Studies on the Diapause in the Planthoppers and Leafhoppers (Homoptera)

II. Arrest of Development in the Fourth and Fifth Larval Stage Induced by Short Photoperiod in the Green Rice Leafhopper, *Nephotettix bipunctatus cincticeps* UHLER[1]

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INTRODUCTION

The green rice leafhopper, *Nephotettix bipunctatus cincticeps* UHLER,[2] hibernates as the fourth or fifth instar larvae among the weeds grown near paddy fields. It has been said that this species shows no clear arrest of development which can be considered as the true diapause, larvae in the overwintering state being able to develop whenever these are put into effective temperature. Moreover, the larvae are unable to live completely without suitable food during winter (MIYAKE, 1932; SHINKAI, 1954). The small brown planthopper, *Delphacodes striatella* FALLÉN, which was considered to have the true diapause in the 4th larval stage (MIYAKE, 1932; KISIMOTO, 1958 etc.) shows a similar reaction to high temperature, namely, larvae in diapause develop at 30°C without any pre-treatment necessary for the completion of diapause (KISIMOTO, 1958).

Larvae in the overwintering show a dark pigmentation compared with those during other seasons. On the other hand, the green rice leafhopper has a seasonal polymorphism, the spring form and the summer form, which differ from each other in the pigmentation (ESAKI & HASHIMOTO, 1937). The spring form is often obtainable among the overwintering generation. These facts suggest that some physiological changes may occur during the overwintering.

Effect of photoperiod on the induction of diapause has been much studied during these years. Recently, MÜLLER (1954, 1955) found that the seasonal polymorphism was also determined by photoperiod, the spring form being induced by short photoperiods and the summer form by long photoperiods, in *Euscelis plebejus* and *E. lineoratus*.

Suggestions and criticism of Prof. S. UTIDA of this laboratory are much acknowledged.

MATERIAL AND REARING METHODS

Three to five larvae were put into test-tubes (2 cm in diameter and 17.5 cm in length) within 24 hours of hatching, with a leaf blade or a seedling of the rice plant in each for food. A few drops of water were poured into each tube. Food and container were renewed every few days. The rearing was carried out in glass houses in which temperature was regulated at 10, 20 and 30°C respectively, and photoperiods over the natural day length were supplemented by artificial light of enough intensity.

Initially the materials used were collected from a rice field at Kitashirakawa, Kyoto in early June, 1957, and larvae of the 2nd to the 4th generation were offered to the present experiments..

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[1] Contribution from the Entomological Laboratory, Kyoto University, No. 308.

[2] H. Hasegawa proposed *Nephotettix cincticeps* UHLER instead of *Nephotettix bipunctatus cincticeps* UHLER at the 2nd Ann. Meet. Japanese Soc. Appl. Ent. Zool. 1958.

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RESULTS

Rearing under a short day and a long day photoperiod at 20 and 30°C. — Rearings under 8 hr and the natural day length (*ca.* 14 hr 30 min) were carried out from the middle of June. Curves showing the progression of instar are shown in Fig. 1. Mortality during the larval period was almost negligible.

Arrest of development in the 4th and the 5th larval stage is clearly shown under a short photoperiod of 8 hr at 20°C. Developmental period of each larva varies in a considerable degree, the shortest one being near to that under a long photoperiod and the longest exceeding two months. On the other hand, a well uniform 5th moulting and emergency curves were obtained under a long photoperiod. Retardation of development was also observed in the 3rd larval stage, though not so conspicuous as in the 4th and the 5th larval stage. Rates of increase of the developmental period of the 4th and the 5th instar comparing to those under the long photoperiod are rather parallel and special instar showing a particular elongation of developmental period was not easily determined.

The larvae in the state of arrest of development look dark after the 3rd and the 4th moulting, while the larvae under the long photoperiod present a greenish yellow pigmentation, especially on the dorsal part of thorax. This pigmentation seems to originate from the pigment in the wing bud which can be seen through the transparent body wall. Indeed, the larvae of the former group too present a similar pigmentation approaching to the moulting.

At 30°C no apparent effect of photoperiod on the developmental speed was observed.

Rearing under a short day and a long day

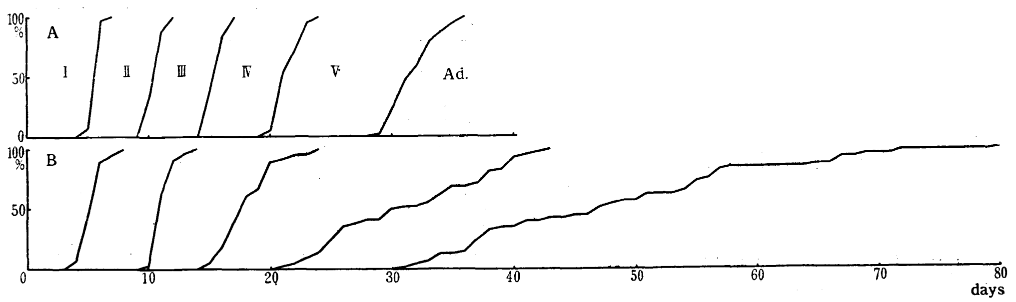

Fig. 1. Accumulated moulting curves of each instar showing the progression of instar at 20°C. A: under a long day photoperiod of 14 hr 30 min. B: under a short day photoperiod of 8 hr.

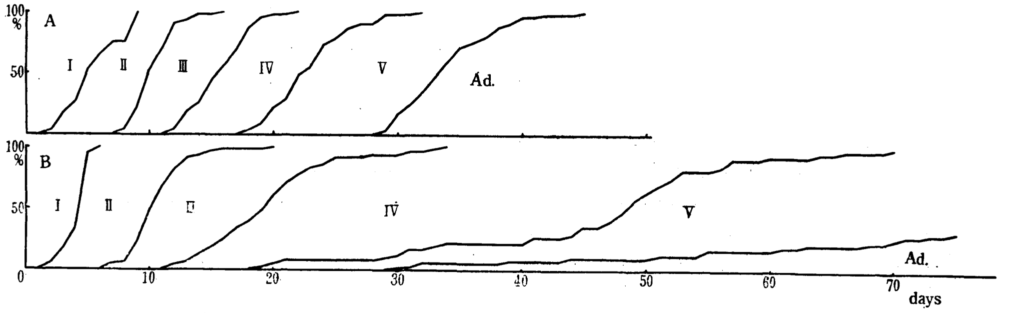

Fig. 2. Curves showing the progression of instar at alternating temperature between 30°C (8 hr) and 10°C (16 hr). A: under permanent illumination. B: under illumination at 30°C and darkness at 10°C, namely under a short photoperiod.

photoperiods at alternating temperature between 30 and 10°C.—To detect the effect of low temperature on the induction of arrest of development, alternating condition of temperature between 30°C for 8 hr and 10°C for 16 hr was set. In one group, a darkening phase of 16 hr was coincided with 10°C and in another group no darkening phase was given. Temperature of 10°C seems to be low enough for the induction of diapause if it is effective. The result is shown in Fig. 2. Rearing was stopped at the 70th day from the beginning of rearing. Larval mortality was negligible.

Clear elongation of the developmental period was found in the 4th and the 5th larval stage under the short photoperiod. On the other hand, under permanent illumination the larval development takes place steadily though the individual variation of developmental period increases a little with instar.

The elongation of larval period is shown to be primarily induced by the short photoperiod. Low temperature of an appropriate range is of course necessary but its effect is not direct. Under a long photoperiod larvae seem to develop accumulating the intermittent growth which may take place at 30°C and considerably high developmental speed can be found. This ability seems to be unobtainable or depressed to a very low level under a short photoperiod.

Effect of a long day photoperiod and high temperature on the 4th instar larvae reared under a short day photoperiod at 20°C.—The larvae reared under a short photoperiod of 8 hr at 20°C until the 3rd moulting were thereafter transferred to the condition of permanent illumination at 20°C and 30°C. The result is shown in Fig. 3.

Effect of permanent illumination to accelerate the larval development which is photoperiodically suspended, so to speak, at 20°C is clearly shown. High temperature of 30°C is also responsible for the acceleration of development, but the effect is incomplete without a fulfilment of the photoperiodical condition. A little long 5th larval period and a little large variation of larval period under the short photoperiod indicate the residual effect.

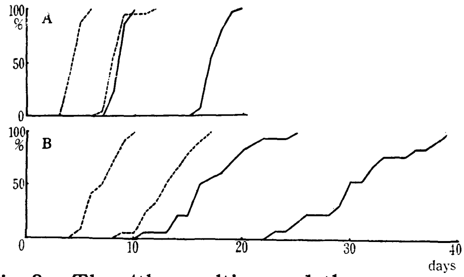

Fig. 3. The 4th moulting and the emergency curves of the larvae put into permanent illumination and 8 hr illumination at 20 and 30°C. The larvae were reared until the 3rd moulting under a short photoperiod of 8 hr at 20°C. A: under permanent illumination. B: under a short photoperiod. Broken line: at 30°C. Whole line: at 20°C.

Relation between the 1st to 3rd larval period and the 4th to 5th larval period, and that between the 4th and the 5th larval period under a short day photoperiod at 20°C. The results are shown in Fig. 4 and 5 from the experiments described in Fig. 1.

It is shown that the larvae having longer I-III larval period present clearer elongation of IV-V larval period. The larvae having extremely short I-III larval period

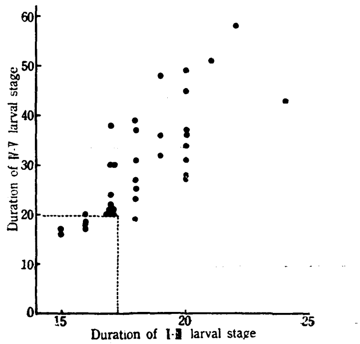

Fig. 4. Relation between the duration of the 1st to 3rd larval stage under a short photoperiod at 20°C. Broken line shows the maximum duration of the larvae under a long photoperiod at the same temperature.

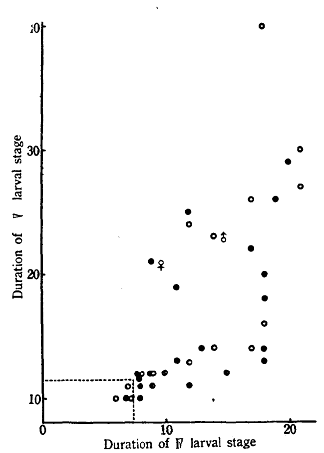

Fig. 5. Relation between the duration of the 4th and the 5th larval stage. Other explanation is similar to Fig. 4.

show no difference from the larvae under a long photoperiod. This fact is also applicable to the relation between the 4th and the 5th larval period. Those larvae which have longer I-III larval period than the border line present without exception the elongation of development in the 4th and the 5th larval period, but not true in *vice versa*.

Absolute length of the 5th larval period is longer than that of the 4th larval period as shown in Fig. 5. But under a long photoperiod mean durations of the 4th and the 5th larval period are 6.0 and 10.3 days. It is difficult to decide which is more sensitive for the effect of short photoperiod to induce the elongation of larval period.

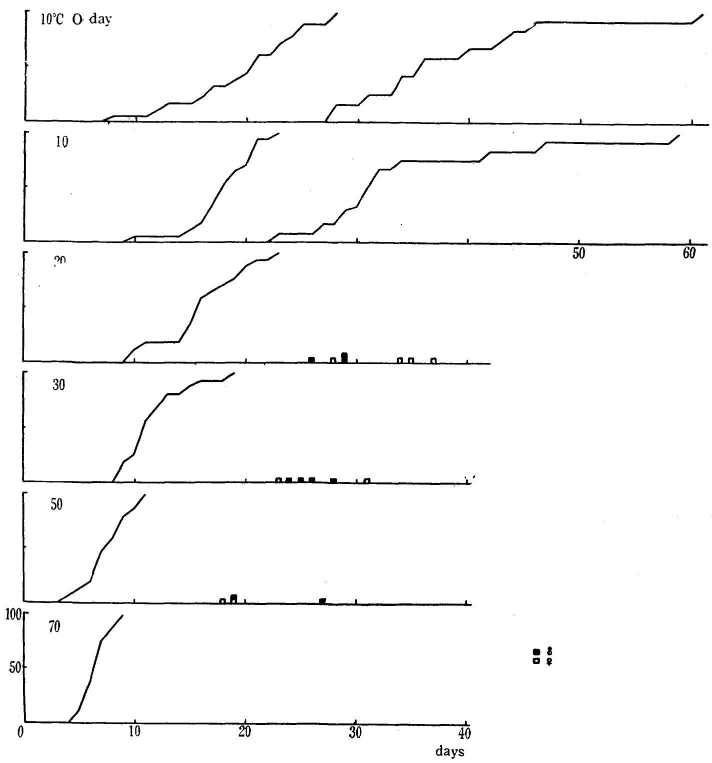

Fig. 6. Effect of chilling at 10°C for various period under a short photoperiod of 8 hr after the 3rd moulting. The larvae were reared under a short photoperiod at 20°C until the 3rd moulting. Curves present the 5th moulting and the emergency curves. Number of adult emerged are shown in figures of the larvae chilled for over 20 days.

Effect of low temperature on the completion of the arrest of development.—Following to the ordinary method for the completion of diapause, larvae reared under a short photoperiod at 20°C until the 3rd moulting were chilled at 10°C within 24 hr of the moulting for 10, 20, 30, 50, 70 days under the same photoperiod. During the chilling, it seemed to be necessary to renew the food plant, and wilting of food lead larvae to death. After the chilling. the larvae were returned to the same condition of temperature and photoperiod as before the chilling. At 10°C the rice seedling easily wilts probably because of the low temperature, and high mortalities during the treatment seemed to be induced in most part by it. The result is shown in Fig. 6.

High mortalities obtained in the 5th larval period, especially in those larvae which were chilled for longer periods, were also because of the unfavourability of the food used in this experiment adding to low resistivity of the larvae to the low temperature. Number of abults emerged is shown in figure instead of emergency curve, for the high mortalities obtained may lead the emergency curves inexact.

Chilling within 20 days has no effect on the development of larvae treated, the 4th moulting curves being on a parallel position from the day when the larvae were returned to 20°C. Chilling for over 50 days lead the larvae to moult promptly and uniformly. The 4th larval period after returning to 20°C become equivalent to that of the larvae reared under a long photoperiod at the same temperature. The 5th larval period is exactly unknown, but a trend of prompt and uniform emergence can be perceived.

Cold-hardiness at 0°C was studied with the larvae reared under a short photoperiod of 8 hr and a long photoperiod of 16 hr at 20°C but the hardiness is very low in both groups of larvae and all larvae died within a few days. The low resistivity to low temperature seems to be partly connected with the necessity of presence of fresh food during the chilling. In the case of the diapausing larvae of the small brown planthopper the cold-hardiness at 0°C is considerably high (unpublished result). In the central and southern part of Japan temperature of microhabitat of overwintering larvae is considered to reach scarcely to 0°C, and more resistivity to low temperature may be shown in other conditions. The present result does not necessarily mean the difficulty of overwintering of this species.

DISCUSSION

The green rice leafhopper has been considered, as stated already, to have no true diapause. In fact, it seems to be true in some points, excluding the diapause-like behaviour mentioned above. As BONNEMAISON (1945) and recently LEES (1955) stated, distinction between diapause and quiescence became difficult as researches were advanced. It seems inappropriate to consider that the arrest of development induced by a short photoperiod as in the present case is caused by unfavourable condition, and therefore as quiescence. In LEES' words (1955), "photoperiod is a stimulus which, unlike temperature, cannot be regarded as immediately favourable or unfavourable". COUSIN (1932) qualified diapause as "tous les arrêts d'activité et d'évolution accompagnés d'un ralentissement du métabolisme, qu'elles qu'en soient les causes déterminantes" (in BONNEMAISON, 1945).

From these points it is impossible to deny that the present result on the arrest of development is to be recognized as diapause.

On the other hand, the requirement of fresh food during the arresting period and low cold-hardiness studied preliminary in the present experiments remain as the favourable characters for considering the arrest of development as non-diapause. Metabolic adjustment of the larvae in the state of arrest is remained to be solved, but it is clear that some physiological changes are induced in the larvae under a short photoperiod comparing to those under a long photoperiod from the fact that the development is accelerated and reaches to a well normal developmental speed in the 5th larval stage if the larvae in the state of arrest are put under a long photoperiod at the same temperature.

The fact that the development of larvae is accelerated and becomes uniform after appropriate periods of chilling seems to offer another point favourable for considering the arrest of development as diapause, though further studies are to be undertaken.

Requirement of fresh food during the arrest of development does not diminish the possibility of overwintering of the larvae, for in most of Japan winter gramineous weeds which are suitable for the green rice leafhopper, grow near paddy fields. Indeed, larvae can overwinter on these weeds in the field and in laboratory condition. The arrest of development can be considered to be adaptive for waiting the season when host plants are abundant and temperature becomes favourable for population growth of the species.

Comparing to the diapause in the small brown planthopper, *Delphacodes striatella* Fallén (KISIMOTO, 1958) the followings are concerned. The arrest of development is induced by a short photoperiod of favourable temperature and prevented by a long photoperiod, in both species. The larvae in the state of arrest of development are induced to develop promptly and uniformly whenever they are put into a long photoperiod at the same temperature. The larvae are considered to retain the sensitivity to a long photoperiod during the state of arrest of development in both species. At high temperature, such as 30°C no arrest of development is induced, larvae developing completely in the same speed without regard to the photoperiod. This fact is similar to the ordinary cases.

On the other hand, some differences are also found out. Duration of the arrest of development is longer in the small brown planthopper than in the green rice leafhopper at 20°C and the arresting stage is almost restricted to the 4th larval stage in the former species, but in the latter it is difficult, in the present state, to decide which is the more suitable stage to be concerned as the arresting stage the 4th stage or the 5th stage. Cold-hardiness at 0°C and the resistivity to food shortage are much higher in the former than the latter.

SUMMARY

The green rice leafhopper, a pest of the rice plant, *Nephotettix bipunctatus cincticeps* UHLER, was reared under a long photoperiod and a short photoperiod at 20°C and 30°C, and the following results were obtained.

1. At 20°C a clear elongation of the duration of the 4th and the 5th larval stages was found under a short photoperiod of 8 hr, while under a long photopeeriod of *ca.* 14 hr 30 min a normal development was found.
2. At 30°C no effect of the photoperiod on the development was found.
3. At alternating temperature between 10°C for 16 hr and 30°C for 8 hr per day, much clear elongation of the developmental period was found if the larvae were kept in darkness at the phase of 10°C. On the other hand, normal development was obtained under permanent illumination.
4. The larvae in the arrest of development were induced to develop promptly if they were put in a long photoperiod even at the same temperature of 20°C. High temperature, such as 30°C is also effective without regard to the photoperiod in which the larvae are to be put, though it is more effective under a long photoperiod than under a short one.
5. The development of the larvae in the state of arrest is induced to normal if the larvae are chilled at 10°C for more than 50 days.
6. It was discussed whether or not the arrest of development can be considered as a diapause. As affirmative characters the followings are concerned, that is, the arrest of development is induced by a short photoperiod and the arrest is completed by chilling for appropriate durations. As negative characters, larvae in the arresting state need succulent food without which they soon die and cold-hardiness at 0°C is low compared with those characters in the small brown planthopper.

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摘　　要

ウンカ類の休眠に関する研究

Ⅱ. ツマグロヨコバイの幼虫発育に及ぼす日長と温度の作用

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ツマグロヨコバイは幼虫態で越冬するが，休眠はしないといわれてきた。しかし条件によつてはいろいろな休眠様現象を示すことがわかつた。

1) 20°C で短日（8時間照明）および自然日長（約14時間30分）で初令より飼育すると，前者では4,5令で明らかな発育遅延が見られ，幼虫は暗色を帯びる。一方後者では正常に発育し，脱皮直後も黄緑色を帯びる（第1図)。

2) 照明時間（8時間）中を 30°C，暗黒時間（16時間）中を 10°C とするような変温下では．幼虫の発育遅延はさらに明らかになるが，同じ変温条件下でも連続照明下では発育は正常である（第2図)。

3) 30°C では長日，短日ともに発育遅延は見られなかつた。

4) 20°C，8時間照明下で4令化した幼虫を連続照明下に移すと発育は促進される。また同じ幼虫を 30°C 下においても発育は促進されるが，同じ 30°C 下でも長日下のほうが促進の程度は高い（第3図)。

5) 同じ幼虫を 10°C で 50 日以上低温処理するとその後 20°C，8時間照明下においても正常に近い発育をするようになる傾向が見られた（第6図)。

6) ここで見られた発育遅延は，その誘起に対してある範囲内の温度での短日の効果が明らかであり，その他以上の諸点よりみて，やはり一種の休眠状態にあるものと考えられる。

7) ヒメトビウンカ幼虫における休眠と比較し，多くの類似点を見出すことができた。

抄　　録

小麦への施肥とムギのアブラムシ

DANIELS, N. E. (1957) Greenbug populations and their damage to winter wheat as affected by fertilizer applications. J. Econ Ent. 50(6): 793～794.

ARANT and JONES (1951) および BLICKENSTAFF ら (1954) は大麦やライ麦でのムギノアブラムシ *Toxoptera graminum* の繁殖が窒素質肥料の施用量と逆比例の関係にあることを示した。筆者はさらに窒素を燐酸，カリおよびカルシウムと組合せて施用して栽培した小麦におけるムギノアブラムシの繁殖を調査した。温室内の試験では，1本の小麦あたりのアブラムシ数は，前に報告されたと同様に無窒素区で多く，窒素施用区で少なかった。また燐酸単用区，窒素-燐酸区，窒素-燐酸-カリ区ではアブラムシの繁殖は少なかったが，窒素とともにカルシウムを施用すると，アブラムシの数は著しく増加した。この結果を小麦植物の重量あたりに換算すると，アブラムシの数は窒素-燐酸区，窒素-燐酸-カリ区で少なく，燐酸区，無窒素区，窒素-カルシウム区で多かった。

野外試験の結果も窒素を与えると小麦の生育が良好となり，小麦植物の重量あたりのアブラムシ数はきわめて少なく，これに燐酸を組合せても同様の傾向がみられた。これらの結果からみてムギノアブラムシの場合，窒素，燐酸およびカリ肥料を適当に多量に与えることは植物の生育を良好にするためにも，またムギノアブラムシの繁殖を抑える効果からも有用であろう。

（農技研　平野千里）