Chapter 9

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Pheromones of Lepidopterous Insects

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INTRODUCTION

A decade has passed since I (W. L. R.) joined the New York State Agricultural Experiment Station, and in that time it has become obvious to me that the Experiment Stations play an important role in agriculture. They not only serve as a unique bridge between "ivory tower" research and grower extension services, but also encourage activities on both ends of this bridge. Thus, basic studies can be directed toward and brought along a continuum to the very practical end. In China university professors are required to work several months a year in the fields or factories to keep in touch with the needs of the masses. Laboratory researchers at Experiment Stations can get this feeling for reality without deserting the research programs by working very closely with colleagues who conduct research on the experimental farms and with individual growers.

In the insect pheromone area, the bridge between basic research and its application has been a very busy two-way street. Findings obtained in the laboratory are brought to the field, and data from the field reveal that more research is required in the laboratory. At first, pheromone research was held up until instrumentation became sufficiently sophisticated to allow chemists to identify pheromone compounds. In the course of this work it became obvious that the chemistry was dependent on good behavioral analyses in the laboratory

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and, particularly, in the field. When the pheromone components were identified, it was found that their use in the field was not straight-forward. Every species seemed to have its own optimum release rate, component ratio, trap design, trap placement, etc. Once a good attractant trap was developed by the combined efforts of chemists and entomologists, other questions arose, such as: 1) how does trap catch reflect population density; can it relate to the necessity of the timing of insecticide applications? 2) can the trap be economically used at a density that will suppress a pest population? 3) can pheromones be used to disrupt mating by atmospheric permeation; if so, what would be the most effective disruptant when dispersed throughout the field—the natural pheromone blend or just one of the pheromone components? and 4) what is the most economical way of dispersing the disruptant in the air to obtain the appropriate concentration for an entire insect flight?

These questions can be answered only by the coordinated efforts of chemists, biologists, economic entomologists, ecologists, and industry. Further development of the promising disruption technique may depend on more detailed knowledge of how pheromones are perceived and how they modify behavior. In this paper we wish to describe some of the efforts that we have made to define the individual roles of pheromone components. This will be the basis for a general survey of related pheromone blends, and will lead to a discussion on a current speculative hypothesis on the origin of pheromones.

Last year at the Cornell Centennial Symposium (Roelofs 1975) I described some of the studies that were carried out on our research animal, the redbanded leafroller moth (RBLR), *Argyrotaenia velutinana* (Wlkr.). Briefly, we have: 1) followed with light and electron microscopy the development of the female sex phermone gland through the pupal and adult stages; 2) defined the chemistry of the pheromone components; 3) conducted various male behavioral tests with the pheromone in the laboratory and the field; 4) studied electroantennogram responses to the pheromone components; and 5) conducted field studies on the use of the pheromone in monitoring insect abundance, mass trapping for control, and in male orientation and mating disruption tests. The next step was to define the role of each pheromone component, with the anticipation that more knowledge of their behavioral effects would help develop better mating disruption programs.

PHEROMONE COMPONENTS OF THE REDBANDED LEAFROLLER

The pheromone components are a mixture of *cis*-11-tetradecenyl acetate (c11-14:Ac), *trans*-11-tetradecenyl acetate (t11-14:Ac), and dodecyl acetate (12:Ac) (Fig. 1) (Roelofs et al. 1975). In field trapping studies, a definite ratio of ca. 8% t11-14:Ac in c11-14:Ac gave the best catches, and the addition of dodecyl acetate in a 3:2 or 2:1 ratio to the 14-carbon components resulted in up

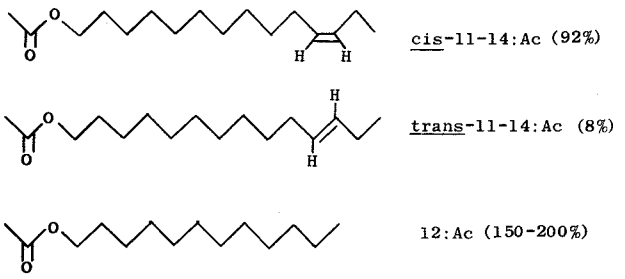

FIGURE 1 *Pheromone components of the redbanded leafroller moth.*

to 10-fold increases in trap catch. It would appear that dodecyl acetate is a potent synergist of attractancy, since it does not attract males by itself. However, counting the number of males caught in a trap does not reveal anything about the behavior that has occurred prior to their capture. To understand better the behavior effected by each component, the compounds were tested separately and in combination in electroantennogram studies, in laboratory stimulation and orientation behavioral assays, and in field behavioral observations (Baker 1975, Baker et al. 1976).

Field Behavioral Studies

Field studies with the pheromone components provide some interesting insights into the behavior effected by each. In one experiment the components were used alone and in various combinations in wicks placed in traps of various sizes (Fig. 2). The only treatments capturing more than two males were the 92:8 mixture of c11- and t11-14:Ac, and the mixture containing all three chemicals (Table 1). The presence of 12:Ac was most important with small traps, which require insects to orient very closely to the pheromone source before they can land. The table top traps captured the males almost at the periphery of the trap and showed only a two-fold increase with 12:Ac. These results indicate that dodecyl acetate is important only for close-range behavior, and that the correct blend of pheromone components is much more important when using the small traps.

Observations were made as males approached non-sticky table tops and Pherocon traps. In approaches to the table tops, males could be observed from as far away as 15 m. The males flew in low to the ground and landed periodically in the grass as they approached the pheromone source. Characteristic behavior exhibited on landing was antennal preening, followed immediately by wing fanning, walking up to the top of the grass blade, and flight. When finally in the vicinity of the table top, a male usually spent many seconds casting at the edge of the metal surface before landing. Observations of 108 males (Table 2) showed

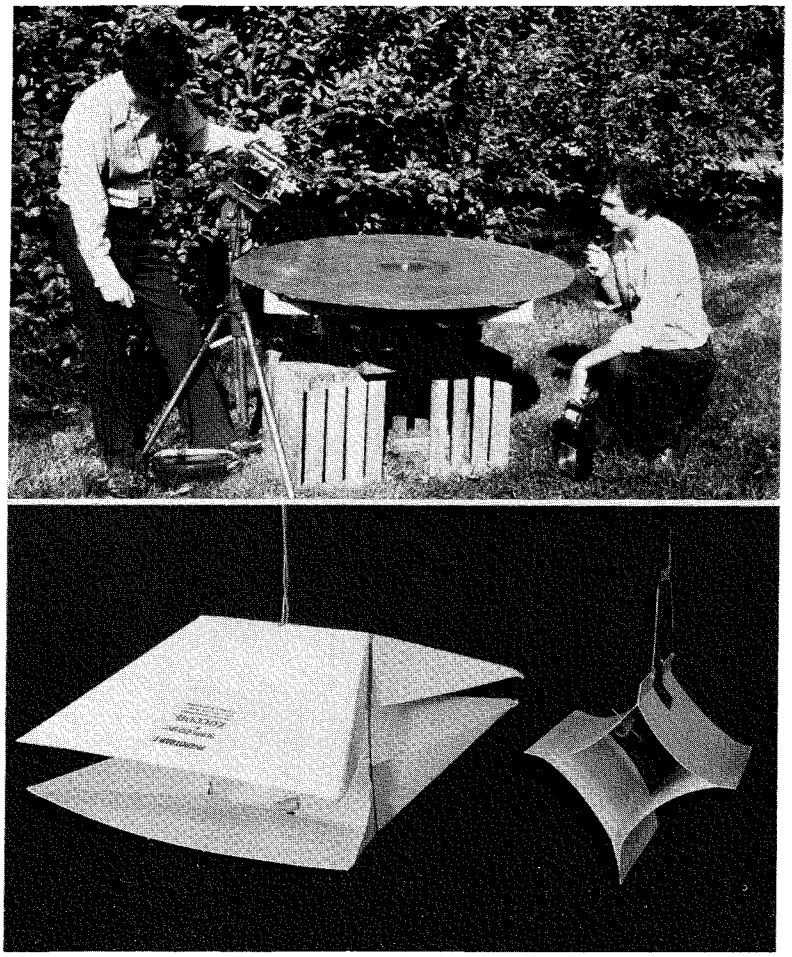

FIGURE 2 *(Top) Table top trap used with sticky surface to trap redbanded leafroller males, and used with a non-sticky surface to observe male behavioral responses to chemicals positioned in the center. (Bottom left) Pherocon*^{R} *IC trap. (Bottom right) Sectar I trap. Bottom traps are from Zoecon Corp. (Palo Alto, CA).*

the importance of 12:Ac in effecting close-range responses. With 12:Ac present, there was a significant increase in the number of males landing, in wing fanning, and in walking close to the pheromone source. Since there was no significant difference in the number of males approaching the table tops for the two treatments, the data show that 12:Ac does not "synergize" long-distance "attractancy", but rather elicits close-range responses.

These results were supported further by observing males approaching a non-sticky Pherocon trap. In this situation, males slowed their forward progress

TABLE 1 *The effect of 12:Ac on male RBLR captures with various trap sizes*

Type of trap	*Mean no. males captured/trap* Att.[a]	Att. + 12:Ac[a]	Ratio of males caught without/with 12:Ac
Table top, 60 cm radius	9.7	19.7	1:2.0
Pherocon IC, 14 cm radius	2.7	14.7	1:5.4
Sectar traps, 7.6 cm radius	2.0	24.6	1:12.3

[a]Attractant (Att.) = c11-14:Ac/t11-14:Ac (92:8), 10 mg; in second treatment 12:Ac, 15 mg.

as they neared the trap edge and engaged in short distance vertical or horizontal casting for as long as 17 sec before attempting to land. The males rarely flew directly into the trap, but landed somewhere on an outside surface and then walked into the trap while fanning. Again, treatments with and without 12:Ac brought an equivalent percentage of males to within 0.5 m of the trap (Table 3). The presence of 12:Ac, however, caused 100% of the males approaching the trap to land whereas only 31% of the approaching males landed with the treatment not emitting 12:Ac. With the 12:Ac, all of the males that landed also engaged in wing-fanning behavior and entered the trap. It is obvious from the data that 12:Ac effected large trap-catch increases in previous field studies because it caused many more males to land and to enter the trap.

Laboratory Behavioral Studies

In the field, no significant differences were found in the frequency or duration of wing fanning between the two treatments (without and with 12:Ac) once males had landed on the trap surfaces. This indicated that the close-range

TABLE 2 *Behavioral observations of RBLR males to table top pheromone sources*

Male behavior	Att.[a]	Att. + 12:Ac[a]
No. males observed	41	67
% approaching to 0.5 m	70.7	82.1 NS
% landing on table	19.0	71.6 **
% fanning while walking	26.8	56.7 **
% approaching to 10 cm of dispenser	17.1	52.2 ***

[a]Attractant (Att.) = c11-14:Ac/t11-14:Ac (92:8), 10 mg; in second treatment 12:Ac, 15 mg.
**$p < 0.01$
***$p < 0.001$

TABLE 3 *Behavioral observations of RBLR males to non-sticky Pherocon traps*

Male behavior	Att.[a]	Att. + 12:Ac[b]
No. of males observed	49	40
% approach to 0.5 m	85.7	87.5 NS
% landing on trap	26.5	87.5 ***
% males entering trap	20.4	87.5 ***
% males touching dispenser	14.3	62.5 ***

[a]Attractant (Att.) = c11-14:Ac/t11-14:Ac (92:8), 10 mg.
[b]12:Ac, 15 mg.
***$p < 0.001$

behavioral modification effected by 12:Ac occurs primarily while the male is in flight. In the overall sequence of precopulatory responses, 12:Ac appears to be important in getting males, which are casting about the pheromone source, to land. Since we could not duplicate this casting flight in our present laboratory stimulation and orientation behavioral tests, it was difficult to observe any behavioral effects attributable to 12:Ac in the laboratory. It did become obvious, however, that any behavioral modifications effected by the pheromone components are dependent on the quantity and quality of the stimulus. For example, at the 2 ng level (Fig. 3), 12:Ac did not elicit any response from RBLR males, whereas a 92:8 mixture of c11-14:Ac/t11-14:Ac, with or without 12:Ac, produced ca. 75% stimulation. It would appear that t11-14:Ac is inhibitory to these responses when present in percentages above 8% since the responses rapidly decrease as the amount of t11-14:Ac increases. Further studies, however, show that this is more likely caused by the differences in threshold levels needed to elicit responses by each mixture. Data (Fig. 4) from a dose-response series show that even pure t11-14:Ac can elicit good wing-fanning responses if present at high enough dosages. Again, the threshold of response was lowest for the 8% mixture. The dosage of 8% mixture needed to produce 50% wing fanning was 100 times less than that required with pure c11-14:Ac and 10,000 times less than that required with pure t11-14:Ac.

The third component, 12:Ac, was added to treatments of pure t11-14:Ac, pure c11-14:Ac, and the 8% mixture in stimulation and orientation bioassay tubes. Dosages of each treatment that elicited less than 50% wing fanning in previous studies did not elicit very different stimulation or orientation responses even though 12:Ac was added (Fig. 5). At higher dosages of the various treatments, 12:Ac was effective in maintaining throughout the 60 sec. period the initial high level of wing fanning produced by the pure c11-14:Ac and by the 8% mixture treatments. Without 12:Ac, wing fanning dropped in 30 sec. to ca. half the initial level.

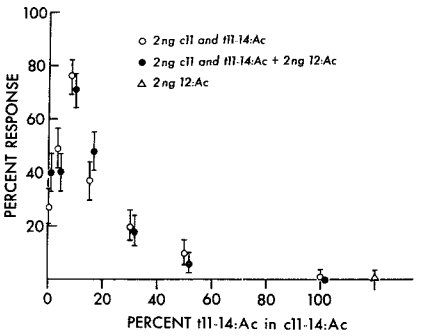

FIGURE 3 *Laboratory activation responses of redbanded leafroller males to pheromone component mixtures.*

In brief, RBLR male behavioral studies both in the laboratory and in the field revealed that these insects are very sensitive to a definite ratio of c11-14:Ac/t11-14:Ac components and that this ratio is needed to elicit and sustain the long-distance precopulatory flight. They also revealed that an additional component, 12:Ac, is used to effect close-range behavior once the moth has undergone the appropriate preceding precopulatory behavior.

Male Orientation Disruption

Since the long-distance components, c11-14:Ac and t11-14:Ac, are used in a 92:8 ratio, the question arises as to whether it would be better to disrupt male orientation with the minor component, t11-14:Ac, or with the correct pheromone blend. To answer this question, plots (0.25 ha each) in a vineyard

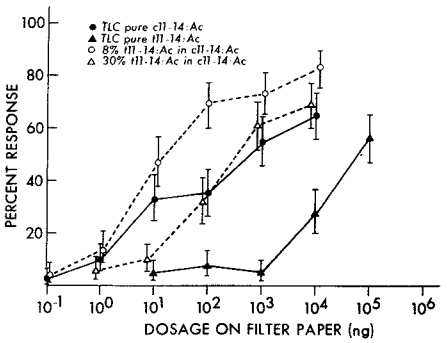

FIGURE 4 *Male redbanded leafroller wing fanning responses to pheromone components in box olfactometers.*

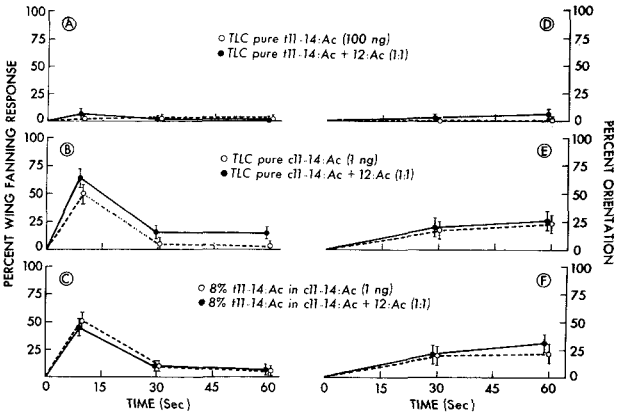

FIGURE 5 *Male redbanded leafroller wing fanning and orientation responses to pheromone components in glass tube olfactometers.*

were treated with microencapsulated (Pennwalt formulation) c11-14:Ac/t11-14:Ac mixtures in 89:11, 50:50 and 0:100 ratios. The three replicates of treated plots and their corresponding check plots were monitored with RBLR pheromone traps. The results (Table 4) (Roelofs et al. 1976a) indicate that the natural pheromone blend, 89:11, is the most effective disruptant, and the minor component, t11-14:Ac, is the least effective. Based on the laboratory behavioral observations, the disruption data could be interpreted as follows: The threshold for response is the lowest for the 89:11 mixture and the highest for t11-14:Ac.

TABLE 4 *Disruption of communication of male RBLR moths*

Treatment c11-14:Ac to t11-14:Ac	$\bar{x}$ males/plot[a]	$\bar{x}$% disruption[b]
89:11	1.0 d	98 a
Check	49.0 a	
50:50	4.6 c	89 b
Check	43.7 a	
0:100	13.0 b	67 c
Check	39.3 a	

[a]Means followed by an uncommon letter differ at the 5% level according to an analysis of variance of the number of males per plot transformed to $\sqrt{x + 0.5}$ and Duncan's new multiple range test.

[b]Percentages followed by an uncommon letter differ at the 5% level according to an analysis of variance of the percentages of disruption per plot transformed to the arcsin $\sqrt{\text{percentage}}$ and Duncan's new multiple range test.

The concentration of disruptant used in this test may not have been high enough to strongly affect the behavioral response with t11-14:Ac, whereas the 89:11 mixture concentration may have been above the threshold level for response with a resulting disruptant effect.

Pheromone Components of Other Leafrollers

The above discussion of the redbanded leafroller pheromone shows that the males are attuned to a particular combination of components. This is particularly important in maintaining specificity in the field in the presence of other species utilizing the same components. A review of pheromones of some other leafrollers (Table 5) shows that a number of species use their own particular ratio of c11-14:Ac/t11-14:Ac as their pheromone. Some other species use a very definite ratio of the positional isomers c11-14:Ac and c9-14:Ac, while others use a mixture of functional group analogs. In all cases reported, the female produces the components in approximately the same ratio that optimally attracts males in the field. Thus, it appears that the females emit a very precise

TABLE 5 *Pheromone blends of leafrollers (Tortricidae: Tortricinae)*

Species	Pheromone components: 14:Ac's *cis*-11	*trans*-11	Other components	Reference
1 Obliquebanded leafroller	92%	8%		Roelofs and Tette 1970
2 Redbanded leafroller	92	8	12:Ac (200%)	Roelofs et al. 1975
3 Fruittree leafroller	70	30	12:Ac (400)	Roelofs et al. 1974
4 Fruittree tortrix	50	50		Persoons et al. 1974
5 Omnivorous leafroller	12	88		Hill and Roelofs 1975
6 *Clepsis spectrana*	90	-	c9-14:Ac (10)	Minks et al. 1973
7 European leafroller	85	-	c11-14:OH (15)	Roelofs et al. 1976b
8 Smaller tea tortrix	35	-	c9-14:Ac (65)	Tamaki et al. 1971a
9 Orange tortrix	30	-	c11-14:ALD (70)	Hill et al. 1975
10 Summerfruit tortrix	10	-	c9-14:Ac (90)	Meijer et al. 1972 Tamaki et al. 1971b
11 Tufted apple bud moth	-	50	t11-14:OH (50)	Hill et al. 1974

1 *Choristoneura rosaceana* (Harris)
2 *Argyrotaenia velutinana* (Wlkr.)
3 *Archips argyrospilus* (Wlkr.)
4 *Archips podana* Scopoli
5 *Playnota stultana* Walsingham
6 *C. spectrana* (Treitschke)
7 *Archips rosanus* L.
8 *Adoxophyes fasciata* Walsingham
9 *Argyrotaenia citrana* (Fernald)
10 *Adoxophyes orana* (Fischer von Roeslerstamm)
11 *Platynota idaeusalis* (Wlkr.)

blend of chemicals to which the corresponding males are particularly sensitive. The origin of these chemicals and their variability within a species' pheromone is the subject of a current speculative hypothesis that has received much publicity in the lay press. The next section will discuss some of the research we have conducted on the oak leafroller moth, *Archips semiferanus* (Wlkr.), the insect that was involved in the development of the hypothesis.

SEX PHEROMONE OF THE OAK LEAFROLLER

Previous reports (Hendry et al. 1974, 1975a) on the oak leafroller (OLR) suggested that this moth was different from the other leafrollers because it utilized *cis*-10-tetradecenyl acetate (c10-14:Ac) as a major pheromone component along with at least 17 other monounsaturated 14-carbon acetate isomers in its pheromone system. These reports were of interest to us because the electroantennogram (EAG) responses of male OLR moths to various standards (Hendry et al. 1975b) did not support c10-14:Ac as the major component, and the large number of suggested pheromone components was inconsistent with the specific blends of other leafrollers. Further interest was generated when it was reported (Hendry et al. 1975c) that: 1) the OLR females did not produce pheromone if reared on semisynthetic diet without oak leaves; 2) the males appeared to be attracted to various 14-carbon acetate isomers at distinctly different times during the flight period, leading to the speculation that the oak leafroller was evolving subgroups on different species of oak; and 3) different 14-carbon acetate isomers were found in varying composition in leaves of several oak species suggesting that the subgroups were deriving their particular pheromone from the leaves on which the larvae had fed. These reports had implications for the general field of pheromones, so we investigated the pheromone of this "unusual" leafroller.

Pheromone Components in Female OLR

OLR eggs were obtained from Moshannon State Forest, Pa. and the larvae successfully reared on a pinto bean-based artificial medium (Shorey and Hale 1965) without addition of oak leaves or oak extract (Miller et al. 1976). OLR larvae and pupae also were collected from the foliage of oak trees within a natural infestation of OLR on Boone Mountain, 3 mi. north of Penfield in Elk County, Pa. Efforts were concentrated on obtaining specimens from chesnut (*Quercus prinus* L.), black (*Q. velutina* Lam.), and white (*Q. alba* L.) oaks. Leaves from the appropriate species were used in the laboratory to feed 5th instar larvae until pupation.

The abdominal tips of 2- to 3-day-old females 4 h into scotophase (16:8 LD) were extracted by soaking in methylene chloride. GLC analyses on an XF-1150 column (Fig. 6) showed that extracts from oak-reared females

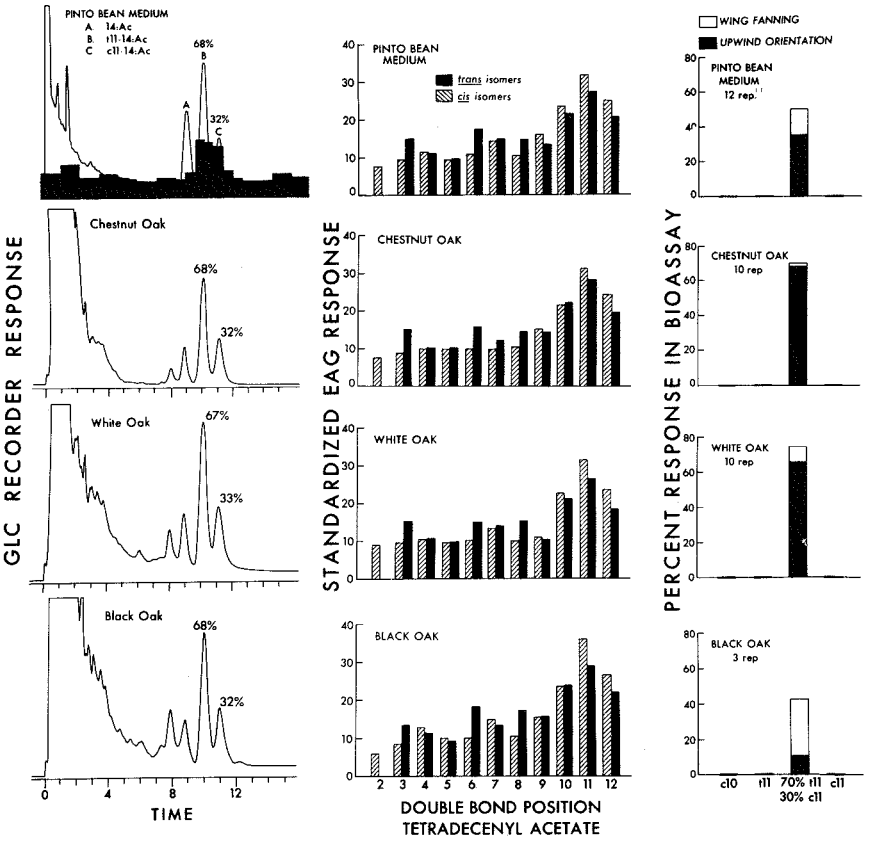

FIGURE 6 *Comparative a) pheromone gland GLC analyses, EAG activity is shaded in the pinto bean tracings, b) male antennal responses, and c) laboratory behavioral responses of oak leafrollers reared on a pinto bean diet, black oak leaves, white oak leaves, and chestnut oak leaves.*

produced the same three peaks (A, B, and C) as found with extracts from medium-reared females. These three components of all extracts showed the following similarities: a) identical GLC retention times; b) virtually identical ratios—the ratios of peak A to peaks B and C varied from 15 to 30%, but the B:C ratio was constant at $\bar{x}$ = 67:33 or 68:32; and c) presence in total quantities of 35-50 ng per individual.

EAG assay of 1-min collections of crude extract effluent from a nonpolar GLC column (OV-1) revealed only one area of EAG activity, which coincided with the retention times of 14-carbon acetates and included the retention times of all three components A, B and C. EAG-active material from OV-1 was

collected in 1-min fractions from XF-1150 with subsequent EAG assay. This showed that only components B and C elicited good antennal responses with the minute quantities involved in these extract aliquots (Fig. 6). The three components A, B and C had CLC retention times identical to those of tetradecenyl acetate, *trans*-11-tetradecenyl acetate and *cis*-11-tetradecenyl acetate on OV-1 and on XF-1150 columns (Miller et al. 1976). Saponification of the three components produced products with retention times identical to those of the corresponding alcohols on XF-1150, and treatment of the hydrolysis products with acetyl chloride gave products with the original component retention times on XF-1150.

Although the predominant pheromone components from the various female extracts appeared to be *trans*-11- and *cis*-11-tetradecenyl acetates, special efforts were made to determine if any of the other reported 14-carbon acetate isomers were present. Crude abdominal tip extract was separated by $AgNO_3$- silica gel TLC and the plates scraped in three bands corresponding to saturated-, *trans*-, and *cis*-compounds. GLC analysis (XF-1150) of each band revealed a single peak corresponding to components A, B and C, respectively, and no evidence of any other 14-carbon acetate isomers. Additionally, the 14-carbon acetate fraction from OV-1 of each type of female extract was subjected to microozonolysis. Each extract produced a large peak on OV-1 corresponding to 11-acetoxyundecanal, and another large peak corresponding to the unozonized tetradecenyl acetate (Fig. 7). These data confirmed the assigned Δ-11-tetradecenyl acetate structures for components B and C, and also showed that there were no detectable amounts (<1%) of the other positional isomers (Fig. 7).

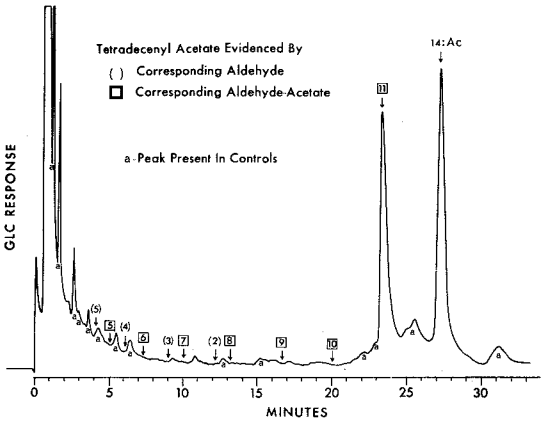

FIGURE 7 *Microozonolysis products on OV-1 of female abdominal tip extract from pinto bean diet-reared oak leafrollers.*

Male OLR Responses to Pheromone Components

EAG profiles were obtained for newly-emerged OLR males from the various oaks and the artificial medium (Fig. 6). Throughout the various series of 10- to 16-carbon acetates, alcohols and aldehydes, the four "types" of OLR males all responded similarly, with the greatest antennal responses elicited by the pheromone components, *cis*-11 and *trans*-11-tetradecenyl acetates.

The various 'types' of OLR males were used also in laboratory excitation and orientation bioassays (Baker et al. 1976, Miller et al. 1976). Again, the specificity of response was similar among all 'types', with only a 70:30 ratio of *trans*:*cis* mixture of Δ-11-tetradecenyl acetates eliciting responses in a series that included *cis*-10-, *cis*-11- and *trans*-11-tetradecenyl acetates (Fig. 6). The responses of the black oak males are shown to be lower than those shown for the other 'types', but this is attributed to the lack of these males for adequate replication, rather than a statistically different specificity.

The most important data, however, on the biological activity of the pheromone components are from field studies. To test the specificity of the OLR males in Pennsylvania to various ratios of the identified pheromone components and to other isomers previously reported to be pheromone components, we used the small Sectar and Pherocon IC traps (Fig. 2). As noted above with the redbanded leafroller studies, the smaller traps require a more precise blending of the pheromone to lure the males closer to the odor source and to get them to enter the traps. The treatments were replicated between 4–10 times for the various tests, and, more importantly, traps were re-randomized every night in most tests to average out possible population gradients and "hot spots" of OLR adults in the forest.

Specificity of OLR males for a blend of *trans*-11- and *cis*-11-tetradecenyl acetate is dramatically shown in Table 6. The *cis*-4- and *cis*-10-tetradecenyl acetates, as well as the individual pheromone components *cis*-11- and *trans*-11-tetradecenyl acetates did not attract any males, whereas a 7:3 mixture of the latter two compounds attracted 744 males in 2 days. Data from live female pairs show that the synthetic pheromone blend is as attractive as live females, and also show that males responded to all three "types" of OLR females in this test period.

Several other field attractancy tests (Miller et al. 1976) indicated that 1 mg of the pheromone blend on a rubber septum was more attractive to OLR males than lower quantities, and that 10 mg of the blend in polyethylene caps (used for many other leafrollers) was not attractive. Addition of tetradecenyl acetate, identified from OLR abdominal tips, did not increase trap catch, and decreased trap catch when present at >25% of the mixture. A series of *trans*-11/*cis*-11 mixtures was field tested to determine the specificity for the 67:33 ratio found in female tips. The data (Fig. 8) showed a surprisingly narrow range of attractive

TABLE 6 *Male oak leafroller attractancy studies, July 5-6, 1975*

Treatment[a]	$\bar{x}$ males/trap
cis-4-tetradecenyl acetate	0
cis-10-tetradecenyl acetate	0
cis-11-tetradecenyl acetate	0
trans-11/*cis*-11 (7:3)	124.2
(3-day-old) virgin females	
3 pairs from white oak	81.0
2 pairs from black oak	60.0
1 pair from chestnut oak	120.0

[a]Synthetic treatments were 1 mg chemical on a rubber septum; 6 replicates rerandomized daily.

ratios, with a significant difference obtained between ratios of 66:34 and 70:30. This narrow range of male responsiveness, along with the unvarying component ratios in the females, underscore the lack of pheromonal variation of oak leafrollers in Pennsylvania and further negate the possibility that some oak leafroller populations are evolving quite different pheromone systems in this area. At the conclusion of the 1975 field tests conducted in a very light OLR infestation, 4,242 oak leafroller males had been attracted to the pheromone

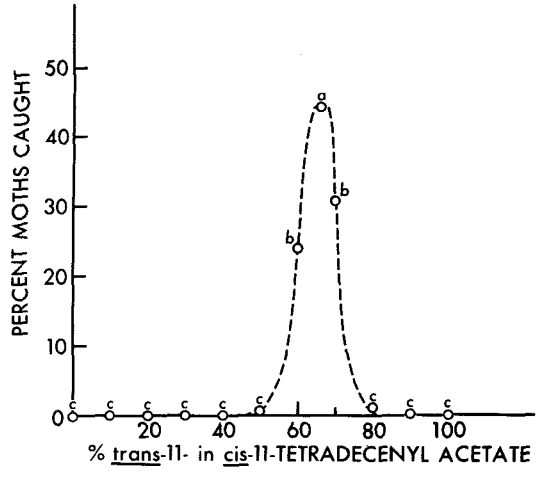

FIGURE 8 *Field attractancy test for oak leafroller males with varying ratios of t11- and c11-14 Ac. The test was conducted from July 6-16, 1975 using Sectar I traps spaced 15-20 m apart. The 6 replicates were re-randomized each day between July 8-11. Mean for the treatments marked by the same letter were not significantly different at the 5% level.*

blend of *trans*-11/*cis*-11 (7:3), and 0 males had been caught in traps baited with the series of individual isomers.

SUMMARY

The oak leafroller study showed that this species is similar to the other leafrollers. It can be reared successfully on diets in the laboratory, it utilizes a specific blend of pheromone components that are common to the other leafrollers, the pheromone components elicit the greatest EAG responses, the blend elicits the greatest laboratory behavioral responses, and the blend is as attractive in the field as virgin females.

Pheromones, therefore, have been shown to be important in reproductive isolation of a complex of sympatric leafrollers. Individual pheromone components are used in precise ratios to effect this specificity. As shown for the redbanded leafroller, additional components are sometimes used to mediate close-range behavior. Knowledge of these pheromone components and the behavioral responses mediated by them is increasingly important as efforts are directed toward the manipulation of pheromone communication for insect control.