ECOLOGY AND BEHAVIOR

Mating Disruption of Two Sympatric, Orchard-Inhabiting Tortricids, Choristoneura rosaceana and Pandemis limitata (Lepidoptera: Tortricidae), with Pheromone Components of Both Species' Blends

M. L. EVENDEN,^{1, 2} G.J.R. JUDD,³ and J. H. BORDEN¹

J. Econ. Entomol. 92(2): 380-390 (1999)

ABSTRACT In British Columbia, several pheromone blends were tested as possible mating disruptants for 2 sympatric, orchard-inhabiting leafrollers (Lepidoptera: Tortricidae), the obliquebanded leafroller, Choristoneura rosaceana (Harris), and the threelined leafroller, Pandemis limitata (Robinson). Z9-tetradecenyl acetate (Z9-14:OAc), a minor pheromone component of the P. limitata pheromone and known pheromone antagonist of C. rosaceana, was tested alone and in combination with Z11-tetradecenyl acetate (Z11-14:OAc), the major pheromone component of both species, and additional minor components of the C. rosaceana pheromone, as mating disruptants of both species. Disruption of mating, assessed using tethered virgin females of both species, was tested in 0.1-ha plots (33.3 by 33.3 m), using fiber-tape dispensers releasing ≈10 mg/ha per hour. Z9-14:OAc applied alone did not significantly disrupt mating of either species. All treatments containing Z11-14:OAc and Z9-14:OAc in a \approx 1:1 ratio equally reduced mating of both species. Furthermore, an \approx 91:6 ratio of Z11-14:Oac : Z9-14:OAc, which is highly attractive to P. limitata, was no more effective than a less attractive pheromone blend containing a, ~1:1 ratio of these components. Unattractive blends combining the major component, Z11-14:OAc and the inhibitor, Z9-14:OAc, disrupted mating of C. rosaceana as effectively as the major component alone. These results indicate that false-trail following was not an important mechanism of mating disruption for either of these species in this experimental setting. We conclude that Z11-14:OAc could be used alone or in combination with Z9-14:OAc to disrupt mating in both leafrollers simultaneously.

KEY WORDS Choristoneura rosaceana, Pandemis limitata, leafroller, mating disruption, pheromone, orchard

ALTHOUGH THE TWO sympatric leafrollers (Lepidoptera: Tortricidae) the obliquebanded leafroller, *Choristoneura rosaceana* (Harris), and the threelined leafroller, *Pandemis limitata* (Robinson), are secondary pests of pome fruits in the Okanagan and Similkameen Valleys of British Columbia they are important. Implementation of a sterile insect release program to control *Cydia pomonella* (L.) (Dyck et al. 1993), the key insect pest of pome fruits, will likely cause these and other leafroller species to become more serious pests (Judd and McBrien 1994) that will require a noninsecticidal management strategy if growers are to increase organic or insecticide-free fruit production.

The pheromone blend of western Canadian populations of *C. rosaceana* has been identified as a 100:2: 1.5:1 ratio of Z11-tetradecenyl acetate (Z11-14:OAc), E11-tetradecenyl acetate (E11-14:OAc), Z11-tetradecenyl alcohol (Z11-14:OH), and Z11-tetradecenyl aldehyde (Z11-14:Ald), respectively (Vakenti et al. 1988, Thomson et al. 1991). Female *P. limitata* share Z11-14:OAc as the major pheromone component with C. rosaceana, but release it with Z9-tetradecenyl acetate (Z9-14:OAc) in a 91:9 blend; but a 94:6 blend of these components was optimally attractive to male P. limitata in trapping experiments (Roelofs et al. 1976).

Pheromone-based mating disruption has been used successfully to control several species of insect pests (Cardé and Minks 1995), but there are few examples of successful multiple-species mating-disruption systems (Ridgway et al. 1990). Sympatry of *C. rosaceana*, *P. limitata*, and other leafroller species in British Columbia requires an integrated approach to the development of a multiple-species mating-disruption system (Judd and McBrien 1994). One approach to achieving this goal is the use of common pheromone components (van Deventer and Blommers 1992, Pfeiffer et al. 1993, Deland et al. 1994), but another might be the use of interspecific antagonists (Bengtsson et al. 1994).

Z9-14:OAc, the minor pheromone component of the *P. limitata* pheromone, was demonstrated to be a pheromone antagonist for populations of *C. rosaceana* in western Canada (Evenden et al. 1999a) and has also been cited as a pheromone antagonist for eastern North American populations (Cardé and Baker 1984). Although pheromone antagonists alone have not been effective mating disruptants (Kaae et al. 1974, Roths-

April 1999

EVENDEN ET

child 1974, Daterman et al. 1975) the mulate cross species attraction (St 1983). In combination with pherom released from the same dispenser t miting disruption (Bengtsson et al. 1 Shaw 1995, Suckling and Burnip 199 1996), for instance, by causing treated areas (Bengtsson et al. 199 search showed that complex and si blends, independent of attractivent effective as mating disruptants aga indicating that false-trail following other mechanisms (Bartell 1982, (vided by less attractive formulation setting (Evenden et al. 1999b). Addi to the pheromone blend of C. rosace response of males of both C. rosaced to traps baited with virgin female: 1999a), indicating the potential of mone components from both speci ruptant for both species.

In this study, we tested Z9-14:0 combination with Z11-14:OAc, the component of both species, and components for *C. rosaceana*, to de blend could be developed that we factory disruption of mating in both

Materials and Meth

General protocol. All experimer in Cawston, British Columbia (B.C. using a small-plot protocol (Roelo Evenden et al. 1999a) (Fig. 1). E plots (33.3 by 33.3 m) were estable managed orchards. Plots were at l a minimum of 10 m from the edg Treatments were assigned to plots design and rerandomized so that cupied each plot for a maximum o control plot was included in each

Five atmospheric semiochemica b) were applied using Conrel fi (Ecogen, Billings, MT). The small 14:OAc and E9-14:OAc in blends were inescapable by-products of isomers. In each plot, dispenser upper 3rd of the tree canopy on t tree. Dispenser density was mai Except where otherwise mentio release rate was $\approx 10 \text{ mg/ha per l}$ gen; Weatherston et al. 1985). N deployed at the beginning of ea 48 h before assessing the effect of ments on mating disruption.

Disruption of mating was assivirgin female *C. rosaceana* and *P.* laboratory at 24°C and a photopon a modified pintobean-based d 1965). Pupae were sexed and individually in 150-ml cups and p source. Females aged 6-96 h

¹ Centre for Pest Management Department of Biological Sciences, Simon Fraser University, Burnaby, BC, Canada V5A 186.

² Current address: Department of Entomology, College of Agriculture, S-225 Ag Science Building N, University of Kentucky, Lexington, KY 40546–0091.

³ Agriculture and Agri-food Canada, Pacific Agri-food Research Centre, Summerland, BC, Canada V0H 1Z0.

April 1999

Inhabiting Tortricids, tata (Lepidoptera: Both Species' Blends

BORDEN¹

ssted as possible mating dis-": Tortricidae), the obliqueleafroller, Pandemis limitata component of the P. limitata ed alone and in combination nponent of both species, and g disruptants of both species. cies, was tested in 0.1-ha plots our. Z9-14:OAc applied alone containing Z11-14:OAc and rthermore, an ≈91:6 ratio of no more effective than a less onents. Unattractive blends k:OAc, disrupted mating of C. licate that false-trail following e species in this experimental nbination with Z9-14:OAc to

er, mating disruption, phero-

ne major pheromone component with t release it with Z9-tetradecenyl ace-:) in a 91:9 blend; but a 94:6 blend of its was optimally attractive to male P. ing experiments (Roelofs et al. 1976). ased mating disruption has been used control several species of insect pests iks 1995), but there are few examples ultiple-species mating-disruption syset al. 1990). Sympatry of C. rosaceana. other leafroller species in British Co an integrated approach to the develultiple-species mating-disruption sy McBrien 1994). One approach to ;oal is the use of common pheromone van Deventer and Blommers 1992 993, Deland et al. 1994), but anothe e of interspecific antagonists (Benge

the minor pheromone component pheromone, was demonstrated to be agonist for populations of *C. rosaccia* ada (Evenden et al. 1999a) and has a pheromone antagonist for easter on populations (Cardé and Baker 1990) omone antagonists alone have not be of disruptants (Kaae et al. 1974, Rol child 1974, Daterman et al. 1975) they are reported to stimulate cross species attraction (Stadlebacher et al. 1983). In combination with pheromone components released from the same dispenser they could cause mating disruption (Bengtsson et al. 1994, Suckling and Shaw 1995, Suckling and Burnip 1996, Witzgall et al. 1996), for instance, by causing emigration from treated areas (Bengtsson et al. 1994). Previous research showed that complex and simple pheromone blends, independent of attractiveness, were equally effective as mating disruptants against C. rosaceana, indicating that false-trail following did not augment other mechanisms (Bartell 1982, Cardé 1990) provided by less attractive formulations in a small plot setting (Evenden et al. 1999b). Addition of Z9-14:OAc to the pheromone blend of C. rosaceana disrupted the response of males of both C. rosaceana and P. limitata to traps baited with virgin females (Evenden et al. 1999a), indicating the potential of combining pheromone components from both species as a mating disruptant for both species.

In this study, we tested Z9-14:OAc alone and in combination with Z11-14:OAc, the main pheromone component of both species, and minor pheromone components for *C. rosaceana*, to determine whether a blend could be developed that would provide satisfactory disruption of mating in both species.

Materials and Methods

General protocol. All experiments were conducted in Cawston, British Columbia (B.C.) during 1994-1997 using a small-plot protocol (Roelofs and Novak 1981, Evenden et al. 1999a) (Fig. 1). Experimental 0.1-ha plots (33.3 by 33.3 m) were established in organically managed orchards. Plots were at least 40 m apart and a minimum of 10 m from the edge of each orchard. Treatments were assigned to plots after a Latin-square design and rerandomized so that each treatment occupied each plot for a maximum of 14 d. A nontreated control plot was included in each replicate.

Five atmospheric semiochemical treatments (Table 1) were applied using Conrel fiber-tape dispensers (Ecogen, Billings, MT). The small percentages of E11-14:OAc and E9-14:OAc in blends 4 and 5 (Table 1) were inescapable by-products of synthesis of the Z iomers. In each plot, dispensers were hung in the upper 3rd of the tree canopy on the north side of the tree. Dispenser density was maintained at 1,000/ha. Except where otherwise mentioned, semiochemical release rate was $\approx 10 \text{ mg/ha}$ per hour at $\approx 20^{\circ}$ C (Ecoter, Weatherston et al. 1985). New dispensers were deployed at the beginning of each replicate, at least 16 h before assessing the effect of atmospheric treatments on mating disruption.

Disruption of mating was assessed using tethered in female C. rosaceana and P. limitata reared in the boratory at 24°C and a photoperiod of 16:8 (L:D) h modified pintobean-based diet (Shorey and Hale 5). Pupae were sexed and females were placed bidually in 150-ml cups and provided with a water rce. Females aged 6-96 h were immobilized at



5 m

Fig. 1. Plot design used to test mating disruption in experiments 1-6. Four 0.1-ha plots were established in each experiment in organically managed orchards in Cawston, BC. PC, plot center. φ , positon of 2 tethered females (of each species in experiments 4-6), one high and the other low in the canopy, except for experiment 1 in which females were placed only high in the canopy.

0.5°C, tethered with a loop of polyester thread secured around 1 forewing, and transported to field sites individually in plastic cups housed in refrigerated containers. Females of both species were placed at both high (upper 3rd of canopy) and low (head height) positions in the tree canopy at each of 6 locations near the plot center (Fig. 1) during late afternoon and collected early the following morning. Females were placed on a leaf and secured by taping the thread to a branch. Placement of each female was marked with flagging tape. Females recovered from experimental plots were dissected to reveal the presence (mated) or absence (virgin) of a spermatophore in the bursa copulatrix. Females were omitted from the data set if they were dead and not mated upon recovery. Tethered females were placed in experimental plots on 2-3 nights in each replicate to ensure that the proportion of females mating was based on 15–30 live females per treatment per replicate. In 2 instances in experiment 1 (see below), extremely high mortality rates caused proportions to be based on 9 and 7 individual females.

Experiments. Experiments 1-3 were conducted to test the hypothesis that blends containing the major pheromone component of both species and minor components of the *C. rosaceana* pheromone, blends that are all effective mating disruptants for *C. rosaceana* (Evenden et al. 1999b), would disrupt mating by *P. limitata.* Experiment 1, conducted from 18 July to 15

JOURNAL OF ECONOMIC ENTOMOLOGY

Table 1. Blend compositions used in mating-disruption experiments against C. rosaceana and P. limitata

Experiment number	Blend no.	% component in blend					
		Z11-14:OAc	E11-14:OAc	Z11-14:OH	Z11-14:Ald	Z9-14:OAc	
1, 2, 3, 4	1	95.7	1.9	1.4	1.0		E9-14
1, 4	2	96.7	1.9	1.4	1.0	- 37	STATES.
1, 4, 5, 6	3	98.0	2.0	14	_	- 1052	
5	4	91.4	2.4	_		- 36	
4, 5, 6	5	01.1	2.4	—	—	6.1	0.
-, 0, 0					—	97.8	U.

Compositions of blends 1-3 were as determined by Ecogen and verified by gas chromatograph (GC) analysis. Contents of blends 4 were as determined by GC analysis.

September 1994, tested blend 1, a four-component pheromone of *C. rosaceana*, and simpler partial blends 2 (lacking Z11-14:Ald) and 3 (Z11-14:OAc + E11-14: OAc) (Table 1). In this experiment, females were placed only at high levels in the canopy on open platforms with a square cardboard base of 42 cm² and a circular roof of 64 cm².

Experiments 2 and 3 tested blend 1 at various release rates to determine the optimum dose required to disrupt mating in *P. limitata*. In experiment 2, conducted from 7 June to 4 August 1995, dispensers with 25, 50 and 100 fibers per dispenser provided approximate release rates of 2.5, 5, and 10 mg/ha per hour, respectively, at $\approx 20^{\circ}$ C (Ecogen; Weatherston et al. 1985). In experiment 3, conducted from 20 June to 28 July 1996, disruption dispensers with 1, 6, and 13 fibers per dispenser produced release rates of ≈ 0.1 , 0.6, and 1.3 mg/ha per hour, respectively.

Experiments 4-6 were conducted to determine the minimum number of components in the pheromone of *C. rosaceana*, that alone, or in combination with Z9-14:OAc, would provide simultaneous mating disruption of both *C. rosaceana* and *P. limitata*. Experiment 4, conducted from 21 June to 24 July 1996, compared atmospheric treatments of blends 1, 2, and 3 in combination with Z9-14:OAc in a \approx 1:1 ratio. Dispensers with 100 fibers of blends 1, 2, or 3 were attached to disruption dispensers containing 100 fibers of Z9-14: OAc (blend 5) producing an approximate combined release rate of 20 mg/ha per hour, 10 mg from each dispenser type.

In experiment 5, conducted from 12 August to 30 August 1996, treatments included the major component of both species with E11-14:OAc (blend 3) plus Z9-14:OAc (blend 5) in a 1:1 ratio, and blend 4, an attractive blend to *P. limitata* containing Z11-14:OAc, E11-14:OAc, Z9-14:Oac, and E9-14:OAc in a 91.4:2.4: 6.1:0.2 ratio (Table 1). In treatment 1, fiber-tape disruption dispensers with 100 fibers of blend 3 were attached to dispensers containing 100 fibers of blend 5 with a release rate of ~10 mg/ha per hour from each dispenser.

In experiment 6, conducted from 14 June to 19 July 1997, the 3 treatments were 100 fibers of blend 3, 100 fibers of blend 5, and 100 fibers each of blends 3 and 5 in a 1:1 ratio. Release rates were $\approx 10 \text{ mg/ha per hour for each blend.}$

Statistical Analyses. Proportional data generated in all mating disruption experiments were analyzed by logistic regression techniques, a more poweful method of analyzing proportional data (Levesque 1990) than either chi-square tests or analysis of varance (ANOVA) on arcsine transformed data (Za-1984). Selecting the most powerful method reduces the possibility of committing a type II error (i.e., accepting the null hypothesis when it is false [Zar 1984]). We used logistic regression models (GLM 1985) [i.e., generalized linear models that determine the relationship between a binomially distributed response variable (p_i) , of the form y/n, where y =number of successes (e.g., number of insects mating out of n = total number tested) and 1 or more explanatory variables x_{I}].

The model used has the form:

$$p_i = \exp(\beta_0 + \beta_1 x_{1i} + \ldots + \beta_k x_{ki})/1 + \exp(\beta_0 + \beta_1 x_{1i})$$

 $+ \ldots \beta_{k} \mathbf{x}_{ki}$

Vol. 92, no. 1

April 1999

where the relationship between p_i and the x_i is sigmoidal, but it can be shown (Collett 1989) that the logit (p_i) of this function is linearly related to x_i .

logit
$$(p_i) = \log (p_i/(1-p_i)) = \beta_0 + \beta_1 x_{1i} + \dots + \beta_k x_{ki}$$

Proportions of tethered female C. rosaceana that were mated after being exposed for 1 night in pheromonetreated or control plots were compared by a linear logistic regression model (GLIM 1985) in which disruption treatment was the explanatory variable, and replicates over time and plot position were treated as dummy variables. In experiment 2, 3, and 4 the dose of blend 1 could be considered as a continuous variable but a categorical model was used, because it allowed the dose at which mating disruption became ineffective to be identified. Fitting of the logistic regression model was followed by Z-tests to compare individual proportions using a procedure similar to a multiple comparisons test on means. The α -value was adjusted using the Bonferroni inequality to control for type I errors, which depend on the number of comparisons being made (Zar 1984). In all cases the experimentwise $\alpha = 0.05$.

Results

Atmospheric treatment in experiment 1 with pheromone blends 1-3 containing Z11-14:OAc, the major component of both species and minor components of *C. rosaceana*, resulted in a 63-81% reduction in the

0.7 E.) proportion of P. limitata females mated 0.6 а 0.5 0.4 0.3 0.2 Mean (± S. 0.1 0.0 control Z11-14:OAc 0 E11-14:OAc O 0 Z11-14:OH Z11-14:Ald 0

Approximate release rat

Fig.2. Proportions of mated, tethered pheromone (blend 1) and 2 partial blen with the same letter are not significant!

Proportion of mating among tether tata (Fig. 2). However, all 3 blends equal in effectiveness. Mating disrup Provided in experiments 2 and 3 by omone of *C. rosaceana*, was signifirelease rates ranging from 0.6-10.0(Fig. 3). Atmospheric treatment wit at 0.1 mg/ha per hour in experiment proportion of mating in female *P. 1* with a nontreated control (Fig. 3).

Evenden et al

382

ıd						
14:Ald	Z9-14:OAc	E9-14:OAc				
.0						
	—					
	6.1	0.2				
	97.8	2.2				

h (GC) analysis. Contents of blends 4 and 5

Vol. 92, no. 2

techniques, a more powerful ing proportional data (Levesque chi-square tests or analysis of variin arcsine transformed data (Zar ie most powerful method reduces ommitting a type II error (i.e., achypothesis when it is false [Zar logistic regression models (GLIM lized linear models that determine stween a binomially distributed re v_i), of the form y/n, where y =ies (e.g., number of insects mating number tested) and 1 or more exs x_I].

l has the form:

$$+ \dots \beta_k x_{ki} / 1 + \exp(\beta_0 + \beta_1 x_{1i} + \dots \beta_k x_{ki}),$$

nship between p_i and the x_i is sigbe shown (Collett 1989) that the nction is linearly related to x_i ,

$$(1-p_i) = \beta_0 + \beta_1 x_{1i} + \ldots + \beta_k x_k$$

nered female C. rosaceana that were exposed for 1 night in pheromone-I plots were compared by a linear model (GLIM 1985) in which diswas the explanatory variable, and ne and plot position were treated as In experiment 2, 3, and 4 the dose of considered as a continuous variable model was used, because it allowed mating disruption became ineffeced. Fitting of the logistic regression ed by Z-tests to compare individual ; a procedure similar to a multiple on means. The α -value was adjusted oni inequality to control for type I end on the number of comparisons 1984). In all cases the experiment-

Results

eatment in experiment 1 with pher 3 containing Z11-14:OAc, the major th species and minor components of ulted in a 63-81% reduction in the



Approximate release rates (mg/ha per h) of semiochemical components

Fig.2. Proportions of mated, tethered female *P. limitata* in nontreated plots or plots treated with the complete *C. rosaceana* pheromone (blend 1) and 2 partial blends (2 and 3) in experiment 1, 18 July-15 September 1994, Cawston, BC, n = 4. Bars with the same letter are not significantly different, Z-test, P > 0.05.

proportion of mating among tethered-female *P. limitata* (Fig. 2). However, all 3 blends were statistically equal in effectiveness. Mating disruption of *P. limitata* provided in experiments 2 and 3 by blend 1, the pheromone of *C. rosaceana*, was significant and equal at release rates ranging from 0.6–10.0 mg/ha per hour (Fig. 3). Atmospheric treatment with blend 1 released at 0.1 mg/ha per hour in experiment 3, did not alter the proportion of mating in female *P. limitata* compared with a nontreated control (Fig. 3).

Atmospheric treatment in experiment 4 with blends 1-3 in combination with Z9-14:OAc (blend 5) strongly reduced the proportion of mating among tethered female *P. limitata*, but only the combination of blends 2 + 5 resulted in a significant reduction in mating by *C. rosaceana* (Fig. 4). No treatment differences were detected for the 3 semiochemical blends tested in experiment 4 for either species. In experiment 5, blends 3 + 5, equivalent to an off-ratio pheromone blend for *P. limitata*, were tested against blend 4, a



Approximate release rate of atmospheric treatment with blend 1 (mg/ha per h)

Fig. 3. Proportions of tethered female P. limitata mating in nontreated plots or plots treated with blend 1 at various release rates in experiment 2 (7 June-4 August 1995) and experiment 3 (20 June-28 July 1996), Cawston, BC, n = 4 in both experiments. Within each experiment bars with the same letter are not significantly different, Z-test, P > 0.05.

blend close to the P. limitata pheromone. As in experiment 4, treatments containing Z9-14:OAc produced a greater reduction in mating in P. limitata (81-83%) than C. rosaceana (Fig. 5). For C. rosaceana, only blends 3 + 5 resulted in a significant reduction (73%) in the proportion of females that mated.

In experiment 6, Z9-14:OAc alone (blend 5) the minor component of the P. limitata pheromone did not reduce mating in either species, whereas Z11-14:OAc (blend 3), the major component of both species, did (Fig. 6). Blends 3 + 5, the off-ratio blend of the P. limitata pheromone, were no more effective as a mating disruptant against P. limitata than Z11-14:OAc (blend 3) the major component alone. For C. rosaceana, treatment with blends 3 + 5 significantly reduced mating, but was no more effective than Z11-14:OAc alone (blend 3) (Fig. 6).

Discussion

Our data suggest that simultaneous disruption of mating in the sympatric species C. rosaceana and P. *limitata* can be achieved by treating the atmosphere with Z11-14:OAc, the compound that comprises the majority of the pheromone in both species or with a blend containing both Z11-14:OAc and Z9-14:OAc, the minor component for P. limitata and antagonist to C. rosaceana.

In experiments 1-3, the reductions in the proportion of tethered, female P. limitata that mated was most likely caused by neurophysiological effects resulting from exposure to Z11-14:OAc. Trap capture of male P limitata is inhibited by the addition of 6% E11-14:OAc to its pheromone blend (Roelofs et al. 1976). It is not known if Z11-14:OH or Z11-14:Ald is perceived by P limitata males and acts interspecifically in some manner. Blends 1 and 2, containing Z11-14:OH and Z11-14:Ald, were no more effective at reducing mating in P. limitata than blend 3, which contained 98% Zll-14:OAc with 2% E11-14:OAc. As Z9-14:OAc, the minor component of the P. limitata blend is required for attraction of males of this species (Roelofs et al. 1976) it is highly unlikely that disruption using any of blends 1-3 alone (Table 1) was the result of false-trail following. Although it may be possible to camouflage a plume with an incomplete pheromone blend (Minks and Cardé 1988), it is most likely that neurophysiological effects caused the observed reduction in mating of P. limitata in experiments 1-3. Preexposure or constant exposure to single pheromone components in the laboratory (Linn and Roelofs 1981, Liu and Haynes 1993a) and in the field (Flint and Merkle 1984, Judd et al. 1995) has resulted in upwind flight of males to off-ratio pheromone blends that is best explained by neurophysiological adaptation or habituation.



Approximate release

Fig. 4. Proportions of tethered fe treated with C. rosaceana pheromone Cawston, BC, n = 4. Within each speciproportions that approached 0 for wh

EVENDEN ET AL

April 1999



Approximate release rates (mg/ha per h) of semiochemical components

Fig. 4. Proportions of tethered female C. rosaceana and P. limitata mating in experiment 4 in nontreated plots or plots and with C. rosaceana pheromone (blends 1-3) in combination with Z9-14:OAc (blend 5) in a 1:1 ratio, 21 June-24 July 1996, score, BC, n = 4. Within each species, bars with the same letter are not significantly different, Z-test, P > 0.05. Asterisks indicate portions that approached 0 for which standard errors could not be estimated by the logistic regression function.



pts treated with blend 1 at various release ly 1996), Cawston, BC, n = 4 in both ly different, Z-test, P > 0.05.

1-3, the reductions in the proportion le P. limitata that mated was most neurophysiological effects resulting Z11-14:OAc. Trap capture of male P. ed by the addition of 6% E11-14:OAc blend (Roelofs et al. 1976). It is not OH or Z11-14:Ald is perceived by P. 1 acts interspecifically in some man-12, containing Z11-14:OH and Z11nore effective at reducing mating in plend 3, which contained 98% Zll-11-14:OAc. As Z9-14:OAc, the minor ie P. limitata blend is required for s of this species (Roelofs et al. 1976 ly that disruption using any of blends 1) was the result of false-trail foli it may be possible to camouflage a complete pheromone blend (Minks , it is most likely that neurophysic used the observed reduction in malin experiments 1-3. Preexposure of e to single pheromone components y (Linn and Roelofs 1981, Liu and nd in the field (Flint and Merkle 1954 has resulted in upwind flight of male mone blends that is best explained by cal adaptation or habituation.

386 JOURNAL OF ECONOMIC ENTOMOLOGY EVENDEN ET Vol. 92, no. April 1999 1.0 0.8 C. rosaceana а 0.7 0.8 0.6 Mean (± S. E.) proportion of females mated 0.6 0.5 proportion of females mated 0.4 а 0.4 0.3 0.2 0.2 ab b 0.1 0.0 0.0 1.0 P. limitata 0.8 0.8 0.7 Э ш 0.6 i 0.6 Mean (± 0.5 0.4 0.4 0.3 0.2 h 0.2 b 0.1 0.0 blend 3 control blend 4 + blend 5 0.0 Z11-14:OAc control 0 9.8 91.4 E11-14:OAc 0 0.2 2.4 0 Z11-14:OAc Z11-14:OH 0 0 0 E11-14:OAc 0 Z11-14:Ald 0 0 0 Z11-14:OH 0 Z9-14:OAc 0 9.8 6.1 0 Z11-14:Ald E9-14:OAc 0 0.2 0.2 0 Z9-14:OAc E9-14:OAc 0

Approximate release rates (mg/ha per h) of semiochemical components

ſ

Fig. 5. Proportions of tethered female C. rosaceana and P. limitata mating in experiment 5 in nontreated plots or plots treated with the P. limitata pheromone (blend 4) or blend 3 in combination with Z9-14:OAc (blend 5) in a 1:1 ratio, 1^2 August-30 August 1996, Cawston, BC, n = 4. Within each species, bars with the same letter are not significantly different, Z-test, P > 0.05.

Approximate release

Fig. 6. Proportions of tethered for treated with Z9-14:OAc alone, blend July 1997, Cawston, BC, n = 4. Withi



ing in experiment 5 in nontreated plots or plan ion with Z9-14:OAc (blend 5) in a 1:1 min h the same letter are not significantly different

Approximate release rates (mg/ha per h) of semiochemical components Fig. 6. Proportions of tethered female C. rosaceana and P. limitata mating in experiment 6 in nontreated plots or plots and with 29-14:OAc alone, blend 3 alone, or blend 3 in combination with 29-14:OAc (blend 5) in a 1:1 ratio, 14 June-19 1997, Cawston, BC, n = 4. Within each species, bars with the same letter are not significantly different, Z-test, P > 0.05.

The significant reduction in the proportion of female *P. limitata* that mated over a wide range of release rates of blend 1 in experiments 2 and 3, except at the lowest release rate of 0.1 mg/ha per hour (Fig. 3), is in contrast to observations that release rate of pheromone is important in preventing mating and providing crop protection in several mating-disruption systems (Schwalbe and Mastro 1988, Webb et al. 1990, Suckling and Shaw 1992). Blend 1 also reduced mating by tethered *C. rosaceana* females at pheromone release rates >1.3 mg/ha per hour (Evenden et al. 1999b).

Atmospheric treatments composed of components from both species' blends disrupted mating in both species to varying degrees. In experiments 4 and 5, blends incorporating Z9-14:OAc disrupted mating of P. limitata but were less effective against C. rosaceana (Figs. 4 and 5). Mechanisms that may be acting to prevent P. limitata from mating in these experiments include camouflage of female-produced plumes, adaptation, and habituation. In experiment $\overline{5}$, the tested blends contained the same components in different ratios. Blend 4, an ≈91: 6 ratio of Z11-14:OAc to Z9-14:OAc is an attractive blend to P. limitata, and could therefore have invoked false-trail following. The other treatment, blends 3 + 5, represents an off-ratio blend for P. limitata with an approximate 1:1 ratio of these components. Experiment 5 (Fig. 5) shows that at the tested release rate, the attractive blend 4 was no more effective as a mating disruptant of P. limitata than the off-ratio blend. Because of the presence of the antagonist Z9-14:OAc, the reduction in mating of C. rosaceana in these same plots, could only be the result of neurophysiological effects or emigration from treated areas. In support of this finding, Evenden et al. (1999b) demonstrated that partial pheromone blends (blends 2 and 3) were equally effective as mating disruptants of C. rosaceana as the more attractive blend 1.

Blends containing antagonists and pheromone components have been used as mating disruptants for several species. Large-scale mating disruption of the light brown apple moth, Epiphyas postvittana (Walker), was achieved using a formulation that contained a behavioral antagonist, produced as a by-product of pheromone synthesis, which rendered the formulation unattractive (Suckling and Shaw 1995). Suckling and Burnip (1996) found no difference in disruption of mate location of Planotortrix octo (Dugdale) (Lepidoptera: Tortricidae) when an attractive pheromone disruptant treatment and an unattractive partial pheromone containing an antagonist were compared. Bengtsson et al. (1994) demonstrated that male pea moths emigrated from treated areas when isomerization of a pheromone component resulted in the production of an inhibitory isomer in the disruptant formulation.

In experiment 6, unlike in experiments 4 and 5, mating in both species was reduced significantly when the atmosphere was treated with blend 3 alone and blends 3 + 5 in a 1:1 ratio (Fig. 6). Blends 3 + 5reduced mating of *C. rosaceana* females by 85% in experiment 6, which is greater than the 73 and 65% reductions in experiments 4 and 5, respectively. The latter 2 experiments were conducted the year before experiment 6 in different orchards with differing composition opy structures, and with greater population pressures as measured by monitoring traps adjacent to experimental plots. The relatively low proportion of female that mated in the control plots in experiments 4 and 5 may thus reflect a high level of competition from females.

Treatment with Z9-14:OAc (blend 5) alone had no effect on the proportion of females of either species that mated. For C. rosaceana this was expected be cause Z9-14:OAc is a known pheromone antagonid (Cardé and Baker 1984, Evenden et al. 1999a), and treatment with pheromone antagonists alone has not provided effective mating disruption in other studie (Kaae et al. 1974, Rothschild 1974, Daterman et al 1975). Pheromone antagonists are not perceived as antagonists unless they are present in the same plume as the pheromone components (Liu and Haynes 1993b, Rumbo et al. 1993). Furthermore, there are antennal receptors (ie. Den Otter and van der Haagen 1989) and glomeruli in the macroglomerular complex in the antennal lobe of some insects that process response to pheromone antagonists alone (Mustaparta 1996), and over stimulation of this pathway does not appear to alter pheromone blend integration and upwind flight to females. For P. limitata, however, 29-14:OAc is a minor pheromone component (Roelofs et al. 1976). There was a slight, nonsignificant reduction in mating of P. limitata in plots treated with Z9-14:OAc alone (Fig. 6). In other species, minor components alone may be effective as mating disruptants (Yashima et al. 1975, Miyashita et al. 1976, Kanno et al. 1978, Stadlebacher et al. 1983). We previously demonstrated (Evenden et al. 1999a) that Z9-14:OAc does not alter capture of male P. limitata in female-baited traps. It appears that the major pheromone component, Z11-14:OAc, is required to provide adequate mating disruption of both P. limitata and C. rosaceana.

Acknowledgments

We thank H. L. McBrien for advice and review of the manuscript; R. Gries and H. D. Pierce, Jr., for chemical analyses; C.A. Levesque and J. Hall for statistical advice; M.G.T. Gardiner and L.J. Chong for technical advice and assistance; and N. C. Delury, N. L. Weremy, G. Zilahi-Balogh, and L. E. Delury for field assistance; and R. Schneider, A. Turner, and T. Wills for welcoming research in their orchards. We thank Ecogen, Incorporated, for preparation of pheromone dispensers. This research was supported by the Science Council of British Columbia, the Similkameen Okanagan Organic Producers' Association, the British Columbia Fruit Growers' Association, Phero Tech Incorporated, and the Natural Sciences and Engineering Research Council of Canada.

References Cited

- Bartell, R. J. 1982. Mechanisms of communication disruption by pheromone in the control of Lepidoptera: a review. Physiol. Entomol. 7: 353-364.
- Bengtsson, M., G. Karg, P. A. Kirsch, J. Löfqvist, A. Sauer, and P. Witzgall. 1994. Mating disruption of pea moth Cydia

Vol. 92, no. 1

April 1999

Indexicana F. (Lepidoptera: Tortricidae blend of sex pheromone and attra J. Chem. Ecol. 20: 871-887.

- Garde, R. T. 1990. Principles of mating dist In R. L. Ridgway, R. M. Silverstein, a
- In R. L. Ridgway, R. M. Shverstein, e leds.], Behavior-modifying chemicals f ment: applications of pheromone and Marcel Dekker, New York.
- Cardé, R. T., and T. C. Baker. 1984. Sexu with pheromones, pp. 355-376. In W. Cardé [eds.], Chemical ecology of insu derland, MA.
- Cardé, R. T., and A. M. Minks. 1995. Co mating disruption: successes and const Entomol. 40: 559-585.
- Collett, D. 1989. Modelling binary data. New York.
- Daterman, G. E., G. Doyle Daves, Jr., ar Comparison of sex pheromone versu disruption of pheromone communica *buoltana*. Environ. Entomol. 4: 944-9
- Deland, J.-P., G.J.R. Judd, and B. D. Roitb tion of pheromone communication leafroller (Lepidoptera: Tortricidae) British Columbia. Environ. Entomol.
- Den Otter, C. J., and M. M. van der pheromone attractants and inhibito armyworm, *Mamestra brassicae* L. electrophysiological discrimination. I 235-242.
- Dyck, V. A., S. H. Graham, and K. A. B mentation of the sterile insect rele eradicate the codling moth, *Cydia pc* idoptera: Olethreutidae), in British pp. 285-297. *In* Proceedings of Intern on Management of Insect Pests: N Molecular and Genetic Techniques. I Energy Agency, Vienna, Austria. IAJ
- Evenden, M. L., G.J.R. Judd, and J. H. multaneous disruption of pheromon *Choristoneura rosaceana* (Harris) an (Robinson) with pheromone and J. Chem. Ecol. (in press).
- 1999b. Pheromone-mediated mating of toneura rosaceana: is the most attrace most effective? Entomol. Exp. Appl
- Flint, H. M., and J. R. Merkle. 1984. (Lepidoptera: Gelechiidae): alterat to gossyplure by release of its comp Econ. Entomol. 77: 1099-1104.
- GLIM. 1985. The statistical system fc interactive modelling, 3.77. Numeric Oxford Science Publications, Oxfor
- Judd, G.J.R., and H. L. McBrien. 199 mating disruption of pome fruit pest a multiple-species approach. In Pro Research, Development and C Semiochemicals in Insect Pest Ma National conference of the Ento Canada, 19 October 1994, Winnipeg agement Alternatives Office, Natur Canada.
- Judd, G.J.R., H. L. McBrien, and J. H. ification of responses by *Campyl* eroptera: Miridae) to pheromone l permeated with synthetic sex phe components. J. Chem. Ecol. 21: 19

fferent orchards with differing canid with greater population pressure nonitoring traps adjacent to experirelatively low proportion of females control plots in experiments 4 and 5 high level of competition from feral

1 Z9-14:OAc (blend 5) alone had no portion of females of either species C. rosaceana this was expected beis a known pheromone antagonist r 1984, Evenden et al. 1999a), and heromone antagonists alone has not e mating disruption in other studies 4. Rothschild 1974, Daterman et al. ie antagonists are not perceived as s they are present in the same plume ne components (Liu and Havnes t al. 1993). Furthermore, there are rs (ie. Den Otter and van der Haagen ruli in the macroglomerular complex obe of some insects that process renone antagonists alone (Mustaparta stimulation of this pathway does not heromone blend integration and upmales. For P. limitata, however, Z9r pheromone component (Roelofs et was a slight, nonsignificant reduction vitata in plots treated with Z9-14:OAc n other species, minor components ective as mating disruptants (Yashima shita et al. 1976, Kanno et al. 1978, al. 1983). We previously demonn et al. 1999a) that Z9-14:OAc does e of male P. limitata in female-baited that the major pheromone compoic, is required to provide adequate n of both P. limitata and C. rosaceano

Acknowledgments

. McBrien for advice and review of the ries and H. D. Pierce, Jr., for chemiel vesque and J. Hall for statistical advice and L.J. Chong for technical advice are C. Delury, N. L. Weremy, G. Zilahi-Bador for field assistance; and R. Schneide Wills for welcoming research in the k Ecogen, Incorporated, for preparation nsers. This research was supported by us of British Columbia, the Similkameen Oco oducers' Association, the British Columis sociation, Phero Tech Incorporated ces and Engineering Research Council

References Cited

 Mechanisms of communication disr mone in the control of Lepidoptera Entomol. 7: 353-364.
Karg, P. A. Kirsch, J. Löfqvist, A. Sauer, se 994. Mating disruption of pea moth Generation. nigricana F. (Lepidoptera: Tortricidae) by a repellent blend of sex pheromone and attraction inhibitors. J. Chem. Ecol. 20: 871-887.

- Cardé, R. T. 1990. Principles of mating disruption, pp. 47-71. In R. L. Ridgway, R. M. Silverstein, and M. N. Inscoe [eds.], Behavior-modifying chemicals for insect management: applications of pheromone and other attractants. Marcel Dekker, New York.
- Cardé, R. T., and T. C. Baker. 1984. Sexual communication with pheromones, pp. 355–376. In W. J. Bell and R. T. Cardé [eds.], Chemical ecology of insects. Sinauer, Sunderland, MA.
- Cardé, R. T., and A. M. Minks. 1995. Control of moths by mating disruption: successes and constraints. Annu. Rev. Entomol. 40: 559-585.
- Collett, D. 1989. Modelling binary data. Chapman & Hall, New York.
- Daterman, G. E., G. Doyle Daves, Jr., and G. Smith. 1975. Comparison of sex pheromone versus an inhibitor for disruption of pheromone communication in *Rhyacionia* buoliana. Environ. Entomol. 4: 944-946.
- Deland, J.-P., G.J.R. Judd, and B. D. Roitberg. 1994. Disruption of pheromone communication in three sympatric leafroller (Lepidoptera: Tortricidae) pests of apple in British Columbia. Environ. Entomol. 23: 1084–1090.
- Den Otter, C. J., and M. M. van der Haagen. 1989. Sex pheromone attractants and inhibitors in the cabbage armyworm, *Mamestra brassicae* L. (Lep.: Noctuidae): electrophysiological discrimination. Insect Sci. Appl. 10: 235-242.
- Dyck, V. A., S. H. Graham, and K. A. Bloem. 1993. Implementation of the sterile insect release programme to eradicate the codling moth, *Cydia pomonella* (L.) (Lepidoptera: Olethreutidae), in British Columbia, Canada, pp. 285–297. In Proceedings of International Symposium on Management of Insect Pests: Nuclear and Related Molecular and Genetic Techniques. International Atomic Energy Agency, Vienna, Austria. IAEA, Vienna.
- Evenden, M. L., G.J.R. Judd, and J. H. Borden. 1999a. Simultaneous disruption of pheromone communication in *Choristoneura rosaceana* (Harris) and *Pandemis limitata* (Robinson) with pheromone and antagonist blends. J. Chem. Ecol. (in press).
- 1999b. Pheromone-mediated mating disruption of *Choristoneura rosaceana:* is the most attractive blend really the most effective? Entomol. Exp. Appl. (in press).
- Flint, H. M., and J. R. Merkle. 1984. The pink bollworm (Lepidoptera: Gelechiidae): alteration of male response to gossyplure by release of its component Z, Z-isomer. J. Econ. Entomol. 77: 1099-1104.
- CLIM. 1985. The statistical system for generalized linear interactive modelling, 3.77. Numerical Algorithms Group, Oxford Science Publications, Oxford, England.
- G.J.R., and H. L. McBrien. 1994. Pheromone-based mating disruption of pome fruit pests in British Columbia: multiple-species approach. In Proceedings, Workshop: Research, Development and Commercialization of Semiochemicals in Insect Pest Management in Canada. National conference of the Entomological Society of Canada, 19 October 1994, Winnipeg, Manitoba. Pest Manment Alternatives Office, Natural Resources, Ottawa, Canada.
- G.J.R., H. L. McBrien, and J. H. Borden. 1995. Modfiction of responses by *Campylomma verbasci* (Hetrepter: Miridae) to pheromone blends in atmospheres permeated with synthetic sex pheromone or individual components. J. Chem. Ecol. 21: 1991-2002.

- Kaae, R. S., H. H. Shorey, L. K. Gaston and H. H. Hummel. 1974. Sex pheromones of lepidoptera: disruption of pheromone communication in *Trichoplusia ni* and *Pectinophora gossypiella* by permeation of the air with nonpheromone chemicals. Environ. Entomol. 3: 87-89.
- Kanno, H., S. Tatsuki, K. Uchiumi, M. Kurihara, and J.-I. Fukami. 1978. Disruption of sex attraction in the rice stem borer moth, *Chilo suppressalis* Walker, with components of the sex pheromone and related chemicals. Appl. Entomol. Zool. 13: 321-323.
- Levesque, C. A. 1990. The nature and significance of fungal colonizers in the herbicidal effect of glyphosate. Ph.D. dissertation, Simon Fraser University, Burnaby, BC, Canada.
- Linn, C. E., Jr., and W. L. Roelofs. 1981. Modification of sex opheromone blend discrimination in male Oriental fruit moths by pre-exposure to (E)-8-dodecenyl acetate. Physiol. Entomol. 6: 421-429.
- Liu, Y.-B., and K. F. Haynes. 1993a. Pheromone-mediated responses of male cabbage looper moths, *Trichoplusia ni*, following various exposures to sex pheromone or (Z)-7dodecenol. J. Chem. Ecol. 19: 503-515.
- 1993b. Impact of (Z)-7-dodecenol and turbulence on pheromone-mediated flight manoeuvres of male *Trichoplusia ni*. Physiol. Entomol. 18: 363-371.
- Minks, A. K., and R. T. Cardé. 1988. Disruption of pheromone communication in moths: is the natural blend really most efficacious? Entomol. Exp. Appl 49: 25–36.
- Miyashita, K., K. Kawasaki, Y. Uesumi, and T. Sugiura. 1976. Mating suppression of Spodoptera litura F. (Lepidoptera: Noctuidae) in green-houses by a component of its sex pheromone. Appl. Entomol. Zool. 11: 364-367.
- Mustaparta, H. 1996. Central mechanisms of pheromone information processing. Chem. Senses 21: 269-275.
- Pfeiffer, D. G., W. Kaakeh, J. C. Killian, M. W. Lachance, and P. Kirsch. 1993. Mating disruption to control damage by leafrollers in Virginia apple orchards. Entomol. Exp. Appl. 67: 47–56.
- Ridgway, R. L., R. M. Silverstein, and M. N. Inscoe. 1990. Behavior-modifying chemicals for insect management: applications of pheromones and other attractants. Marcel Dekker, New York.
- Roelofs, W. L., and M. A. Novak. 1981. Small-plot disorientation tests for screening potential mating disruptants, pp. 229-242. In E. R. Mitchell [ed.], Management of insect pests with semiochemicals. Plenum, New York.
- Roelofs, W. L., A. Cardé, A. Hill, and R. T. Cardé. 1976. Sex pheromone of the threelined leafroller, *Pandemis limitata*. Environ. Entomol. 5: 649-652.
- Rothschild, G.H.L. 1974. Problems defining synergists and inhibitors of the oriental fruit moth pheromone by field experimentation. Entomol. Exp. Appl. 294-302.
- Rumbo, E. R., S. M. Deacon, and L. P. Regan. 1993. Spatial discrimination between sources of pheromone and an inhibitor by the light-brown apple moth *Epiphyas postvit*tana (Walker) (Lepidoptera: Tortricidae). J. Chem. Ecol. 19: 953–962.
- Schwalbe, C. P., and V. C. Mastro. 1988. Gypsy moth mating disruption: Dosage effects. J. Chem. Ecol. 14: 581-588.
- Shorey, H. H., and R. L. Hale. 1965. Mass rearing of the larvae of nine noctuid species on a simple artificial medium. J. Econ. Entomol. 58: 522-524.
- Stadlebacher, E. A., M. W. Barry, A. K. Raina, and J. R. Plimmer. 1983. Fatal interspecific mating of two *Heliothis* species induced by synthetic sex pheromone. Experientia 39: 1174-1176.

JOURNAL OF ECONOMIC ENTOMOLOGY

Suckling, D. M., and P. W. Shaw. 1992. Conditions that favor mating disruption of *Epiphyas postvittana* (Lepidoptera: Tortricidae). Environ. Entomol. 21: 949–956.

1995. Large-scale trials of mating disruption of lightbrown apple moth in Nelson, New Zealand. N.Z. J. Crop Hortic. Sci. 23: 127-137.

- Suckling, D. M., and Burnip, G. M. 1996. Orientation disruption of *Planotortrix octo* using pheromone or inhibitor blends. Entomol. Exp. Appl. 78: 149-158.
- Thomson, D. R., N.P.D. Angerilli, C. Vincent, and A. P. Gaunce. 1991. Evidence for regional differences in the response of obliquebanded leafroller (Lepidoptera: Tortricidae) to sex pheromone blends. Environ. Entomol. 20: 935-938.
- Vakenti, J. M., A. P. Gaunce, K. N. Slessor, G.G.S. King, S. A. Allan, H. F. Madsen, and J. H. Borden. 1988. Sex pheromone components of the obliquebanded leafroller, *Choristoneura rosaceana* in the Okanagan Valley of British Columbia. J. Chem. Ecol. 14: 605-621.
- Van Deventer, P., and L.H.M. Blommers. 1992. Mating disruption of several leaf feeding orchard leaf-roller species with a single sex pheromone component. Acta Phytopathol. Entomol. Hung. 27: 615-620.
- Weatherston, I., D. Miller, and J. Lavoie-Dornik. 1985. Commercial hollow-fiber pheromone formulations: the

degrading effect of sunlight on celcon fibers causing creased release rates of the active ingredient. J. Cher Ecol. 11: 1631-1644.

- Webb, R. E., B. A. Leonhardt, J. R. Plimmer, K. M. Tatma V. K. Boyd, D. L. Cohen, C. P. Schwalbe, and L. W Douglass. 1990. Effect of racemic disparlure relation from grids of plastic ropes on mating success of go moth (Lepidoptera: Lymantriidae) as influenced by and population density. J. Econ. Entomol. 83: 910-91
- Witzgall, P., A. C. Backman, M. Svensson, M. Bengtsson, C. Unelius, J. Vrkoc, P. A. Kirsch, C. Loriatti, and J. Löfmid 1996. Potential of a blend of E8, E10-12OH and E8, E10-12OH and E8, E10-12Ac for mating disruption of codling moth, Code pomonella (L.) (Lep., Tortricidae). J. Appl. Entomol. 12 611-614.
- Yashima, T., Y. Tamaki, S. Kamano, and M. Oyama. 1973. Suppression of mating of the armyworm moth, Spodogeera litura, by a component of its sex pheromone. Appl Entomol. Zool. 10: 237-239.
- Zar, J. H. 1984. Biostatistical analysis, 2nd ed. Prentice-Hall Englewood Cliffs, NJ.

Received for publication 10 July 1998; accepted 11 January 1999.

Estimating Ec a

OCTAVIO

Centro Agronómico Tropical de I

ABSTRACT An alternative developed and illustrated. A relations involved in determi a more manageable model o sents a simpler but conceptua and pest control costs are a f thresholds can result in lower but could also be less costly economic threshold that resu functions.

KEY WORDS economic t

THE USE OF injury levels and thres improved the practice of pest manag last half of the 20th century. Stern e duced to the entomological literatu economic injury level (EIL) and eco revolutionizing pest control decisio et al. 1983, Mumford and Norton 19 the EIL as the lowest population cause enough economic damage to artificial control measures. They als nomic threshold as the density at w sures should be determined to prepest population from reaching the 1959).

To eliminate ambiguity and to m more rigorous economically, Hea Southwood and Norton (1973) rec the density at which the cost of equals the economic loss prevented the control tactic. Based on the forr defined the economic threshold as sity that represents a future popula which will prevent economic loss e implementing the control tactic. general formulas based upon the ϵ of the EIL and the economic thres tions developed by Southwood a which, unlike in Chiang (1982) (1986), are not restricted to syst relationships between insect den

¹Department of Agricultural and Applied University, Box 42132, Lubbock, TX 79409-5 sity is a co-sponsor of this research.

Vol. 92, no. .

390