum lure in plots under mating disruption. However, this outcome did not hold in 2003, when traps baited with 10× to 1000× membrane lures captured significantly fewer moths than a trap baited with a single 1× membrane lure in plots under mating disruption. Thus, increasing lure loading above that of 1× monitoring lures (rubber septa or membrane-type) does not appear to reliably increase the effectiveness of monitoring of males of either leafroller species in orchards where pheromone ropes are deployed at recommended densities.

The results of this study indicate that Isomate-OBLR/PLR ropes, currently marketed for mating disruption of *C. rosaceana*, disrupt the orientation of this species less than has been documented in previous studies that used similar dispensers lacking traces of the antagonist *Z*9-14:Ac (Deland *et al.* 1994; Knight *et al.* 1998). Evenden *et al.* (1999*c*) found that application of dispensers containing a 1:1 mixture of

Z9-14:Ac and the four-component western *C. rosaceana* pheromone (Vakenti *et al.* 1998) in small-plot trials achieved levels of disruption of orientation to traps baited with virgin females (>83%) that were approximately equal to those achieved with dispensers containing the pheromone alone. Perhaps these differing responses of *C. rosaceana* in British Columbia and Michigan are due to "racial" differences between these geographically separated populations.

Based on their results, Evenden *et al.* (1999*a*, 1999*b*, 1999*c*) concluded that mating disruption was unlikely to be mediated by false-plume-following and more likely to be mediated by camouflage or receptor adaptation, given that dispensers with incomplete blends or those containing a behavioral antagonist were not less effective than those containing multicomponent attractive blends. Furthermore, it was suggested that both *C. rosaseana* and *Pandemis limitata* Robinson, 1869 (Lepidoptera: Tortricidae) could be controlled concurrently using dispensers releasing the pheromone components of both species, despite the presence of a behavioral antagonist for *C. rosaceana* within such a blend (Evenden *et al.* 1999*a*, 1999*c*). Thus, the undeclared addition of Z9-14:Ac by Shin-Etsu Chemical Co. (Tokyo, Japan) to Isomate-OBLR/PLR dispensers also containing the major components of both *C. rosaceana* and *P. limitata* was likely made to improve the effectiveness of this dispenser for concurrent mating disruption of these two sympatric leafroller species.

Our recent laboratory (Stelinski *et al.* 2004*a*) and field (Stelinski *et al.* 2004*b*) studies in Michigan suggest that false-plume-following is an important mechanism mediating mating disruption of *C. rosaceana* by polyethylene-tube dispensers such as Isomate-OBLR/PLR Plus. Despite the presence of the antagonist Z9-14:Ac, *C. rosaceana* are attracted to and closely approach or contact Isomate-OBLR/PLR Plus dispensers in flight tunnel studies (Stelinski *et al.* 2004*a*) and under natural apple orchard conditions (Stelinski *et al.* 2004*b*). However, the addition of this behavioral antagonist of *C. rosaceana* to such dispensers may have made them less effective by decreasing attractiveness relative to dispensers lacking this compound. Further work should be conducted to determine whether the presence of this antagonist in dispensers affects mating disruption of *C. rosaceana* in Michigan and in the eastern United States. In contrast, orientation disruption of *A. velutinana* was high using Isomate-OBLR/PLR dispensers, suggesting the potential use of such dispensers for effective control of this species.

Acknowledgements

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