Higher Densities of Distributed Pheromone Sources Provide Disruption of Codling Moth (Lepidoptera: Tortricidae) Superior to That of Lower Densities of Clumped Sources

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ABSTRACT Field experiments quantified the effect of synthetic pheromone release-site density and distribution on 1) orientational disruption of male codling moths, *Cydia pomonella* (L.) (Lepidoptera: Tortricidae), to pheromone-baited traps; and 2) fruit injury. A clustering test varied pheromone release-site density from 0 to 1,000 Isomate-C Plus dispensers per ha while maintaining the total number of dispensers at 1,000. Percentage of orientational disruption of pheromone-baited traps increased significantly as a function of increasing density of release sites. Fruit injury decreased as the density of release sites increased and was lowest in plots treated with Isomate-C Plus dispensers distributed as 1,000 point sources per ha. We also manipulated point source density of 0.1-ml paraffin-wax drops containing 5% codlemone [(*E,E*)-8,10-dodecadien-1-ol], and thus the total amount of pheromone deployed per hectare. The percentage of disruption of traps baited with either 1.0- or 0.1-mg codlemone lures increased with increasing density of wax drops deployed. Both trapping and field observations confirmed that wax drops were attractive to male codling moths, suggesting that disruption was mediated by competitive attraction. Development of dispensers that can be mechanically applied at high densities has potential to improve the efficacy and economics of codling moth disruption at high population densities.

KEY WORDS mating disruption, false-plume following, competitive attraction, camouflage, desensitization

Mating disruption of codling moth, *Cydia pomonella* (L.), (Lepidoptera: Tortricidae), in the United States is implemented on >54,000 ha of pome fruits and walnuts, with varying degrees of success (Gut et al. 2004). The predominant formulation currently used in the United States is the Isomate-C Plus polyethylene tube dispenser (Shin-Etsu Chemical Co., Tokyo, Japan, Thomson et al. 2001) applied at densities of 500–1,000 dispensers per ha, which equates with ≈1–2 dispensers per fruit tree. Some researchers (Shorey and Gerber 1996, Knight 2004) suggest that efficacy can be maintained while reducing the density of release sites, if overall release rate per hectare is maintained or increased. A savings in labor is postulated for a given number of Isomate dispensers assembled into clusters rather than distributed individually (Knight 2004). However, Suckling and Angerilli (1996) falsified this idea for light brown apple moth, *Epiphyas postvittana* (Walker). Their study revealed that if the total number of dispensers was held constant, plots with higher densities of release sites best-disrupted moth catches in pheromone traps.

There are several commercially available disruption products for codling moth in addition to Isomate-C dispensers. For example, Isomate-CTT (Shin-Etsu Chemical Co., Tokyo, Japan) dispensers contain twice as much pheromone as the Isomate-C Plus dispenser and are designed for application at a rate of 500 dispensers per ha (Alway 2002). Other products, such as Hercon Disrupt CM flakes (Hercon, Emigsville, PA) and Scentry NoMate CM Fibers (Scentry, Billings, MT) are applied at higher densities (≈37,000 per ha), compared with Isomate dispensers, and release pheromone at rates similar to those emitted by female moths (Swenson and Weatherston 1989, Welter and Cave 2005). Understanding how distribution of pheromone release devices in an orchard affects orientational disruption of male moths is necessary to optimize efficacy of mating disruption for codling moth.

The overall goal of this investigation was to determine whether codling moth disruption is improved by increasing density and distribution of pheromone release sites. Studies were also conducted to determine whether male moths approach dispensers to provide insight into the mechanism(s) by which disruption may be operating. Our specific objectives were to determine whether 1) a given number of Isomate-C Plus dispensers was equally efficacious whether clumped or distributed, and 2) codling moth disruption could be improved over that by Isomate dispens-

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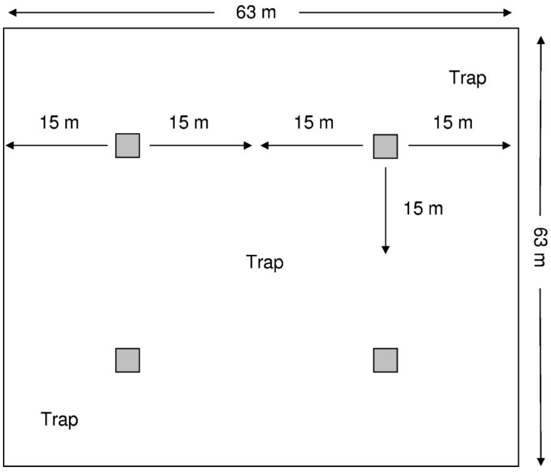

Fig. 1. Diagram of a 0.4-ha orchard plot containing four release sites of clustered Isomate-C Plus dispensers. Shaded boxes (not to scale) represent 100 clustered Isomate-C Plus dispensers. Other release-site densities were likewise regularly distributed.

ers if multiple paraffin-wax drops were deployed per tree as Stelinski et al. (2005a) demonstrated was effective for oriental fruit moth, *Grapholita molesta* (Busck). A trapping study and direct field observations were conducted to determine whether wax drops attract male codling moth. Pheromone release rate from wax drops also was quantified by gas chromatography.

Materials and Methods

Experiment 1: Reducing Release Site Density while Maintaining Total Pheromone Applied per Hectare Constant. This study was conducted from 10 May to 30 September 2003. The objective was to evaluate the effect of clustering pheromone release sites on disruption efficacy while maintaining a total of 1,000 Isomate-C Plus dispensers per ha. These dispensers contained 205 mg of 53.0% codlemone [(*E,E*)-8,10-dodecadien-1-ol], 29.7% 12:OH, 6.0% 14:OH, and 11.3% inert ingredients. Densities of release sites per hectare were 0, 10, 25, 100, 500, and 1,000. Dispensers were applied individually in the top m of trees for the 500 and 1,000 dispensers per ha treatments. Two dispensers were spaced 2.5 cm apart in the 500 release site per ha treatment. Multiple dispensers in the 10, 25, and 100 release site/ha treatments were attached to horizontally mounted, (one intersection per cm^2) galvanized-metal hardware cloth (TWP Wire Mesh, Berkeley, CA), each dispenser spaced 2.5 cm apart as per Suckling and Angerilli (1996). The 100 release sites per ha treatment consisted of 10 dispensers per cluster; the 25 release sites per ha treatment consisted of 40 dispensers per cluster; and the 10 release sites per ha treatment consisted of 100 dispensers per cluster. Pheromone release sites were spaced equidistantly throughout each 0.4-ha plot (Fig. 1). Experimental design was a randomized complete block with two

Table 1. Description of orchards used in experiment 1 in which density of release sites (Isomate-C Plus dispensers) per hectare was varied without varying total amount of pheromone deployed per hectare

Orchard no.	Cultivar(s)	Tree age (yr)	Canopy ht(m)	Tree spacing (m)
1	'Red Delicious'	16	3.5–4.5	3 by 6
2	'Golden Delicious'	10	3.5–4.5	1.8 by 4.6
	Red Delicious	10	3.5–4.5	3 by 5.5
	Red Delicious	20	4–5	3 by 5.5
	'Rome'	8	3–4	2.4 by 5.5
3	'Braeburn'	7	2.4–3.1	2.7 by 4.9
	'Macintosh'	7	2.4–3.1	2.7 by 4.3
	'Fuji'	7	2.4–3.1	2.4 by 4.6
	Jonagold'	7	2.4–3.1	2.4 by 4.6
	'Northern Spy'	7	2.4–3.1	2.4 by 5.5
4	'Gala'	20	2.4–3.1	2.4 by 4.6
	Gala	20	3–4	2.7 by 4.9

replicates (blocks) located at the Trevor Nichols Research Complex (TNRC) of Michigan State University in Fennville, MI, and one each in two commercial orchards in South Lyon and Flushing, MI. The two blocks at TNRC were separated by at least 300 m, and treatment plots at all commercial orchards were separated by at least 45 m. Experimental sites and tree composition are described in Table 1. Disruption of male moth orientation to sex pheromone was assessed using three pheromone traps (LPD Scenturian Guardpost, Suterra, Bend, OR) per 0.4-ha plot baited with 1-mg codlemone rubber septum lures and placed in the upper one-third of tree canopies on a diagonal transect across each plot (Fig. 1). Lures were red rubber septa loaded with codlemone (>98% isomeric and chemical purity, Suterra, Bend, OR). New pheromone lures were deployed every 2 wk during each moth generation. Moths captured in traps were counted and removed once weekly.

Codling moth fruit injury was evaluated in all plots after first generation moth flight and immediately before harvest. Thirty apples (*Malus* spp.) per tree, 15 apples high in the canopy and 15 apples low in the canopy, were examined from 20 trees per plot (600 fruit per plot total).

Experiment 2: Increasing Both Point-Source Density and Total Pheromone Applied per Hectare from Paraffin-Wax Drops. Paraffin-wax dispensers (Stelinski et al. 2005a) were used because a larger range of densities could be compared than with Isomate-C Plus dispensers, while applying less total pheromone per hectare than could be achieved with Isomate-C Plus dispensers. This study was conducted from 13 May to 3 June of 2004 at TNRC. This experiment ran for only 2 wk because disruption efficacy was rapidly lost thereafter. Experimental site, tree composition, and maintenance protocol of orchards are described in Stelinski et al. (2005a). Orientational disruption trials were conducted comparing five application densities of 0.1-ml drops of paraffin wax containing 5% pheromone. Paraffin-wax dispensers were formulated as described in Stelinski et al. (2005a). Briefly, paraffin-wax formulation consisted of: 30% paraffin wax (Gulf wax, Royal Oak Sales, Inc., Roswell, GA), 4% soy oil (Spectrum Naturals, Inc., Petaluma, CA), 2% Span 60 (Sorbitan monostearate, Sigma-Aldrich, St. Louis, MO), 1% vitamin E [(±)-α-tocopherol, Sigma-Aldrich), 5% codlemone (Bedeukian Co., Danbury, CT, >98% purity confirmed by gas chromatography), and 58% (by total weight) deionized water. Wax drops were hand-applied to branches of trees by using 5-ml plastic syringes. Densities of wax drops compared were zero per tree, three per tree (820 per ha, 3.3 g [AI]/ha), 10 per tree (2,700 per ha, 11 g [AI]/ha), 30 per tree (8,200 per ha, 33 g [AI]/ha), and 100 per tree (27,300 per ha, 109 g [AI]/ha). Experimental design was a randomized complete block with treatments applied to 0.07 (16-tree)-ha plots replicated five times. Replicate orchards (blocks) were separated by at least 35 m and treatment plots by at least 15 m. Orientational disruption of male catches was assessed using two pheromone traps, baited with either 1.0 or 0.1 mg of codlemone, placed in two of four central trees of each plot. Traps were hung ≈2–3 m above ground level in the upper third of the tree canopy. Wax dispensers were never placed closer than 50 cm from monitoring traps. Moths captured in traps were counted and removed twice weekly.

Experiment 3: Evaluating Attractiveness of Paraffin-Wax Dispensers to Male Codling Moths. We compared captures of male codling moth in traps baited with 0.1-ml paraffin-wax drops formulated as described above with that of rubber septum lures loaded with 1 mg of codlemone (described above) known to be highly attractive. These tests were conducted from 6 July through 19 September 2004 in plots not being used for mating disruption studies. Paraffin-wax dispensers containing pheromone were pipetted onto 2- by 5-cm strips of aluminum foil and allowed 24 h to dry before strips were deployed in traps. Fresh lures were installed every 2 wk into plastic delta traps deployed in unsprayed 0.4-ha plots of apples, as described above. Unbaited traps were used as a negative control. Paraffin-wax treatments were replaced every 4 wk. The experiment was arranged in a randomized complete block with six replicates. Traps were spaced ≈26 m apart and rotated weekly. Traps were hung ≈1.5–2 m above ground level in the upper third of the tree canopy. Moths captured in traps were counted and removed twice weekly.

Experiment 4: Direct Observation of Codling Moth Males in Plots Treated with Various Densities of Wax Drops. Direct observations of male codling moth visits to wax drops in trees were conducted as detailed in Stelinski et al. (2005a). Observations were conducted on 17 nights during first codling moth generation. One wax drop containing pheromone was observed in control plots that were otherwise untreated.

Experiment 5: Measuring Pheromone Release Rate from 0.1-ml Wax Drops. Release Rate of codlemone from paraffin-wax dispensers was determined using protocol reported by Stelinski et al. (2005a). Briefly, paraffin-wax drops (0.1 ml) were applied to 1- by 5.5-cm pieces of flat, wooden Craft Sticks (Diamond Brands, Cloquet, MN) by using an Eppendorf repeat pipetter. Resulting drops were ≈7 mm in diameter and 2 mm in thickness. Samples were attached with plastic ties to branches of five 5–7-m-tall apple trees at a height of 2–3 m within the tree canopy. Samples were maintained in the field and in a laboratory fume hood from 3 August to 8 October 2004. Five samples were collected immediately at application to determine pheromone concentration in wax drops at test onset. Thereafter, three samples were collected approximately every 24 h for 4 d and then every other d for 80 d. Pheromone extracted from samples was quantified using a gas chromatograph (HP-6890, Hewlett–Packard, Palo Alto, CA.) fitted with a DBWAXETR polar column (model 122-7332, J&W Scientific, Folsom, CA) of length 30 m and internal diameter 250 μm. Initial oven temperature was 130°C for 2 min, and then it was ramped at a rate of 2.5°C/min to 160°C, where it was held for 2 min. The program then ran at 40°C/min to a final temperature of 230°C. The carrier gas, He, entered the column at 20 psi.

Statistical Analysis. For orientational disruption and trapping studies, data were transformed to ln $(x + 1)$ (which normalized distributions and homogenized variance) and then subjected to analysis of variance (ANOVA). Fruit injury data were arcsine transformed before ANOVA. Differences in pairs of means were separated using the least significant difference (LSD) test (SAS Institute 2000). Fruit injury data also were subjected to regression analysis to describe the overall relationship between fruit injury and $\log_{10}$ of pheromone release-site density. Observational data of moth visits to paraffin-wax drops in the field were subjected to chi-square analyses. Percentage of orientational disruption was calculated as 1 − (mean moth catch per trap in the pheromone-treated plot/mean moth catch per trap in the control plot) × 100.

Results

Experiment 1: Reducing Release-Site Density while Maintaining Total Pheromone Applied per Hectare Constant. Overall, percentage of disruption of pheromone-baited traps increased significantly as a function of increasing density of pheromone release sites (Fig. 2A). Traps in plot centers treated with 1,000 or 500 release sites per ha captured significantly (F = 14.2; df = 5, 18; $P < 0.01$) fewer males than those in plots treated with 0, 10, or 25 release sites per ha (Fig. 2A). Also, significantly ($P < 0.01$) fewer males were captured in plots with 1,000 release sites per ha than in plots with 100 release sites per ha (Fig. 2A). There was no significant ($P > 0.05$) difference in male catch in central traps among plots treated with 10 and 25 release sites per ha (Fig. 2A).

Traps placed on plot borders treated with 500 and 1,000 point sources per ha captured significantly (F = 8.3; df = 5, 18; $P < 0.01$) fewer males than those placed on plot borders with 0, 10, 25, or 100 release sites per ha (Fig. 2B). There was no significant difference among male captures in border traps of plots treated with 10 or 100 release sites per ha (Fig. 2B). As with central traps, orientational disruption of border traps

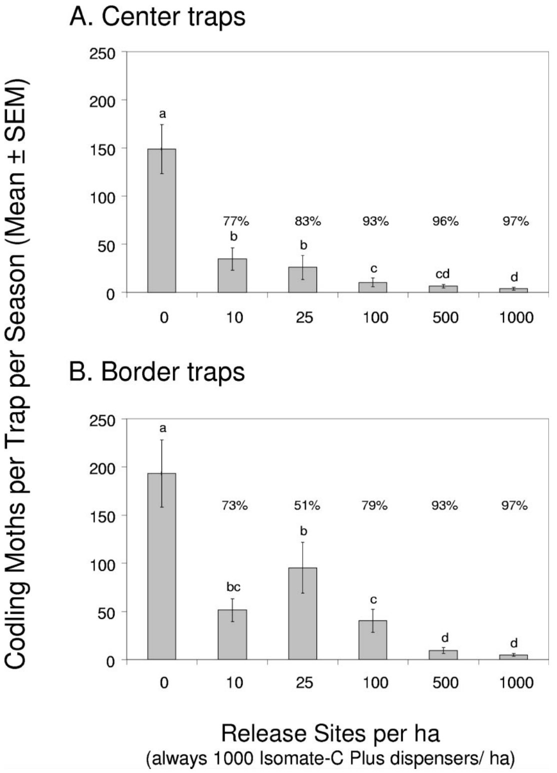

Fig. 2. Mean captures of codling moth males in lure-baited delta traps in centers (A) and borders (B) of plots containing various release-site densities of Isomate-C Plus dispensers while maintaining the total number of dispensers at 1,000 per ha. Means followed by the same letter are not significantly different at $\alpha < 0.05$.

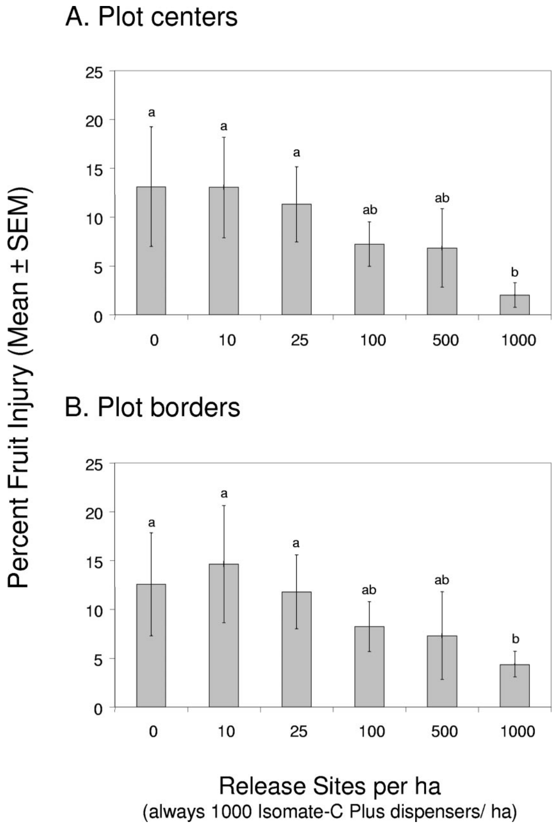

Fig. 3. Mean percentage of fruit injury due to codling moth larval infestation in centers (A) and borders (B) of plots containing various release-site densities of Isomate-C Plus dispensers while maintaining the total number of dispensers at 1,000 per ha. Means followed by the same letter are not significantly different at $\alpha < 0.05$.

was highest for the two highest release-site density treatments (Fig. 2B).

Percentage of infested fruit decreased as density of release sites increased. Fruit injury in both plot centers and borders was significantly (F values = 4.4, 5.0, respectively, df = 5, 18; $P < 0.01$) reduced relative to the control in plots treated with 1,000 release sites per ha (Fig. 3A and B). Among pairs of means, there was no significant ($P > 0.05$) difference between fruit injury in plots with 100 through 1,000 release sites per ha. Overall relationships between decreasing fruit injury as a function of increasing $\log_{10}$ of release-site density were described by $y = -0.23x + 3.8$ ($R^2 = 0.84$) and $y = -0.25x + 4.2$ ($R^2 = 0.8$) for plot centers and borders, respectively. Slopes for these relationships were significantly (F values = 20.5, 13.1, respectively; df = 1, 5; $P < 0.05$) negative.

Experiment 2: Increasing Both Point-Source Density and Total Pheromone Applied per Hectare from Paraffin-Wax Drops. Mean numbers of moths captured in traps decreased as a function of increasing wax-drop density. Significantly (F values = 11.4, 12.2, respectively; df = 4, 20; $P < 0.01$) fewer males were captured in traps baited with 1.0- and 0.1-mg lures in plots treated with 27,300 wax drops per ha than in plots with 0, 820, and 2,700 drops per ha (Fig. 4A and B). However, this analysis of pairs of means revealed no significant ($P > 0.05$) differences in numbers of males caught with both lure loadings between plots with 8,200 and 27,300 point sources (Fig. 4A and B). Overall, percentage of disruption of traps baited with either 1.0- or 0.1-mg lures increased with increasing density of point sources deployed (Fig. 4A and B). Ninety-four and 99% orientational disruption was achieved with 27,300 point sources per ha for 1.0- and 0.1-mg lures, respectively.

Experiment 3: Evaluating Attractiveness of Paraffin-Wax Dispensers to Male Codling Moths. Significantly ($F = 16.2$; df = 3, 20; $P < 0.01$) more male codling moths were captured in traps baited with each pheromone treatment than in blank controls, which captured 0.06 ± 0.05 (mean ± SE) males over the season. There was no statistical ($P > 0.05$) difference in mean number of males captured in traps baited with red septa (65.5 ± 13.4), 0.1-ml wax drops with 98% pure codlemone (81.8 ± 18.5), or 0.1-ml wax drops with codlemone extracted from Isomate-C Plus dispensers (74.3 ± 9.2).

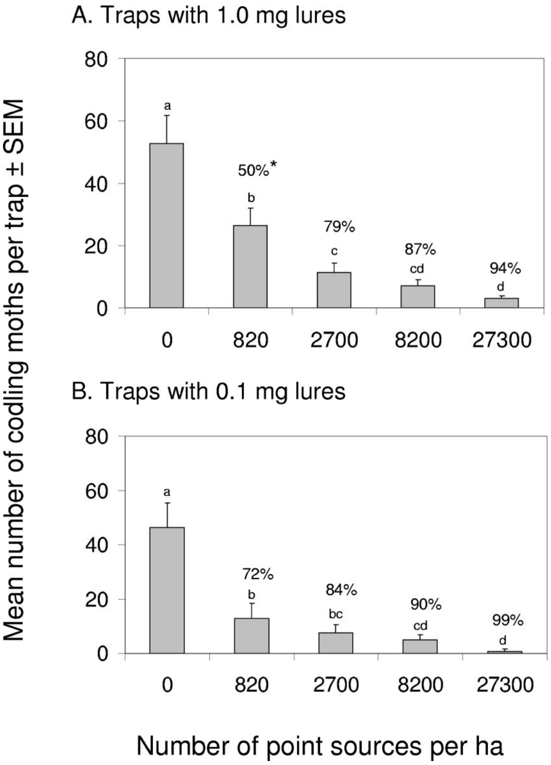

Fig. 4. Mean captures of codling moth males in lure-baited delta traps in plots containing various densities of 0.1-ml paraffin-wax drops containing 5% codlemone. Means followed by the same letter are not significantly different at $\alpha < 0.05$.

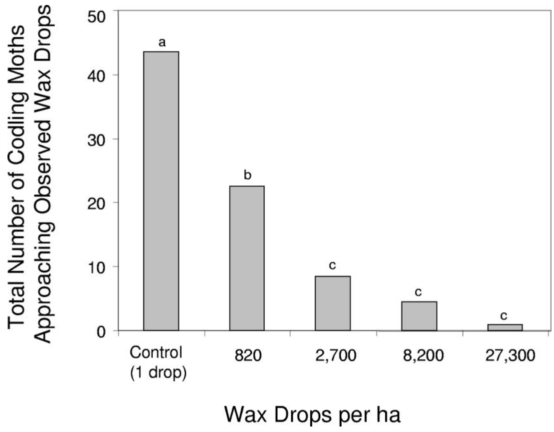

Fig. 5. Numbers of codling moth males observed approaching paraffin-wax drop dispensers of pheromone in plots receiving various densities of dispensers. All moths observed approached within 130 cm of dispensers. Observations were conducted on 17 evenings between 17 May and 12 June. Means followed by the same letter are not significantly different at $\alpha < 0.05$.

Experiment 4: Direct Observation of Codling Moth Males in Plots Treated with Various Densities of Wax Drops. Codling moth males approached wax drops in treated plots at all dispenser densities (Fig. 5). Significantly ($\chi^2 = 7$, df = 1, $P < 0.01$) more males approached a single drop under observation in otherwise untreated plots than in plots with 820 drops per ha and likewise significantly ($\chi^2 = 20$, df = 1, $P < 0.01$) more males approached a single drop under observation in plots treated with 820 drops per ha than in plots treated with 2,700 drops per ha. Sixteen of 81 males observed made direct contact with drops, 88% of observed males approached within 20 cm of wax drops, and all observed moths came within 130 cm. After landing on foliage near wax drops, males fanned their wings and walked rapidly. None of the visits lasted longer than 2 min, and 90% flew away from dispensers within 60 s.

Experiment 5: Measuring Pheromone Release Rate from 0.1-ml Wax Drops. Release profiles of codlemone from wax drops in a laboratory fume hood and in the field are shown in Fig. 6, fitted with exponential decay curves. Laboratory samples yielded an R^2 of 0.98 and a decay constant value of −0.028, whereas field samples gave an R^2 of 0.94 and a higher decay constant value of −0.051. Release rate of codlemone from a wax drop was ≈2.1 and 3.3 μg/h over the first 14 d of release in the laboratory and field, respectively. Between day 14 and 35, release rate decreased to ≈1.3–0.5 μg/h.

Discussion

The highest density of pheromone-dispenser release sites yielded the best orientational disruption of male codling moth to traps and lowest fruit injury. Increased orientational disruption as a function of increasing release-site density occurred both when the total amount of pheromone per hectare was increased, and when it was held constant. These results corroborate findings of previous studies of release-site density on disruption for other moth species (Charlton and Cardé 1981, Palaniswamy et al. 1982, Suckling et al. 1994, de Lame 2003). In the current study, 96–97% orientational disruption was achieved with 1,000 Isomate C Plus ropes per ha distributed as 1,000 point sources per ha, and 94–99% disruption was achieved with 27,300 paraffin-wax drops per ha. Given that Isomate-C Plus dispensers release pheromone at ≈20 μg/h (Knight 1995), and paraffin-wax drops released ≈2 μg/h during the first 2 wk in the field, the amount of pheromone released per hectare per hour for 1,000 Isomate dispensers and 27,300 wax drops was ≈20 and 55 mg, respectively.

Alford and Silk (1983) and Suckling and Angerilli (1996) also varied release-site density while maintaining total number of pheromone point sources per hectare constant. The former study was conducted with the spruce budworm, *Choristoneura fumiferana* (Clemens), and Hercon flakes (Hercon, Emigsville, PA) as the dispenser of synthetic pheromone. Intermediate densities of 33 and 100 points per m^2 of 60 and 20 flakes per release site yielded higher disruption than a uniform distribution of single flakes or nine

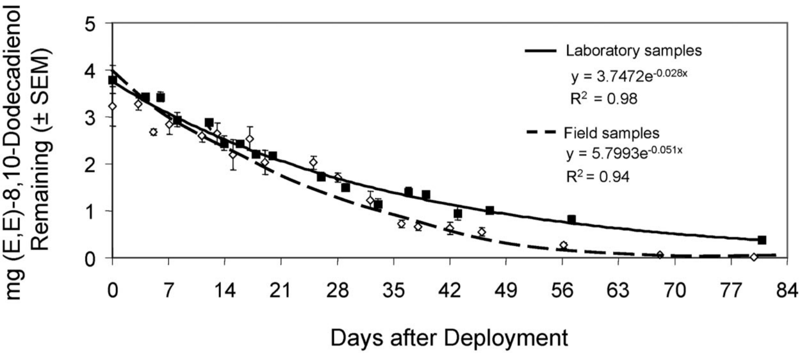

Fig. 6. Release profiles of 0.1-ml paraffin-wax drops containing 5% codlemone fitted with exponential decay curves.

release sites of 222 flakes per site. These results are consistent with the current study in that the treatment with fewest release sites disrupted the least. That intermediate densities of flakes proved slightly better than the completely uniform distribution of one flake per release site in the Alford and Silk study is likely because clumps of 20 and 33 flakes per site competed with females to a higher degree than single flakes per site, given the low pheromone release rate from these dispensers. However, even with intermediate clumping, treatments with 20 and 33 flakes per release site were applied at high densities of 2,000 and 660 total release sites per ha. Suckling and Angerilli (1996) studied the light brown apple moth and used polyethylene, reservoir-type dispensers similar to those used in our study. Our results were consistent with the above studies in that clumping of dispensers decreased disruption.

Current results are inconsistent with those of Knight (2004), who found that highly spaced clusters of 100 Isomate-C Plus dispensers (four per ha) disrupted codling moth males comparably to 500 dispensers per ha distributed individually. However, Knight's cluster treatment was supplemented by a 10–20-m-wide border application of Isomate-C Plus dispensers at a density equivalent to 1,000/ha, which was not applied to the highly distributed Isomate dispenser treatment. In addition, codling moth density in the current study was high (>300 moths per trap for the season in control plots based on three traps per 0.4 ha) but was low in the Knight study (< 8 moths/trap for the season in control plots based on two traps per ha). Thus, contradicting results between our study and Knight's are probably due to differences in experimental design and codling moth population density.

On both plot borders and in plot centers, fruit injury was lowest when Isomate-C Plus dispensers were most highly distributed. Fruit injury in the 1,000 point source per ha treatment was almost two-fold less than in the 500 point source per ha treatment (Fig. 3A and B). In addition, there was a significant overall relationship between increased release site density and decreased fruit injury. It is important to note that seemingly small differences in percentage of disruption as measured by traps (e.g., 93–96 versus 97–99%) may be associated with widely differing crop protection outcomes.

Codling moth males have been observed orienting to and landing within proximity (mean 50 cm) of Isomate-C Plus dispensers placed directly within trees in pheromone-treated orchards (Stelinski et al. 2005b). In our recent flight tunnel studies with codling moth males, preexposure of moths to Isomate-C Plus dispensers decreased male responsiveness to otherwise highly attractive lures (Stelinski et al. 2006). This suggests that desensitization after preexposure to Isomate dispensers may have contributed to disruption of codling moth. More research will be required to determine relative importance of desensitization after preexposure to high-release, reservoir dispensers versus pure competitive attraction to false plumes.

Both trapping experiments and field observations confirmed that wax drops were highly attractive to male codling moth, suggesting that orientational disruption by wax drops functioned primarily by competitive attraction (false-plume following). Deployment of paraffin-wax dispensers at 8,200 and 27,300 drops per ha has recently been shown to provide better mating disruption of *G. molesta* than standard applications of Isomate-M Rosso dispensers in small plot trials (Stelinski et al. 2005a). However, this wax formulation still needs improvement for codling moth under high population densities in Michigan. Although 99% orientational disruption was achieved in the current study with 27,300 drops per ha, this result lasted only ≈2 wk, after which disruption was not better than 50% relative to control plots. This may have been due to the drop in codlemone release rate after day 14 (Fig. 6) or codlemone degradation (Millar 1995) after this interval. That wax drops deployed within delta traps were attractive to codling moth for up to 4 wk in our trapping study, whereas disruption failed after 2 wk, suggests photodegradation of codlemone was a problem. A recently improved formulation incorporating antioxidants as well as UV and visible light blockers deployed at 27,300 drops per ha proved equally effective to Isomate C-Plus dispensers at 1,000/ha for an entire moth generation (L.L.S. et al., unpublished data) and holds promise as a cost-effective alternative mating disruption formulation for codling moth that can be machine-applied. The addition of insecticides to this formulation might enhance efficacy through removal of attracted males (Krupke et al. 2002).

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