Identification and possible functions of the hairpencil scent of the yellow peach moth, *Conogethes punctiferalis* (Guenée) (Lepidoptera: Pyralidae)¹

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Abstract

Male hairpencil scent of *Conogethes punctiferalis* was analyzed and its function was studied. A component detected by GC-EAD, was identified as (*E*)-2-methyl-2-butenic acid (tiglic acid) by GC, GC-MS. Males had no tiglic acid right after emergence but tiglic acid concentrations increased to an average of 1–2 µg/male by 2 weeks. Males with hairpencils from which tiglic acid was washed away by hexane and with removed hairpencils showed significantly lower mating success than control males. Less mating success occurred in females antennectomized bilaterally and normal males than with normal pairs. Tiglic acid was concluded to be a sex pheromone which functions in conspecific male recognition and also may be important as an aphrodisiac pheromone. Small numbers of males were attracted to hairpencil extracts or tiglic acid in a wind tunnel, but females showed no orientation or attraction to tiglic acid.

Key words: *Conogethes punctiferalis*, hairpencil scent, male sex pheromone, tiglic acid, mating behavior

INTRODUCTION

The yellow peach moth, *Conogethes punctiferalis* (Guenée), is a serious pest of various fruits and some field crops in tropical and temperate Asia and Australia. Female moths of this species release sex pheromone during the course of mating behavior. (*E*)-10-Hexadecenal and (*Z*)-10-hexadecenal, at a ratio of 9:1, have been identified as the main components of this female sex pheromone (Konno et al., 1982). A synthetic lure consisting of these components has been used for mass-trapping, monitoring and disruption in Japan, Korea and China.

Generally, mating behaviors of nocturnal lepidopteran species are regulated with a sophisticated female sex pheromone system, but male adults of some species also produce and release various volatile semiochemicals as pheromones from specific organs, hair pencils, hair brushes or wing androconias. With the hairpencils extruded, *C. punctiferalis* males posteriorly approach calling females and contact the females' bodies with their antennae be-

fore copulation (Konno et al., 1980). A sex pheromone of a sibling species, *Conogethes* sp., with a different host-plant range has almost the same chemical profile as that of *C. punctiferalis* (unpublished data). However, pre-mating and post-mating reproductive isolations have been established (Konno et al., 1981; Honda, 1986). These behavioral characteristics in conspecific or heterospecific interactions undoubtedly suggest an important biological function(s) of male sex pheromones.

We report here the chemical identification of a male sex pheromone and discuss its function in the mating system of *C. punctiferalis*.

MATERIALS AND METHODS

Insect. The yellow peach moth was reared on either an artificial diet (Honda et al., 1979), chestnut or corn. Adults were sexed at the pupal stage and kept separately in cages at 25±1°C, 55–70% R.H. and 15L–9D photoperiod and were provided with a 10% sugar solution from cotton pads. A 40 W red lamp was used for scotophase observations.

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Extracts and chemicals. The hairpencils of 3 virgin males (kept from females) were extruded by slight finger pressure on the abdomen and removed with ophthalmic scissors at 4 h after lights-off. When pharate male adults (0 day) were subjected to extraction, their puparium were carefully removed with fine forceps just before emergence. The hairpencils were extracted with a small volume of hexane in a conical glass vial for 5 min at room temperature. After filtration through a glass wool filter in a pipet, the extracts were concentrated to the appropriate volume using N_2 and stored at -20°C until use. Authentic *E*-2-methyl-2-butenic acid (tiglic acid), *Z*-2-methyl-2-butenic acid (angelic acid), *E*-2-pentenoic acid and 3-pentenoic acid were obtained from Sigma and Tokyo Kasei.

Gas chromatography (GC) and electroantennographic detection (GC-EAD). GC analysis was conducted on a Shimadzu GC-17A equipped with an HP-INNO WAX fused silica column ($25\text{ m} \times 0.25\text{ mm}$ ID, Yokokawa Hewlett-Packard, Tokyo, Japan) and a flame ionization detector (FID) under the following conditions: oven temperature was held at 80°C for 2 min, then increased to 200°C at $4^\circ\text{C}/\text{min}$, the temperatures of the detector and injector were 240°C , the carrier gas was He, and samples were injected in a splitless mode. The split valve was opened 1 min after injection. Retention times of the GC-EAD active components in the extract and authentic chemicals were compared on a polar column (DB-WAX) and an apolar column (DB-1; $30\text{ m} \times 0.25\text{ mm}$ ID, J & W Scientific, Folsom, California).

The GC-EAD was basically similar to that described by Arn et al. (1975). An HP-INNO WAX column ($25\text{ m} \times 0.25\text{ mm}$ ID, Yokokawa Hewlett-Packard) was installed in a Hewlett-Packard 5890 Series II GC. Injections were splitless. The oven temperature was held at 50°C for 2 min and then increased to 150°C at a rate of $10^\circ\text{C}/\text{min}$. The effluent from the column was split at a 1:1 ratio between a flame ionization detector (FID) and an electroantennographic detector (EAD). Humidified air at 21°C delivered the GC effluent to the antennal preparation which was bridged between a pair of drops of 0.1 M KCl saline on Ag-AgCl electrodes.

Gas chromatography-mass spectrometry

(GC-MS). GC-MS analysis was conducted by the coupling of a mass selective detector (MSD) (Hewlett-Packard 5972 Mass Engine) and a Hewlett-Packard 5890 Series II GC equipped with a DB-WAX column ($30\text{ m} \times 0.25\text{ mm}$ ID, J & W Scientific). The column oven temperature was held at 60°C for 2 min then increased to 200°C at $4^\circ\text{C}/\text{min}$. The interface was maintained at 280°C .

Methylation and dimethyl disulfide (DMDS) adduct. Authentic mono-unsaturated acids and crude extracts were converted to the corresponding methyl esters and subsequently derivatized to DMDS adducts to determine the position of the bound olefinic. A 50 ml aliquot of etherial diazomethane was added to the ether solution of authentic acids or the crude extract and the mixtures were allowed to react for 30 min at room temperature. An aliquot of the products was subjected to GC and GC-MS analyses. As described by Buser et al. (1983), 20 μl of DMDS and 4 μl of 1% iodine solution in ether were added to 5 μl of a hexane solution of the methylated authentic acids or the extracts. The mixtures were sealed in glass ampules and incubated at 40°C for 12 h, and then extracted with 100 μl of hexane three times after addition of 5% $\text{Na}_2\text{S}_2\text{O}_3$. The extracts were dehydrated with anhydrous Na_2SO_4 and concentrated for GC-MS.

Bioassay in cages. To clarify the functions of male hairpencil components in mating behavior, 3-day-old male and female moths were subjected to the following treatments. In the first experiment, 7 males were anesthetized with CO_2 and their hair pencils were surgically removed with fine forceps. Each hairpencil of the 7 other males was washed with 3 μl of hexane after CO_2 anesthesia (a preliminary GC analysis confirmed that tiglic acid contents of washed males was 1/10 less than those of normal males). Seven pairs of these male moths and normal female moths were housed in a plastic cage ($23\text{ cm} \times 41\text{ cm} \times 29\text{ cm}$). Their mating success was observed hourly for 6 to 9 h during the scotophase. Mating pairs were removed. The numbers of moths performing each behavior were compared using a χ^2 2×2 test of independence with Williams' correction. Statistical significance was detected at the $p < 0.05$ level.

In the second experiment, two-choice tests by males in the cage were conducted: 5 normal male moths were allowed access to (a) 5 normal females vs. 5 females with antennae removed, (b) 5 females with half binary antennae removed vs. 5 normal females, (c) 5 females fully antennectomized vs. 5 normal females and (d) 5 females with fully antennectomized vs. 5 females with half binary antennae removed. Antennectomization was done under CO₂ anesthesia.

In both experiments, male moths used as a control were treated in the same manner but hair pencils and antennal segments were left intact. All observations were conducted for 7 days under the conditions mentioned above.

Bioassay in a wind tunnel. Responses to hairpencil extracts or authentic chemicals were examined using a wind tunnel (200 cm × 30 cm × 30 cm). The fresh air stream in the tunnel was controlled by an electric fan blower at a speed of 0.3 m/s. The 3- to 6-day old males were tested individually and the following behavior categories were recorded: catch plume, close to source (within 5 cm), contact with the source. A hexane solution of authentic baits or hairpencil extracts of 5 males was applied to strips of filter paper. Controls were treated with 5 μ l of hexane only. The filter paper strip was suspended about 15 cm from the top and 15 cm from the upwind end of the tunnel. After the stimulus source was set, males were introduced into the tunnel about 15 cm from the top and 15 cm from the downwind end of the tunnel. All experiments were conducted for 5 to 7 h during the scotophase at 22 ± 2°C under 1.5 lux red lamp. Three behavioral categories were recorded: (1) catch plume (catch the pheromone plume at center of wind tunnel); (2) close to source (within 5 cm of the source and hovering around it); (3) source contact. The numbers of moths performing each behavior were compared using a χ^2 2 × 2 test of independence with Williams' correction. Statistical significance was detected at the $p < 0.05$ level.

RESULTS

Chemical identification of male scent

GC-EAD analysis of hairpencil extracts for ten males revealed that a female-antennal re-

sponse was associated exclusively with a peak (compound A) during a retention time of 10.3 min (Fig. 1). The molecular weight and fragmentation patterns of compound A were determined by GC-MS analyses. Compound A gave the following diagnostic ion peaks; parent peak at m/z 100, m/z 85 ($M^+ - 15$) and m/z 55 ($C_4H_7^+$) (Fig. 2A), which corresponds to an unsaturated molecular structure of $C_5H_8O_2$. The methylation product of compound A by ethereal diazomethane gave a corresponding methyl ester with a molecular ion peak at m/z 114 by GC-MS (Fig. 2B). This indicates that compound A could be an unsaturated carboxylic acid. As shown in Fig. 2C, the DMDS adduct of methylated compound A gave two characteristic diagnostic ions at m/z 75 ($C_2H_4SCH_3^+$) and 134 ($C_2H_3COOCH_3SCH_3^+ + H$), indicating an unsaturated double bond between C₂ and C₃ or C₃ and C₄. From these spectral data, 2-methyl-2-butenic acid and 3-pentenoic acid were proposed as candidate structures for compound A.

The GC-retention time of the methylated compound A was compared with that of four authentic compounds including the above candidates. As shown in Table 1, methyl *E*-2-methyl-2-butenate (methyl tiglate), methyl *Z*-2-methyl-2-butenate (methyl angelate), methyl *E*-2-pentenoate and methyl 3-pentenoate were clearly discriminated by their retention times on

Fig. 1. GC-EAD analysis of female antennal responses to hairpencil extract of male *C. punctiferalis*.

Fig. 2. GC-EI mass spectra of compound A from hairpencil extract of male moths, authentic *Z*-2-methyl-2-butenic acid and their derivatives.

Table 1. Retention times of methylated compound A and authentic chemicals on polar and apolar GC columns

Chemicals	INNO-WAX (polar)	DB-1 ^c (apolar)
Compound A	8.69 ^a	—
Tiglic acid	8.68 ^a	—
Methyl 2-pentenoate	8.51 ^b	6.00
Methyl 3-pentenoate	8.09 ^b	5.46
Methyl tiglate	8.21 ^b	6.02
Methyl angeliate	6.58 ^b	5.19
Methylated compound A	8.22 ^b	6.03

^a 60°C (2 min)–20°C/min–170°C, ^b 40°C (2 min)–4°C/min–120°C, ^c 40°C (2 min)–1°C/min–120°C.

polar (INNO-WAX) and apolar (DB-1) columns. The retention time of compound A when converted to a methyl ester coincided well with that of methyl tiglate.

Mass-spectra of compound A and its derivatives by GC-MS were almost the same as those of tiglic acid, methyl tiglate and DMDS adduct of methyltiglate (Fig. 2C, D, E, F). Tiglic acid also evoked female antennal response as well as compound A in GC-EAD.

Relationship between male scent content and male age or larval foods

Male hairpencils of pharate adults (0 day) contained no tiglic acid, but this acid was found at low levels on the day of emergence and increased gradually to ca. 1.5 µg/male by 14 days after emergence (Fig. 3). There was no significant difference in the levels of tiglic acid production by males reared on the artificial diets, chestnut or corn.

Biological functions of male scent

As shown in Table 2, when males with hairpencils washed with hexane were allowed to mate with female adults in bioassay-1 (non-choice test), their mating success was 21.4% and this was significantly lower than that of control pairs (71.4%). Similar decreased mating (28.5%) was also observed in pairs of males without hairpencil. A second bioassay (choice test) was designed to confirm whether olfactory detection of male scent by females was essential for the acceptance of males. Females were antennectomized in different fashions and allowed to mate with normal males (Table 3). There was

Fig. 3. Tiglic acid content in the hairpencil extract of male *C. punctiferalis* at various ages.

Table 2. Mating success by male *C. punctiferalis* with removed hairpencils or without tiglic acid as compared to normal male moths

Treatments	No. pairs tested	Mating success (%)
Intact (control)	21	71.4 a
Washed with hexane	56	21.4 b
Hairpencils excised	14	28.5 b

Within columns, percentage followed by a common letter do not differ significantly at $p < 0.05$ according to the chi-square test of independence with Williams correction.

no significant difference in matings between males and intact females or females with either antenna removed or with half-cut antennae. However, mating success between females antennectomized bilaterally and males was significantly decreased. In this combination, it was frequently observed that antennectomized females refused final contact or copulation with males by flapping their own wings vertically or moving away. During these two bioassays, normal calling behaviors were observed in most females tested, and male moths with washed hairpencils also showed normal oriented flights to calling females.

In the wind tunnel test, low percentages of male moths were attracted to and contacted the filter paper strip treated with crude extract or tiglic acid (Table 4). Approximately 22.9% of males showed typical behavior of 'catch plume,'

Table 3. Mating responses of *C. punctiferalis* males to antennectomized females

Antennal excision in females	No. of pairs tested	No. of pairs mated
A vs. B		A vs. B
One antenna vs. intact	10	5:4
Both half antennae vs. intact	15	7:6
Both antennae vs. intact	20	2:17
Both antennae vs. both half antennae	25	3:18

Table 4. Behavioral responses of male *C. punctiferalis* to tiglic acid in a wind tunnel

Tiglic acid (µg)	N	Percentage of males responding		
		Catch plume	Close to source	Source contact
Control	30	0 a	0 a	0 a
0.05	20	5.0 ab	5.0 ab	5.0 a
0.5	25	16.0 abc	12.0 ab	8.0 a
5	35	22.9 bc	11.4 ab	8.6 a
50	50	34.0 c	22.0 b	2.0 a
Male extract ^a	25	16.0 abc	12.0 ab	12.0 a
Female (5 µg) ^b	20	0	0	0

^aFive male equivalents.

^bFemales were exposed to 5 µg of tiglic acid.

Within columns, percentage followed by a common letter do not differ significantly at $p < 0.05$ according to the chi-square test of independence with Williams correction.

and 8.6% of males contacted the filter paper with 5 µg tiglic acid. The lower the dose of tiglic acid the less males responded. Extracts of hairpencils of five males equivalent to 5 µg also provoked biological activity in males. No females were attracted to tiglic acid.

DISCUSSION

Many species of nocturnal moths produce and release odorous compounds from specialized scales such as hairpencils, hair brushes or androconias. In over ten species of Noctuidae, various aromatic compounds including 2-phenylethanol, benzyl alcohol and benzaldehyde have been reported as male specific scents (Aplin and Birch, 1968, 1970; Meinwald et al.,

1971; Clearwater, 1972; Birch et al., 1976; Jacobson et al., 1976; Bestmann et al., 1977; Hirai, 1977, 1980a, b; Hirai et al., 1978; Rong et al., 1997). Most of these compounds are found with other related compounds, but others also occur with short-chain aliphatic acids. The male scents of *Leucania conigera*, *L. impura* and *L. palleas* (Aplin and Birch, 1968, 1970), and of *Pseudaletia separata* (Rong et al., 1997) contain iso-butyric acid and acetic acid, respectively, in addition to aromatic compounds. In *Cucullia umbratica*, male scents consist of only free fatty acids, 2-methylpropanoic acid and 2-methylbutanoic acid (Birch, 1972). Our finding of tiglic acid from male hairpencils of *C. punctiferalis* is the first report of an unsaturated fatty acid as male scent (sex pheromone), although it has been reported as a defense substance of Carabid beetles (Schildknecht, 1970; Kanehisa and Kawazu, 1982; Attygalle et al., 1991).

The male scents (pheromones) of lepidopteran insects possess various kinds of biological functions. In the case of butterflies, male scents have been recognized as aphrodisiac pheromones (Pliske and Eisner, 1969). Male pheromones of the Oriental fruit moth, *Grapholitha molesta*, attract sex-pheromone-releasing females for a short distance (Baker et al., 1981; Nishida et al., 1982). In *Galleria mellonella*, male pheromones elicit typical female sexual behaviors (Leyrer and Monroe, 1973; Thibout et al., 1994), and there are no attractive pheromones for the males. In some species of moths, male scents function as an arrestant (aphrodisiac) to the female, stimulants for calling by the female (Clearwater, 1972; Hendricks and Shaver, 1975), or inhibitors of approach and copulatory behaviors for conspecific competitors (Hirai et al., 1978).

Despite normal calling, antennectomized *C. punctiferalis* females showed lower mating success with normal males than intact or females missing only one antenna or half of antennae in choice tests. This lower mating success results from a failure to detect a male pheromone by females rather than the effect of antennal trauma. Similar results have also been found in *Ostrinia nubilalis* (Royer and McCeil, 1992). Although male adults of *Leucania separata* and *Mamestra brassicae* have odorous hair brushes,

their mating success was not effected by removal of these organs or female antennae (Hirai, 1977).

Significantly decreased mating success in male *C. punctiferalis* without hairpencils or tiglic acid and in antennectomized females indicates that tiglic acid in the hairpencils is indispensable for establishing normal mating behaviors in this species, and that tiglic acid can be defined as a sex pheromone of this species. Female moths may discriminate conspecific males from other species because tiglic acid was not found in a sibling species, *Conogethes* sp. which had almost the same female sex pheromones as *C. punctiferalis* (unpublished data). Another possible function is selection of new virgin males from the male population.

The crude extract from hairpencils and tiglic acid attracted a lower percentage of males. If the male attraction to the hairpencil scent was involved in reproductive behaviors, a higher percentage of males should have responded. Such exclusive attractiveness to conspecific males by male sex pheromones has not been reported thus far. Both sexes of the saltmarsh moth, *Ectingmene acraea* (Willis and Birch, 1982) and the cabbage looper moth, *Trichoplusia ni* (Noctuidae) (Landolt and Heath, 1990; Landolt et al., 1996) were reported to be attracted to the male corematal scents. These bisexual attractions were explained as an aggregation to make leks for mating behavior. There has been, however, no evidence of lek formation in *C. punctiferalis* in the field and, thus, the precise biological significance of the male response to the male sex pheromone remains to be clarified.

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REFERENCES

- Aplin, R. T. and M. C. Birch (1968) Pheromones from the abdominal brushes of male noctuid Lepidoptera. *Nature* 217: 1167-1168.
- Aplin, T. R. and M. C. Birch (1970) Identification of odorous compounds from male Lepidoptera. *Experientia* 26: 1193-1194.
- Arn, H., E. Städler and S. Rauuscher (1975) The electroantennographic detector—a selective and sensitive tool in the gas chromatographic analysis of insect pheromones. *Z. Naturforsch.* 30C: 722-725.
- Attygalle, A. B., J. Meinwald, J. K. Liebherr and T. Eisner (1991) Sexual dimorphism in the defensive secretion of a carabid beetle. *Experientia* 47: 296-299.
- Baker, T. C., R. Nishida and W. L. Roelofs (1981) Close-range attraction of female oriental fruit moths to herbal scent of male hairpencils. *Science* 214: 1359-1361.
- Bestmann, H. J., O. Vostrowsky and H. Platz (1977) Pheromone. XII. Männchenduftstoffe von Noctuiden (Lepidoptera). *Experientia* 35: 874-875.
- Birch, M. C. (1972) Male abdominal brush-organs in British noctuid moths and their values as a taxonomic character (Part I). *Entomologist* 105: 233-244.
- Birch, M. C., G. G. Grant and U. E. Brady (1976) Male scent brush of *Peridroma saucia*: chemistry of secretion. *Ann. Entomol. Soc. Am.* 69: 491-492.
- Buser, H. R., H. Arn, P. Guerin and S. Rauscher (1983) Determination of double bond position in mono-unsaturated acetates by mass spectrometry of dimethyl disulfide adducts. *Anal. Chem.* 55: 818-822.
- Clearwater, J. R. (1972) Chemistry and function of a pheromone produced by the male of the southern armyworm *Pseudaletia separata*. *J. Insect Physiol.* 18: 781-789.
- Hendricks, D. E. and T. N. Shaver (1975) Tobacco budworm: male pheromone suppressed emission of sex pheromone by the female. *Environ. Entomol.* 4: 555-558.
- Hirai, K. (1977) Observations on the function of male scent brushes and mating behavior in *Leucania separata* W. and *Mamestra brassicae* L. (Lepidoptera, Noctuidae). *Appl. Entomol. Zool.* 12: 347-351.
- Hirai, K. (1980a) Male scent emitted by armyworms, *Pseudaletia unipuncta* and *P. separata* (Lepidoptera: Noctuidae). *Appl. Entomol. Zool.* 15: 310-315.
- Hirai, K. (1980b) Behavioral function of male scent in moths (Lepidoptera: Noctuidae). *Bull. Chugoku Natl. Agric. Exp. Stn.* E16: 1-32.
- Hirai, K., H. H. Shorey and L. K. Gaston (1978) Competition among courting male moths: Male-to-male inhibitory pheromone. *Science* 202: 644-645.
- Honda, H. (1986) Post-mating reproductive isolation between fruit- and Pinaceae-feeding types of the yellow peach moth, *Conogethes punctiferalis* (Guenée) (Lepidoptera: Pyralidae). *Appl. Entomol. Zool.* 21: 489-491.
- Honda, H., J. Kaneko, Y. Konno and Y. Matsumoto (1979) A simple method for mass-rearing of the yellow peach moth, *Dichocrocis punctiferalis* Guenée (Lepidoptera: Pyralidae) on an artificial diet. *Appl. Entomol. Zool.* 14: 464-468.
- Jacobson, M., V. E. Adler, A. N. Kishaba and E. Priesner (1976) 2-Phenylethanol, a presumed sexual stimulant produced by the male cabbage looper moth, *Trichoplusia ni*. *Experientia* 32: 964-966.
- Kanehisa, K. and K. Kawazu (1982) Fatty acid components of the defensive substances in acid-secreting carabid beetles. *Appl. Entomol. Zool.* 17: 460-466.
- Konno, Y., K. Arai, K. Sekiguchi and Y. Matsumoto (1982) (E)-10-Hexadecenal, a sex pheromone component of the yellow peach moth, *Dichocrocis punctiferalis* Guenée (Lepidoptera: Pyralidae). *Appl. Entomol. Zool.* 17: 207-217.
- Konno, Y., H. Honda and Y. Matsumoto (1980) Observations on the mating behavior and bioassay for the sex pheromone of the yellow peach moth, *Dichocrocis punctiferalis* Guenée (Lepidoptera: Pyralidae). *Appl. Entomol. Zool.* 15: 321-327.
- Konno, Y., H. Honda and Y. Matsumoto (1981) Mechanisms of reproductive isolation between the fruit-feeding and the Pinaceae-feeding types of the yellow peach moth, *Dichocrocis punctiferalis* Guenée (Lepidoptera: Pyralidae). *Jpn. J. Appl. Entomol. Zool.* 25: 253-258 (in Japanese with English summary).
- Landolt, P. J. and R. R. Heath (1990) Sexual role reversal in mate-finding strategies of the cabbage looper moth. *Science* 249: 1026-1028.
- Landolt, P. J., O. H. Molina, R. R. Heath, K. Ward, B. D. Dueben and J. G. Millar (1996) Starvation of cabbage looper moths (Lepidoptera: Noctuidae) increases attraction to male pheromone. *Ann. Entomol. Soc. Am.* 89: 459-465.
- Leyrer, R. L. and R. E. Monroe (1973) Isolation and identification of the scent of the moth, *Galleria mellonella*, and a revaluation of its sex pheromone. *J. Insect Physiol.* 19: 2267-2271.
- Meinwald, J., W. R. Thompson and T. Eisner (1971) Pheromones. VII. African monarch: major components of the hairpencil secretion. *Tetrahedron Lett.* 38: 3485-3488.
- Nishida, R., T. C. Baker and W. L. Roelofs (1982) Hairpencil pheromone components of male oriental fruit moths, *Grapholitha molesta*. *J. Chem. Ecol.* 8: 947-959.
- Pliske, T. E. and T. Eisner (1969) Sex pheromone of the queen butterfly: biology. *Science* 164: 1170-1173.
- Rong, K., Y.-S. Chow and H.-Y. Ho (1997) Chemical composition of hair pencil extract in male Oriental armyworm *Pseudaletia separata* Walker (Lepidoptera: Noctuidae) in Taiwan. Abst. 3rd Asia-Pacific Conf. Entomol., p. 104.
- Royer, L. and J. N. McCeil (1992) Evidence of a male sex pheromone in the European corn borer, *Ostrinia nubilalis* (Hubner) (Lepidoptera: Pyralidae). *Can. Entomol.* 124: 113-116.
- Schildknecht, H. (1970) Die Wehremie von Land- und Wasserkäfern. *Angew. Chem.* 82: 17-25.
- Thibout, E., S. Ferary and J. Auger (1994) Nature and role of sexual pheromones emitted by males of *Acrolepiopsis assectella* (Lep.). *J. Chem. Ecol.* 20: 1571-1581.
- Willis, M. A. and M. C. Birch (1982) Male lek formation and female calling in a population of the Arctiid moth *Estigmene acrea*. *Science* 218: 168-170.