

Title	Geographic variation in the seasonal life cycle of <i>Mamestra brassicae</i> (LINN) (Lepidoptera : Noctuidae)
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GEOGRAPHIC ADAPTATION IN THE SEASONAL LIFE
CYCLE OF *MAMESTRA BRASSICAE* (LINNÉ)
(LEPIDOPTERA : NOCTUIDAE)¹⁾

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INTRODUCTION

Mamestra brassicae (LINNÉ) has a wide geographic range. In almost everywhere in the Palaearctic region, various kinds of vegetable crops are actually or potentially exposed to the attack by this insect. The common occurrence over such a vast area is undoubtedly a proof of its remarkable success in adaptation. The adaptation seems to rely, at least in part, on the genetic variability of local populations.

It has been worked out that this species forms a photoperiodic cline between 40° and 60°N in eastern Europe, through which the onset of winter diapause is adjusted to the seasonal changes at different latitudes (DANILEVSKII, 1961). In the Japanese Islands, the pupa may become dormant not only in winter but also in summer, and the summer diapause seems to be important for the geographic adaptation. The species is highly variable in the incidence and intensity of this diapause (MASAKI, 1956; MASAKI and SAKAI, 1965). In Hokkaido (41°30'–45°30' N) the local populations do not aestivate. In northern Honsyu (about 40°N) some pupae undergo a brief period of aestivation, but others do not. Both the incidence and intensity of summer diapause are gradually enhanced southward, and near the southern limit of distribution (27°–28°N) it is comparable in duration to the winter diapause. The pupae in the Amami Islands are thus in diapause for the warm five months from May to September, as well as for the cooler five months from November to March (SAKAE, unpublished data).

As each local population establishes adaptation to a particular environment, it would become restricted in adaptive plasticity. In such circumstances, a local genotype may fail to survive when it is transferred to an extremely different climatic area. Experiments by PREBBLE (1941) with *Gilpinia polytoma* and by DANILEVSKII (1957) with *Acronycta rumicis* provide such examples. In both species, the southern stocks were killed by frost when transferred to the northern areas within the species range. The ultimate cause of their extinction was the failure to enter diapause before winter. In view of these results, a method of autocidal control by using genes which are responsible for geographic adaptation may be proposed.

The present work has been undertaken in order to explore the possibility of such a method. Two strains of *Mamestra brassicae*, which were derived from widely separated parts of the Japanese Islands, were bred side by side at Hirosaki. They were exposed to a seasonal fluctuation of environment and their seasonal cycles of develop-

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ment were compared. Based on these results, the survival of each strain in northern and southern climates is considered.

MATERIAL AND METHOD

Source of material

The Hirosaki and Naze strains of *Mamestra brassicae* were available for the present work. The former was derived from egg batches which were collected during the first week of June, 1966, on the university campus (40°35'N). The latter was originated from one egg batch found at Naze (28°23'N) in the last week of October, 1965, and sent to the laboratory at Hirosaki. The larvae that hatched were kept under short-day conditions at 20°C in order to obtain diapause pupae capable of overwintering. The resulting pupae were stored at a low temperature until the following spring. In May, 1966, they were returned to a warm temperature. Moths emerged from them and laid eggs in the first week of June. Thus the rearing of the two local strains started at the beginning of the normal feeding season of this moth in Aomori prefecture.

Method of rearing

The larvae were reared in petri dishes and were provided with cut leaves of *Polygonum cuspidatum* as food. In order to avoid over-crowding, the number of insects per vial was decreased as they grew, and there were less than five in each 12 × 3 cm vessel at the final instar. When fully fed, the larvae were transferred to another petri dish loosely filled with moist tissue paper. Newly formed pupae were removed every day and weighed individually and then kept on moist filter paper in a petri dish. They were examined every day and the duration of the pupal stage of each individual was recorded.

Conditions of rearing

Four groups of larvae of each strain were reared in a series of photoperiodic boxes (MASAKI, 1966) with 12, 13, 14, and 15 hours of light per day. In the first brood at Hirosaki, feeding larvae are normally found from the first week of June to the second week of July, so that they are subject to long days of about 15 hours. The longest daily photophase used in the experiments approximated the natural day-length. The temperature in the photoperiodic boxes was not controlled. The weekly mean varied from 21 to 25°C. The average during the whole period of larval growth was about 23°C, being a few degrees higher than in the field.

Most of the larvae pupated during the first two weeks of July. The pupae were removed from the photoperiodic boxes and were placed under natural daylight conditions in a rearing room. In this room, the daily mean temperature fluctuated seasonally between 4° and 26°C. The mean temperature for the period of about one year from June 1966 to May 1967 was 14.7°C. This is comparable to an annual mean which may be encountered in 34°-35°N of the Japanese Islands. The range of diurnal as well as seasonal fluctuation was of course smaller in the rearing room than in the field. However, the seasonal trends were parallel in the room and field conditions.

Local climates

The original places of the two strains widely differ in climatic conditions. The

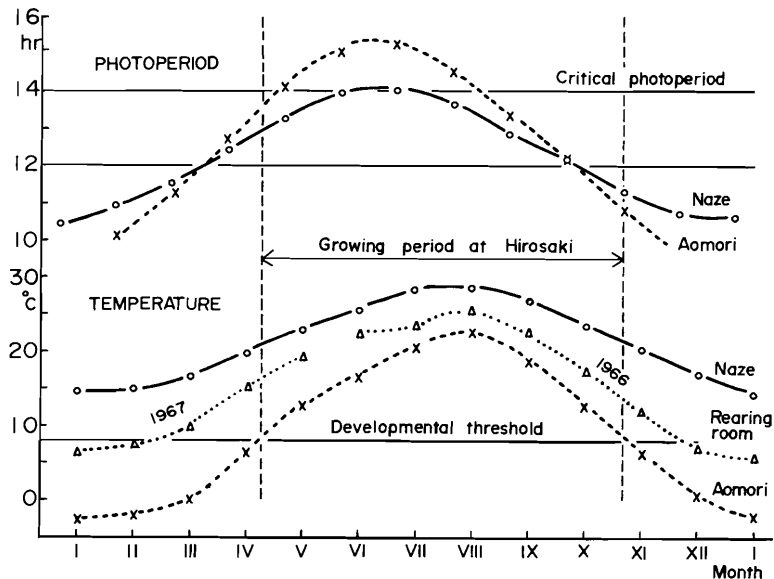


Fig. 1. Seasonal cycles of day-length and temperature at Aomori ($40^{\circ}49'N$) and Naze ($28^{\circ}23'N$) and monthly means of temperature recorded in the rearing room.

annual mean temperature is $9.1^{\circ}C$ at Aomori ($40^{\circ}49'N$) as against $21.1^{\circ}C$ at Naze ($28^{\circ}23'N$). The annual sum of effective temperature above $8^{\circ}C$ is 1621 degree-days at Aomori, while it is almost threefold as much, 4810 degree-days, at Naze. The two places are separated from one another by about 12 degrees of latitude, so that there is a difference of more than one hour in day-length at the summer solstice. As indicated in figure 1, the room conditions under which the two strains were grown were intermediate between the field conditions of the northern and southern habitats with respect to temperature.

RESULTS

Larval development

Table 1 gives the developmental time of larvae of the two strains. In the Hirosaki strain, the mean remained almost constant at 25 days in photoperiods of 12, 13, or 14 hours. The larvae pupated a few days earlier than this in a photoperiod of 15 hours. In the Naze strain, the mean duration of larval development varied within a range of only 1.2 days among different photoperiodic treatments. The variation was so small that any effect of photoperiod was not conceivable.

In each photoperiod, the two strains were similar in their developmental time. The difference between them was statistically significant only at the longest photoperiod. Even in this case, the northern strain pupated only 1.3 days earlier than did the southern strain. In spite of the contrasting climatic conditions of their original places, the northern and southern larvae are like each other in their developmental velocity.

The rate of larval growth could also be compared on the basis of size gains per unit time. The size gains during the larval stage might be represented by the pupal

TABLE 1
Developmental time (days) of larvae of northern and southern strains of *Mamestra brassicae* reared in different photoperiods at a mean temperature of 23°C

Photoperiod	Hirosaki, 40°35' N			Naze, 28°23' N		
	<i>n</i>	\bar{x}	$s_{\bar{x}}$	<i>n</i>	\bar{x}	$s_{\bar{x}}$
12 hr	83	25.6	0.19	143	26.0	0.17
13	110	25.6	0.15	138	25.4	0.18
14	86	25.9	0.17	99	25.6	0.16
15	96	23.5	0.18	91	24.8	0.17
Total	375	25.1	0.10	471	25.5	0.09

n = sample size. \bar{x} = mean. $s_{\bar{x}}$ = standard error of mean.

TABLE 2
Pupal weight (mg) of the northern and southern strains of *Mamestra brassicae* reared as larvae in different photoperiods at a mean temperature of 23°C

Photoperiod	Hirosaki, 40°35' N			Naze, 28°23' N			
	<i>n</i>	\bar{x}	$s_{\bar{x}}$	<i>n</i>	\bar{x}	$s_{\bar{x}}$	
♂	12 hr	47	457	7.2	73	443	5.8
	13	56	472	5.4	64	424	5.6
	14	42	422	9.6	47	412	6.9
	15	49	391	10.6	40	437	4.6
	Total	194	435	4.7	224	430	2.4
♀	12 hr	36	494	6.9	70	504	5.8
	13	54	509	6.1	74	462	8.1
	14	41	465	8.7	52	472	7.5
	15	46	459	11.9	51	483	6.2
	Total	177	483	4.6	247	480	3.7

n = sample size. \bar{x} = mean. $s_{\bar{x}}$ = standard error of mean.

weight. Table 2 gives the means of the pupal weight in different photoperiodic treatments. The pupal weight was highly variable among different groups, but no definite trend of its variation could be detected in relation to either photoperiod or geographic origin. A consistent variation was found only between the sexes; the female was on the average about 40 to 50 mg heavier than the male at any photoperiod in each strain. In each sex, the difference between the northern and southern pupae was small. Therefore, the rate of larval growth seems to be relatively stable among local populations (cf. HIRATA, 1962b).

Pupal development

In figure 2 are shown the numbers of emerging moths from all the surviving pupae obtained in the rearings stated above. The pupae were kept in the rearing room throughout the whole period of observation. Since most of the pupae had been formed in the first half of July, the extremely variable time of their development was at once noticeable in this figure. Moths began to emerge from late July and continued to do so until the middle of May of the next year. The duration of pupal stage ranged from only a few weeks to more than 300 days. During this time lapse of ten months, four more or less distinct peaks of moth emergence were found.

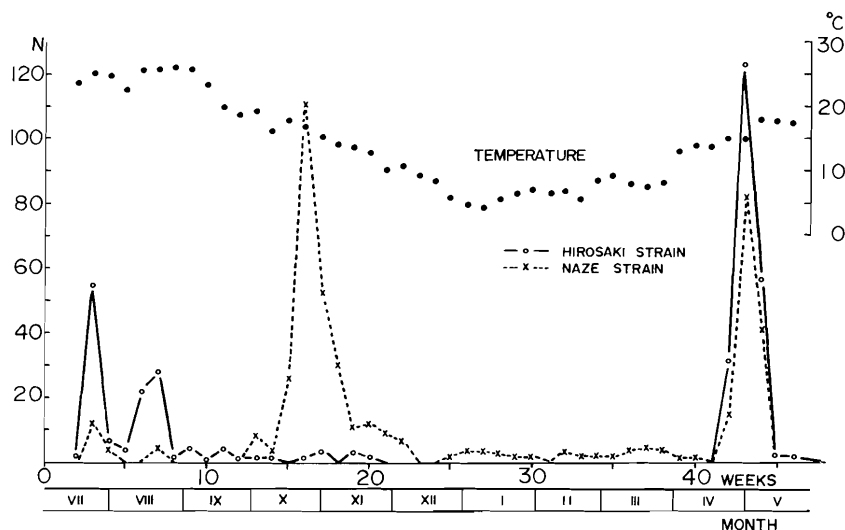


Fig. 2. Numbers of moths emerging from pupae of the northern (Hirosaki) and southern (Naze) strains. The pupae were formed in July in various artificial photoperiods.

The first one occurred soon after pupation at the end of July. This undoubtedly represented the nondiapauses development, since the sum of effective temperature attained to about 300 degree-days by the peak date. This value about corresponded to the known heat requirement by the diapauses-free pupae (SANTA, 1955 ; MASAKI, 1956a; HASEGAWA, 1967). As seen in the figure, most of the pupae belonging to this group were of the northern origin, and only a very small number of the southern pupae were involved.

The next peak was found in late August. This was again mostly comprised of moths emerging from the northern pupae, and few of the southern pupae developed at this period. The time lapse between the first and second peaks was about four weeks, which represented the duration of aestivation in the northern pupae. This brief diapauses in summer is a characteristic of the northern Honshu populations (MASAKI, 1956 ; MASAKI and SAKAI, 1965).

The third peak of emergence occurred at the end of October, about two months after the completion of the northern summer diapauses. This peak was mainly due to moths emerging from the southern pupae that had experienced a long summer diapauses. A few moths thereafter emerged sporadically from the persisting southern pupae. This was probably caused by an intense summer diapauses, which delayed the resumption of development until the cold season. Since the southern and northern larvae pupated at the same season, and since the pupae of the different origins were kept under the same external conditions, the remarkable delay of moth emergence from the southern pupae was a doubtless indication of the hereditary strength of their summer diapauses.

The last peak of emergence appeared in the following spring. The pupae giving rise to adults at this season could be regarded as successful overwinterers. Many of both the northern and southern pupae survived the winter. There was no difference in the peak date of emergence between the two strains. They were therefore similar

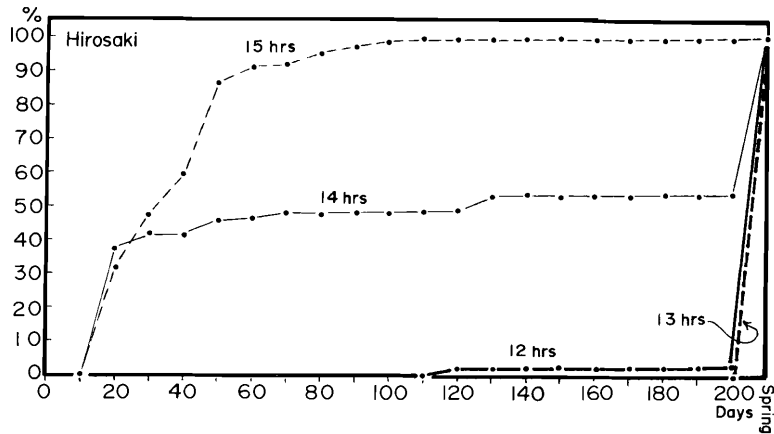


Fig. 3. Moth emergence from the northern pupae reared in different photoperiods. Ordinate: cumulated number of emerging moths. Abscissa: time in days from pupation.

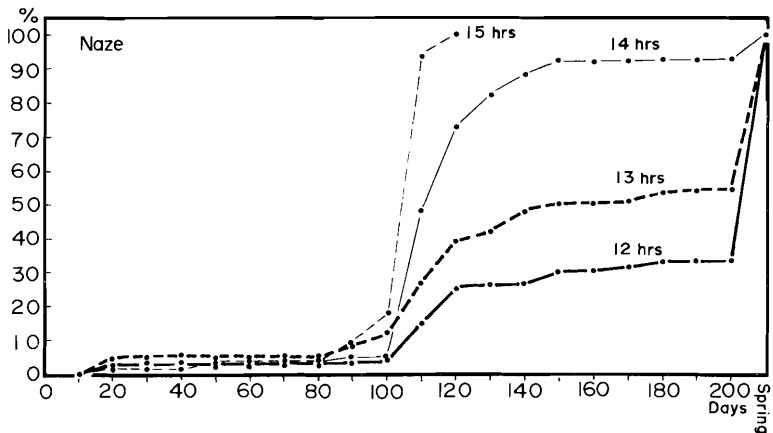


Fig. 4. Moth emergence from the southern pupae reared in different photoperiods. Ordinate: cumulated number of emerging moths. Abscissa: time in days from pupation.

in their thermal requirements after hibernation. The sum of heat units accumulated in the spring amounted to 270 degree-days by the peak date. This value was in agreement with that obtained for the post-diapause development at Tokyo (SANTA, 1955), Iwate (HASEGAWA, 1967) or Sapporo (MASAKI, 1956a; MATSUMOTO, 1956).

The local strains seem to be rather similar in the intensity of winter diapause and also in the thermal requirement after hibernation. Variations between them are mainly found in the incidence, maintenance or termination of summer diapause.

Photoperiodic response

As described above, the pupal development of *Mamestra brassicae* was highly variable. The factors causing this variation seem to be the photoperiod during the larval stage and the geographic origin. The first factor can be seen in each of figures 3

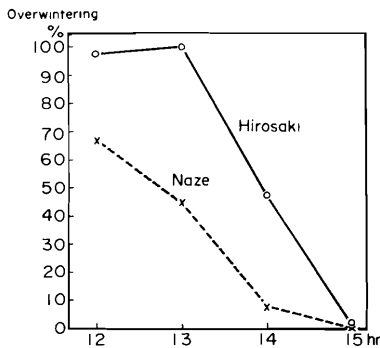


Fig. 5. Incidence of overwintering pupae at different photoperiods in the northern (Hirosaki) and southern (Naze) strains.

and 4. The second factor may become evident by comparing these two figures. This comparison and figure 5 may also suggest an interacting effect between photoperiod and strain, that is, the response to photoperiod differs in the different strains.

Figure 3 shows the emergence of moths of the northern strain in various photoperiods. At a photoperiod of 15 hours, about one-third of the pupae averted any kind of diapause, giving rise to moths within 20 days. The emergence progressed further with time, and few pupae persisted more than three months. Almost two-thirds of the pupae were therefore referable to the aestivating type. Only one persisted through the winter. At a 14-hour photoperiod also, about

one-third of the pupae were free of diapause, but the rest lay dormant for long periods and did not resume to develop until the next spring. At still shorter photoperiods of 12 or 13 hours, almost all the pupae passed through the winter.

Figure 4 illustrates the photoperiodic response of the southern strain. The curves of moth emergence in this diagram differ conspicuously from those described above. At any photoperiod, the percentage emergence remained at a very low level for about three months after pupation. The emergence curve then rose sharply, and at a 15-hour photoperiod all the survivors completed development just before winter. A similar sequence of adult emergence was observed at a 14-hour photoperiod except some pupae persisting until the next spring. At 12- or 13-hour photoperiods, only less than half of the pupae gave rise to adults concurrently with those raised at the longer photoperiods. The rest overwintered.

The northern and southern strains were similar in that a short photoperiod was required for the induction of overwintering diapause. As shown in figure 5, however, they are not identical in the critical photoperiod for this induction. It is 14 hours in the Hirosaki strain while about 12 hours 30 minutes in the Naze strain. Moreover, the level of induction of this diapause is generally higher in the northern than in the southern strain. In addition to the characteristics of summer diapause, these local differences should also have an important bearing on the adjustment of the seasonal life cycle to the northern and southern climates.

Seasonal life cycle

The climatic indices at Aomori and Naze are given in the 1965 edition of *Rikanyempo* compiled by the Tokyo Astronomical Institute. Based on these data, the photothermographs which represent the accumulation of heat in relation to the change of day-length at the two localities are drawn in figure 6. On these curves, the larval stages sensitive to the influence of photoperiod are represented by rectangles. In Aomori prefecture, the occurrence of the sensitive stages of the two broods can be predicted from the accumulation of effective temperatures above 8°C. About 280 degree-days are required for emerging of adults from hibernated pupae, as already cited. Moths mate and lay eggs soon after their emergence. The egg stage lasts 4 days at 25°C (ISHIKURA and OZAKI, 1958) or 3 days at 30°C (OTUKA, SANTA and SUTO,

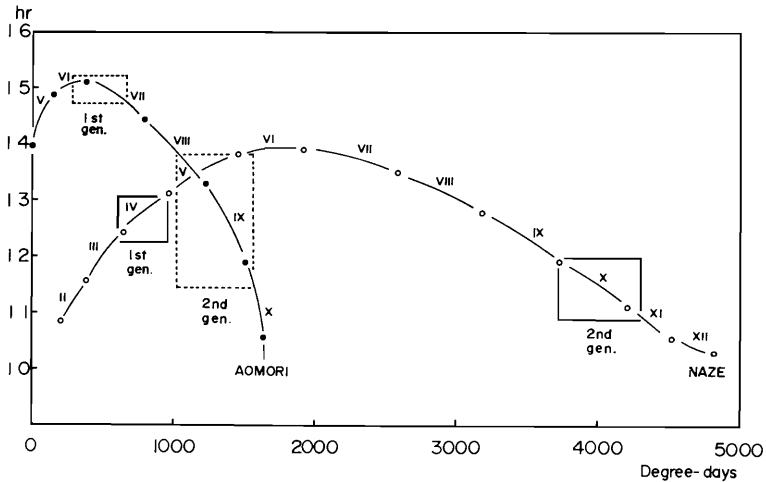


Fig. 6. Photothermographs at Aomori and Naze for understanding the seasonal life cycle of *Mamestra brassicae*. By rectangles are indicated the larval stages sensitive to photoperiod.

1953), requiring about 60-70 degree-days. The larvae of the first brood would therefore appear from the middle of June when the heat accumulation attains to about 350 degree-days. Since some of them give rise to nondiapause pupae, a further accumulation of about 700 degree-days that is necessary for one nondiapause generation (MATSUMOTO, 1956) should bring forth the second brood. The sensitive stage of the second brood is consequently expected to begin from the middle of August. However, the progeny of aestivating pupae would appear somewhat later, and larvae in the sensitive state might exist at least until late September. These predictions do not contradict with field observations by HIRATA (1962a, 1963). It is clear in figure 6 that the first-brood larvae grow in long days of about 15 hours, while the second-brood larvae feed in short days of about 14 hours or less. The critical photoperiod of this local population lies between the day-lengths experienced by the two broods. The seasonal life cycle is understood from the photoperiodic response.

It seems rather difficult to account for the seasonal life cycle at Naze in a similar way. In the southern island, any extensive field survey of the seasonal development of this moth has not been carried out. The only data pertaining to the life cycle are provided by SAKAE (unpublished observations), who kept the local specimens throughout the year in an insectary. Based on this information, the sensitive stages are indicated on the photothermograph. As seen in the graph, the sensitive stage of the first brood occurs later than the period predicted from the accumulation of heat. As stated before, however, the Hirosaki and Naze strains developed at the same rate after hibernation in the laboratory. This discrepancy should not therefore be attributed to any genetic difference between the local populations. It may be supposed that the delayed spring emergence at Naze is caused by the mild winter which may prevent the rapid termination of diapause. At Naze, in fact, the monthly mean temperature does not fall below the developmental threshold (8°C) even during the coldest month (figure 1). In order to predict the date of spring emergence under such circumstances, it is necessary to examine the maintenance and termination of diapause in the overwintering

pupae.

As demonstrated in the rearing room, the long summer diapause belongs to the genetic characteristic of the Naze strain. Since most, if not all, of the first-brood pupae would aestivate at Naze, the occurrence of the second brood cannot be predicted from the accumulation of heat. According to observation by SAKAE, the second-brood larvae mainly feed in October and November. As shown in figure 6, the day-length in the sensitive stage of the first brood is more than 12 hours, while it is less than 12 hours in the second brood. The critical day-length for determination of the type of diapause should be around 12 hours. The experimental results plotted in figure 5 conform to this phenological requirement, showing the median photoperiod of about 12 hours 30 minutes for inducing hibernation in the Naze strain. The response around the critical photoperiod was, however, not sharp. The difference of less than one hour between the day-lengths in the first and second broods would be insufficient for complete switching over of diapause from the summer to the winter type. Factors other than day-length may be involved.

DISCUSSION

The northern and southern strains of *Mamestra brassicae* differ in the incidence, maintenance or termination of summer diapause and in the critical photoperiod for inducing winter diapause. Because of these differences, the two strains maintain their different seasonal life cycles even when they are kept in the same climatic conditions. The local strains would fail to accomplish the seasonal regulation of their developmental cycle, if they are removed far from their birth-place and released in the field. The results of rearing show that the Hirosaki strain is of course able to maintain successive generations in the northern environment. Most of the first-brood pupae of this strain give rise to moths before the end of August, so that there is a sufficient amount of heat before winter for development of their offspring. So far as temperature concerns, the first-brood adults must appear before the first week of September at Hirosaki in order to produce progeny which overwinter successfully.

Most of the Naze pupae fail to emerge as moths until October or November owing to the prolonged summer diapause in the first brood. It is evident that if they were transferred to the northern locality, their progeny would perish by frost at an early stage of larval life. It might be suspected further that the moths of the first brood would fail to emerge on cold autumn nights at Hirosaki. For these reasons, the southern population would be annihilated when it is released in northern Honsyu or Hokkaido.

On the contrary, the northern population would not be successful in the southern environment, because it requires a relatively long day-length in order to avert overwintering diapause. Figure 6 suggests that at Naze the day-length during the larval development ranges from 12 to 13 hours in the first brood, being apparently shorter than the critical level for the northern strain. As a result, the northern pupae would be forced to enter hibernation already in late spring under the photothermal conditions at Naze. The life cycle would become univoltine. The pupae would lie dormant for as long as 10 months. During this long period of immobility, they would suffer high mortality, being exposed to hot weather or other environmental stresses.

The southern genotype would apparently be lethal in the northern climate, and the northern genotype would fail to use the rich southern environment. This fact may

be considered in developing a method of autocidal control (KNIPLING, 1960). The use of local adaptive genes for such a purpose seems to have some advantage as compared with lethal mutants or some sterilizing agencies. In many cases, the geographic adaptation seems to be accomplished by a cline, so that a genotype suitable for the purpose can be selected from a graded series of local genotypes. An effective genotype can be located by means of the photothermographic analysis of local climates. Introduced genes would not decrease the viability or activity of their carriers, because the lethal influence would be achieved only by disharmonization between the life cycle and the seasonal changes.

The use of adaptive genes seems to be promising, but it remains to be a mere possibility unless at least the genetic relationships between the local traits and the degree of mating success between local strains are made clear. Solution of these questions is also significant for understanding the evolution of geographic adaptation.

SUMMARY

Northern (Hirosaki, 40°35'N) and southern (Naze, 28°23'N) strains of *Mamestra brassicae* (LINNÉ) were bred in a rearing room at Hirosaki where the seasonal fluctuation of temperature was comparable to that encountered in 34°–35°N of the Japanese Islands. Both strains hatched in June and were fed in photoperiods of 12, 13, 14 or 15 hours. They were similar in the rate of larval development as well as in the pupal weight, although conspicuously different in the incidence and maintenance of summer diapause and in the median photoperiod for the induction of winter diapause. Summer diapause, which may be invoked by a long photoperiod, lasted much longer in the southern than in the northern strain. As a result, moths emerged from the southern pupae in late autumn, so that their progeny would not survive in the northern climate. The critical photoperiod for the induction of winter diapause was longer in the northern than in the southern strain. Because of its long critical photoperiod, the northern strain would enter hibernation already in the first brood if it is transferred to the southern island. Based on these results, a possible use of local genes for the autocidal control is suggested.

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