配偶行動時の昆虫性フェロモンの役割I

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Role of Insect Sex Pheromone in Mating Behavior I. Theoretical Consideration on Release and Diffusion of Sex Pheromone in the Air

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An equation concerning sex pheromone diffusion was obtained through micrometeorological knowledge. By assuming a model moth with its sex pheromone and sex pheromone-effective sphere, analyses of role of male's flight and sex pheromone were attempted. Consequently, the relationship among size of sex pheromone-effective sphere, release rate and threshold concentration was found to be very important.

INTRODUCTION

Sex pheromone, released by a virgin female, is diffused into the air and is percieved by flying sex pheromone-sensitive males. The male response results in copulation, which is the last step in the whole process of mating. Knowledge of the process and its utilization in pest control are a subject of insect sex pheromone biology. While isolation, identification and synthesis of sex pheromone have been noticeably developed, the process from the time of female pheromone release to copulation has rarely been studied. A primary subject of insect sex pheromone biology is to investigate how an insect utilizes sex pheromone in the air. Therefore, not only isolation, identification and synthesis of sex pheromone but also the study on this process is so important that both must be studied together. On each step of the process, the effectiveness of sex pheromone is related to its physical properties and insect behavior. For example, sex pheromone extension into the air can be described not only by the release rate and/or threshold concentration of sex pheromone (BOSSERT and WILSON, 1963), but also by mating behavior (HIDAKA, 1972). However, the release rate or the threshold concentration of sex pheromone are hardly measured and the mating behavior of field insects are scarcely revealed in detail. This paper will consider the relationship among factors which constitute the process from female pheromone release to male perception. In order to examine this process, a model system will be analyzed on physicochemical, ethological and micrometeorological standpoint.

Bases of an equation for sex pheromone diffusion[1]

Suppose in this model that an insect has a mating behavior similar to that of *Hyphantria cunea* DRURY (Lepidoptera : Arctiidae) and that lauryl acetate or myristyl acetate is its sex pheromone. Since physicochemical properties, especially those related

[1] Table 1 explaining variables.

Table 1. VARIABLES USED IN EQUATIONS

C_0 :	Saturated vapor density (μg/ml)
C' :	Vapor density outside boundary layer (μg/ml)
$C(X)$:	Concentration of sex pheromone at the distance downwind from a virgin female (μg/ml)
D_M :	Diffusion coefficient (cm^2/sec)
G :	Gustiness (non-dimensional)
P :	Vapor pressure (mmHg)
P_0 :	Amount of sex pheromone in unit distance (μg/cm)
Q :	Minimal concentration of sex pheromone which changes male random-flight into zigzag one, threshold concentration (μg/ml)
r :	Radius of sex pheromons releaser (cm)
$S(X)$:	Cross-section area of diffusion plume (cm^2)
U :	Mean wind velocity (cm/sec)
W_0 :	Release rate of sex pheromone (μg/sec)
$(W)_0$:	Ratio of release rate to threshold concentration (ml/sec)
X :	Distance downwind from a virgin female (cm)
X_M :	Maximal sex pheromone-effective distance downwind from a virgin female (cm)
$\overline{y^2}$:	Mean variance of wind variation (cm^2)
α :	Factor of wind (cm/sec)
δ :	Thickness of boundary layer (cm)

to vaporization of moth sex pheromone, seem to be analogous[2] to those of lauryl acetate or myristyl acetate, we choose these materials as the model sex pheromone. An idea for the relationship between sex pheromone-effective sphere and a change in male's flight pattern was postulated from an observation on mating behavior of *H. cunea* (HIDAKA, 1972), so that this insect is adopted as a basic animal for this model. This hypothesis was reconfirmed by our field observation. We found that maximum distance from a virgin female to a point where flying males randomly began to fly in a zigzag way was 5–6 m and that the males approached the female along this distance for 15–30 sec. A concept of the distance is alternative to that of the pheromone-effective sphere (Fig. 1). On the other hand, medium of pheromone diffusion is the air. Therefore properties of air turbulence must be known to examine behavior of sex pheromone in the air. These properties show that a relationship between size of space of the phenomenon investigated and the averaging-time should be found (INOUE, 1952). The relationship was considered in our observation of mating behavior of *H. cunea.*

When evaporation of pure lauryl acetate and so on are assumed as release of sex pheromone, their vapor pressures and size of pheromone releaser should be known in order to give the release rate of sex pheromone from the model female. The vapor pressures were measured by the gas-saturation method. Saturated vapor densities were calculated from the value of these vapor pressures and the ideal gas law. Diffusion coefficients were estimated by Gilliland's semi-theoretical equation. The values were obtained as follows (Table 2): vapor pressure, $P=10^{-4}$—10^{-3} mmHg; saturated vapor density, $C_0=10^{-3}$—10^{-2} μg/ml; diffusion coefficient, $D_M=4\times10^{-2}$ cm^2/sec.

[2] This analogy is concerned with molecular size, intermolecular force and so on.

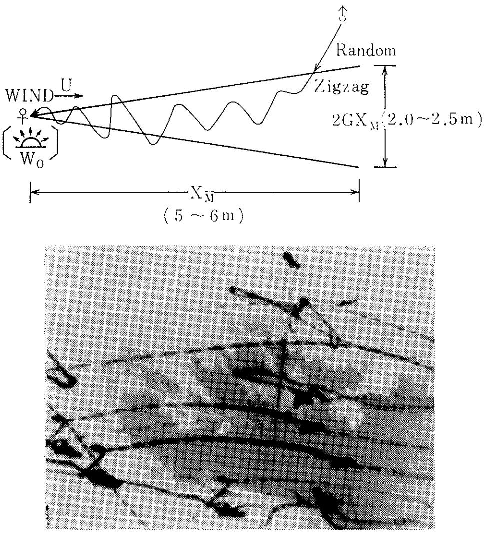

Fig. 1. A scheme of mating behavior of a model moth and a photograph of field flying male of *H. cunea*. As soon as a flying male randomly comes into conical pheromone-effective sphere of sex pheromone released by a virgin female, the male begins to seek the female in a zigzag way, approaches to the female and finally copulates with her. ♀, a virgin female; ♂, pheromone-sensitive male; G, gustiness; U, mean wind velocity; W_0, release rate; X_M, maximal pheromone-effective distance downwind from a virgin female.

Table 2. VAPOR PRESSURE, P, SATURATED VAPOR DENSITY, C_0, AND DIFFUSION COEFFICIFNT, D_M, AT 25°C

	LA	MA	CA
P(mmHg)	1.3×10^{-3}	4.3×10^{-4}	2.2×10^{-4}
C_0(μg/ml)	1.6×10^{-2}	7.4×10^{-3}	3.3×10^{-3}
D_M(cm²/sec)	4.5×10^{-2}	4.2×10^{-2}	3.9×10^{-2}

LA, lauryl acetate; MA, myristyl acetate; CA, cetyl acetate

An equation for pheromone diffusion

Release rate of sex pheromone may be related to surface area and surface condition of a pheromone releaser. Since the surface of actual pheromone releasing gland is covered with many hairs, true surface area must be rather large. The hairs on the gland can promote evaporation of the sex pheromone. If the virgin female possesses an adequate quantity of the pheromone, a vapor layer (laminar boundary layer) can always be present over the pheromone releaser. Then, the form of apparent surface of the gland, related to pheromone release rate, is that of the vapor layer (e.g. hemisphere). Now in our model the hemisphere with radius, r, is assumed as the releaser. The pheromone release rate, W., is given as follows:

$$W_0=2\pi r^2 D_M(C_0-C')\frac{1+(\delta/r)}{\delta} \qquad (1)$$

where δ is thickness of boundary layer and C′ is vapor density outside the layer. Since $C' = 0$ and $\delta/r \gg 1$ were assumed, (1) is rewritten as

$$W_0 = 2\pi r D_M C_0 \qquad (2)$$

The radius, r ($r = 0.03$—0.3 cm), is so small that wind velocity does not influence the evaporation rate of sex pheromone.

The sex pheromone released with the rate, W_0, flows downwind with velocity, U. Sex pheromone released in unit time[3] moves downwind in the corresponding time. Consequently this can be distributed uniformly in the distance where wind moves in unit time (wind velocity). The amount of this spread pheromone (amount of sex pheromone in unit distance), P_0, is given by the following equation:

$$P_0 = W_0/U \qquad (3)$$

On the other hand, cross-section area, S(X), of pheromone-diffusion plume at a point of a distance, X, downwind from a virgin female is given by

$$S(X) = \pi\overline{y^2} \qquad (4)$$

Gustiness,

$$G = \sqrt{\overline{y^2}}/X \qquad (5)$$

shows fluctuation of air turbulence. When (5) is substituted into (4), the equation,

$$S(X) = \pi G^2 X^2 \qquad (6)$$

is obtained. Since the pheromone amount, P_0, is spread homogeneously in this area, its concentration at the point, X, is:

$$C(X) = P_0/S(X) = W_0/\pi U G^2 X^2 \qquad (7)$$

Now, if the spread of sex pheromone shall be assumed as normal distribution, then the sex pheromone concentration, C(X, Y, Z,), at a point, (X, Y, Z), is expressed as follows:

$$C(X, Y, Z) = W_0/\pi\overline{y^2}U \exp\{-(Y^2+Z^2)/2\overline{y^2}\} \qquad (8)$$

and (5) is put into (8),

$$C(X, Y, Z) = W_0/\pi G^2 X^2 U \exp\{-(Y^2+Z^2)/2G^2X^2\} \qquad (8')$$

is gained. When (8′) is thought of only in the vicinity of X axis, $(Y^2 + Z^2) / X^2$ becomes about zero. Then, we have

$$C(X) = W_0/\pi G^2 X^2 U \qquad (9)$$

This equation is equal to (7).

In this way the two equations of (7) and (9), are identical, though obtained by respectively different ideas. The process of male guidance to a virgin female will be analyzed by this equation.

ANALYSES

Effect of wind velocity

Substituting the maximal sex pheromone-effective distance downwind from a virgin female, X_M, and the sex pheromone concentration at this point, Q, that is, minimal concentration which can change male flight pattern (threshold concentration) into (7), we have the following equations:

$$W_0/Q = (W_0) = \pi U G^2 X_M{}^2 \qquad (10)$$

$$(W)_0 = \alpha X_M{}^2 \qquad (10')$$

where $\alpha = \pi U G^2$. In this equation, $(W)_0$ is a ratio of W_0 to Q. Since each value of W_0 and Q can be determined by each species, $(W)_0$ is constant with respect to each

[3] The amount of sex pheromone released in unit time is the release rate.

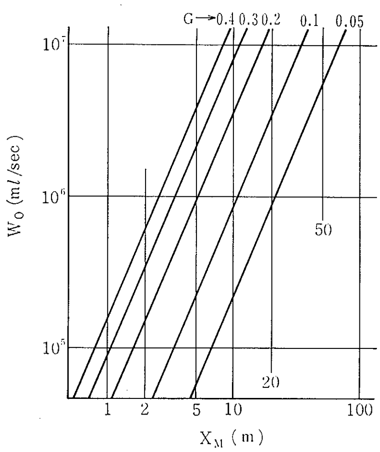

Fig. 2. Relation between $(W)_0$ and X_M in case of U=30 cm/sec. $(W)_0$, ratio of release rate to threshold concentration; X_M, maximal pheromone-effective distance downwind from a virgin female; U, mean wind velocity; G, gustiness.

animal. According to units of $(W)_0$, i.e. ml/sec, $(W)_0$ means that the larger its value is, the larger space size is used by the insect in unit time. Considering the value of $(W)_0$ constant, X_M is a function of α, that is

$$X_M = f(\alpha) \qquad (10'')$$

X_M is merely related with α which is given by mean wind velocity, U, and gustiness, G.

Observing mating behavior of *H. cunea*, we measured mean wind velocity and gustiness to be less than 50 cm/sec and 0.05—0.4 respectively. These values give α=0.1—20 cm/sec[4]. In Fig. 2, $(W)_0$ is plotted as a function of α with U=30 cm/sec and G=0.05—0.4. The straight lines in this log-log graph move slightly along the Y axis if the value of mean wind velocity changes. The graph shows that meteorological factors such as mean wind velocity and gustiness hardly cause size of sex pheromone-effective sphere, X_M, to change: for example, the values of X_M at which the lines with G=0.1—0.3 cut the line of $\log(W)_0=6$ are 3—10 m. The range of these values is not large. Therefore, the size of the effective sphere, X_M can be fixed on every species and is not necessarily related to meteorological elements.

If so, what is primary factor determining X_M? The most significant factor must be that male moths fly randomly. It has been noted only that sex pheromone is carried by wind. However, it is shown by the above formula that male flight should be more remarkable than the sex pheromone current itself. Thus, the relationship between the sex pheromone-effective sphere and the change of male flight pattern is the most important in this model. Male flying is a primary element defining X_M when the attention is given to the final step[5] of the male approach to a virgin female. However, if this point of view is carried further, this factor can be changed and then male flight is not always the most significant.

[4] If mean wind velocity is more than 50 cm/sec, the value is in the same range.
[5] Less than 10-m distance from a virgin female.

Bossert-Wilson's equation

Bossert and Wilson (1963) derived the following equation from Sutton's equation:

$$(W)_0 = 0.1256UX^{7/4} \quad (11)$$

It is apparent that this equation is formally equal to (10). However, they did not check the interrelation among W_0, Q and X when they analyzed (11). A basis of connection was not assumed. This is the worst flaw. It is doubtful that the values of W_0, Q and X are related to one another. It is not evident that each determined value means. The relation among sex pheromone release and perception and male response should be well known in order to examine the relationship among W_0, Q and X. Field observation on male responses against sex pheromone is very significant. In (10), a factor determining the interrelation among W_0, Q and X is the change of male flight pattern (Hidaka, 1972).

Release rate and threshold concentration of sex pheromone

Pheromone release rate W_0, was estimated from the above values; r, D_M and C_0, and equation (2) as

$$W_0 = 10^{-5} - 10^{-3} \quad (\mu g/sec)$$

A value of X_M is assumed to be less than 10 m because it was known by an observation of *H. cunea* that X_M was 5—6 m (Hidaka, 1972). From (10') the values of α give those of $(W)_0$ followed as Fig. 2.

$$(W)_0 = 10^5 - 10^7 \quad (ml/sec)$$

By substituting the value of W_0 and $(W)_0$ in (10), the value of Q was obtained as expressed in Table 3.

Table 3 shows that the threshold concentration of the model insect is 10^5—10^6 molecules/ml (10^{-11}—10^{-10} μg/ml), which is similar to that expected. For examole, in *Trichoplusia ni* W_0 and Q were measured as $W_0 = 2\times10^{-5}$—4×10^{-4} μg/sec and $Q = 3\times10^{-11} - 3\times10^{-9}$ μg/ml (Sower et al., 1971). By using these values, value of $(W)_0$ was calculated as

$$(W)_0 = 10^4 - 10^7 \quad (ml/sec)$$

This value shows that the size of the sex pheromone-effective sphere of *T. ni* seems to be as same as that of this model[6].

CONCLUSION

The process of release, diffusion and perception of sex pheromone was analyzed

Table 3. The Relation Among Values of Release Rate, W_0, and Threshold Concentration, Q, of Sex Phfromone and Ratio of W_0 to Q Assuming X_M Less than 10 m

	W_0 (μg/sec)		
	10^{-3}	10^{-4}	10^{-5}
(W_0) (ml/sec	$10^5 - 10^7$	$10^5 - 10^7$	$10^5 - 10^7$
Q(μg/ml)	$10^{-8} - 10^{-11}$	$10^{-9} - 10^{-12}$	$10^{-10} - 10^{-13}$
(molecules/ml)	$10^8 - 10^5$	$10^7 - 10^4$	$10^6 - 10^3$

[6] The female of *T. ni* has an excessive amount of sex pheromone. This may be an example satisfying the concept that sex pheromone release is similar to evaporation of pure material.

by introducing a micrometeorological model into a concept of a sex pheromone-effective sphere. It is doubtful whether the model is adequate to the actual process of mating. However, in order to define the relation between sex pheromone-effective sphere and threshold concentration, a rule such as the change of flight pattern is necessary. This process was proved by such a rule. In other words, it is very important and necessary that sex pheromone effectiveness is discussed not only in physiological aspects but also in an aspect concerned with mating behavior.

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