

GEOGRAPHIC VARIATION OF DIAPAUSE IN INSECTS*

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I. INTRODUCTION

Diapause as an important adaptive trait has been known to occur in many species of insects inhabiting various parts of the world. Among other things, it takes a leading part in the seasonal regulation of the life cycle. Through the timely onset and close of diapause, insects are able to synchronize the time of growth and breeding with the favourable season of the year. They would have thus a greater chance than otherwise to survive a great deal of seasonal changes in the environment. The available information presents a number of such examples, for which the reader is referred to the reviews by BONNEMEISON (1945), BODENHEIMER (1952), ANDREWARTHA (1952), EMME (1953), LEES (1955) or DANILEVSKY (1956). The general account of diapause is also given in these extensive works.

It would seem reasonable to presume that this physiological faculty of seasonal regulation have evolved under the influence of the long-term process of natural selection. As a consequence of this adaptation, insects have attained an impressive degree of fitness to the seasonal cycle of the environment. At the same time it might be suspected that some species are highly specialized in their mode of annual cycle, so that they could no longer endure any shift in the rhythm of the seasonal changes. If an insect would have lost the plasticity in its way of seasonal regulation, it would be limited to a climatically uniform area or to particular places protected from violent fluctuations of external conditions. As a matter of fact, however, some species are found thriving in a wide variety of climatic conditions. In the Japanese Archipelago, for instance, the cabbage moth *Mamestra brassicae* is a serious pest of vegetables on the subtropical isles of Amami as well as on the cool, snowy island of Hokkaido or even in the severe climate of Sakhalin (MASAKI, 1956). Many more examples of this sort could be quoted and in most, if not all, of such cases some adaptive changes in the mechanism of the seasonal regulation should have taken place to cope with the diversity of local conditions.

Although the available data are as yet far from sufficient to understand all the elaborate aspects of the problem, it seems worthwhile to sketch briefly the known facts and to extract the essential features in order to promote further intensive studies about this fascinating subject. This is the aim of the present work, which is not

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intended to cover all the available information.

II. INCIDENCE OF DIAPAUSE

In certain species of insects, the number of brood per year is strictly constant throughout the whole range of distribution. They are mostly univoltine, as shown by a familiar example of the gipsy moth *Lymantria dispar*. The obligatory intervention of diapause everywhere is the direct cause of their constant voltinism. In others, the voltinism varies from place to place. This is accomplished by the variable incidence of diapause. Now, two factors seem to be responsible for the local variation in the incidence of diapause. One is the local difference in climatic conditions and the other is the local variation in the genetic constitution of the populations. The latter would be elucidated when phenologically different local populations were compared in the same environmental conditions.

The two striped grasshopper *Melanoplus bivittatus* is univoltine in Prairie Provinces in Canada, while it is semi-voltine, i. e. it completes one life cycle in two years, at Kersley in the interior of British Columbia. The heritable variation in diapause is involved in this locally different cycles. In the laboratory the eggs from Kersley enter diapause twice at different stages of development; at each stage a prolonged period of cold exposure is necessary to become free of diapause, and as a result the majority of the eggs have to pass two winters before hatching in the field. In contrast, most of those from Prairie Provinces hatch after one period of diapause (PUTNAM and HANDFORD, 1958). The Lethbridge population enters diapause also only once as demonstrated in experiments by CHURCH and SALT (1952).

A similar variation is found in the case bearer *Fumea crassiorella*. In Portugal it is univoltine with a larval diapause, while in central Europe it is partly semi-voltine, a certain proportion of the larvae hibernates twice before pupation. This difference is probably based on the different genetic constitutions of the local stocks, for even in the warm climate of Portugal about half of the offspring from Prague required two winters to complete development (MATTHES, 1953).

The special ability of the northern populations of these insects to enter diapause twice in the life cycle has likely evolved as an adaptation to the short growing season insufficient for completing development. Semi-voltinism with twice diapause in the life cycle is also found in other species such as the grasshopper *Pardalophora apiculata* or the saturniid moth *Pseudohazis eglanterina* in the cold climate of Canada (PICKFORD, 1953; EVANCE, 1958). But it is not known if there is a local difference of this life cycle and diapause. It should be noted that semi-voltinism is not always accomplished by diapause; Some species of the Canadian grasshoppers pass the first winter as diapausing eggs but the second winter as quiescent nymphs. Many more examples of this sort might be found in alpine butterflies.

Variation in the incidence of diapause is more conspicuous and widespread among those species which have the potential capacity of continuous development. These species are usually multivoltine in the southern part of their range, and the number of annual generations decreases northward until they become univoltine in the northern reaches. In parallel to this, diapause tends to be obligate and increasing proportion of individuals enters diapause in each generation, as reviewed by LEES (1955). He cited as examples the corn borer *Pyrausta nubilalis* in the United States (BABCOCK, 1924 and others),

the spruce sawfly *Gilpinia polytoma* in eastern Canada (PREBBLE, 1941a, b), the white butterfly *Pieris napi* in Fennoscandinavia (PETERSEN, 1947), and the saturniid moth *Telea polyphemus* in the United States (DAWSON, 1931).

A similar geographic tendency might be found in many other species with multiple generations in certain parts of their range. When the larvae of *Acronycta rumicis* from different localities of Russia were reared in diapause-preventing conditions, a considerable proportion of the pupae of the Leningrad population entered diapause while those from southern localities were completely free of it (DANILEVSKY, 1957). The same tendency was also found in several other species such as *Spilosoma menthastri*, *Pieris rapae*, *Capua reticulana*, *Mamestra brassicae*, *Pandemis corylana*, *Acronycta leporina*, *A. megacephala*, *Demas coryli*, and *Smerinthus populi*. In all these species, the Leningrad stocks showed more or less a stronger tendency to enter diapause than the Belgorod stocks. The failure of the Leningrad insects to escape from diapause in a long photoperiod does not necessarily indicate the obligate nature of their diapause, for it was elucidated in *Acronycta rumicis* that diapause could be prevented by continuous illumination at a temperature higher than 27.5°C. There can be little doubt, however, that the northern populations of these insects have at least a strong tendency to enter diapause over a wide range of external conditions as compared with the southern ones, and also that some of them might have the genetic property of obligatory diapause. In the last three species named above, indeed, the tendency towards diapause was so strong that all individuals entered diapause in the long photoperiod when they came from Leningrad.

Considering from its geographic incidence, diapause of obligatory type seems to have evolved in the northern populations as a result of selection by the scarce natural resources that permit to produce only one generation a year. By the regular onset of diapause in each generation, the population is prevented from responding to a temporary shift in climatic conditions that may otherwise invoke an untimely growth. In warmer southern climates, on the other hand, facultative diapause might be more preferable, since it enables the population to repeat active generations before winter and thus to exploit more environmental resources available for multiplication. Further south, even diapause of facultative type might have no survival value, but it would become a handicap in the competition with other non-diapause species. In the region where there is almost unlimited supply of food and warmth, insects might enjoy the rich environmental resources, breeding and growing throughout the the year by the complete omission of diapause.

Thus the tropical subspecies of the migratory locust *Locusta migratoria migratorioides* always develops without arrest, while the populations in France (LE BERRE, 1952, 1953) and southern Russia (YAKHIMOVICH, 1950) undergo diapause. Another strain with facultative diapause also occurs in the southern part of France (LEBERRE, cited in LEES). The subspecies *Locusta migratoria danica* enters an embryonic diapause in Japan, where it is virtually univoltine, while diapause is absent or at least facultative in the bivoltine population which forms migrating swarms in China (UMEYA, 1946).

The brown-tailed moth *Euproctis pseudoconspersa* affords another example of this kind. It is bivoltine in the main island of Japan and exclusively hibernates in the egg stage (MINAMIKWA, 1951a), whereas it shows no conspicuous arrest in Formosa where

it has six annual generations and various stages of development can be found all the year-round (SONAN, 1927).

The Japanese subspecies of the Eri silkworm *Philosamia cynthia pryeri* is mostly bivoltine with a facultative diapause in the pupal stage, though in Nagano Prefecture it is univoltine. The tropical subspecies *Philosamia cynthia ricini* entirely lacks the capacity for diapause and repeats several generations in Assam, its homeland (KOID-SUMI and SHIBATA, 1938). In this form no attempt to induce diapause by controlling the day-length and temperature during the egg and larval stages was successful (KAWAGUCHI and KANEMURA, 1941). Despite this remarkable diversity in the diapause behaviour, the different subspecies are physiologically not isolated; the hybrids between them could have been reared for five or more successive generations without reducing the viability (YAMAGUCHI, 1949). Hence a complete series of graded variation from obligatory diapause through facultative to nondiapause could be seen in this moth. *Locusta migratoria* would provide another example of this gradational variation. In other species referred to above, the genetic property of the local populations varies from nondiapause to facultative diapause, or from facultative to obligatory one. From

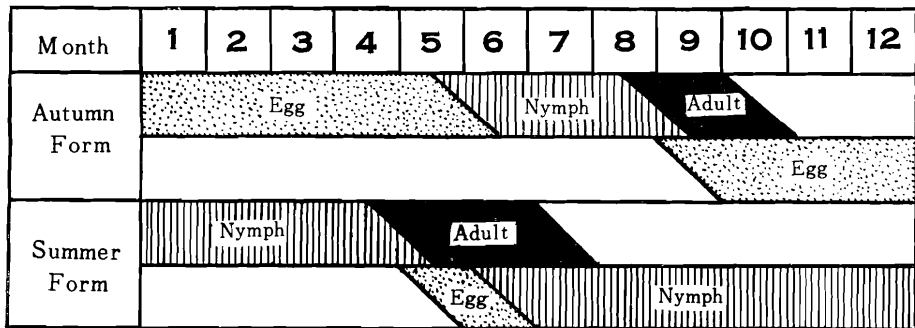


FIG. 1. Two different types of life cycle of *Scapsipedus aspersus* in certain southern districts of Honshu (after OHMACHI and MATSUURA).

this mode of variation, it would seem that facultative diapause is the necessary intermediate step to attain the genetic change from nondiapause to obligatory diapause. But this is not always the case, as indicated by the following example.

The cricket *Scapsipedus aspersus* is strictly univoltine throughout Japan and most populations enter obligatory diapause in the egg stage (OHMACHI and MATSUURA, 1951; MASAKI, 1960). Nondiapause specimens are, however, sparsely found among the ordinary ones in certain southern prefectures facing the Pacific ocean. They are frequently confined to such micro-habitats as southern exposures of hillocks where the winter temperature presumably tends to be higher than in other sites. In spite of the absence of diapause in the egg stage, this form grows slowly and has only one generation a year as well (OHMACHI and MATSUURA, personal communications): It might be inferred from its pattern of distribution that these small populations would represent the northern pioneers from the south, where the nondiapause populations with a multivoltine life cycle would be thriving. It is, however, yet to be determined whether this variation indicates a complete omission of diapause or a mere shift of diapause from the egg to the nymphal stage.

It will be noted that this divergence in diapause behaviour effectively segregates the

two partly sympatric strains (see fig. 1). The nondiapauses populations are usually heard singing from May to July in advance of the autumn song of the predominating populations. The reproductive seasons of the two forms are thus well separated, though there is no detectable difference in their song. In the laboratory fertile hybrids can easily be obtained between them (OHMACHI and MATSUURA). A similar variation seems to exist between the spring and autumn broods of the American field cricket *Acheta pennsylvanicus*, however the geographic distribution of the two types of life-cycle has not been elucidated (ALEXANDER, 1957):

If speciation by the seasonal isolation of this kind would have progressed further, a pair of closely related species, one with diapause and the other without it, would share the territory into northern and southern parts. Such a situation is perhaps illustrated by the distribution and diapause behaviour of the very closely allied species of the field cricket in Japan: The Emma field-cricket *Gryllulus* (= *Acheta*) *mitratus* occurs almost everywhere in the suitable habitat from the central part of Hokkaido to the southern tip of Kyushu, but its habitation on the isles of Amami and further south is in doubt; while the Taiwan field-cricket is restricted to the coast of the southwestern districts and is also found in the Ryukyu Islands, probably extending its range to Formosa or further south (OHMACHI and MATSUURA, 1951b). The Emma shows a univoltine life cycle with an obligatory diapause in the egg stage (MASAKI, 1960a), but the Taiwan has no diapause at all, with two generations a year at least on the southern coast of Kii peninsula, and usually hibernates as nymphs at half-grown stages. The hybrid sterility between the two siblings is now complete, as demonstrated by intercrossing experiments in the laboratory.

Such a seasonal segregation is less pronounced between strains with obligatory diapause and with facultative one, for they hibernate at the same stage of development and have a higher chance of concurrent emergence from diapause in spring, which might result in intercrossing. When the diapausing pupae of different local stocks of *Acronycta rumicis* were kept hibernating in the natural conditions of Leningrad, the moths emerged almost simultaneously from them, in spite of their different genetic constitutions with respect to the incidence of diapause (DANILEVSKY, 1957). The seasonal segregation of the univoltine and multivoltine strains of the corn borer *Pyrausta nubilalis* in the Lake States (the United States) is not complete, and the two are intermingled, forming heterozygous populations in certain areas where they encounter one another (VANCE, 1939; ARBUTHNOT, 1944; NEISWANDER, 1947).

III. REACTION THRESHOLD IN FACULTATIVE DIAPAUSE

Variations in the incidence of diapause stated above might be due to the varying threshold of external stimuli for the evocation of diapause: If an insect has an extremely low threshold, it would enter diapause in a very wide range of environmental conditions, and fail to avert diapause within the limits of survival. Conversely, if the threshold is extremely high, the conditions which induce its diapause might be non-existent in the ordinary range of environment. Between these extremes there would be an intergraded series of the reaction threshold. If a species has an intermediate threshold value, its diapause would be induced by some regimes but not by others, namely it is facultative (cf. LEES, 1955). The reaction threshold has thus little ecological meaning if it is greatly departed from the limits of ordinary fluctuations

of the environmental conditions. Therefore, the geographic variation manifested by the varying reaction threshold deserves consideration especially in diapause of facultative type.

Among other external factors, the length of daylight has been known by far the most important for the evocation of facultative diapause in many insects. It varies regularly with the progress of season, and also with latitude or altitude, and so insects should respond to different regimes of this factor in order to enter diapause in the proper season at different geographic locations. Recent works by DANILEVSKY (1957a, b) clearly illustrate this point. He took samples of *Acronycta rumicis* from different localities ranging from Leningrad to Sukhumi on the coast of the Black

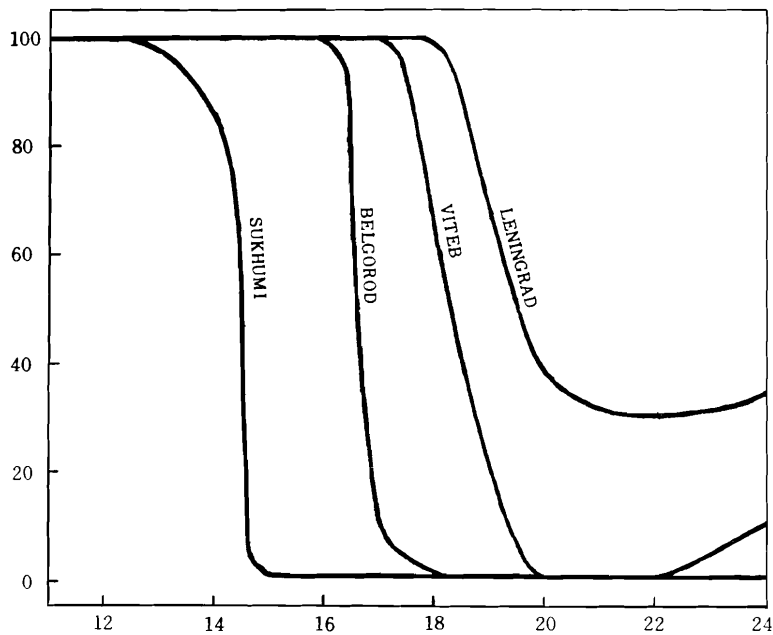


FIG. 2. The photoperiodic response of four local strains of *Acronycta rumicis* from different latitudes in Russia. Ordinate, percentage of diapausing pupae; abscissa, length of photoperiod per day during the larval stage (after DANILEVSKY).

Sea, and measured the critical length of photoperiod by rearing them in different durations of daily illumination. The results show that the critical day-length for the prevention of pupal diapause varies considerably between local strains. It was 19 hours in the Leningrad (60°N) strain, 18 hours in the Viteb (55°N), 16–17 hours in the Belgorod (50°N), and 15 hours in the Sukhumi (42°N) (see fig. 2). Except the representatives from Leningrad, the local stocks completely averted diapause in the day-lengths exceeding the critical value characteristic for each strain.

Since this clinal variation is related to the latitudinal gradient of day-length during the latter half of the growing season, it might be expected that many other insects sensitive to day-length show parallel geographic differentiations. Thus in *Spilosoma menthastri* the critical length of photoperiod was about 19 hours in the specimens

taken from Leningrad, but about 15 hours when they came from Sukhumi. Further examples might be given by comparing the results of similar experiments conducted on the same species at different latitudes. At Cambridge in England the mite *Tetranychus telarius* gave rise to the females of winter (diapause) type in a photoperiod less than 14 hours, while at Leningrad the same effect was obtained in 16 hour daily light (LEES, 1953; BONDARENKO, 1950). The contradiction between the results obtained by DICKSON (1949) and CHAUDHRY (1956) might also suggest the local differentiation of *Cydia molesta* in the mode of diapause, but a direct examination of the local stocks used by these authors is necessary for the conclusion.

Although day-length is the most precise signal of the seasonal changes, the magnitude of its variation during the growing season is not great, especially at lower latitudes. By this reason insects have attained a remarkable degree of precision in their photoperiodic response. For instance, even at the low latitudes in tropical Africa where day-length fluctuates by only 50 minutes from 11 hr 40 min to 12 hr 30 min, the red locust *Nomadacris septemfasciata* is responsive to this slight change (NORRIS, 1959); It is not surprising therefore that the local populations not separated from each other by a great latitudinal distance show a slight but significant difference in the critical length of day for the evocation of diapause.

In *Chilo suppressalis*, the Saigoku strain, inhabiting the southwestern parts of Japan, averts diapause in daily light of 14 hours, but the Shonai strain, occurring on the Japan Sea coast of northern Honshu, requires a photoperiod of about 30 minutes longer than this to be free of diapause (INOUE and KAMANC, 1957). A slight but significant difference in the photoperiodic response has also been found between the Hokuriku (the Japan Sea coast of central Honshu) and Kyushu populations of the green rice-leafhopper *Neplotettix bipunctatus cincticeps*. The nymphal diapause of this insect is determined before birth by external factors acting upon the parents, but whether the diapausing nymphs resume to develop or remain in diapause is controlled by the photoperiod operating directly upon them. The critical length of daily light for this resumption of development is about 13 hours in the Hokuriku population. This is about 30 minutes longer than that in the Kyushu population (NASU, 1960).

Geographic variations in the photoperiodic reaction seem to be associated with variations in the response to temperature. Generally speaking, in the northern populations a higher temperature is necessary to avert diapause than in their southern counterparts. This is clearly indicated in *Acronycta rumicis* either in a short diapause-inducing photoperiod or a long diapause-preventing one (DANILEVSKY, 1957). In 12 hour daily light about one-half of the pupae of the Sukhumi strain averted diapause at 27.5°C; while only less than a half of the Belgorod strain could do so at a higher temperature of 30°C; and more than a half of the Leningrad stock failed to escape from diapause at a still higher temperature of 32.5°C, which was close to the limit for normal growth. Similarly, in continuous light, the Sukhumi strain almost completely escaped diapause even at a temperature as low as 15°C, while the Leningrad one required a temperature higher than 27.5°C to do so. The stock from Belgorod showed an intermediate response between the two.

As summarized by LEES (1955), the Scandinavian populations of *Pieris napi* probably show a similar trend of geographic variation (PETERSEN, 1947). The range of temperature over which diapause occurs extends to a higher scale in the populations from the Arctic Circle than in those from southern Sweden. The Nebraska and

Minnesota stocks of the moth *Telea polyphemus* may also be different in their response to temperature (DAWSON, 1931), but in this and also some other earlier works no caution had been taken to control the effect of light so that the response to temperature could not properly be appreciated. It might be expected that the geographic variation in the threshold temperature as well as in the critical length of photoperiod for the onset of diapause would be widespread in those insects which occur over a wide range of latitude.

Although in many cases both day-length and temperature are playing the decisive roles, this cannot exclude the possibility that local populations undergo differentiations in the mode of their response to other factors of minor importance. Moreover, there might be another type of variation in the response to environment. Populations may enter diapause in response to different stimuli at different localities; that is, the relative sensitivity to various external agencies may be variable. The recent findings by TSUJI (1960) suggest this possibility. He was able to select several physiological strains from a stock of *Plodia interpunctella*. They enter diapause in response to external factors of different categories. In a strain, the larvae were induced to enter diapause by either a high population density or a low temperature, while another strain was insensitive to the density of rearing but went into diapause at a low temperature.

IV. RESPONSE TO TEMPERATURE DURING DIAPAUSE

During hibernation populations of insects would be exposed to different local conditions of temperature. They might therefore be variable in their response to temperature in order to complete diapause at the proper time of the year. In *Austroicetes cruciata* the western race completes diapause at the highest rate at a temperature of 13°C; this is about three degrees higher than the optimum for the eastern race inhabiting the cooler part of the range. The higher temperature optimum in the former race is probably an adaptation to the warmer winter of its habitat (ANDREWARTHA, 1944).

In *Acronycta rumicis* the limit of temperature for the completion of diapause extends to a higher range in southern populations as compared with a northern one. The pupae derived from Belgorod or Sukhumi could complete diapause at a constant temperature of 20°C, while those from Leningrad was able to do so only below 14°C. Above these limits they suffered a high mortality within six months (DANILEVSKY, 1957a).

In the planthoppers *Sogata furcifera* and *Nilaparvata lugens*, the diapausing eggs of populations in northern Japan require cold temperatures to resume development, while those from Kyushu are able to hatch when kept continuously at a high temperature. That is to say, the upper limit for diapause development is much lower in the northern populations than in the southern ones (NASU, 1960).

Similar difference between geographic populations might also be expected in the lower limit for the termination of diapause. This was observed in the Emma field-cricket. A considerable proportion of the eggs of Hokkaido and northern Honshu populations could begin to develop promptly after an exposure to 0–1°C for about three months, but the same treatment was not so effective in the southern populations (fig. 3). In the latter only a few eggs could resume to develop under these conditions, and no further increase in hatchability was observed by longer exposures. Instead, the

eggs were so adversely affected by cold that many were found dead during a month of incubation after the treatment.* In this cricket, the upper limit of temperature for the termination of diapause is almost identical with that for the morphological development, and there is no diversity in this respect between local strains examined. Again, there was little difference in the optimum temperature between them, and most remarkable variation was found in the length of diapause as will be stated later.

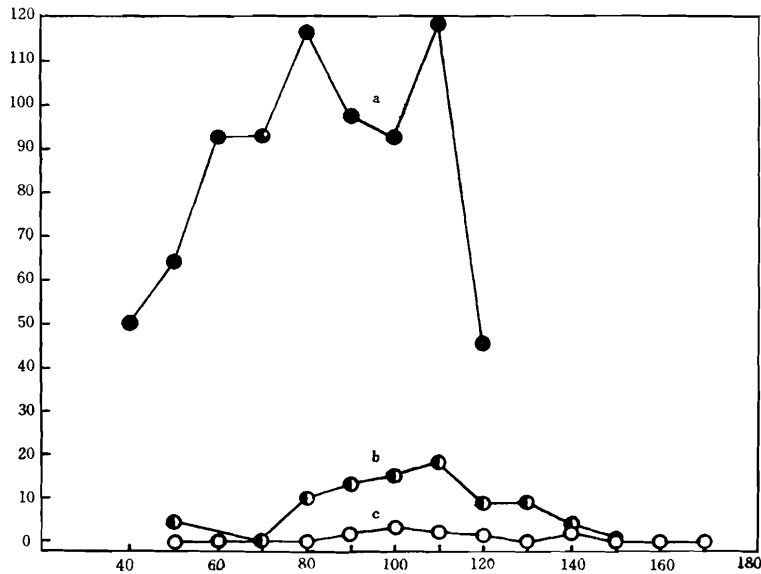


FIG. 3. The effect of a low temperature near the threshold for diapause development upon the hatchability of local strains of *Gryllulus mitratus*. a, Sapporo; b, Tokyo; c, Koti. Ordinate, number of eggs that hatched on incubation at 25°C per 150 eggs; abscissa, the duration of previous exposure to 0-1°C in days (after MASAKI).

These examples, though scanty, may suggest that an untimely close of the resting period otherwise occurring in different climates may be avoided to a certain extent by the geographic variation in the thermal requirements for diapause development. Apparently, however, this is not the whole story, because the end of diapause is primarily determined by the intensity or inherent length of diapause. Namely two heritable traits seem to be involved in the completion of diapause — the duration of diapause and the mode of reaction to temperature. The geographic variation in the intensity of diapause will be dealt with in the next section.

*In *Acheta* (= *Gryllulus*) *commodus*, diapause in the eggs can be terminated in a very short time at sub-zero temperatures, the process of which might be different from that at milder ones (HOGAN, T. W. *Austr. Jour. Biol. Sci.* **13**: 527-540, 1960). The same is probably the case in *Gryllulus mitratus*. The response to the low temperature (0-1°C) of local strains here stated should be taken as indicating their different *ecological* limits of temperature for the successful termination of diapause. The physiological limits may be much lower. The detailed account of the Hogan's interesting paper was not accessible to the writer before the proof-reading.

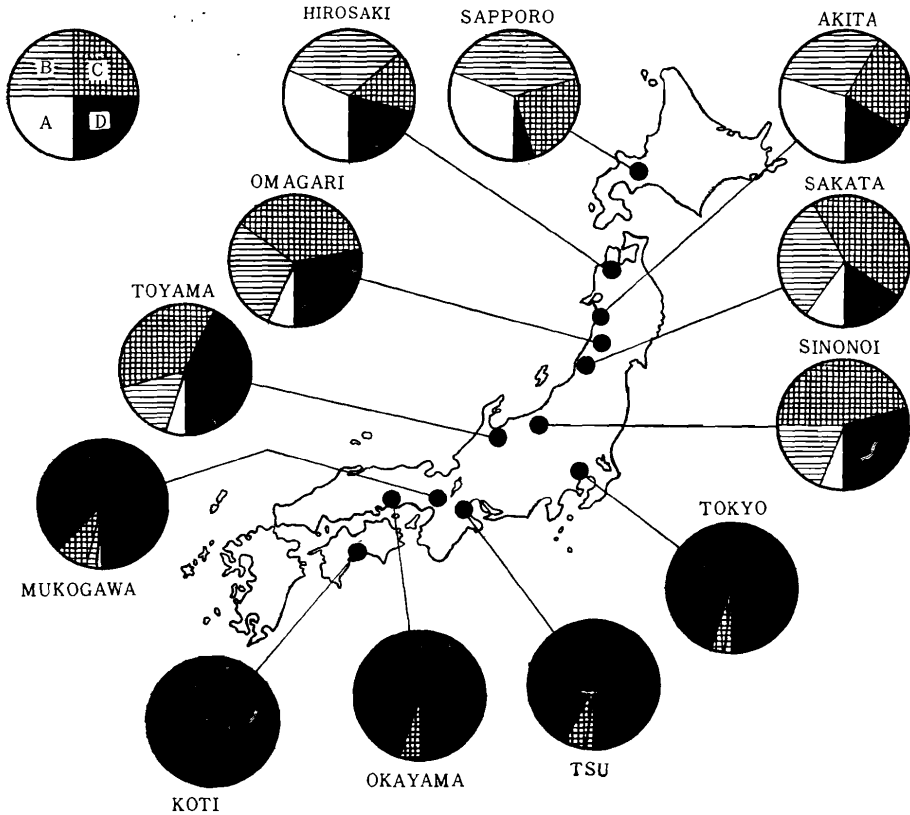


FIG. 4. Geographic variation in the duration of diapausing egg stage of *Gryllulus* (= *Acheta*) *mitratus* at 20°C. Fan-diagram indicates the percentage of eggs that hatched: A, within 100 days; B, between 101 and 110 days; C, between 111 and 130 days; and D, after 131 days or longer (after MASAKI).

V. DURATION OF DIAPAUSE

As stated before, several ecological races of the rice-stem borer *Chilo suppressalis* occur in Japan. One of the important physiological traits differentiating them is the intensity of winter diapause, which supervenes at the end of the larval growth usually in the second generation of the year. The intensity of diapause in the local strains of this borer was measured by the period of time taken to pupate when removed to a high temperature of 25°C at various times during hibernation. In all trials, the northern Shonai strain pupated in a shorter time and showed a higher percentage of pupation than the southern Saigoku strain; The former thus undergoes a weaker diapause as compared with the latter. Between these two ecological forms there are populations showing intermediate strengths of diapause (FUKAYA, 1951 and others). Further microgeographic differentiations seem to occur within the region of each ecological type: Northern populations of the Saigoku strain terminate diapause in a shorter time than do southern populations of the same strain (INOUE and KAMANO, 1959); Another race has been found on the Pacific coast of Sikoku, where

it repeats three generations a year and its diapause lasts for a relatively short period (TSUTUYAMA *et al.* 1959). The local variation of diapause in *Chilo suppressalis* seems rather complicated. Broadly speaking, however, the larvae in the southern warmer districts enter a longer or more firmly fixed diapause than their counterparts in the northern or snowy parts of Honshu. This is true only in the regions where the borer has two annual broods — an important fact in considering the geographic trend of variation as will be discussed in Section IX.

A similar trend was found in the Emma field-cricket. When the eggs deposited by the adults of various local strains were kept under the same laboratory conditions, nymphs hatched earlier from the eggs of Hokkaido and northern Honshu strains than from those of more southerly ones (fig. 4, MASAKI, 1960 b). At a constant temperature of 20°C, the length of diapausing egg stage ranged on the average from 100 to 120 days in the northern populations, while it varied from 150 to 170 days in the

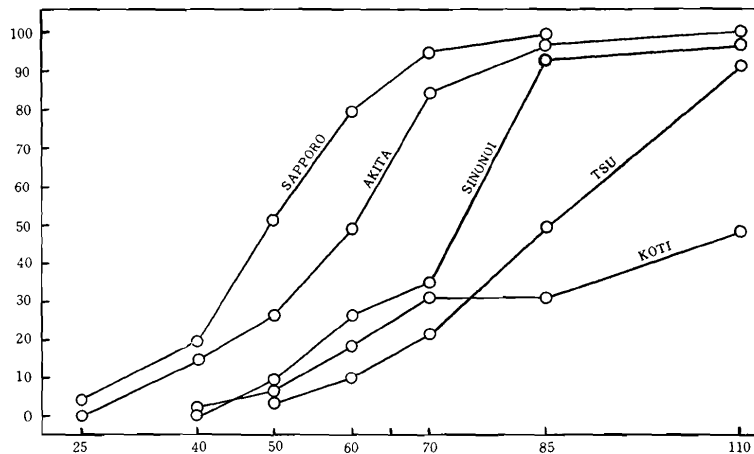


FIG. 5. Percentage of nymphs that hatched at 24°C after various periods of cold exposure (5-12°C) in several local strains of *Gryllulus mitratus*. Ordinate, percentage of hatching; abscissa, duration of cold exposure in days (after MASAKI).

southern Honshu populations, and a still longer egg stage of about 190 days was met with in the Koti strain derived from the warm Pacific coast of Sikoku. Apparently, these conspicuous differences in the length of egg stage represent the variation in the duration of diapause. In experiments breaking diapause by cold, the northern populations required a shorter period of cold exposure for prompt hatching at a high temperature than did the southern ones (fig. 5).

The examples of similar nature could be cited further: In the gipsy moth *Lymantria dispar*, the overwintering period of the egg lasts longer in the Mediterranean race than in the central European; and also the Hokkaido race hatches earlier than the Honshu races, though there are rather vague minor variations apart from this broad tendency (GOLDSCHMIDT, 1932, 1938). In *Austroicetes cruciata* cited before, the western race, the inhabitant of the warmer area, has to pass a longer embryonic diapause than the eastern race over a wide range of temperature (ANDREWARTHA, 1944).

In these examples, a common tendency could be pointed out. Diapause is shorter in

the population inhabiting the northern or cooler parts of the range than in those occupying the southern or warmer parts: The length of winter diapause in these forms is not proportional to the duration of the cold season.

On the other hand, the geographic gradient of variation is quite reversed in another group of insects. The small bivoltine cricket *Pteronemobius fascipes* commonly found in Japan may afford an example of this. When compared in the laboratory, the length of embryonic diapause was found much longer in the strain originated from Hirosaki near the northern tip of Honshu than in the strain from Tsu on the coast of the Ise Bay (MASAKI, 1960b). The average length of the egg stage at 20°C was about 165 days in the former while it was 105 days in the latter. Similar differences were also observed at higher temperatures of 25 or 30°C. It should be noted that in this small

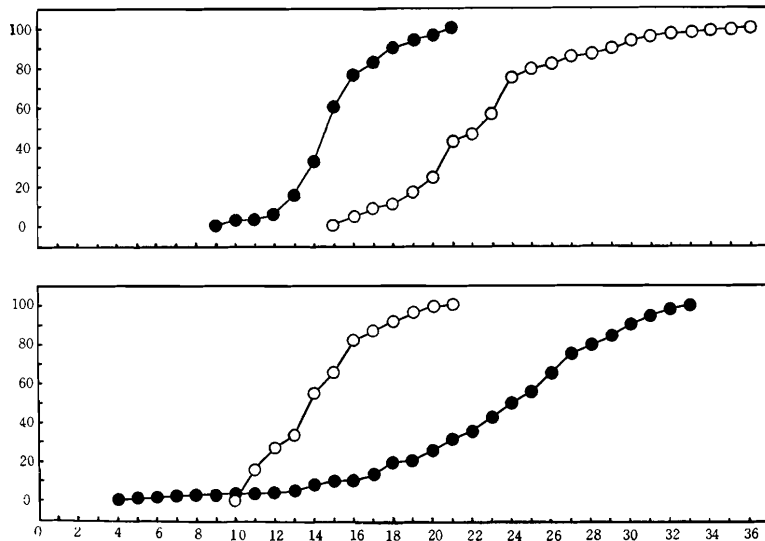


FIG. 6. Showing reversed tendencies of geographic variation in the length of diapause. The upper, *Gryllulus mitratus*; the lower, *Pteronemobius fascipes*. Open circles, Tsu strain; closed circles, Hirosaki strain. Ordinate, cumulative percentage of nymphs that hatched; abscissa, time in weeks at 20°. The eggs were kept at this temperature from the deposition (after MASAKI).

cricket a bivoltine annual cycle is predominant in the southern locality, but only a negligible partial second brood, if at all, might be produced at Hirosaki.

A similar situation has been known of the corn borer *Pyrausta nubilalis* in the United States. Diapause in the univoltine race is considerably longer than in the multivoltine one (ARBUTHNOT, 1944). In eastern Canada, the New Brunswick population of *Gilpinia polytoma* has two annual generations, but the Gaspé population has only one: Again, diapause tends to last for a very longer period in the latter than in the former. Many adults emerged from the hibernating New Brunswick samples when incubated in December, but the same result was not obtained in the Gaspé ones until January or February (PREBBLE, 1941 b). In the Arctic Circle of Fennoscandia, the butterfly *Pieris napi* fails to produce more than one annual brood because of the short summer, and its diapause lasts longer than in the southern bivoltine

strains (PETERSEN, 1947). Finally, in *Acronycta rumicis* the Leningrad strain which is virtually univoltine in nature requires a longer period of cold treatment to terminate diapause than do the stocks derived from central or southern parts of Russia, where the moth produces from two to four annual generations (DANILEVSKY, 1957 a).

All these examples lead to the conclusion that diapause tends to be longer as the number of annual generation is progressively reduced northward. One exception to this tendency, however, has been known at present. That is the Yezo field-cricket, a close relative of the Emma field-cricket. The eggs of the Obihiro strain underwent a considerably longer period of diapause than those of the Sapporo strain at both temperatures above and below the threshold for morphogenesis (fig. 7). The winter is considerably severer and the summer is a little cooler at Obihiro, but the cricket is strictly univoltine in both localities.

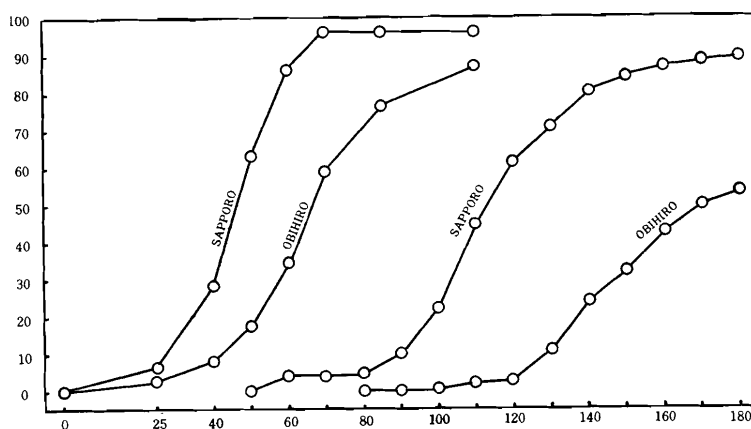


FIG. 7. Comparison of the diapausing egg stage between two local strains of the Yezo field-cricket. Left two curves show the percentage hatching at 25°C (ordinate) after previous exposure to 5-12°C (abscissa, in days). Right two curves indicate the cumulative percentage of hatching (ordinate) at a constant temperature of 20°C (abscissa, time in days at 20°C) (after MASAKI).

VI. AESTIVATION DIAPAUSE

Diapause occurring in summer has hitherto attracted little attention of entomologists in temperate countries, conceivably because there are fewer species of insects manifesting the arrest of this kind than those resting in winter. Under certain climates, especially of the Mediterranean type, the summer is the most adverse season, liable to check all the active life of insects either directly by the intense heat and drought or indirectly through perishing the food plants. Under these circumstances, aestivation diapause, if it occurs, should have an enormous survival value. The annual activity of insects might then be separated by the occurrence of two periods of arrest in both summer and winter, if the winter is also severe; or else it might be restricted to the cooler and moister half of the year if the winter is mild, and the cycle of activity is just reversed from that prevailing in the regions with luxuriant vegetations in summer (cf. WILTSHIRE, 1956). RIVNAY (1958) reported that the northern

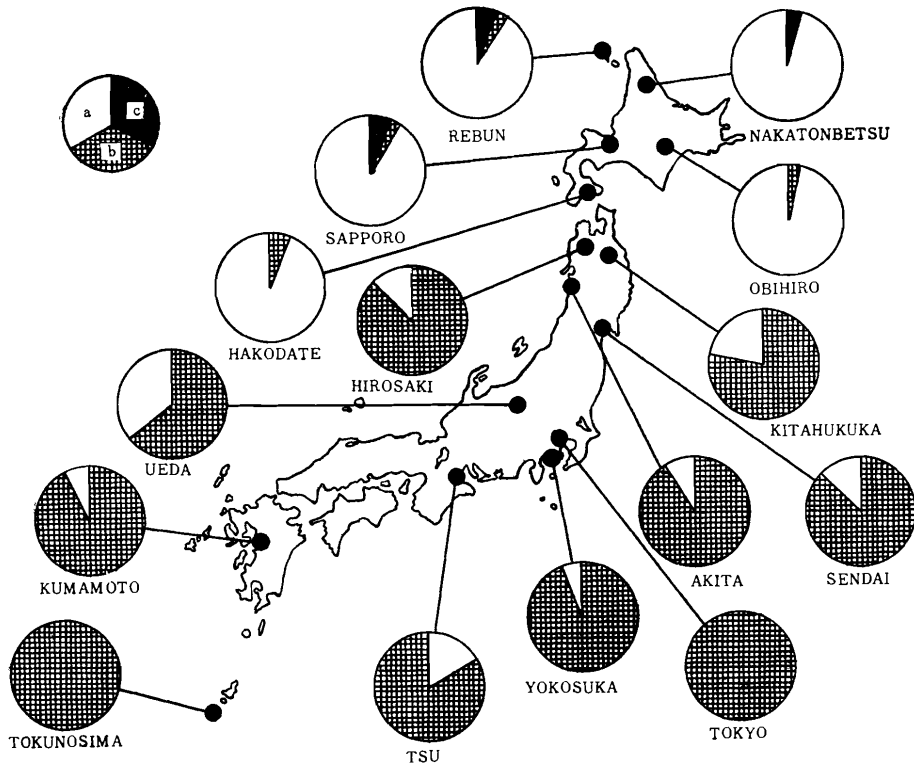


FIG. 8. Geographic variation in the incidence of aestivation diapause of *Mamestra brassicae* in Japan. The larvae of different local strains were reared at a high temperature (25°C) in a long photoperiod (16 hours), and the pupae were kept at 26°C. a, Non-diapause pupae; b, aestivation diapause pupae; c, hibernation diapause pupae (after MASAKI).

species of chafer beetles hibernate while the Mediterranean ones aestivate; that is to say, diapause is shifted from the winter in the northern countries to the summer in the Mediterranean region.

Such a substantial change in the life cycle occurs in a single species which extends its range over both regions. The onion fly *Hylemyia antiqua* is mostly dormant from May to November in Israel, though in England the resting stage is from October to April (RIVNAY, 1958). In this case the diapause behaviour of the Israeli population must radically be different from that of the northern populations, for the environmental conditions preceding the arrest are quite distinct so that diapause should be induced by different regimes of external stimuli. Furthermore, the conditions of temperature required for the completion of diapause in the two countries should also be different, because the aestivating insects terminate diapause at the end of the hot season, while the hibernating ones resume to develop at the beginning of the warm season.

In some arid regions the local population might acquire the disposition to enter aestivation diapause without losing their ability of hibernation diapause, which they might have inherited from the northern populations. The isolated population of the swallow-tail butterfly *Papilio machaon centralis* in the Bagdad gardens indicates

this. It passes about three months of the hot and dry season in the state of pupal arrest and also enters diapause in winter (WILTSHIRE, 1958). On the other hand, some of the northern subspecies have only a trace of the ability of summer diapause, though their winter rest could be prolonged over six months (MANLEY, 1935).

Aestivation diapause occurs in the milder climates as well, probably as an adaptation to the seasonal cycle of the food plant or other ecological factors. The local populations of aestivating species are variable in the genetic ability of this faculty, as the length of the hottest season varies from one locality to another.

As stated before, the cabbage moth *Mamestra brassicae* is distributed throughout the Japanese Archipelago, from the northernmost island of Hokkaido to the southernmost isles of Amami. In spite of the remarkable diversity of climatic conditions within these parts of its range, the moth virtually persists its bivoltine annual cycle throughout. What is more, a puzzling fact has been known about the geographic variation in its phenology. The moths from hibernating pupae emerge progressively earlier toward the south as might be expected from the increasing amount of effective temperature, but the reverse is true in the next flight. The second flight of the year is normally observed in the latter half of August and the first half of September at Sapporo (MATSUMOTO, 1956), while it is delayed until as late as November in Amami-Osima (SAKAE, personal communication). This is caused by the variations in the incidence and intensity of summer diapause among local populations (fig. 8; MASAKI, 1956 b). In Hokkaido, the most of the offspring from the hibernating brood does not enter diapause at all, giving rise to the adult early in autumn. At the northern tip of Honshu, however, a certain proportion of the pupae is found dormant in the mid-summer (HIRATA, unpublished observations). Further south, aestivation diapause also prevails throughout the country. This conspicuous difference between the Hokkaido and the more southerly populations was observed when different local stocks were bred at a temperature of 26°C in a photoperiod longer than 16 hours. They are less variable in the response to low temperatures and short photoperiods, and all enter winter diapause under these conditions. The two types of diapause could be distinguished by the conditions of temperature required for their termination.

It was further found that there was another aspect of the geographic variation in the disposition of aestivation diapause. The duration of aestivation in *Mamestra brassicae* is partly modified by temperature in such a way that it is shortened by the earlier onset of cool autumn in the north and prolonged by the hot summer lasting longer in the south. In addition to this, the timing of the autumn emergence from aestivation is controlled by intrinsic factors. When the aestivating pupae of various local stocks were kept at the same temperature (26°C) those from northern Honshu completed diapause in about two months; those from the southern parts required about three months before emergence; and the progenies originated from Tokunosima, south of Amami-Osima, remained in diapause for the longest time — over four months. A correlation seems to exist between the hereditary length of summer diapause and the duration or the average temperature of the hot season in the native localities. In the northern districts the period of hibernation is much longer than that of aestivation under natural conditions as well as in the laboratory; conversely, on the isles of Amami, near the southern border of the distribution, the moth prolongs its summer arrest to about six months while it is dormant only three winter months.

A geographic variation parallel to this seems to occur in the beet-leaf mining

maggot *Pegomyia hyoscyani*. When the two groups of the aestivating pupae, which had been derived from Sapporo and Hukuoka, respectively, were kept under the same laboratory conditions, the northern flies began to emerge from the beginning of September in advance of the southern flies doing so in the middle of October. The southern strain had entered aestivation about a month earlier than the northern one; the actual difference in the length of aestivation diapause between them was therefore as great as three months. The same tendency firmly persisted in the broods of the next summer (NISHIJIMA, personal communication).

A further example of this sort might be found in the winter moth *Operophtera brumata* which is widely distributed in the Palaearctic region. In Switzerland, SCHNEIDER-ORELLI (1932) reported that the moths appear earlier in the cooler mountain forest than in the warmer plains. This difference was observed even when the aestivating pupae from different altitudes were kept at the same place. He thought therefore that the winter moth was differentiated into ecological races at different altitudes.

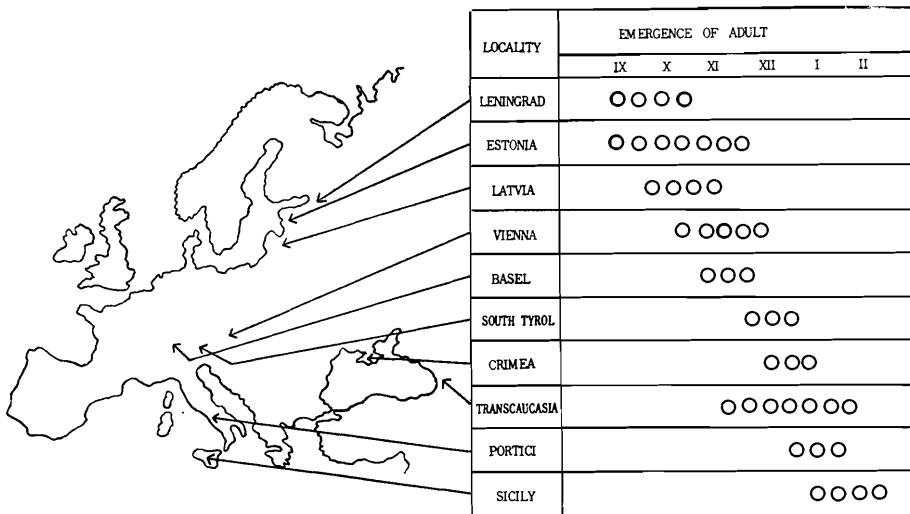


FIG. 9. Geographic variation in the season of the adult emergence of *Operophtera brumata* in Europe (from various sources).

Similar variations can also be seen in the phenology of this moth in relation to latitude. The moths are found progressively earlier as we go from the Mediterranean coast or Transcaucasia to the cooler districts of northern Europe (KOZHANCHIKOV, 1950; REIFF, 1953; RUSS, 1956; ZIRNITZ, 1953; ZOLK, 1933; UVAROV, 1931). This geographic trend of the phenology is similar to, though much more conspicuous than, that of the second flight season of *Mamestra brassicae* in the Japanese Archipelago, which suggests the existence of a similar differentiation of local populations in the character of aestivation diapause. Some authors tried to explain this locally different phenology on the basis of the particular response to temperature of the aestivating pupae (KOZHANCHIKOV, 1950), and did not admit the physiological differentiation of the local populations (SILVESTRI, 1941.) In view of the findings by SCHNEIDER-ORELLI

and also by SPEYER (1938), the possibility cannot be ruled out that some hereditary variation is at least partly involved in this variable phenology. Recently WYLIE (1960) experimentally demonstrated the genetic difference in the length of the pupal stage as well as in the rate of embryonic development between several populations from western Europe.

Yet, it is not certain whether a true diapause is involved in the prolonged period of aestivation of *Operophtera brumata*. Even though the process of metamorphosis in the aestivating pupae is not ceased at all, it is obvious that the rate is abnormally slow and is affected by temperature in such a particular fashion that is seldom found in any other process of morphogenesis. It could not be denied that the particular pattern of the annual cycle of the moth is moulded by the particular physiological state of aestivation — and whether one calls it diapause or not is immaterial in considering the problem of seasonal regulation and its geographic variation as an adaptation of insects to a wide variety of environment.

VII. CLIMATIC LIMITS FOR SURVIVAL

In most, if not all, of the diapausing species, the performance of seasonal regulation seems to be a prerequisite for a permanent existence in a district, which means that this capacity is one of the factors determining the geographic limits for survival. The tolerance of an insect to extreme conditions of some physical agencies has been studied in the past to elucidate the factors limiting the distribution of insects. It is clear that such studies might provide only an incomplete information. For a more profitable approach, the capacity of seasonal regulation should be tested.

It might be surmised that differentiation in the diapause character of the local populations confers on the species as a whole broader limits for survival than otherwise. On the other hand, each population might be restricted to a narrower climatic range and have a less chance to survive a drastic shift in environmental conditions. It is of course not an easy work to determine the limits of the capability of seasonal regulation in a local strain, because it requires to equip a series of artificial seasonal changes simulating climates at various geographic locations. At present no trial of this sort has been carried out on a large scale. Some suggestions on the importance of this problem might, however, be obtained from either intentional or accidental transports of insects from their homeland to other parts of the world.

Thus the tropical subspecies of the Eri silkworm *Philosamia cynthia ricini* had been introduced into Korea and northern China for its silk, but as it had no capacity to diapause it failed to overwinter there unless protected by some artificial measure (TANAKA, 1943). The occurrence of diapause in the subspecies of temperate districts, *Philosamia cynthia pryeri* and *P. c. walkeri*, is therefore an essential physiological trait to survive. In other words, this species has been able to spread northward by evolving the ability of diapause. However, even if a population is capable of diapause, it is not always successful to survive a colder climate. When the bivoltine strain of *Gilpinia polytoma* was transferred from New Brunswick to Gaspé Peninsula where a univoltine population predominates, the former persisted its bivoltine cycle and the second brood was killed by the earlier frost before reaching the diapause stage. Probably, the day-length during the growing season at Gaspé was longer than the critical value for the evocation of diapause in the New Brunswick strain, though this was not experi-

mentally tested. The converse transference of the Gaspé strain to New Brunswick was not fatal, but the univoltine strain had only one brood a year as in its original locality in spite of the longer growing season in New Brunswick (PREBBLE, 1941 a):

The photoperiod dependence of facultative diapause would provide a unique problem in considering the limits of survival of local strains. The critical day-length for the onset of diapause in a local population must lie somewhere between the longest day-length of the year and the day-length at the close of the growing season. The day-length in summer becomes longer and the growing season ends earlier toward the north. Naturally the higher the latitude of the habitat, the longer will be the critical day-length of the local strain, as shown by examples in Section III. If, then, a local strain is transferred to a higher latitude where the shortest day-length of the growing

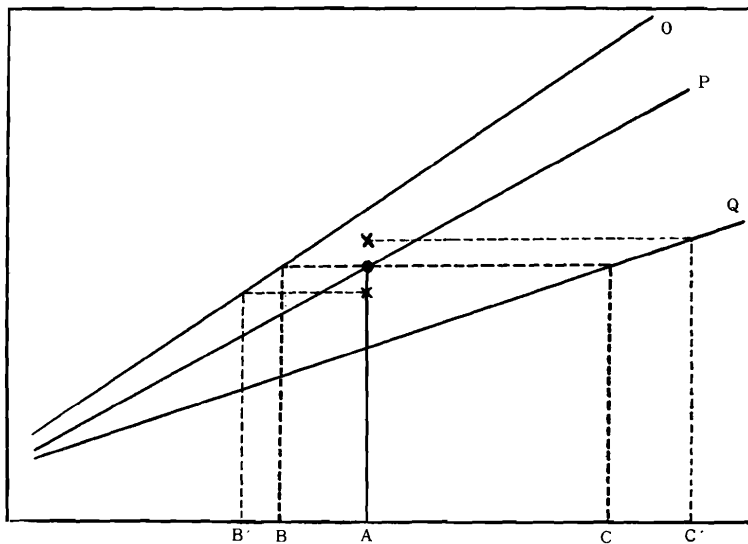


FIG. 10. Schematic representation of the latitudinal limits for survival of a local strain set by the gradient of day-length. Ordinate, day-length; abscissa, latitude. O, the longest day-length; P, the critical day-length; Q, the day-length at the close of the growing season. The local strain inhabiting at the latitude A cannot retain its multivoltine cycle beyond B. It fails to enter diapause beyond C. If an exogenous modification occurs in the photoperiopic response, these limits will be extended to B' and C', respectively. For further explanation, see text.

season exceeds the critical value, it will not survive because of the failure to enter diapause before winter (see fig. 10). Conversely, if it is taken to a lower latitude where the longest day-length does not reach the critical value, it would fail to utilize the abundant environmental resources because of the premature onset of diapause. In the latter case, the immigration does not always lead to extermination. The fate of the colonists might largely be influenced by other ecological factors. In the former case the day-length itself likewise does not directly exert any detrimental effect upon the immigrants, but in extreme cases it completely excludes them by disturbing their life cycle:

These rigid situations might be improved to a certain extent by the phenotypical modification of the photoperiodic reaction. In *Chloridea obsoleta*, the critical length of

photoperiod is prolonged by about 1 hour 30 minutes for each reduction of 5°C in the environmental temperature (GORYSIN, 1953, cited in DANILEVSKY, 1956). If this is a general tendency, it would extend greatly the latitudinal limits for the survival of a local strain. The dissipation of the long-day effect by the action of subthreshold temperature at the beginning of daily light hours might be another factor contributing to the phenotypical improvement of the response, since at a high latitude such a condition is likely to be induced by cold mornings in nature (DANILEVSKY, 1956). The otherwise severe limitation of latitudinal range for a local strain would be widened to a certain extent in this way. These phenotypical modifications are, however, not entirely successful to overcome the latitudinal gradient of day-length:

This is most instructively demonstrated by DANILEVSKY with *Acronycta rumicis* in Russia. When the larvae of different local stocks were fed in the white-night summer at Leningrad, those from central and southern Russia gave rise to nondiapaue pupae in response to the 'extremely long day-length, and being exposed to the killing frost, all were wiped out. The native stock entered diapause and was able to survive the winter as usual. In this case, it was the failure in the seasonal regulation that was fatal to the southern strains, for it was tested that they could survive the winter under natural conditions of Leningrad if they were in diapause: On the other hand, it was surmised that if the Leningrad strain was transferred to a farther southern locality where the longest day-length in summer was shorter than the critical value for the prevention of diapause of this strain, it would not avert diapause altogether. The annual cycle would then be univoltine, and the resulting diapause pupae would have to endure the long hot season before winter. This might reduce their viability, since in experiments the diapausing pupae eventually died without developing when kept continuously at a high temperature. Under the same conditions, the southern strains are able to repeat active generations, since their diapause is prevented by the long summer day.

From these examples, an impression may arise that local strains are so differentiated that they could hardly exist outside their habituated districts. But this is not always the case. Since the Colorado potato beetle *Leptinotarsa decemlineata* has colonized in western Europe, it has been extending eastward, crossing countries of different climatic conditions. What is more, this remarkable extension has presumably been achieved without conspicuous genetic change in the mode of diapause, for there is as yet no detectable difference in the critical day-length for the induction of the imaginal diapause among the Dutch, Hungarian and Russian populations (GORYSIN, 1956; DE WILDE *et al.*, 1959): Again, several species of insects introduced into Hawaii from temperate regions have retained their diapause under the stable tropical climate, though the ultimate fate of these insects cannot be predicted: Among them, the solitary wasp *Sphex harrisi* persists in diapause for a very long period of time ranging from 6 to 13 months (NISHIDA, 1955). It would seem that the life cycle does not coincide with the cycle of years. This is probably caused by the absence of winter cold in these tropical islands: In its native temperate country, the cold season might perhaps bring about a rapid and synchronized emergence from diapause. Under severer circumstances, the wasp could not have existed with this disturbed annual cycle. The mild climate or the absence of formidable enemies and competitors in Hawaii might have enabled the wasp to get along.

The chance of a local strain to survive immigration may thus be different accor-

ding to different ecological situations. Some of the examples given above, however, suggest that because of its specialized mode of diapause a strain may get only a thin chance to establish a new territory conspicuously different in climatic conditions as well as in the latitudinal location. The point of this story is that a local strain is best adapted to its homeland. It seems not adequate to emphasize that insects have lost their plasticity to survive a diversity of environmental conditions. An accidental immigration over an immense distance is not a normal way of extending the distribution. The normal process of changing the distribution should have taken a very long time, long enough for insects to respond by genetic variabilities to natural selection. The geographic differentiation of populations would not be directed to a blind alley. It is the proof of the genetic versatility in the physiological traits of insects, which is one of the most important factor determining the range of distribution:

VIII. INTRAPOPULATION VARIATION OF DIAPAUSE

We have seen that a great deal of genetic changes have taken place in the diapause character of insects as they have extended over different climatic areas. In this connexion it seems significant to deal with the plasticity of diapause in a local population.

In a population of *Locusta migratoria gallica* inhabiting southern France, there are found a few nondiapause individuals among predominating diapause ones. From this material LE BERRE (1952, 1953) was able to select a nondiapause strain as well as another one which exhibits a firm obligatory diapause. As stated elsewhere, the tropical subspecies of this locust lacks in the ability of diapause, and has the remarkable habit of migration over an immense distance; which means that the genetic heterogeneity of this population might have been derived from occasional invaders from the south.

The meal moth *Ephestia kueiella* is virtually univoltine in warehouses in London, but BADSEN was able to select a strain that could avert diapause when fed on midlings at a temperature of 25°C (WALOFF, 1948, 1949). Similarly the Indian meal moth *Plodia interpunctella* is highly heterogenous in its character of diapause, for several strains distinguished by the mode of response to external factors were isolated from a sample collected at Kyoto (TSUJI, 1960; see Section III). Both these insects are the inhabitants of warehouses and have a high opportunity of being transported with commercial foodstuffs, and a population in a locality, or even in a warehouse, might comprise of different strains.

In the United States, heterozygous populations of *Pyrausta nubilalis* occur at the border between the univoltine and bivoltine areas; the Teledo population is such one, which shows intermediate characters in the incidence and duration of diapause. From this population a strain which is almost indistinguishable from the pure univoltine one was selected (ARBUTHNOT, 1944). Since the borer is an immigrant from Europe, and since the territory relations of the univoltine and multivoltine races are as yet not stabilized, the heterozygous population might have been formed by intercrossing of the two distinct races differentiated in Europe (LEES, 1955).

Beside these examples of more or less unstable situations, genetic diversities in the incidence of diapause have also been found in more stable situations. *Melanoplus differentialis* is virtually univoltine in Iowa, entering an embryonic diapause when the

eggs are kept at a high temperature of 25°C. From a very few exceptional individuals averting diapause, a strain was obtained by selection that developed continuously at a high temperature; Also, another strain was isolated by the counter selection that did not produce even an exceptional nondiapause eggs (SLIFER, 1951).

In insects of some commercial value, such exceptional individuals might provide a starting material to breed a new race. From a stock of *Antheraea pernyi* with facultative diapause, two strains could have been isolated by selection through several successive generations under artificially controlled day-length; one strain showed a stronger tendency to enter diapause than the field stock; the other could avert diapause almost completely in an intermediate photoperiod of 14 hours (TANAKA, 1951); Such a selection might be effected unconsciously when a stock of insects has long been kept in constant laboratory conditions. Thus UMEYA and HARADA (1955) had kept a culture of a bivoltine race of the silkworm *Bombyx mori* under the conditions of a long-day treatment in the egg stage. That is, the generations were succeeded one after another by producing diapause eggs; After twelve successive diapause generations, the stock was subjected to a short-day treatment that had been completely effective on preventing diapause in the original generation. In the last generation, however, the trial was not successful, and diapausing eggs were predominant in the resulting egg batches; It is not known whether any transformation of genes had been involved in this change, though a plausible interpretation might be afforded by the theory of genetic assimilation (cf. WADDINGTON, 1957);

The genetic variability of diapause is sometimes concealed in natural populations, and a particular genotype requires particular external conditions for its phenotypic expression; In such a case, it might be revealed by some artificial treatment; At Leningrad several species of moths have univoltine life cycles in nature, but their heterogeneity in the disposition of diapause was elucidated by rearing them at a temperature higher than in the average summer in a long photoperiod. Under these conditions some pupae developed without arrest while others entered diapause (DANILEVSKY, 1957); Probably the strains with obligatory and facultative diapause, respectively, could be isolated by artificial selection.

In the spruce budworm *Choristoneura fumiferana*, the populations in eastern Canada are effectively univoltine. If they were subjected to long photoperiods, at least one larva in more than half of the families produced by field insects can develop without diapause. Selection over six generations yielded a strain that is virtually free of diapause when subjected to continuous light; This stock has been reared for a further six generations and still retained this photoperiod-dependence of diapause. It responds to light in an unusual way as compared with the majority of the insects naturally sensitive to day-length; for the proportion of diapause decreases gradually as the photoperiod is prolonged from 15 to 24 hours, and no sharp critical change occurs within a narrow range of photoperiod (HARVEY, 1957). This may well be due to the fact that this photoperiodic response has not been subjected to selection. It seems not impossible to obtain strains responding to different critical day-lengths by a further selection under different lengths of daily light;

Another aspect of the intrapopulation variation might be found in the duration of diapause. In many experimental works, more or less conspicuous individual variations in the length of diapause have generally been observed. This is particularly striking when diapausing insects are placed at a constant high temperature. To take examples from

crickets: at a temperature of 20°C the diapausing egg stage lasted from 66 to 147 days in *Gryllulus mitratus*, 93 to 165 days in *Scapsipedus aspersus*, 94 to 273 days in *Loxoblemus arietulus*, 39 to 236 days in *Pteronemobius fascipes*, 33 to 152 days in *P. taplobanensis*, and 37 to over 300 days in *P. ohmachii*; all these results were obtained with the samples taken at Hirosaki (MASAKI, 1960). A wide range of variation may also be found at a temperature lower than the threshold of growth. In the Sapporo strain of *Mamestra brassicae* a few pupae terminate diapause after a cold exposure to 5°C lasting shorter than a month, while some are still diapausing after three months of cold rest (MASAKI, 1956 a).

It is not known if these variations are of genetic nature. Whatever the cause might be, there is reason for them existing in natural populations. For the successful overwintering, an insect should be in diapause at least until the onset of the cold season and free of it before the end of that season. Individuals undergoing various lengths of diapause between these limits are able not only to survive the winter but also to resume development simultaneously in the next spring. For instance, when an egg of *Gryllulus mitratus* laid in September, as usual at Hirosaki, terminates its diapause in about one month, namely in October, it will overwinter successfully, for the temperature is already below the threshold for development at that time. Even if a similar egg requires as long as six months to do so, it will begin postdiapause growth concurrently with the former, because the temperature at Hirosaki does not rise above the threshold until the middle of April.

If the variation spreads over a much wider range, exceeding these limits, it may result in a striking diversity between individual life cycles. A part of the population will be free of diapause during the first hibernation and emerge in the following spring, but another part will fail to do so and pass the second, third or even more winters before resuming to develop. As a result the adults from one brood will emerge in different seasons. The most striking example has been known in the wheat blossom midge *Sitodiplosis mosellana*; in an outdoor insectary the larvae pass from one to twelve winters before emerging as adults (BARNES, 1952). The delayed emergence of this kind is especially of common occurrence among the sawflies. The adults of *Gilpinia polytoma* emerge from the cocoons of the same generation after passing from one to six winters in Gaspé peninsula; In New Brunswick, the emergence of the adults from one brood covers three years (PREBBLE, 1941 b). It is interesting that the incidence and extent of delayed emergence differ between the two populations. This might suggest that there is a genetic difference between individuals emerging in different years from each population.

The cocoons of *Cephalcia abietis* enter diapause at two different stages and give rise to adults after passing from one to three winters. This is explained by NOVAK (1957) on the basis that the amount of cold during one winter is insufficient for breaking diapause of some individuals. Therefore, the proportion of individuals passing two or three winters in diapause would vary from year to year with the fluctuation in winter temperature. In Czechoslovakia this sawfly requires, in the normal years, two winters to complete diapause, but in 1956 when an exceptionally severe winter was followed by a cool summer, the majority of the populations gave rise to adults before the next winter, probably because the requirement for cold by the diapausing larvae was fulfilled earlier than usual.

In *Megastigmus spermotrophus*, the rhythmic factor seems to be responsible for

a similar diversity of adult emergence; the action of low temperature for the termination of diapause attained its maximum effect in about 20 weeks, and then diminished again, so that individuals passing this peak without resuming development would require another period of cold in the next winter. (HUSSEY, 1955) In this case also, the split emergence of the adults may not occur without variation between individuals in the intensity of diapause.

It is then likely that the different cycles are not genetically fixed, but it is the intensity of diapause that is subject to striking variation. And yet, whether this intrapopulation variation in the intensity of diapause is controlled by genetic factors or not is open to question. The genetic nature of the variation might be elucidated by selection for a particular length of diapause. Any trial of this kind has not been carried out as yet.

IX. FACTORS OF VARIATION

Diapause is not the only possible way of adaptation in insects to survive a great diversity of climatic conditions, for there are those insects which exist in cold as well as warm regions without any faculty of diapause. For example, the Asian common looper *Plusia nigrisigna* has no genetic capacity of diapause, though it thrives in both the cold highland at an altitude of 1300 m in Nagano Prefecture and warmer plains around Tokyo (ICHINOSE and SHIBUYA, 1959). Even in the species capable of diapause, variations in some physiological traits other than diapause might be needed to improve the fitness of the species to the local conditions. The rate of development is one of such variable traits; in *Chilo suppressalis* the larvae of the Shonai strain develop much faster than those of the Saigoku strain (FUKAYA, 1951); in *Gryllulus mitratus* the northern strains mature in a shorter time than do the southern ones (MASAKI, unpublished data). There would, however, exist the relatively narrow limits of variation of this sort. The rapid growth of the northern strains of the Emma field-cricket is in fact achieved at the expense of the body size; their adults are conspicuously smaller than those of the southern strains. Were the rate of sexual maturation increased further, the body size would accordingly be reduced. There might be the limits of body size beyond which the continuity of the species is likely to be broken. Furthermore, the reduction in the body size might perhaps lower the number of eggs produced by a female.

On the other hand, a much greater range might be allowed for the variability of diapause, because diapause is not a biochemically indispensable part of morphogenesis, and moreover it is such a physiological state in which the expenditure of energy is kept at the lowest level. Its intervention in the development would scarcely influence the somatic vigour of the resulting adult. This is strongly exemplified in the remarkable diapause, lasting over ten years, of the wheat blossom midge (BARNES, 1952). The point is further illustrated by the pattern of the local differentiation of *Acronycta rumicis* in Russia; different local strains show little variation in the speed of development while they are strikingly differentiated in the mode of diapause (DANILEVSKI, 1957).

There is thus a good deal of evidence that physiological character of diapause varies greatly from one local population to another in a species of insect. This is conceivably a prerequisite for the species to have spread over the present range, as suggested by the results of transferring experiments stated in Section VII. Natural

selection should have been operative in the process of such a physiological divergence of local forms, which might have the potential variability in diapause to cope with the challenge of the environment. Mutability might afford in the long run a further basis for responding to natural selection. The currently predominating theory of mutation and selection might be one of the workable hypotheses for tackling the problem of geographic variation in diapause. At present, however, there has been no valid evidence of any mutational change in the diapause behaviour of insects, even of such a domesticated one as the silkworm that has been under the care of people for a very long time and studied in detail about the physiology and heredity of its diapause. The difficulty to realize any mutational appearance of a new diapause character may well be due to the fact that diapause is not controlled by a single gene, but by a set of multiple genes as demonstrated by the mode of inheritance of vultinism in the silkworm (MURUGA, 1943; NAGATOMO, 1951; MOROHOSHI, 1957). The photoperiodic reactions in *Acronycta rumicis* and *Choristoneura fumiferana* are also probably governed by multiple genes (DANILEVSKI, 1957; HARVEY, 1957).

Many factors might have been responsible for the natural selection of local characteristics of diapause. The relative importance of such selecting agents is probably different from species to species according to the ecological or physiological characteristics, and also from place to place according to the peculiarities of the local environment. For instance, if a species of insect feeds on a particular food which is available only in a short particular time of the year, the seasonal arrangement of the active and dormant stages would mainly be limited by the food supply. Other rich environmental resources could not be fully utilized. This might result in a strictly univoltine life cycle with a firm obligatory diapause throughout its range, if food is everywhere the limiting factor. The duration of diapause would then be secondarily subjected to selection by the local conditions of temperature or other factors either directly or indirectly through their effect on the food supply. On the other hand, if the species is highly polyphagous or feeds on food constantly available throughout the warmer season, the food might be less important, but another one, say temperature, would determine the duration of the growing season, and hence the number of annual generations. Consequently, the vultinism would vary from place to place depending on the amount of effective temperature if other ecological conditions were favourable. Natural selection would then operate to differentiate the diapause behaviour of local populations. It might therefore be inferred that the adaptive response to the same climatic gradient would be different according to the mode of living of the species; some persist their obligatory diapause throughout but others change their annual cycle from a nondiapause type to a facultative or obligatory diapause one. The general idea of this evolutionary feedback might be represented by figure 11.

As pictured in this figure, the food is undoubtedly one of the most important factors determining the character of diapause. In fact the close connexion between the life cycle of insects and the seasonal cycle of their food plants is impressively indicated by the species which feed on buds or flowers of certain plants fading their blooms in a short time, as pointed out by LEES (1955). The larva of *Cosmia divergens* feeds on the flower of the peach tree and its growth is kept pace with the flowering season by its peculiar pattern of annual cycle. It matures in April, but does not pupate until October since it enters a long summer diapause. The moth emerges in December and deposits eggs. Although diapause in the egg stage has not been studied yet, it is

presumably absent or very weak at least in the non-snowy parts of Japan, and the larva hatches at the beginning of March when peach trees begin to bloom (NOZU, 1915). In this moth, the life cycle should have been varied in such a fashion that the larva is able to hatch at the local flowering time. It should be noticed, however, that the hatching larvae could not directly respond to flowering of the peach tree. The timing must be achieved indirectly through the response to some other factors, probably temperature or day-length, that influence the physiological activity of both the insect and the plant. In northern districts, on the other hand, the length of aestivation diapause might have simply been subjected to natural selection by the

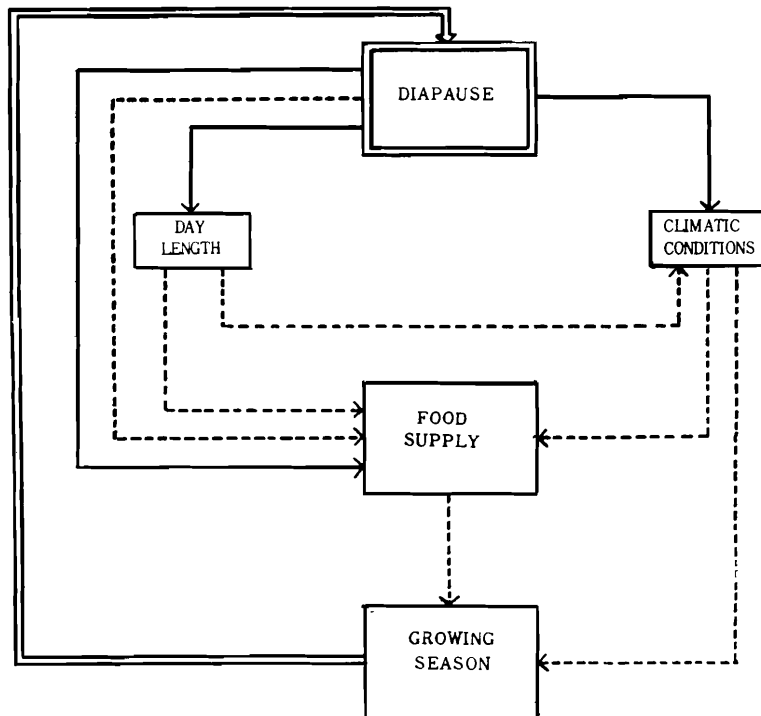


FIG. 11. Diagram showing different courses of moulding the pattern of diapause. Continuous lines indicate the direct response of insects by the diapause mechanism to the factors enclosed in square, which are in turn either superficially or causally correlated to the factors connected by dotted lines. The double line shows the action of selection pressure.

climatic conditions, since the cold and snowy weather would inhibit the late emergence from aestivation. The timing of the hatching season has to be accomplished only by regulating the pace of embryonic development.

The importance of seasonal supply of food as a selecting agency is further suggested by the occurrence of winter species in certain parts of the temperate zone; these insects feed in winter though the weather is not always mild, and some of them pass the summer in diapause. The geometrid moth *Abraxas miranda* is an example. It is partly active in winter but dormant in summer, and this life cycle — being adjusted by the specific mode of diapause — might have been evolved in close connex-

ion with the divergence of the food habit in the subgenus *Calospilos* (MASAKI, 1958, 1959). The occurrence of summer diapause in insects of non-arid regions seems to be related to the seasonal changes in the abundance or quality of the food plants, though detailed field observations and physiological tests are required for the conclusion.

In certain phytophagous insects, the food habit is in fact so delicate that the larva prefers the leaves of a particular quality of its food plant, and this preference would restrict the growing season, and in turn affect the pattern of diapause. In central Japan, two species of large geometrid moth occur in tea-plantations: *Megabiston plumosaria* and *Jankowskia athleta*. Both feed on leaves of the tea-plant, but their preference for the quality is delicately differentiated. The former prefers soft young leaves, but the latter eats old hard ones. Their life cycles are so adjusted that they match with their different food requirements. The larva of *M. plumosaria* pupates in early summer, enters diapause and does not give rise to the adult until late autumn or early winter. The eggs are then laid and hatch in the following spring, when the tea-plants are putting forth their shoots. The life cycle is thus univoltine, with a long aestivation and a short hibernation period. By the intervention of these periods of arrest, the feeding stage is limited only to the two months in late spring (MINAMIKAWA, 1950). On the other hand, *J. athleta* has three annual broods and the hibernating larva does not completely cease to feed (MINAMIKAWA, 1951b). It is able to feed all the year round, because of the constant presence of old leaves. Presumably, the preference for different qualities of the same food plant might have been the factor differentiating their diapause patterns:

One further thing should be argued in this particular case. The delicate divergence of this preference for food might be the outcome of the competition between the two sympatric species. If this be true, then the presence of a competitor might have been the remote cause in evolving the present diapause behaviours of these moths. One may follow out a series of deductions like this in some other cases as well, but it seems useless unless it proves to be true. Although the possibility cannot be ruled out that many factors such as predators, parasites, diseases, competitors or various climatic conditions might be involved in the geographic variation in the incidence of diapause, it is certainly those few factors limiting the growing season that play decisive roles.

The heritable intensity of diapause seems also to be primarily determined by the same factors and secondarily by the conditions prevailing during the diapause stage, because as shown in Section V, the pattern of geographic variation in the intensity of diapause seems to be related to the variability in voltinism. Namely, one of the factors that cause the two reversed trends of variation in the intensity of diapause might be the variability in the incidence of diapause. On this supposition, the paradoxical fact described in Section V could be explained as follows.

In the first place, it should be pointed out that most, if not all, of the diapausing insects are able to endure the severe conditions of winter only in the diapause stage, as demonstrated by some observations stated in Section VIII. It is then indispensable for the survival of these insects to reach the resistant stage before the adverse season. Moreover, to perform its defensive role, diapause should be continued until there is no danger of untimely growth; that is, until the temperature falls below the threshold for growth. It follows therefore that the effective length of diapause might be proportional to the duration or the amount of excess warmth left at the end of the growing season. Suppose that an insect has one brood each year in its northern

reaches of distribution, and also that little amount of effective temperature is left over when it has reached the diapause stage. In such a case, diapause of a short duration might ensure a safe hibernation. If this species extends its range towards southern warmer districts, a longer diapause would be necessary in order to keep spontaneously the standstill state until or after the onset of the severe season. In further south, the insect would be subjected to natural selection of different directions, depending on the ecological circumstances or the physiological characteristics as stressed before. One possible way is to produce an additional generation before winter, utilizing a larger amount of available environmental resources and longer time for growth and breeding. Consequently a shorter diapause will suffice to prevent it from fatal growth before winter. The other way of adaptation is to persist firmly its univoltine life cycle, and to pass the rest of the long warm season in a state of diapause (see fig. 12).

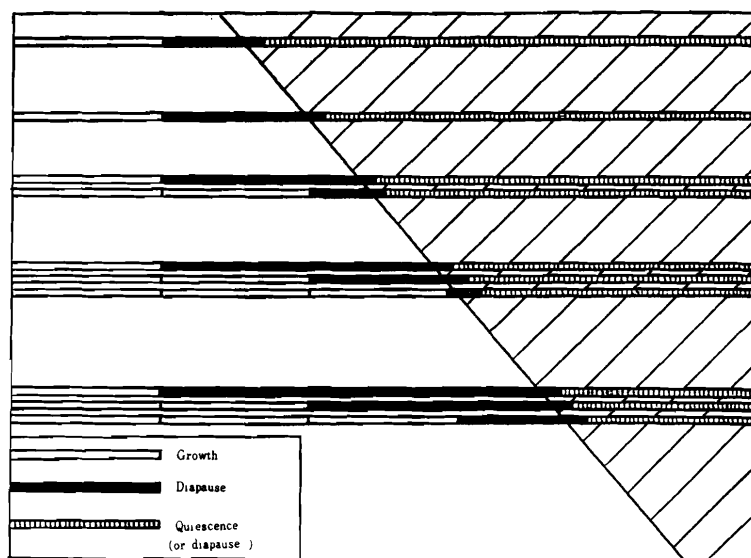


FIG. 12. Schematic diagram showing an interpretation of the geographic variation in the length of diapause. Ordinate, latitude or altitude; abscissa, amount of temperature effective for growth. For further explanation see text.

Within the region where the number of annual brood is constant, diapause would therefore be longer from north to south, but this tendency might be disrupted and reversed in the area where the insect changes its voltinism. In a species with facultative diapause, the intensity of diapause would be increased towards the northern border of the two generation area as the univoltinism becomes predominant. On the contrary, at the southern border where the bivoltine cycle is turning into a trivoltine one, a shorter diapause would be favoured. The occurrence of a trivoltine race in *Chilo suppressalis* on the warm Pacific Coast of Sikoku and its weak diapause as compared with the Saigoku strain could presumably be explained along this line.

The individual life cycles at the critical zone could not be intermediate; it would be either univoltine or bivoltine, etc. Hence, the populations at the border might perhaps be heterogeneous in their genetic constitutions, possibly in a state of physiological

polymorphism; The level of balance between the two different diapause characters might vary from place to place or from year to year in conformity with the gradient or fluctuation of the selection pressure. A situation supporting this assumption could be seen in the rice-stem maggot *Chlorops oryzae*. Though the existence of diapause is obscure in its annual cycle, the local populations of this fly are able to fit their annual cycle to different climates by the intrinsic variations in the rate of development and in the nutritional requirements. The fly has three generations a year in southern Japan, but only two in the northern part. The annual cycle is largely determined by the genetic factors, since the trivoltine race develops faster than the bivoltine one under the same environmental conditions. The change in voltinism is taking place within a narrow zone in Niigata Prefecture where the two cycles are intermingled; The ratio of bivoltine to trivoltine individuals varies regularly from one margin to the other of this zone; Samples taken from one of these intermingled populations are highly variable in the rate of growth; The range of variation in the date of spring emergence of adult flies from the overwintering generation covers the dates of emergence of both the trivoltine and bivoltine strains (HIRAC, 1959; TAMURA *et al.*, 1959).

The interpretation here put upon the two reversed trends of geographic variation in the length of diapause is not as yet standing on valid evidence, for there has been known one exceptional tendency in the Yezo field-cricket, and many more exceptions might be found in the future. Furthermore, other interpretations seem also to be possible. First, in some cases the variation in the mode of response to temperature during diapause might be more important, since a variation in the optimal temperature for the completion of diapause might, in some cases, have the same effect as a variation in the duration of diapause; Unfortunately, this has been explored insufficiently, though it is certain that temperature optimum for the termination of diapause lies between the maximum and minimum temperatures normally experienced by the diapausing population in the local habitat. This is a prerequisite to survive the district with the capacity for diapause. Secondly, there might be no or little primary significance in the geographic variation in the strength of diapause; the duration of diapause might be physiologically associated with the mode of incidence of diapause so that the variation in the latter accompanies the variation in the former. Thus in different races of the silkworm, an obligatory diapause tends to last longer than a facultative one, as demonstrated by the length of cold exposure necessary to hatch the larvae from diapausing eggs (TAKIZAWA and KATSUNO, 1960). Yet, it could not be denied that natural selection have established, or at least allowed, the existence of such a physiological correlation between the incidence and intensity of diapause;

At any rate it is certain that the modes of incidence and completion of diapause have evolved in close connection to each other. As already pointed out, the whole picture of diapause would in turn be related to the way of life of the species; This seems rather axiomatic, because the final goal to be reached by this mechanism of seasonal regulation is to increase the chance for survival of the population. It is the mode of life as a whole that is challenged by the environment.

X. SUMMARY

The mode of diapause in a species of insect may vary a great deal between local populations inhabiting a wide variety of climatic conditions. Diapause tends to be obligate in the cool northern climate, but it would become facultative in the warmer

parts of the range, and no faculty of diapause might be met with further south. On the other hand, there are those insects which retain obligatory diapause throughout their wide range, and this constancy in the incidence of diapause is supposed to be related to the seasonal supply of their food-plants or other ecological factors.

Populations with facultative diapause are further differentiated in their reaction threshold of external stimuli concerning the evocation of diapause. Those from higher latitudes require longer photoperiods and higher temperatures to avert diapause than those from lower latitudes.

The local populations might also differ from one another in the mode of the completion of diapause. This might be observed in the limits and optimum of temperature for the termination of diapause, and also in the intensity or inherent duration of diapause. As to the latter, two reversed trends of geographic variation seem to exist. This might be correlated with the geographic variation in voltinism. If the voltinism is constant, the length of diapause will be longer in warmer districts, while if it is variable, diapause will be shorter in the multivoltine populations than in the univoltine one.

Aestivation diapause occurs in the populations inhabiting those regions where the summer is arid and the phenology of insects' activity is just reversed from that in the milder climates. Aestivation diapause is substantially different in its physiological nature from winter diapause, and certain populations have the capacity to enter diapause of both types. In milder climates, certain species have developed this resting mechanism probably as an adaptation to the seasonal supply of the suitable food, and the local populations might be variable in the incidence as well as in the length of aestivation diapause.

By these differentiations, the climatic limits for the survival of a species is broadened, but a local strain tends to be limited within a relatively narrow zone. If a population is transferred to a locality of a different climate, it will sometimes fail to match the life cycle with the new circumstances and be wiped out. However, each local strain might have a potentiality of further divergence by the genetic versatility of diapause under the influence of natural selection, since the genetic variability of diapause character has been suggested by artificial selection.

Many factors might have been operating in the formation of these geographic variations, and the relative importance of these factors differs between different species, depending on their modes of life and the local conditions of their habitats. Among others, food and temperature might conceivably be most important; in monophagous herbivores the former would exert a decisive effect while in polyphagous insects the latter would be more important. Other ecological factors such as predators, parasites, or competitor might not be neglected.

Namely, it is the mode of life as a whole that is challenged by the environment, which means that the character of diapause is closely linked to other physiological traits as well as ecological habits. The local differentiation of diapause might have been achieved in close connexion with other aspects of the life cycle.

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*The original papers were not accessible.

**Written in Japanese.