

Biology of *Hyphantria cunea* DRURY (Lepidoptera : Arctiidae) in Japan

VII. Delayed Development of Summer Pupae

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INTRODUCTION

A previous study on the photoperiodic response in the Japanese populations of *Hyphantria cunea* shows that the winter diapause is induced by photoperiods shorter than 14.5 hr at 25°C (MASAKI *et al.*, 1968). It is also noted that, under long-day conditions, some pupae undergo a brief period of arrested development and, consequently, that adults may emerge in two distinct periods. In some experiments, there was a time lapse of about one to two weeks between the two peaks of moth emergence, and a few individuals persisted as long as one month or more. The delay in emergence may be much more pronounced. Thus, observations under insectary conditions showed that about half of those pupae which had been formed in early summer postponed their development until autumn.

This timing of seasonal development resembles the aestivating behaviour of the southern populations of *Mamestra brassicae* (MASAKI and SAKAI, 1965). It seems necessary to investigate more closely whether or not this introduced species has an ability of aestivation. Aestivation, if it occurs, may have some bearing on the adaptability of the invader especially in southern localities. It is known in *Mamestra brassicae* that photoperiod and temperature are both important factors involved in aestivation. The influence of these factors has therefore been tested in relation to the delayed pupal development in the summer generation of *Hyphantria cunea*. So far as the writers are aware, no previous reference to this phenomenon is found in the literature on the bionomics of this species.

The present work is the seventh report from the study group on the biology and population dynamics of *Hyphantria cunea* in Japan.

MATERIAL AND METHOD

Source of Material

All works were carried out with materials collected as eggs or ovipositing adults

at Hiratsuka, Kanagawa prefecture. The experiments at Hiratsuka were based on eggs laid by adults that had been collected in early June of 1967, and those at Hirosaki on eggs collected in early June of 1968 and immediately sent by post.

Method of rearing

Larvae were reared in petri dishes (3×12 cm), glass jars (24×18 cm) or wire-screen cages (24×29×40 cm). The type of cage and the density of rearing were changed at appropriate intervals to cope with growing larvae. Foliage of *Cornus controversa* Hemsl. was provided as food in all laboratory tests at Hiratsuka. In a field cage (50×50×60 cm) set in the Horticultural Experiment Station, larvae were fed on leaves of *Salix babylonica* L. Leaves of *Prunus yedoensis* Matsum. were provided in the laboratory rearing at Hirosaki. In every case, food plants were maintained in good conditions by frequent renewal.

When larvae became fully fed, small paper boxes were placed in each cage. A narrow slit was cut on one side of the box, through which larvae searching for pupation sites got into the box. Corrugated sheets of cardboard were put in the box, which offered adequate sites for spinning cocoons. Bands of paper tubes of about 5 mm in diameter and 150 mm in length were provided for the same purpose. These boxes and tubes were opened every day, and newly formed pupae were removed. The date of pupation of each individual was recorded. Pupae were kept in petri dishes lined with sheets of filter paper.

Photoperiod and temperature

The photocycle of 24 hr duration was used throughout this study. At Hiratsuka, experiments were conducted in constant temperature rooms, and desired photophases were provided by 10w "daylight" fluorescent lamps and time switches. At Hirosaki, insects were subjected to various treatments in photoperiodic boxes described elsewhere (MASAKI and OYAMA, 1963). In each box a 10w "daylight" fluorescent lamp was placed above 40 cm from the centre of the rearing cage. The photoperiodic box was not fitted with a cooling unit, so that the temperature could not be kept constant during the hot months. In each series of tests, it fluctuated within a few degrees.

RESULTS

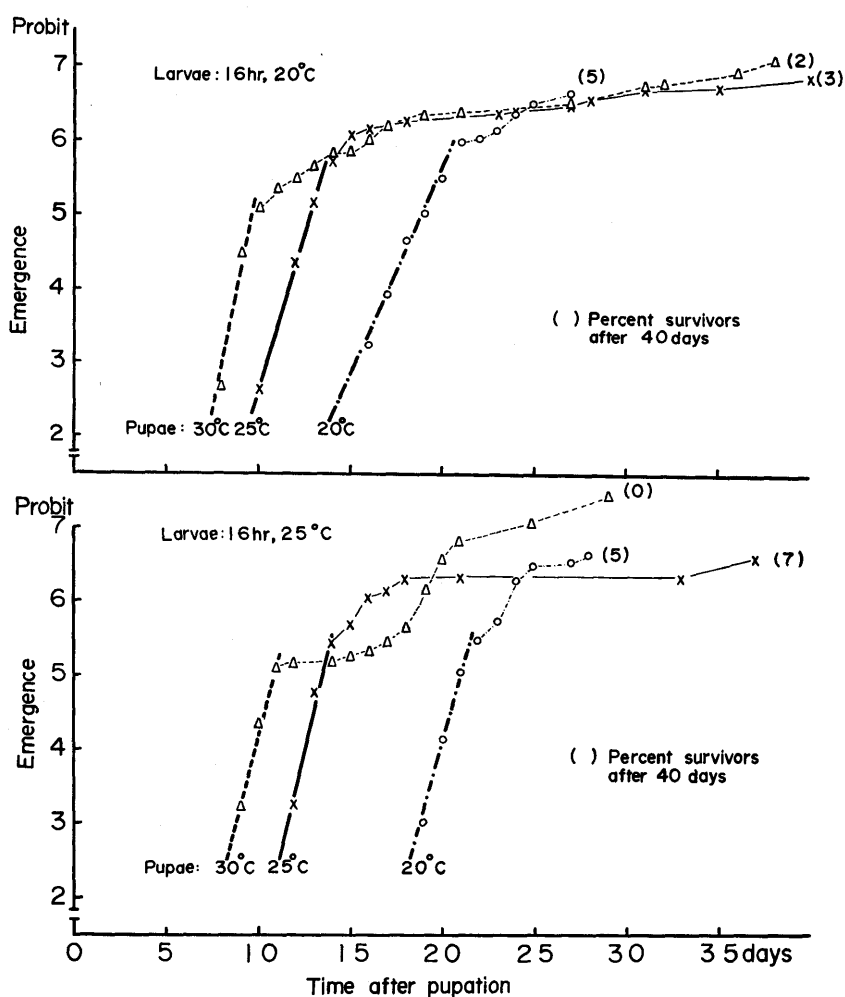
Effect of temperature

Since the present problem concerns with the developmental delay under long-day conditions, larvae were reared at a 16 hr photophase at Hiratsuka. In order to test the influence of temperature, they were fed at two different temperatures, 20° and 25°C. On pupation, each temperature group was divided into five lots, which were subjected to different conditions of temperature at 75% R.H. in darkness. Three lots were thus kept at constant temperatures of 20°, 25° and 30°C. Another lot was subjected to a fluctuating conditions, in which the temperature took a daytime value of 30°C for 8 hours and then gradually fell to a night level of 20°C, giving a

Table 1. MEAN, DURATION OF PUPAL DEVELOPMENT OF *Hyphantria cunea* AT DIFFERENT TEMPERATURES.

Larval stage		Pupal stage (in darkness)			
		20°C	25°C	30°C	20°C-30°C**
20°C	<i>n</i>	116	120	114	115
	\bar{x}	19.9	14.9	13.1	14.6
	<i>s</i>	4.7	6.5	7.1	8.5
25°C	<i>n</i>	86	99	91	90
	\bar{x}	22.0	17.6	14.3	14.3
	<i>s</i>	1.8	11.1	4.9	2.7

* Dially photophase. ** Averaged about 25°C.

n=number emerged as moths. \bar{x} =mean duration in days. *s*=standard deviation.Fig. 1. Progress of moth emergence from non-overwintering pupae of *Hyphantria cunea* at different temperatures.

daily mean of about 25°C. The remaining one was used for a particular test which will be described in the next subsection.

The mean duration of pupal stage in each treatment is given in table 1. In this table is indicated a usual relationship between developmental rate and temperature, which is consistent with the results obtained by Ito *et al.* (1968). There are two points which should be noted further. First, the pupae that had been reared as larvae at 25°C took a slightly longer time to complete their development than those reared at 20°C, even though they were kept at the same temperature during the pupal stage. (A similar trend was also observed in a later experiment.) Second, the variance of the developmental time was rather large and variable. This was related to the occurrence of a few pupae which underwent delayed development. As shown in figure 1, the first part of each emergence curve is linear, which means that the adults began to emerge following a normal pattern of distribution. The insects were, however, not homogeneous as to their developmental rate. There was a lagging tail which conspicuously deviated from the normal distribution. This heterogeneity seemed not to be based on a genetic factor alone. The number of pupae forming the first linear part of the emergence curve became smaller with rising temperature. There were thus more pupae showing delayed emergence at a high than at a low temperature. The day and night fluctuation of temperature between 20° and 30°C had no particular

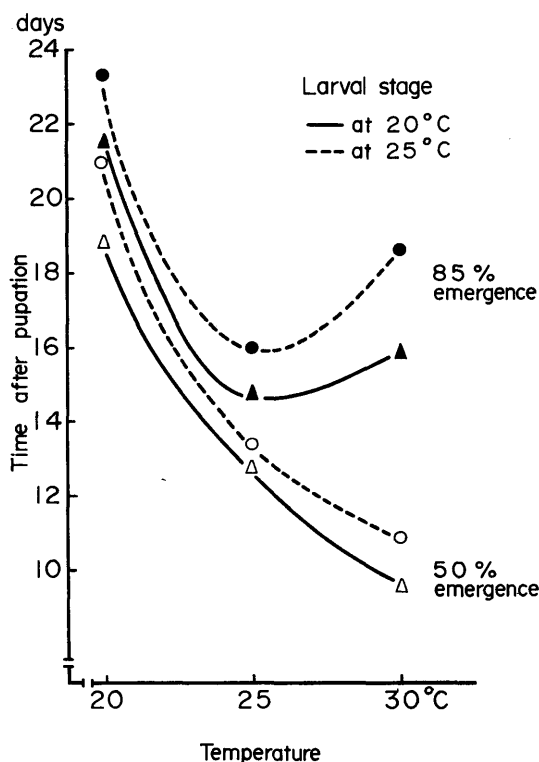


Fig. 2. Relation between the time required for emergence and the temperature during the larval and pupal stages.

influence on this aspect. The same tendency persisted irrespective of whether the insects had been reared as larvae at 20° or at 25°C. The temperature during the larval stage was, however, also influential. The higher rearing temperature tended to enhance the delay after pupation as compared with the low one.

It seems probable that the delayed emergence was not due to a decreased rate of development. A brief period of developmental block might be involved. The elimination of this block might be a process having a particular temperature coefficient. As shown in figure 2, the time required for 50 percent emergence was shortened in a usual fashion as the temperature rose from 20° to 30°C, while the time for 85 percent emergence was the shortest at 25°C, and delayed again at 30°C. Such a trend was quite consistent in the two series of tests. The delayed pupae might have undergone a physiological process with a negative coefficient between 25° and 30°C.

Retardation by heat

If there was such a particular process in the delayed pupae as stated above, their development might be much more severely reatracted at a still higher temperature. One lot was taken from each temperature group that was used in the above experiments. Within a day of pupation this lot was subjected to heating at 35°C in 75% R.H. and darkness. The schedule and result of this test are given as diagrams in figure 3.

When larvae were reared at 20°C and 16hr photophase and the subsequent pupae were subjected to 35°C, only a very few of them gave rise to adults within two weeks. When the pupae in this treatment were examined on the 15th day of heating, it was found that nearly half of them completed metamorphosis but died before emergence. The rest were surviving as pupae. The survivors were then transferred

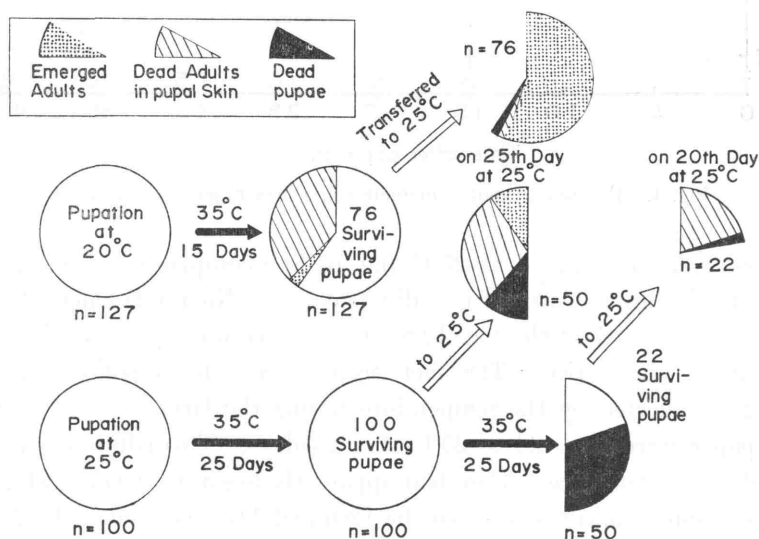


Fig. 3. Schedule and results of experiments of heat exposure with non-overwintering pupae.

to 25°C, at which they gave rise to moths except a few perishing.

The progress of moth emergence in this treatment is given in figure 4. This figure suggests that there were three different categories of pupae as to their time of development. There were those pupae which emerged within 10 days after transference from 35° to 25°C. They initiated development while at 35°C, since they took a considerably less time to emerge at 25°C than what was necessary when kept at 25°C from the beginning. Therefore, the heat treatment did not completely suppress their development. Most of the survivors emerged, however, between the 12th and 14th days at 25°C. This was comparable to the total time required for uninterrupted development at 25°C. These insects were apparently in a dormant state as long as they were kept at 35°C, and began to develop only after they were transferred to 25°C. As shown in figure 4, the progress of their emergence closely coincided with that of those pupae constantly kept at 25°C. Some pupae showed a further delay after the transference to 25°C.

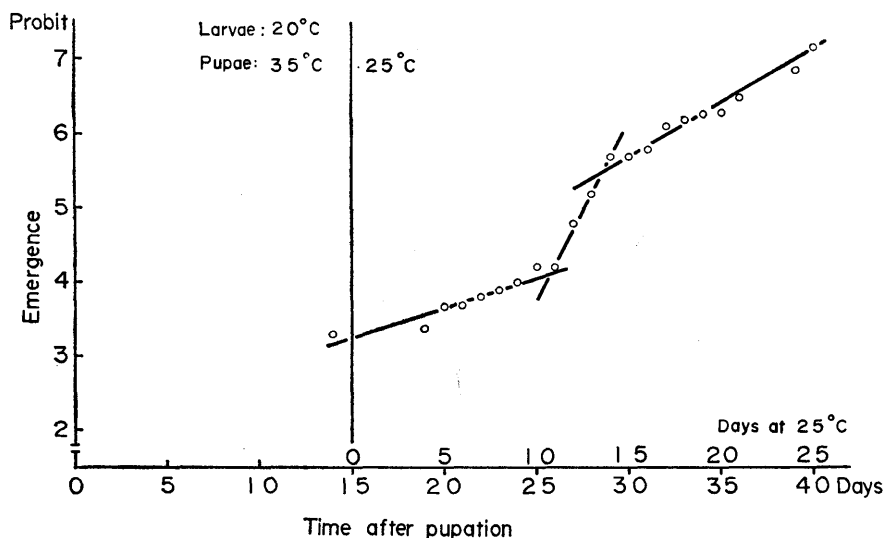


Fig. 4. Progress of moth emergence in a heat-exposure treatment.

If larvae had been reared at 25°C and 16 hr photophase, the resulting pupae responded to the heat treatment in a different way. No adults emerged from them during the first 25 days of the pupal life at 35°C. In no pupae was the adult body moulded during this period. This fact suggests that the response to heat at the pupal stage is affected by the temperature during the larval stage. Half of these dormant pupae were removed to 25°C after 25 days. Two adults emerged on the 6th day of the transference. They had apparently begun to develop while at 35°C. Other seven adults appeared between the 12th and 14th days, undoubtedly starting morphogenesis as soon as the heat inhibition was removed. Most of the rest failed to emerge and died, even though the adult structure was almost complete underneath

their pupal skin. None survived more than 20 days at 25°C.

From the other half of the pupae left at 35°C, no adult emerged for a further period of 25 days. On the 50th day they were examined and half of them were found alive and the other half dead. Any trace of adult structure could be detected in the dead pupae. The surviving pupae were transferred to 25°C. All of them were found dead on the 20th day after the transference, but dissection revealed that in most of the dead pupae was the shape of moth completed. They began, therefore, to develop at 25°C after an arrest of 50 days at 35°C.

A temperature as high as 35°C thus inhibits the adult formation in the pupa of *Hyphantria cunea*. This effect is to some extent reversible. As soon as the pupae are removed from the heat exposure, some of them are able to resume development. One may regard this as a kind of quiescence caused by the direct influence of heat. There is, however, evidence opposing this view. The proportion of pupae affected by this heat dormancy varies with temperature during the larval stage. In other words, the norm of response of the pupae is to a certain degree predetermined.

Retardation at different stages

If the phenomenon described above is a case of simple quiescence, it may occur at any stage of development whenever the insects are exposed to heat. In order to confirm this point, two series of experiments were undertaken at Hirosaki.

In the first series, the insects were reared as larvae at a mean temperature of 28°C (range, 25°–30°C) and a daily photophase of 16 hr. The pupae were divided into five groups. One, as a control, was placed at 25°C throughout the pupal life. The other four groups were subjected to 35°C after 0–1, 3–4, 6–7 or 9–10 days of pupation. When pupae were persisting after 14 days of the heat treatment, they were returned to 25°C. If young pupae were treated, none emerged before the end of the heat exposure so that all the pupae experienced two weeks at 35°C. If older

Table 2. EFFECT OF EXPOSURE AT DIFFERENT PUPAL AGES TO A HIGH TEMPERATURE OF 35°C ON DEVELOPMENT AND SURVIVAL OF *Hyphantria cunea*.

Larval stage	Age of pupae	n	%	\bar{x}	s
A 28°C 16hr photoperiod	Control*	50	98	14.4	3.5
	0–1 day	66	71	24.1	1.6
	3–4	66	30	28.0	1.5
	6–7	66	27	24.4	9.0
	9–10	66	81	13.7	4.4
B 21°C natural long days	Control*	78	100	9.9	2.0
	0–1 day	81	42	25.3	2.7
	3–4	81	11	24.0	8.7
	6–7	82	93	10.2	5.1
	9–10	83	100	10.4	5.8

* Kept at 25°C in series A and at 28°C in series B.

n= number of pupae.

\bar{x} =mean duration of pupal stage in days.

%= percent emerging as moths.

s=standard deviation.

ones were exposed, some moths emerged during the heat exposure so that the time spent at 35°C differed among individuals even in the same group.

In the second series, the larvae were fed in an insectary under natural long-day conditions of 40°35'N in June and July. The mean temperature during the larval stage was 21.3°C. The treatment of the pupae was the same as in the first experiment except that the pupae were kept at about 28°C before and after the heat treatment. The control group was also kept at 28°C.

In both experiments, the pupae received light only during several minutes of daily observations. They were put on moist filter paper in order to avoid extreme desiccation which might occur during exposure to heat.

The results of these experiments are summarized in table 2. The cumulated number of moth emergence in each treatment is illustrated in figure 5. From these data, it is clear that the susceptibility to heat varied with age. Soon after pupation, the insect was almost completely inhibited to develop by the heat exposure. A consider-

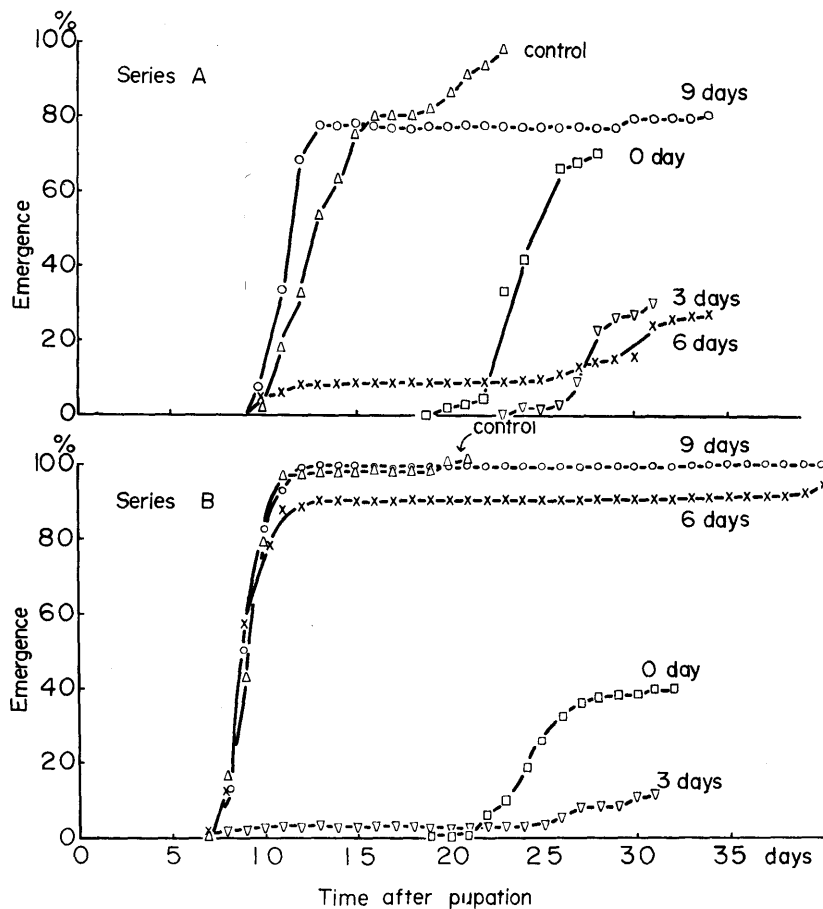


Fig. 5. Progress of moth emergence from pupae which were exposed to heat (35°C) for two weeks or less at different ages. Ages are indicated in days. Control temperature was 25°C in series A and 28°C in series B.

able proportion of pupae survived in a dormant state and resumed to develop when they were transferred to a mild temperature. This is in agreement with the observations stated in the preceding subsection. After a few days, the pupae were similarly retarded by heat, but they became less resistant and many failed to survive. At later stages, the heat exposure was no longer effective in suppressing pupal development. In other words, the pupae lost their ability to lie quiescent at the hot temperature, and their development, having been initiated at 25°C, did not stop even when they were exposed to 35°C.

The tendency stated above was repeatedly recognized in the two series of experi-

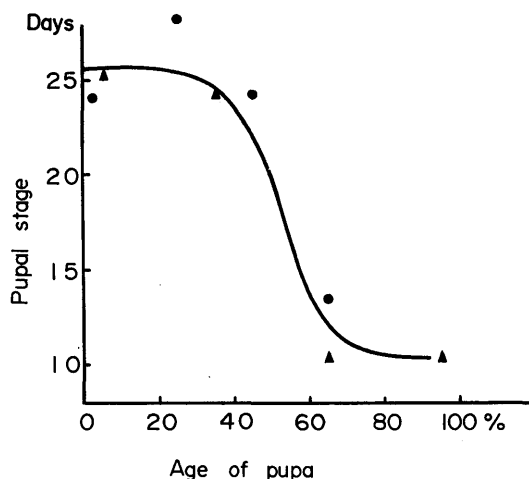


Fig. 6. Mean duration of pupal stage in relation to the age of pupae at which heat treatment (35°C) was applied. Circle—series A. Triangle—series B.

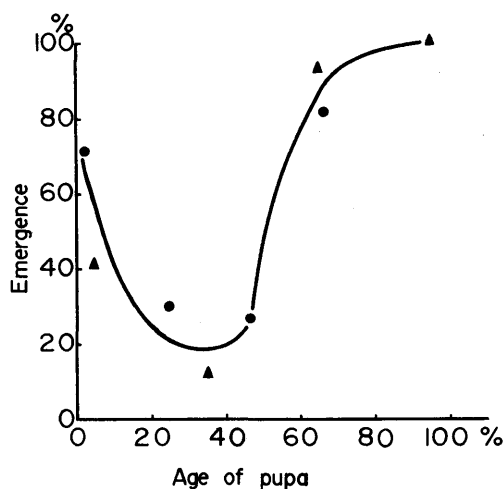


Fig. 7. Percent survival in relation to the age of pupae at which heat treatment was applied. Circle—series A. Triangle—series B.

ments. The results of the different series differed only in the timing of change in the response. This was probably related to the different rates of pupal development. The developmental rate was, as evidenced by the shorter duration of pupal stage of the control group, more rapid in the second than in the first tests. The lower temperature during the larval stage and the higher control temperature during the pupal stage in the second test might be responsible for this. If the age is expressed as percentage of the total life span of the pupa, the timing of change in response is very similar in the two series, as shown in figures 6 and 7. From these diagrams it is clear that the heat dormancy may take place only during the initial stage of the pupal life.

Direct effect of photoperiod

In several species of insects, photoperiod exerts an imminent control upon the maintenance and completion of diapause (HARVEY, 1958; MASAKI and OYAMA, 1963; McLEOD and BECK, 1963; WELLSO and ADKISSON, 1964). In a few species, the pupa has been known to be responsive to day-length (WILLIAMS and ADKISSON, 1964; MANSINGH and SMALLMAN, 1966, 1967). It seems therefore necessary to test the direct influence of photoperiod on the delayed emergence of summer pupae of *Hyphantria cunea*.

Two groups of larvae were reared at Hirosaki in a long photophase of 16 hr. One group was kept at a mean temperature of 24°C (range, 22°–26°C) and the other at a mean temperature of 28°C (range, 25°–30°C). After pupation, each group was divided into four lots, which were subjected to 12, 13, 14 or 15 hr photophases at a mean temperature of 28°C (range, 27°–30°C).

The results are set out in table 3, which shows that both the duration of development and its variance were not influenced by the photoperiod during the pupal stage. The direct action of photoperiod is therefore not involved in the delayed development of summer pupae.

As found in the table and more explicitly illustrated in figure 8, the results of these rearings confirmed the influence of temperature during the larval stage upon the development of pupae. Namely, the mean duration of pupal stage was longer

Table 3. DURATION OF PUPAL DEVELOPMENT OF *Hyphantria cunea*
AT DIFFERENT PHOTOPERIODS.

Larval stanges		Pupal stages		n	\bar{x}	s
Photop.	Temp.*	Photop.	Temp.*			
16hr	24°C	12hr	28°C	46	10.8	1.7
"	"	13	"	46	10.8	1.0
"	"	14	"	43	10.8	0.9
"	"	15	"	47	11.7	1.7
16hr	28°C	12hr	28°C	36	12.6	3.4
"	"	13	"	36	13.0	3.2
"	"	14	"	36	13.8	4.0
"	"	15	"	37	12.6	3.2

* Mean temperature.

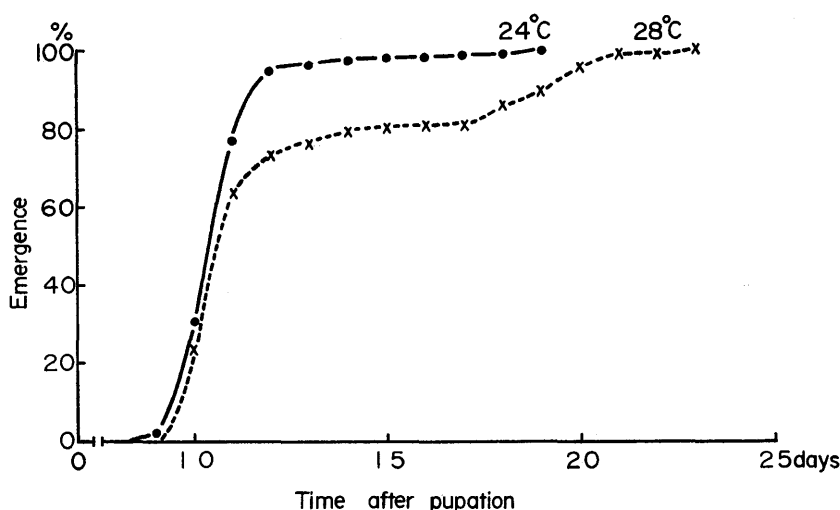


Fig. 8. Progress of moth emergence at about 28°C from two groups of pupae which had been reared at 24° and 28°C, respectively, during the larval stage. Data from different photoperiodic treatments during the pupal stage are lumped together.

in those grown at a higher temperature than in those grown at a lower temperature. Also, the high temperature group was more variable in development. Examination of the emergence curve revealed that this was due to the higher incidence of those pupae which postponed their emergence. In the low temperature group, only two percent of the pupae persisted more than 14 days, while 20 percent did so in the high temperature group.

Emergence under field conditions

In order to know whether or not the delayed emergence in the summer generation occurred in the field, the following observations were carried out.

Last instar larvae feeding on *Salix* sp. were collected on 4 July, 1967, at Hiratsuka. They were reared on the same food plant in a field cage. The cage was examined every day and the date of pupation of each individual was recorded. The pupae were kept in the same cage, although they were enclosed in opaque paper boxes which were provided for pupation.

They pupated in the period from 10 to 15 July. A total of 114 pupae was obtained, of which 98 emerged after 9 to 14 days of pupation. The remaining 16 pupae took from 18 to 73 days to appear as moths. Although the number of delayed pupae was small, this observation suggests the possible occurrence of delayed emergence in the summer generation in the field.

About 70 mature larvae collected at Yokohama in June, 1967, were also kept under observation in a field cage. In this case, the precise pupation date of each individual was not available. Most of them pupated in the last week of June. From the resulting pupae 14 adults emerged before 11 July. After this day, there was no emergence for two months. Five adults, nevertheless, appeared between 11

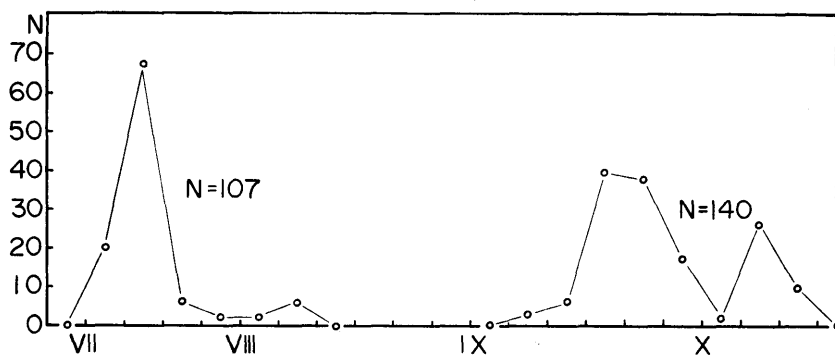


Fig. 9. Separated periods of moth emergence from one group of pupae formed between 21 July and 3 August, 1966, and kept under insectary conditions at Yokohama.

September and 4 October. Others were found dead on later dates.

A much more remarkable case of delayed emergence was observed previously, as briefly referred to in the introductory paragraph. The detail of this is as follows. In June and July, 1966, larvae of *Hyphantria cunea* were reared in a field cage at Yokohama. They pupated between 21 July and 3 August. These pupae were kept in an insectary. As given in figure 9, many adults emerged from them between 30 July and 9 August, and a few delayed ones between 14 and 21 August. After the latter date, there was no emergence from the surviving pupae for one month. From 23 September, however, moths started to emerge again, and continued to do so until the end of October. In this second period of emergence, 140 moths were obtained as against 107 in the first period. Only two pupae persisted to enter hibernation.

Despite this insectary observation, there were no moths caught by the light trap in September and October of the same year at the Horticultural Experiment Station, Hiratsuka. It was therefore not certain that many summer pupae delayed their emergence until autumn under the ordinary field conditions. At the same time, it seemed also possible to infer that the flight activity of delayed moths was prevented by the prevailing low temperatures, hence no trap catches in the autumn.

DISCUSSION

In all experiments described above, test insects were all subjected to the diapause-preventing action of a long-day photoperiod. If they were kept under ordinary seasonal conditions, they would emerge as moths before winter. Such pupae are, under the field conditions, formed in summer so that they might be called summer pupae. Their delayed development does not belong to a kind of hibernation diapause which has hitherto been studied in this moth.

It is not unexpected that the summer pupae may fail to use the photoperiodic calendar since the mature larvae crawl into tree holes and bark crevices, or

under stones and other objects on the ground for pupation so that the pupae may be subject to various light conditions. Also, any tested combination of temperatures during the larval and pupal stages failed to induce a very high proportion of pupae to undergo delayed development. In laboratory tests, indeed, it was not possible to produce the so conspicuous aestivation-like phenomenon that was observed under insectary or field conditions at Yokohama.

The present results suggest, nevertheless, that temperature plays a role in causing the delayed emergence of moths from summer pupae. Manifestation of delayed emergence is, to a certain extent, predetermined by the temperature during the larval feeding stage. If the pupae are kept at the same temperature, the incidence and extent of their delayed emergence varies with the temperature during the larval stage. On the other hand, if the insects are reared as larvae at the same temperature, the occurrence of delayed pupae is increased by a high temperature during the pupal stage. At temperatures below 30°C, the pupae are able to resume development spontaneously at the same temperature at which they have become dormant.

The response of pupae to a sublethal high temperature of 35°C implies a somewhat different feature. As shown in figure 3, some individuals were prevented from developing at this temperature, but they resumed to develop as soon as they were removed to a mild temperature. The cessation of development at 35°C may therefore be considered as a form of quiescence. High mortality after heat exposure indicated that this treatment was more or less harmful for the species. It should, however, be noted that the development could be stopped by the high temperature only during the initial stage of pupal life. Furthermore, the pupae were conspicuously different in their response to the heat treatment, if they were reared at different temperatures during the larval stage. That is, the response of the pupae to a high temperature was predetermined during the larval stage. The observed tendency was the reverse of what might be expected from the acclimatization effect. Those insects reared at a higher temperature were more susceptible to the heat treatment than those reared at a low temperature. This fact throws doubt upon the assumption that the heat dormancy was a simple phenomenon of quiescence. Alternatively, it may be assumed that the heat dormancy was a much stronger manifestation of developmental delay which may be encountered even at temperatures lower than 30°C. A difficulty for accepting this second assumption is that the retarded pupae responded to transference from 35°C to a lower temperature by an immediate resumption of development.

A third hypothesis seems to be possible. The heat treatment stops only the secretory activity of the hormone system which controls metamorphosis. According to this hypothesis, summer pupae are retarded to develop only before the critical period for the hormone secretion. The applied heat treatment suppresses only this secretory activity but not the process of morphogenesis itself. Therefore, those pupae which have passed the critical period do not cease to develop even at 35°C.

Further investigations are required to determine the reliability of these assumptions.

At any rate, it seems most unlikely that this effect of heat exposure is involved in the aestivation-like behaviour of summer pupae as observed at Yokohama in the two years, because the daily maxima of temperature rarely exceed 35°C even in the height of summer in the field. In any laboratory trial, we failed to cause so many pupae to undergo such long periods of dormancy without decreasing their viability.

Although the physiological nature of the delayed development is still obscure, the possibility can not be ruled out that it may occur in the field. If so, a few delayed adults of the summer generation would appear as stragglers late in the season. Their progeny might be still immature in late autumn under the field conditions of the Tokyo-Yokohama district. It seems possible that they may be taken erroneously as representing a partial third brood. It is therefore not always correct to regard the occurrence of young larvae in late autumn as an evidence of a partial third brood.

At present, it can not be inferred whether or not this delayed development in the summer generation would increase the fitness and become prevalent among the populations invading southern hotter regions of this country. It is, on the other hand, obviously fatal in the north. The present results show, however, that this phenomenon would scarcely be manifested in the cool climate.

SUMMARY

As previously shown, *Hyphantria cunea* is a long-day species in that an intense diapause for hibernation is induced by a short-day photoperiod. It was, however, found that some of the pupae, which had been reared as larvae in a long-day photoperiod, underwent brief and variable periods of arrested development. A high temperature during both the larval and pupal stages tended to increase such pupae. A particular temperature reaction, showing a negative coefficient between 25° and 30°C, seemed to be involved in initiating development of the delayed pupae. If young pupae were subjected to a temperature as high as 35°C, some of them stopped to develop but regained activity as soon as they were returned to a mild temperature. The competence to develop at 35°C was partly determined by the temperature during the larval stage. On the other hand, the photoperiod during the pupal stage was not responsible for the occurrence of delayed development. Field and insectary rearings suggested a possible occurrence of delayed emergence in the summer generation. This might be a cause of the existence of stragglers in the late season.

ACKNOWLEDGMENT

The writers are indebted to Dr. Hiroshi KITAJIMA and Mr. Nobuhiko OHO of the Horticultural Experiment Station, Hiratsuka, and to Dr. Syun'ichiro NAKAMURA of the Seed Testing Laboratory, Raw Silk and Horticultural Bureau, for laboratory facilities in doing part of this work at Hiratsuka.

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摘 要

アメリカシロヒトリの生物学的研究

VII. 夏世代蛹の発育遅延

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アメリカシロヒトリは長日昆虫で、その越冬休眠は短日によって誘導される。ところが臨界値以上の長日下にえられたさなぎの中に、羽化のおくれるものが発見された。この実体を知るために、幼虫を長日下に飼育し、えられたさなぎを用いて一連の実験を行なった。その結果は次のようであった。

羽化のおくれるさなぎの割合は、低温よりも高温のほうが多くなる。しかも、さなぎ期のみでなく、幼虫期の温度も同様の効果を与える。遅延個体の羽化は必ずしも温度の上昇にともなって促進されるとはかぎらず、30°C

ではかえっておそくなる傾向がある。さなぎを 35°C におくと、そのあるものは羽化するが、他のものは完全に発育を止めてしまう。こうしたさなぎを再び常温 (25°C) にもどすと、直ちに発育をはじめる。しかし、羽化しえないで、変態完了後に死亡するものもある。35°C で変態を完了する能力は、幼虫期の温度条件に左右され、高温 (25°C) に育ったものは低温 (20°C) に育ったものよりも、発育抑制をうけやすい。発育抑制はさなぎ期の前半期に限ってあらわれ、後半期に入ったものは 35°C にうつしても変態を完了するから、変態ホルモンの分泌阻

害と関連しているのではないかと想像された。さなぎに直接作用する光周期は、羽化抑制と関係がない。

横浜や平塚の野外あるいは飼育室内でも、夏世代に羽化のおくれるさなぎが観察されたので、自然条件でも、このような現象がおこる可能性がある。羽化のおくれた

さなぎの子世代は、秋おそくにも幼虫として発見されるだろう。従来、晩秋の幼虫は3化の証拠と考えられていたが、あるいは羽化遅延個体の子世代であるのかも知れない。