Comparison of Female Attractiveness and Male Response Among Populations of *Choristoneura rosaceana* (Harris) in Western and Eastern U.S. Apple Orchards

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ABSTRACT Female obliquebanded leafrollers, *Choristoneura rosaceana* (Harris), collected from Oregon, Michigan, and New York were deployed in delta traps in Michigan apple orchards to compare their relative attractiveness to Michigan males of the same species. Females originating from Oregon attracted more males than females originating from New York during both generations of leafroller flight in Michigan. Also, females from Oregon attracted more males in Michigan than did "native" Michigan females during the first generation of flight. Analysis of gland extracts from the three populations revealed significantly more of each pheromone component in females originating from Oregon (approximately nine-fold more pheromone per female overall) than those from Michigan. However, there were no significant differences in the relative amounts of each pheromone component between Oregon and Michigan females. A 100:4:5:2 blend of Z11–14:OAc, E11–14:OAc, Z11–14:OH, and Z11–14:Ald was optimal for catching males in Michigan with no added or detrimental effect of Z11–14:Ald, confirming previous studies. However, 100:1 ratios of Z11–14:OAc relative to either E11–14:OAc or Z11–14:OH (also containing 2% Z11–14:Ald) captured more males in Oregon apple orchards compared with 100:4 and 100:10 ratios of Z11–14:OAc relative to either E11–14:OAc or Z11–14:OH. Addition of increasing amounts of Z11–14:Ald relative to Z11–14:OAc (range, 0–8:100) into a blend also containing 4% E11–14:OAc and 5% Z11–14:OH increased male catch in Oregon but not in Michigan. Our results suggest that pheromone blend quantity rather than blend quality may explain greater attractiveness of western compared with eastern female *C. rosaceana* to males in Michigan. Also, an optimized generic blend for monitoring male *C. rosaceana* across North America should contain Z11–14:Ald as has been previously shown, but should not exceed 4:100 ratios of both E11–14:OAc and Z11–14:OH relative to Z11–14:OAc for optimized catch of males in the western United States.

KEY WORDS obliquebanded leafroller, pheromone blends, monitoring, mating disruption

The obliquebanded leafroller, *Choristoneura rosaceana* (Harris), is native to temperate North America and is widely distributed (Chapman et al. 1968). It occurs from British Columbia and Nova Scotia (Venables and Gillespie 1926) south to Florida, but it does not occur in the arid southwest (Chapman et al. 1968). It has an extremely wide host range; the preferred hosts are woody plants within *Rosaceae*, *Ulmus*, *Populus*, *Quercus*, *Betula*, and *Tilia* (Chapman et al. 1968, Chapman 1973).

Choristoneura rosaceana has become an important pest in apple orchards during the past 20 yr. More recently, it has also become a problem in other fruits such as pears (Barnett et al. 1991) and cherries (Long et al. 1997). Larvae feed on developing flowers, leaves, and fruit (Howitt 1993). In apple orchards, early season injury by overwintering larvae results in dropped or disfigured fruit, and second-generation larvae cause shallow mines or deep holes on the surface of the apples. The late season damage is generally more noticeable, because damaged fruit usually remains on the tree (Agnello et al. 1996). Recorded crop damage has ranged from 3 (Agnello et al. 1996) to 20% (Lawson et al. 1996).

The female-produced pheromone components of *C. rosaceana* have been studied from populations spanning North America, which has led to optimized trapping protocols. The major pheromone component, (Z)-11-tetradecenyl acetate (Z11–14:OAc), was first identified by Roelofs and Tette (1970). Studying a New York population of *C. rosaceana*, Hill and Roelofs (1979) later identified an *E*-isomer of 11 tetradecenyl acetate (E11–14:OAc), as well as two additional compounds: (Z)-11-tetradecen-1-ol (Z11–14:OH) and

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(*E*)-11-tetradecen-1-ol (E11–14:OH). Furthermore, the *Z*:*E* isomer ratios of the acetate and alcohol were determined to be 98.3:1.7 and 98.1:1.9, respectively. However, field trials showed that a mixture containing 5–8% of the *E* acetate isomer was more attractive to male moths in New York than the measured ratio of 1.7% *E* acetate (Hill and Roelofs 1979).

Vakenti et al. (1988) identified an additional pheromone component from a population in British Columbia that was initially missed in eastern populations: (*Z*)-11-tetradecenal (Z11–14:Ald). A mixture consisting of the two acetates (96.5% *Z*:2% *E*), the Z alcohol (1.5%), and the aldehyde (1.0% of total blend) was most attractive to western male *C. rosaceana* in field trials. Furthermore, lures without Z11–14:Ald were not species specific and caught European leafrollers, *Archips rosanus* L. in addition to *C. rosaceana.* In a later study, Thomson et al. (1991) compared responses of eastern and western male *C. rosaceana* to pheromone blends with and without the aldehyde. Males from British Columbia were optimally attracted to the blend containing the aldehyde, whereas the eastern (Québec) males did not have a preference for blends with or without Z11–14:Ald. The different component blends in female effluvium and male behavioral responses to blends with and without Z11–14:Ald was thought to be indicative of the presence of western and eastern "races" of *C. rosaceana.*

Most recently, El-Sayed et al. (2003) showed that Z11–14:Ald was present in pheromone gland extracts of female *C. rosaceana* across its North American geographic range in decreasing relative amounts in females from Ontario, Québec, British Columbia, Michigan, and New York. Addition of Z11–14:Ald at 1% to a 97:2:1 blend of the Z and *E* Ac's and OH increased male captures two-fold in British Columbia and Ontario, but had no effect on male captures in Michigan and New York. Furthermore, El-Sayed et al. (2003) found that the relative amounts of each of the four pheromone components decreased successively for females originating from British Columbia, Québec, Ontario, Michigan, and New York. The amounts of Z11–14:OAc, E11–14:OAc, Z11–14:OH, and Z11–14:Ald in glands from western females (British Columbia) were 2- to 18-fold greater than those in glands from eastern females (New York and Michigan).

The objectives of this study were to compare (1) the attractiveness of virgin female *C. rosaceana* collected from western and eastern U.S. populations for attracting conspecific males in Michigan, (2) the effect of varying E11–14:OAc, Z11–14:OH, and Z11–14:Ald relative to Z11–14:OAc on captures of western and eastern male *C. rosaceana*, and (3) the total amounts and relative ratios of pheromone components in glands between western and eastern females.

Materials and Methods

Insects. Insecticide-susceptible *C. rosaceana* larvae were collected in May from unsprayed orchards that had not been previously treated with pheromone for mating disruption in Milton-Freewater, OR; Kalamazoo, MI; and Geneva, NY and raised to pupae on unsprayed apple foliage collected in Fennville, MI. Moths were reared at 24°C and 60% RH under a 16:8 (L:D) photoperiod. Female pupae were placed in 1-liter plastic cages containing 5% sucrose solution for adult emergence. Females were used in trapping and gland analysis tests after emerging on their second scotophase in culture. Special care was taken not to release "non-native" females from Oregon and New York in Michigan orchards.

Geographic Variation in Female Attractiveness. This experiment compared the attractiveness of western versus eastern virgin female *C. rosaceana* to conspecific males in Michigan. Females (1–2 d old) were deployed individually in small wire-mesh cages (4 by 3 by 1 cm) containing a moistened Kimwipe (Kimberly-Clark, Roswell, GA) and hung centrally from the ceiling of delta traps (LPD Scenturian Guardpost; Suterra, Bend, OR). The experiment was conducted at the Trevor Nichols Research Complex (TNRC) of Michigan State University in Fennville, MI, in apple trees with ≈2- to 3-m canopy heights as described by Stelinski et al. (2004). Orchard plots were maintained according to grower standard maintenance protocols in Michigan but did not receive applications of insecticides. The four treatments compared were traps baited with virgin female *C. rosaceana* from (1) Oregon, (2) Michigan, (3) New York, and (4) unbaited control traps. Traps were deployed in six 0.4- to 1.2-ha blocks at least 20 m apart and at least 10 m from plot borders. Blocks were separated by 25–35 m. Traps were hung on the edge of the tree at mid-canopy height, ≈1.8 m from the ground. Females (1–2 d old) were deployed four times during the first (8–24 June) and second (13–29 August) generations of *C. rosaceana* flight and remained in orchard plots for four consecutive nights each time for a total of 16 trapping nights per generation. Traps were inspected daily by counting and removing captured males and subsequently rotated within each block to minimize positional bias.

Effect of Blend Ratios on Male Captures. This experiment tested the effect of varying the amounts of three minor pheromone components relative to Z11–14:OAc on captures of male *C. rosaceana* in Oregon and Michigan. The experiment was conducted in an unmanaged apple orchard in Milton-Freewater, OR, and at the TNRC in Michigan. The orchard in Oregon consisted of a mixed planting of Delicious and Fuji varieties. For each treatment, red rubber septa (The West Company, Lionville, PA) were loaded with 1 mg of total pheromone, varying the amount of a single component. Septa were not pre-extracted before loading with pheromone components. Although certain types of rubber septa have been shown to react with aldehyde components of insect pheromones (Steck et al. 1979), Kamm and McDonough (1980) showed that red septa from The West Company do not, and pre-extraction with dichloromethane does not impact moth captures with aldehyde components compared with nonextracted septa. Three separate trials were conducted in both states, varying ratios of E11–14:

Table 1. Ratios of *C. rosaceana* pheromone components relative to Z11–14:OAc loaded in rubber septa for field trials in Oregon and Michigan

Varied component	Z11–14:OAc	E11–14:OAc	Z11–14:OH	Z11–14:Ald
E11–14:OAc	100	1	5	2
	100	4	5	2
	100	10	5	2
Z11–14:OH	100	4	1	2
	100	4	4	2
	100	4	10	2
Z11–14:Ald	100	4	5	0
	100	4	5	2
	100	4	5	8

OAc, Z11–14:OH, and Z11–14:Ald relative to Z11–14:OAc (Table 1). Pheromone components were obtained from Shin Etsu (>98% isomeric purity; Tokyo, Japan). Pheromone blend solutions used to load rubber septa were prepared in high-performance liquid chromatography (HPLC) grade hexane (Aldrich, Milwaukee, WI) and stored at −18°C. Loaded septa were aged in a fume hood for 24 h before field testing. Septa were pinned centrally to the inside ceiling of delta traps described earlier. Each trial was arranged in a randomized complete block design with six replicates in each state. Treatments were spaced 30 m apart and placed 15 m from plot borders. Traps were hung in the middle of the canopy, ≈1.8 m from the ground. Trials were conducted during first (6 June to 15 July) and second (2 August to 2 September) generations of moth flight. Male moths captured in traps were counted and removed every 2–3 d, followed by trap rotation within each block. Pheromone lures were newly prepared and replaced every 2 wk for each trial.

Pheromone Gland Extraction and Analysis. The amounts of Z11–14:OAc, E11–14:OAc, Z11–14:OH, and Z11–14:Ald in glands of females from Oregon and Michigan were quantified using a slight modification of a procedure reported previously by Delisle and Royer (1994). Glands ($N = 44$ per population) were removed from 2- to 3-d-old females during the second hour of scotophase and placed individually into 2.0-ml gas chromatography (GC) vials (Supelco, Bellefonte, PA) containing 250-μl tapered inserts (Chromatography Research Supplies, Louisville, KY). Glands were extracted, one at a time, with 20 μl of HPLC grade hexane (Aldrich, Milwaukee, WI) with 1.5 ng of methyl decanoate (internal standard) for 20 min; the solvent was evaporated until 2–3 μl remained and was immediately subjected to analysis by GC on a Hewlett–Packard (HP) 6890 Series GC, equipped with a flame ionization detector (FID). The GC was fitted with a Hewlett–Packard HP-20M (30-m length, 0.25 mm ID, 0.2-μm film thickness) carbowax column. The initial GC temperature was held at 75°C for 2 min and ramped at 30°C/min to 225°C, where it was held for 5 min. The He carrier gas entered the column at 13 psi. The amount of each pheromone component in each gland sample was calculated using the internal standard method (McNair and Miller 1998), and the proportion of each component in the blend was determined.

Statistical Analyses. Trapping data were transformed to $\ln(x + 1)$ to normalize the distributions and homogenize variance and subjected to analysis of variance (ANOVA) followed by Fisher protected least significant difference (LSD) with a Bonferroni corrected significance level of $\alpha < 0.05$ to determine significance between treatment means (SAS Institute 2000). Data from female-baited traps in which dead females were discovered during sampling were not used for analysis. Means and SEs in figures are expressed as percentages of total moth catch to facilitate graphical comparisons between relative catch in two geographically separated locations of different population density. The total and relative amounts of pheromone components between females from the two locations were $\ln(x + 1)$ and arcsine transformed, respectively, and compared using Students *t*-tests.

Results

Geographic Variation in Female Attractiveness. During the first generation of moth flight, virgin female *C. rosaceana* from Oregon attracted significantly ($F = 8.3$; df = 11,24; $P < 0.001$) more conspecific males to traps in Michigan than did females originating from Michigan or New York; there was no significant ($F = 1.6$; df = 11,24; $P = 0.1$) difference between attractiveness of Michigan and New York females (Fig. 1A). During the second generation, significantly ($F = 11.4$; df = 10,26; $P = 0.02$) more male *C. rosaceana* were captured in traps with females originating from Oregon or Michigan compared with those from New York; however, there was no significant ($F = 0.6$; df = 10,26; $P = 0.2$) difference in the number of males attracted to Oregon and Michigan females (Fig. 1B). No males were captured in blank traps during either generation (Fig. 1, A and B).

Effect of Blend Ratios on Male Captures. Varying the amount of E11–14:OAc had a significant effect on captures of male *C. rosaceana* in both Michigan ($F = 17.1$ and 19.3 for first and second generations, respectively; df = 2,15; $P < 0.001$) and Oregon ($F = 11.1$ and 21.1; df = 2,15; $P < 0.001$) during both generations (Fig. 2, A and B). The highest captures of Michigan males were recorded with 100:4:5:2 blend of Z11–14:OAc, E11–14:OAc, Z11–14:OH, and Z11–14:Ald, whereas captures of Oregon males were highest with the lowest amount of E11–14:OAc tested (Fig. 2, A and

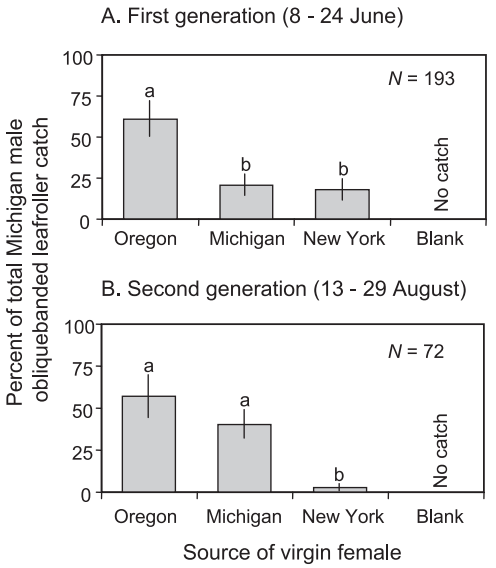

Fig. 1. Percentage captures (% ± SEM) of feral *C. rosaceana* males in traps baited with virgin females originating from the western (Oregon) and eastern (Michigan, New York) United States during the first (A) and second (B) generations of leafroller flight in Michigan. Blank (negative control) traps were left unbaited. *N* = total male catch. Bars with the same letter indicate no significant difference ($P > 0.05$).

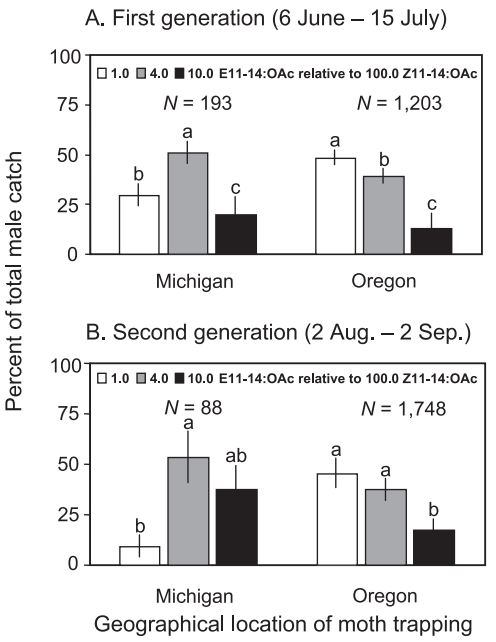

Fig. 2. Percentage captures (% ± SEM) of feral *C. rosaceana* males in Michigan and Oregon with varying ratios of E11–14:OAc relative to Z11–14:OAc during the first (A) and second (B) generations of leafroller flight. *N* = total male catch. Bars with the same letter indicate no significant difference ($P > 0.05$).

B). Varying Z11–14:OH did not significantly ($F = 1.2$ and 1.9; df = 2,15; $P = 0.2$) affect captures of male *C. rosaceana* in Michigan within the range tested (Fig. 3, A and B). However, there was a significant ($F = 34.2$ and 21.5; df = 2,15; $P < 0.001$) effect of varying Z11–14:OH on captures of males in Oregon; most males were captured with the lowest amount of Z11–14:OH tested (Fig. 3, A and B). Varying the amount of Z11–14:Ald had no significant ($F = 1.4$ and 1.7; df = 2,15; $P = 0.31$ and 0.22) effect on captures of male *C. rosaceana* during either generation in Michigan (Fig. 4, A and B). However, significantly ($F = 8.4$ and 20.6; df = 2,15; $P = 0.01$ and <0.001) more male *C. rosaceana* were captured in Oregon with the two and eight ratios of Z11–14:Ald relative to Z11–14:OAc compared with the absence of the aldehyde during both generations (Fig. 4, A and B).

Pheromone Gland Extraction and Analysis. There was a 0.37- to 0.38-min difference in retention time between Z11–14:OAc and E11–14:Oac, with 100% return to the baseline. Significantly more Z11–14:OAc ($t = 22.3$, df = 1, $P < 0.001$), E11–14:OAc ($t = 10.3$, df = 1, $P = 0.01$), and Z11–14:OH ($t = 8.4$, df = 1, $P = 0.02$) were found in gland extracts of females originating from Oregon than from Michigan (Table 2). Although the difference in the amount of Z11–14:Ald in glands of females from the two locations was not statistically significant ($t = 1.7$, df = 1, $P = 0.1$), the average amount of this compound was almost 30-fold higher in Oregon compared with Michigan females. There were no significant ($t = 0.4$–1.7, df = 1, $P >$ 0.05) differences in the relative amounts of the four pheromone components between females collected in Oregon and Michigan (Table 2).

Discussion

Female *C. rosaceana* originating from Oregon attracted more male *C. rosaceana* in Michigan than did "native" Michigan females originating from the location of the study site during the first generation of moth flight. Oregon females were also more attractive than eastern females originating from New York during both generations. There was a slight trend for greater attractiveness of Oregon than Michigan females during the second generation; but the lack of significance may have been caused by lower total male catch during the second generation (less than one half) than during the first (Fig. 1). Greater attractiveness of the western female *C. rosaceana* appears to be explained by greater production of each pheromone component rather than by differences in male moth response to ratios of pheromone blend components. Extracts of glands revealed more than nine-fold more pheromone per Oregon female than per Michigan female. In contrast to the large difference in pheromone amounts, the composition of the pheromone blends in populations from the different regions was very similar, and differences in relative amounts of pheromone components between the different regions were minute. Michigan females contained slightly more Z11–14:OH and Oregon females con-

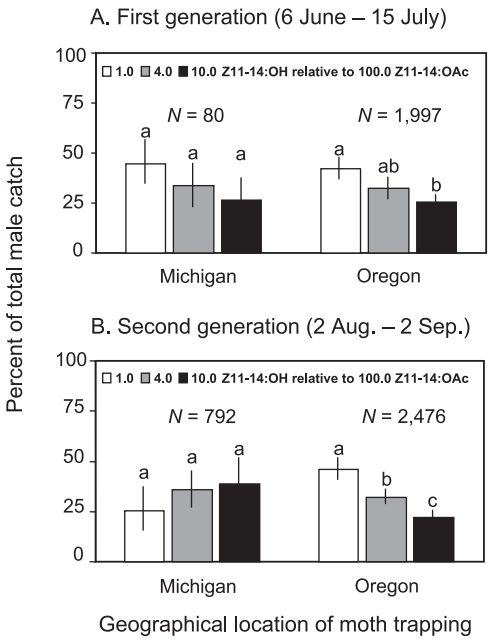

Fig. 3. Percentage captures (% ± SEM) of feral *C. rosaceana* males in Michigan and Oregon with varying ratios of Z11–14:OH relative to Z11–14:OAc during the first (A) and second (B) generations of leafroller flight. *N* = total male catch. Bars with the same letter indicate no significant difference ($P > 0.05$).

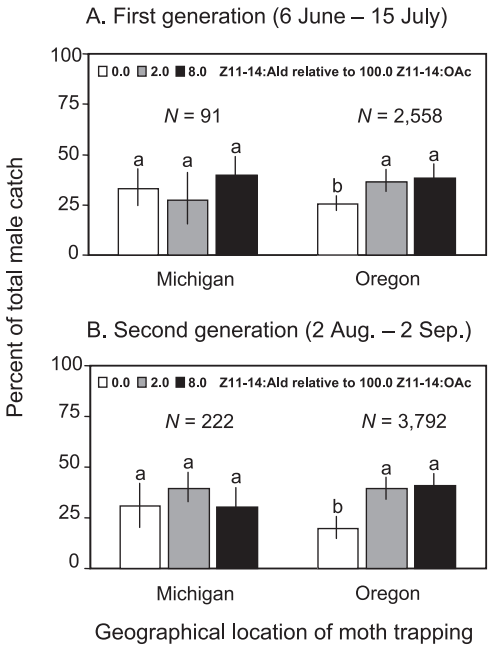

Fig. 4. Percentage captures (% ± SEM) of feral *C. rosaceana* males in Michigan and Oregon with varying ratios of Z11–14:Ald relative to Z11–14:OAc during the first (A) and second (B) generations of leafroller flight. *N* = total male catch. Bars with the same letter indicate no significant difference ($P > 0.05$).

tained slightly more Z11–14:Ald. The marked difference in pheromone quantity between western and eastern females deserves further study. Previous studies have not detected any correlation between female size and pheromone titer in leafrollers (Miller and Roelofs 1980, Delisle and Vincent 2002). El-Sayed et al. (2003) suggested that other factors such as interpopulation differences in pheromone production as a function of diel cycle or age (Delisle and Royer 1994) may contribute to this geographic variation in pheromone production. Future research should address the possibility that the quantitative differences between the western and eastern females' pheromone reported here represent heritable adaptations to the specific localities of larval collection rather than broad transcontinental geographic differences in pheromone quantity per female. A robust sampling of several populations from each region will be required to test this hypothesis.

Given that the relative *Z:E* Ac ratios were nearly identical in gland extracts of western and eastern moths further supports the hypothesis that pheromone blend quantity rather than quality explains the greater attractiveness of western compared with eastern females to Michigan males. Also, this study confirms the results of El-Sayed et al. (2003) that western females produce greater amounts of each pheromone component compared with eastern females; however, female glands from Oregon studied herein contained nearly five-fold more total pheromone, on average, compared with females previously examined from British Columbia (El-Sayed et al. 2003).

Geographic variation in female-produced sex pheromone blends and associated male response has been documented previously in both Lepidoptera and Hymenoptera (Hansson et al. 1990, Wu et al. 1996, Anderbrant et al. 2000, McElfresh and Millar 2002). For example, the regional differences in pheromone blend production and male response in the rice leaffolder moth, *Cnaphalocrocis medinalis*, in Asia are large enough to maintain reproductive isolation (Kawazu et al. 2000). Loading septa with 5 mg of total pheromone, Hill and Roelofs (1979) found that 5–8% E11–14:OAc in Z11–14:OAc acetate optimally attracts male *C. rosaceana* to traps in New York. In this study, the optimally attractive ratio of *Z:E* Ac for males in Michigan with the 1-mg lures was similar. In contrast, more male *C. rosaceana* in Oregon were captured as the amount of E11–14:OAc relative to Z11–14:OAc was decreased from 10.0 to 1.0%. The highest amount of Z11–14:OH relative to Z11–14:OAc tested in this study (10.0%) was at the peak of the 0.5–10.0% range shown to optimally attract male *C. rosaceana* in New York (Hill and Roelofs 1979), and thus it is not surprising that capture of male *C. rosaceana* in Michigan did not differ within this tested range. However, as with E11–14:OAc, decreasing the ratio of Z11–14:OH relative to Z11–14:OAc from 10.0 to 1.0% increased catch of Oregon males. This result is congruent with the findings of Thomson et al. (1991), who also reported increased

Table 2. Mean total (and relative) amounts of four pheromone components from gland extracts of obliquebanded leafroller females from Oregon and Michigan

	Mean ng/gland ± SEM of pheromone components from gland extracts (relative amounts of pheromone components expressed as %)			
Source of female	Z11–14:OAc	E11–14:OAc	Z11–14:OH	Z11–14:Ald
Oregon	249.2 ± 47.8a[a] (85.9 ± 16.5a)	10.8 ± 2.6a (3.7 ± 0.9a)	27.4 ± 8.6a (9.4 ± 3.0a)	2.8 ± 1.5a (1.0 ± 0.5a)
Michigan	24.8 ± 8.3b (78.0 ± 26.1a)	1.4 ± 0.6b (4.4 ± 1.9a)	5.5 ± 1.1b (17.3 ± 3.5a)	0.1 ± 0.2a (0.3 ± 0.6a)

[a] Means of total amounts (and relative) amounts in columns followed by the same letter are not significantly different ($P > 0.05$, *t*-test).

male catch with decreasing Z11–14:OH from 5.0 to 1.5% relative to Z11–14:OAc with a population in British Columbia. It has also been previously documented that addition of Z11–14:Ald to a blend of Z11–14:OAc, E11–14:OAc, and Z11–14:OH increases captures of western *C. rosaceana* males but has no effect on eastern males (Hill and Roelofs 1979, El-Sayed et al. 2003). Similarly, in this study, increasing the relative amount of Z11–14:Ald increased captures of males in Oregon, but had no effect on male catch in Michigan. Collectively, our results show that Oregon and Michigan male *C. rosaceana* differ in their response to varying blend ratios of the four pheromone components. As suggested by El-Sayed et al. (2003), addition of Z11–14:Ald to a general blend for monitoring both western and eastern populations is warranted because this compound does not reduce capture of eastern males. However, a common ratio of E11–14:OAc relative to Z11–14:OAc will not be optimal for monitoring male *C. rosaceana* in both the western and eastern United States given the trend for increasing captures with decreasing E11–14:OAc in Oregon and maximal captures of males with a 4:100 ratio of E11–14:OAc relative to Z11–14:OAc in Michigan (Fig. 2, A and B). Also, the ratio of Z11–14:OH relative to Z11–14:OAc should not exceed 4:100 for optimized catch in both the western and eastern United States. As suggested previously by Thomson et al. (1991), a common blend for monitoring *C. rosaceana* will likely not be optimal throughout its North American geographic range.

In the face of current and future restrictions on broad-spectrum insecticides in U.S. fruit crops, pheromone-based mating disruption (Cardé and Minks 1995) remains a potential biorational control tactic for *C. rosaceana* (Gut et al. 2004). Investigators from across North America and Canada have evaluated mating disruption with mixed results. Disruption efficacy has ranged from poor (50%) to acceptable (98%) in various small plot (range, 0.005–2.4 ha) trials in New York (Reissig et al. 1978, Agnello et al. 1996, Lawson et al. 1996), Ontario (1.5- to 3.5-ha plots) (Trimble and Appleby 2004), and Michigan (0.6-ha plots) (Stelinski et al. 2005). More consistent levels of disruption have been recorded in western North America in both large plot (16.0 ha) trials in Washington (92–99%) (Knight et al. 1998) and small plot trials (0.1 ha) in British Columbia (83%) (Evenden et al. 1999).

It has long been suggested that repeated and sustained mating disruption treatments could impose strong selection pressure on the disrupted pest, leading to evolutionary changes in the pheromone communication system and resulting in resistance (Cardé 1976, McNeil 1992). At least one case of resistance to mating disruption has been reported in Japan for the smaller tea tortrix, *Adoxophyes honmai* Yasuda (Mochizuki et al. 2002). In 1983, mating disruption of this moth pest was initiated in tea fields using a disruptant formulation containing the pheromone Z11–14:OAc (trade name: Hamaki-con). Four years after mating disruption using these dispensers began (1986), crop protection and disruption of male moth catch in pheromone traps was still high (96%). However, by 1996, the percentage of male moth disruption was reduced to 50%. Application of the same disputant formulation to nearby tea fields, where it had not been used previously, yielded disruption of males >99%. Treating the "resistant" population that had been receiving the single component disruptant for a decade with the full four-component pheromone blend resulted once again in excellent disruption (99%), suggesting that resistance had evolved to the single-component pheromone.

Selection for increased pheromone production under prolonged deployment of synthetic pheromones could also be a potential mechanism leading to the evolution of resistance to mating disruption. A significant increase in pheromone production was documented for the pink bollworm, *Pectinophora gossypiella* (Hübner), after 2–3 yr of exposure to mating disruption; however, this was not shown to correlate with improved mating ability (Haynes et al. 1984, Haynes and Baker 1988). Judd et al. (2004) recently hypothesized that higher pheromone production and release by female *C. rosaceana* than female *Pandemis limitata* (Robinson) may explain the lower efficacy of sprayable pheromones in disrupting the former species compared with the latter. These data suggest that female *C. rosaceana* from the western United States are more attractive than conspecifics from the eastern United States because of greater pheromone production. Irrespective of the selection pressures that have resulted in higher pheromone production in the western population of *C. rosaceana*, our results suggest that this phenotype can outcompete females from eastern populations in attracting males. Under mating disruption, selection pressure for increased pheromone production by female *C. rosaceana* may contribute to resistance if higher pheromone production correlates with improved mating ability. This hypothesis will require further testing in pheromone-treated orchards

with varying histories of exposure to mating disruption.

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