Studies on the Diapause in the Planthoppers and Leafhoppers

III. Sensitivity of various larval stages to photoperiod and the forms of ensuing adults in the green rice leafhopper, *Nephotettix cincticeps* UHLER[1]

By Ryôiti KISIMOTO[2]

Entomological Laboratory, Kyoto University, Kyoto

INTRODUCTION

The present author reported that the green rice leafhopper, *Nephotettix cincticeps* UHLER, showed the elongated 4th and 5th larval stages under a short day photoperiod of 8 hr at an adequate low temperature, and the elongation of developmental period was considered to be due to the diapause (KISIMOTO, 1959). In the same paper it was also shown that the larvae at the arrested state of development retained the sensitivity to a long day photoperiod, i. e., the larvae restored the development whenever they were put under a long day photoperiod even at the same temperature.

The adults reared under a short day photoperiod grow up to the spring form and those under a long day the summer form (KISIMOTO, 1958), the two forms differing from each other in the pigmentation, size, etc. (ESAKI & HASHIMOTO, 1937; KISIMOTO, 1958). Recently, MÜLLER (1954, 1957) found that the seasonal polymorphism was determined by photoperiod during the middle instars, the spring form being induced under a short day and the summer form under a long day, in *Euscelis plebejus* and *E. lineoratus* (Homoptera, Auchenorrhyncha).

In the present paper the sensitivity to photoperiod of each larval stage is studied from the view-point of the induction and the maintenance of diapause and the determination of ensuing adult form.

Prof. Dr. Syunro UTIDA of this laboratory is sincerely acknowledged for his encouragement and criticism for this study. Colleagues of this laboratory are also acknowledged.

METHODS OF REARING

Details of the rearing technique have already been shown in the previous papers (KISIMOTO, 1959a, b). The larvae attained to a given stage were put within 24 hr of moulting under the opposite photoperiod from that to which the larvae were hitherto subjected. The rearing was carried out at 20°C under artificial illumination by an electric luminescent tube, illumination being given for 16 hr in the case of a long day photoperiod and 8 hr in a short day.

RESULTS

1. Developmental periods of the 3rd, 4th and 5th larval stages. — Average durations of the 3rd, 4th and 5th larval stages of each treatment are shown in Fig. 1. The emergence and the 4th moulting curves are shown in detail in Fig. 2. The 4th and the 5th larval stages show the longest duration under the short day photoperiod treated throughout the larval development and shortest under the long day. In the former case individual variation is also greatest of all; the larvae having shorter period show the near duration compared with that of non-diapausing larvae.

Followings can be seen in Fig. 1. For the induction of diapause for all larvae it

[1] Contribution from the Entomological Laboratory, Kyoto University, No. 324.

[2] Present address: *Shikoku National Agricultural Experiment Station, Zentsuji, Kagawa Pref.*

(Received for publication, March 18, 1959)

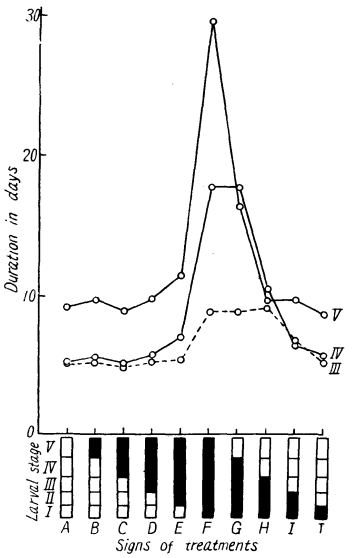

Fig. 1. Average duration of the 3rd, 4th and 5th larval stages under various treatments of photoperiod. Black quadrats mean the short day photoperiod (8 hr) during the stage, white quadrats the long day (16 hr).

is necessary for the larvae to be subjected to the short day photoperiod from the 1st larval stage. When the short day treatment was commenced at the 2nd stage considerable elongation could be observed in some larvae but the most retained the non-diapausing development. The former larvae were considered as diapausing larvae from the view-points of size and pigmentation of ensuing adult, too, as will be mentioned below.

The larval period which attains its largest value under the treatment of the short day throughout the larval development is reduced by the treatment of the long day photoperiod, whenever may it be commenced. In the 1st and the 2nd larval stages no clear difference is found out between the developmental periods of the larvae treated in the two ways. Concerning the 3rd, 4th and 5th larval stages, the developmental speed never attains to the non-diapausing level from the stage the treatment is commenced. It is attained when the treatment is commenced at the preceding stage, i. e., the 5th larval stage attains the non-diapausing level when the larvae are transferred from the short day to the long day at the beginning of 4th larval stage. This trend is similar in both 4th and 5th larval stages, though a little low degree in the 3rd stage. An inverse relation between the 5th and the 4th larval period is, therefore, observed, namely, the 5th larval period becomes shorter than the 4th larval period when the transferring to the long day is made at the 3rd or 4th moulting, and this relation can also be found between the 3rd and the 4th larval periods. Little effect of short day photoperiod given at the 1st and the 2nd larval stages is brought to the 4th and 5th stages unless the short day treatment is continued, but well clearly shown in the 3rd larval stage.

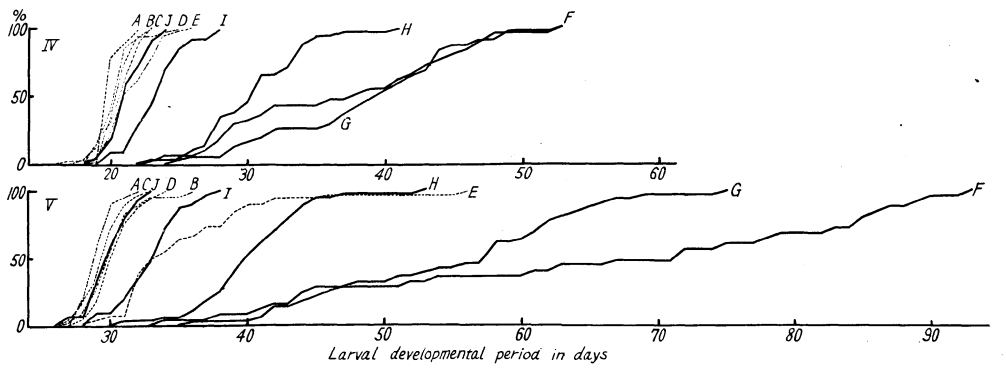

Fig. 2. Accumulated 4th and 5th (emergency) moulting curves in various treatments, the signs, A, B, C, ...corrsponding to those in Fig. 1.

2. Size of adults obtained in the preceding experiment.–Width of head, length of tegmen, length of tibia and femur of the hind leg were measured with an ocular micrometer.

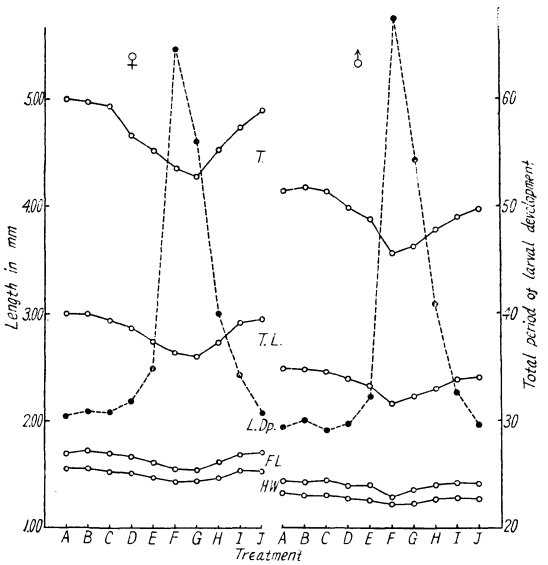

Fig. 3. Average measurements of various parts of adults reared under various treatments of photoperiod. HW: head width, FL: length of femur of the hind leg, TL: length of tibia, T: length of tegmen, LDp: larval developmental period.

Averages of measurements for each treatment are shown in Fig. 3.

Considerable reduction of size is observed in the adults treated with the short day photoperiod throughout the larval development compared with those treated with the long day one, 13.8% reduction in the length of tegmen in the male and 13.1% in the female. Reduction in various parts measured shows a parallel trend for each other, most conspicuous in the length of tegmen and least in the width of head. In the other treatments measurements show intermediate values between the two extremes.

The relation between the length of tegmen and the developmental period is shown by individual in Fig. 4. It is clearly shown that the length of tegmen reduces with elongation of the larval period in curvi-linear proportion. This relation is found also among the members in a given treatment, the longer the developmental period the smaller are the ensuing adults, in both sexes. Reduction of size is clearly shown in the treatments in which the short day exerts its effect elongating the larval period a little over that of non-diapausing larvae, such as in D, E, H, I and J.

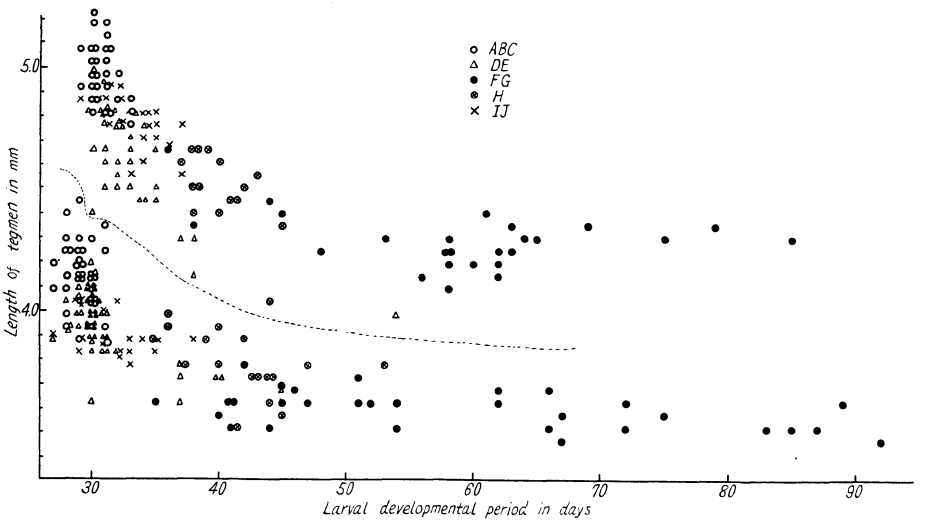

Fig. 4. Relation between the larval developmental period and the length of tegmen of the ensuing adults. Upper : female, lower : male.

3. Coloration and shape of the genital organ. — As already reported preliminary (KISIMOTO, 1958), male adults emerged from diapausing larvae present lighter coloration than those from non-diapausing larvae. Black pigmentation densely deposited on the tip of tegmen and on almost whole lateral side of body and small spotted pigmentation on the legs in the latter adults are much reduced or almost absent in adults emerged from diapausing larvae. Details are shown in Fig. 5. Intermediate forms are easily produced in various treatments.

No clear difference was found in the female except a little dense brown coloration on the lateral side of body in non-diapaused adults.

Shape of the penis and the stylus was examined but no clear difference was found. The size of the two parts is larger in larger adults in proportion.

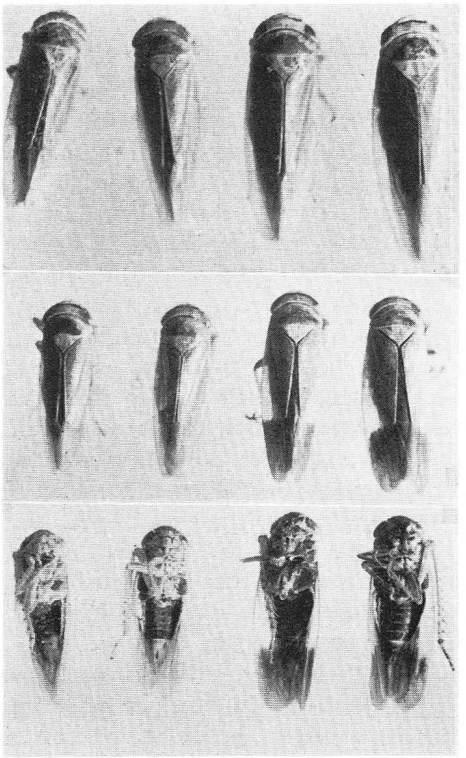

Fig. 5. Photographs showing the typical summer form (right) and the spring form (left). Upper: dorsal view of the female, middle: dorsal view of the male, lower: lateral view of the male.

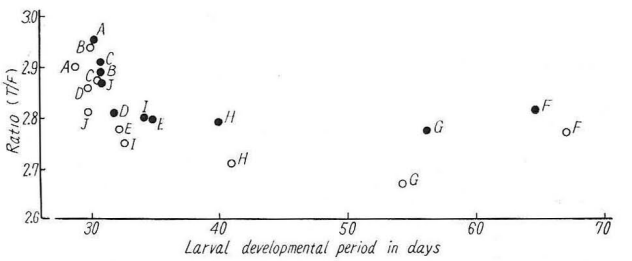

Fig. 6. Ratio of the length of tegmen to the length of femur of the hind leg plotted against the larval developmental period. Ratio is calculated from averages of the two measurements for each treatment. Black circles: female, white: male.

4. Relative growth of the tegmen and the leg. — To study the relative growth a ratio $\frac{\text{length of tegmen}}{\text{length of femur of hind leg}}$ was taken, which was commonly used in the study of the phase of locusts. The ratio is shown against the developmental period in Fig. 6. Ratios were calculated from the average length of tegmen and femur for each treatment. The ratio decreases with developmental period in the similar trend with that in the length of tegmen itself. Similar trend is shown in ratio of the length of tegmen to the width of head. These facts mean that those adults which have shorter larval periods show relatively larger tegmen for their general body size. In other words the length of tegmen is most sensitive to the effect of the treatment reducing the size.

DISCUSSION

A long day photoperiod given at the 1st to 2nd larval stages has almost complete effect in preventing the induction of diapause. Even the long day treatment during only the 1st stage causes about 60 ~70 per cent of larvae to become non-diapause type, the discrimination from the diapausing larvae being tentatively made by the time corresponding to the completion of the 4th or 5th moulting

under the long day photoperiod. It was already reported that the larvae in the diapausing state induced by a short day photoperiod could restore the development whenever they were put under a long day even at the same temperature (KISIMOTO, 1959). The diapause of the green rice leafhopper has thus strict condition for the induction and is always open to the restoration of development. But in detail, the restoration of development takes an elapse of appropriate time to attain to the non-diapausing level. In the present study the critical period when the larvae attained to the non-diapausing level was not determined in the intra-instar development but at least after an elapse of one larval stage it attained to the level. The developmental reaction to the long day treatment is similar in both 4th and 5th larval stages; the fact means that both instar larvae are in the diapausing state as far as the developmental speed is concerned. The elapse of time seems to be due to the time necessary for some hormonal processes intervening in the development attain to the non-diapausing state. It may be a parallel phenomenon to the diapause development in the sense of ANDREWARTHA (ANDREWARTHA, 1952).

The adult forms in respect of the size and pigmentation are, as shown in the present experiment, not discrete for each other, the extremes differing from each other as defined as the spring form (small and light pigmented) and the summer form (large and dark) (ESAKI & HASHIMOTO, 1937). Indeed, some intermediate forms are found between field collected adults of the overwintered and the 1st generation of the year (unpublished data). These facts seem to be due largely to the unstable nature of diapause of this species. But it is certain that the diapause has an important relation to the determination of adult forms probably with the elongation of the developmental period.

MÜLLER (1954, 1957) stated that the seasonal polymorphism in *Euscelis plebejus* FALL. (Homoptera, Auchenorrhyncha) was determined by photoperiod during the middle stages of larval development (2nd to 4th), the summer form being produced under a long day and the spring form under a short day, and the effect of temperature on the determination of the forms was almost excluded. In this study MÜLLER found that *E. incisus* KB. which had been considered as a distinct species was the spring form of the former species. In these papers he discussed the important rôle of photoperiod on the determination of the seasonal forms, not confining the discussion to the leafhopper mentioned, and criticised the prevailing view that the diapause played an important rôle in it. *E. plebejus* has no diapause during the larval development and the larvae reared under different photoperiods show the same larval duration. Moreover, difference in the shape of penis between the two seasonal forms is in such a degree that the two forms had been considered as distinct species. In the present case no clear discrimination was possible between the effect of photoperiod and diapause. A little elongation of the average larval period induced by the short day photoperiod, as in the cases of D and E, is accompanied by a considerable reduction of the adult size. This trend is also appreciable among the members in one treatment having an average developmental period a little longer than that of non-diapausing larvae, such as D, E, H, I and J. In extreme, no difference in the developmental period can be seen from the non-diapausing larvae, while the reduction of size is induced. But at least in this case, the reduction seems to be considered as accompained by an elongation approaching to zero.

In an allied species, *Nephotettix apicalis* MOTSCHULSKY, also the effect of short day inducing a little reduction of the adult size was found (KISIMOTO, 1959). This species has no true diapause but a slight elongation of the larval period is induced under a short day photoperiod.

In the small brown planthopper,

Delphacodes striatella FALLEN, which has a diapause in the 4th larval stage, the brachypterous male is predominantly produced from the larvae diapaused (KISIMOTO, 1956). In this case percentage production of the brachypterous form increases with duration of short day treatment the larvae are subjected, as in the cases of J, I, H, G and F in the present experiment, and naturally the developmental period elongates with elongation of the short day treatment. And it was concluded that the diapause during the larval period provided a condition favourable for the production of the brachypterous male. The seasonal polymorphism in the leafhoppers and the macropterous and brachypterous polymorphism in the planthoppers cannot be always considered as comparable, but the relation between the induction of diapause and the production of the spring form or the brachypterous form is mutually suggestive.

Elongation of the developmental period at low temperatures has no parallel effect on the adult forms to that of the short day photoperiod. Fig. 7 is drawn using the data on the relation between the larval period and the length of the tegmen reared at various temperatures under a

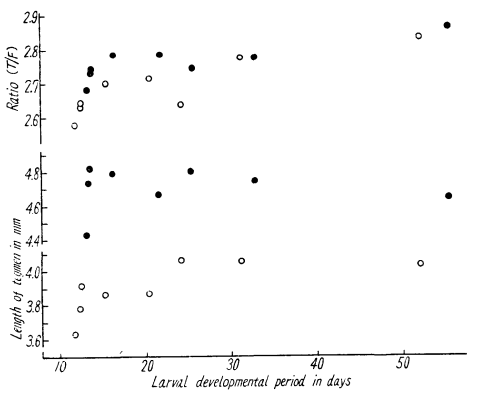

Fig. 7. Relations between the larval duration and the T/F ratio (upper) or the length of tegmen (lower) in adults reared at various temperatures under a long day photoperiod (redrawn from KISIMOTO, 1959b). Black circles: female, white: male.

long day photoperiod reported in the previous paper (KISIMOTO, 1959). The length of tegmen and the ratio, $\frac{\text{tegmen}}{\text{femur}}$, increase with developmental period except the case of the length of tegmen in the female in which a little decrease is found. This fact means that the reduction of adult size is not indiscriminately related to the elongation of developmental period but to that owing to diapause.

JOLY (1954) and JOLY (1956) showed that by implantation of the corpora allata into gregarious nymphs of *Locusta migratoria* L. it was possible to obtain individuals which more or less resembled *solitaria* in the morphological characters and the pigmentation. He assumed that the gregarious phase introduced a hypoactivation of the corpora allata, which is more or less responsible for the development of the morphological characters. FUKAYA & MITSUHASHI (1957, 1958) found that the larval diapause in the rice stem borer, *Chilo suppressalis* WALKER, was characterized in the temporary failure in the activities of brain-prothoracic glands system accompanied with the high activity of the corpora allata. In the larval diapause of the green rice leafhopper it is also supposed that the hormone secreted from the corpora allata plays an important rôle. These two findings lead us to assume that the induction of diapause and the reduction of adult size are phenomena connecting for each other, at least in this case the two phenomena have some connection to the corpora allata as a common centre of action, though may not be ultimate one, which is precursory reactive to environmental factors, such as photoperiod, etc. The weight which of the two reactions, the induction of diapause or the reduction of size, are to be pronounced may be species-specific.

SUMMARY

Some rearing experiments were carried out to determine the stages sensitive to

photoperiod inducing or completing the diapause in the green rice leafhopper, *Nephotettix cincticeps* UHLER. Rearings were carried out in a room of constant temperature of 20°C. 16 hr illumination was given in the long day photoperiod and 8 hr in the short day.

1. For the induction of diapause in all larvae subjected the short day treatment is required since the 1st larval stage. Even the long day during the 1st stage causes 60 to 70 per cent of the larvae to become non-diapause type.

2. The larvae of all stages which are reared under the short day photoperiod retain the sensitivity to the long day photoperiod, the sensitivity being shown in the acceleration of development thereafter.

3. The 4th and the 5th stage larvae which present the most clear elongation of development under the short day photoperiod react to the long day treatment in the similar way for each other, namely, the development is not accelerated in such a degree that the non-diapausing level is attained in that stage the treatment is commenced, but attains to the level provided the treatment is commenced in the preceding stage. It is difficult to determine which is the true diapausing stage the 4th or the 5th stage from the reaction to photoperiod.

The 3rd stage also reacts in the similar way but in a lesser degree.

4. The adults obtained from the various treatments mentioned above were measured in the length of the tegmen, the tibia and femur of the hind leg, and the head width. The typical summer form is obtained under the long day photoperiod throughout the development and the typical spring form under the short day. In the other treatments intermediate forms in the size and pigmentation are obtained, the longer the developmental period the more approaching to the spring form are the ensuing adults. A hyperbolic relation is found between the two variables, the length of tegmen or other body parts and the developmental period.

A ratio, length of tegmen/length of femur of the hind leg, was taken to study the relative growth of body parts. The ratio presents a similar trend with that of the length of tegmen itself with elongation of the developmental period. This fact means that the length of tegmen is most sensitive to the effect of photoperiod.

5. Elongation of the larval period due to low temperature shows no such a relation to the size of ensuing adult as in the former case due to the diapause.

6. Corpora allata are assumed as a common proximate centre of action inducing the diapause and the reduction of adult size.

LITERATURES

ANDREWARTHA, H. G. (1952) Biol. Rev. **27**: 50～107.

ESAKI, T. & S. HASHIMOTO (1937) Minist. Agric. Forest. Nojikairyoshiryo No. 127: 1～135.

FUKAYA, M. & J. MITSUHASHI (1957) Japan. J. Appl. Ent. Zool. **1**: 145～154.

FUKAYA, M. & J. MITSUHASHI (1958) Japan. J. Appl. Ent. Zool. **2**: 223～226.

JOLY, L. (1954) C. R. Soc. Biol. **148**: 579～583.

JOLY, P. (1956) Insectes Sociaux **3**: 17～24.

KISIMOTO, R. (1956) Ōyō-Kontyū **12**: 202～210.

KISIMOTO, R. (1958) Abstract Ann. Meet. Japan. Soc. Appl. Ent. Zool., Tokyo.

KISIMOTO, R. (1959a) Japan. J. Appl. Ent. Zool. **3**: 49～55.

KISIMOTO, R. (1959b) Japan. J. Appl. Ent. Zool. **3**: 128～135.

MÜLLER, H. J. (1954) Beitr. z. Ent. **4**: 1～56.

MÜLLER, H. J. (1957) Zool. Jahrb. Syst. **85**: 317～430.

摘　　要

ウンカ類の休眠に関する研究

Ⅲ. ツマグロヨコバイ幼虫各令の日長作用に対する感受性とそれから羽化した成虫の型について

岸　本　良　一[1]

京都大学農学部昆虫学研究室

幼虫のいろいろな令期に，長日から短日，あるいは短日から長日に変えて，休眠誘起および発育促進の様子を調べた。長日は 16 時間照明，短日は 8 時間照明で，全発育期間中 20°C で飼育した。

1) 全個体が休眠にはいるためには，1 令から短日処理を継続することが必要で，1 令だけ長日にしただけでも 60～70% の個体は非休眠となる（第 1, 2 図）。

2) 全令短日条件では 4 令と 5 令が休眠状態を最も明らかに示すが，長日におくと発育の促進が見られる。しかし，長日に移したその令から直ちに非休眠個体と同じ程度の発育速度にはならず，その前の令から長日条件においた場合にその速度に達する。この傾向は 4 令と 5 令とではっきりした区別はなく，3 令幼虫も低い程度ながら同じ傾向を示す。1～2 令では休眠にはいるものと非休眠のものとで発育に差が見られない（第 1 図）。

3) この飼育で得られた成虫の頭幅，前ばね長，後脚たい節長，けい節長を測った。全令長日条件下で夏型，全令短日条件下で春型が得られるが，その他の条件下では中間型が容易に得られる。体の大きさと発育日数との間には双曲線的関係が見られた（第 4 図）。

4) （前ばね長/後脚たい節長）も，前ばね長だけの場合と同様，発育日数との間に双曲線的関係が見られた。すなわち，長日条件下で得られた個体は，一般的体型に対してはねがよく発達しているといえる（第 6 図）。

5) 休眠の誘起と成虫の型の決定との間には共通したホルモン機構があるのではないかと想像され，アラタ体の作用が注目される。

抄　　録

有機リン殺虫剤抵抗性系統のイエバエにみられる抵抗様式

BUSVINE J. R. (1959) Patterns of insecticide resistance to organo-phosphorus compounds in strains of houseflies from various sources. Ent. exp. & appl. 2 : 58～67.

有機リン殺虫剤に抵抗性を示す 4 系統のイエバエに 14 種のリン剤を接触させて resistance spectra を調べた。その結果著しい傾向として，パラチオンおよびダイアジノンで選抜された抵抗性系統は大体同様の抵抗様式を示し，パラチオン，パラオクソン，EPN，ダイアジノンに強力に抵抗し，マラチオンには抵抗性を示さない。これに反し，マラチオンで選抜された系統はマラチオンには高い抵抗性をもつが，パラチオン，パラオクソン，EPN，ダイアジノンに対する抵抗性は弱い。

メチルパラチオンに対しては各系統はパラチオンに対するとほぼ同様の spectra を示すが，系統間の差はパラチオンに比べわずかである。またクロールチオンに対する抵抗性はいずれの系統も著しい。

パラチオンとダイアジノンとで抵抗性のついた系統を比較すると，一般にダイアジノン抵抗性のハエはパラチオン抵抗性のハエに比べ，アルキルオキシ基としてメトキシを含む化合物よりもエトキシをもつ化合物に対して抵抗性を示すことが認められた。（農技研　平野千里）

---

[1] 現在　四国農業試験場