

## Seasonal Adaptations of Insects as Revealed by Latitudinal Diapause Clines

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**Abstract.** To stimulate further study on seasonal adaptations in insects, two hypotheses are proposed, one accounting for latitudinal variations in diapause intensity and the other pertaining to the phenotypic plasticity of critical photoperiod for diapause induction.

(1) In some species with constant voltinism, diapause intensity increases southward to cope with higher risks of untimely termination of diapause before winter. In other species with variable voltinism, it decreases southward presumably because of stronger selection for nondiapause phenotypes and positive correlations between diapause intensity and incidence.

(2) Clinal variations of critical photoperiod for diapause induction may be mimicked by phenotypic responses to temperature. Such plasticity expands the latitudinal range of adaptation. In a noctuid moth, the critical photoperiod is increased by long photoperiods in the early stage of development, so that photoperiod itself may also be involved in phenotypic adaptation to climatic gradients.

**Key words:** Latitudinal cline, diapause intensity, diapause incidence, critical photoperiod, phenotypic plasticity.

### Introduction

Most species of insects are exposed to latitudinal gradients of climatic conditions (see below). They may cope with such latitudinal gradients mainly by genetic and partially by phenotypic variations in diapause and related physiological traits. A large body of literature has been accumulated on this subject and extensively reviewed (Danilevskii, 1961; Masaki, 1961; Beck, 1980; Saunders, 1982; Tauber *et al.*, 1986; Danks 1987). More up-to-date general discussions on seasonal adaptation in insects are given by Hodek and Danks (both in this issue). Therefore, I will pose only two problems that have not been seriously considered before: (1) the occurrence of clines in diapause intensity that have different directions along the same latitudinal gradients and (2) latitudinal adaptations of the critical photoperiod for diapause induction that mimics latitudinal clines through phenotypic plasticity.

### Latitudinal Clines in Diapause Intensity

#### *Two clinal patterns contrary to each other*

An example of latitudinal gradients of climatic conditions is given in Fig. 1 to illustrate the general

background for the evolution of clinal variations in diapause intensity and incidence. As latitude increases, the summer daylengths increase, summer temperatures decrease and winter temperatures decrease more, so that the temperature difference between summer and winter increases.

I define 'diapause intensity' as the duration of diapause at a certain temperature above the developmental threshold or the time of chilling or other environmental cues (e.g., photoperiod) required for eliminating diapause. Diapause intensity thus defined tends to be highly variable among conspecific local populations. Some examples are given in Fig. 2. All of them show latitudinal clines, probably reflecting adaptation to the climatic gradients. Surprisingly, however, the left and right examples are exactly contrary to each other.

All the clines in the left column of Fig. 2 show decreasing diapause intensity northward. Similar trends are found in *Heliothis zea* (Holtzer *et al.*, 1976) and in *Oxya jezoensis* (Y. Ando, unpub.). In *Pectinophora gossypiella*, the altitudinal gradient in temperature gives a similar effect, i.e. diapause becomes less intense with increasing altitude (Watson *et al.*, 1974). In contrast, all the clines show increasing diapause intensity northward in the right column. In *Chlorops oryzae* also, the winter diapause is more intense in the

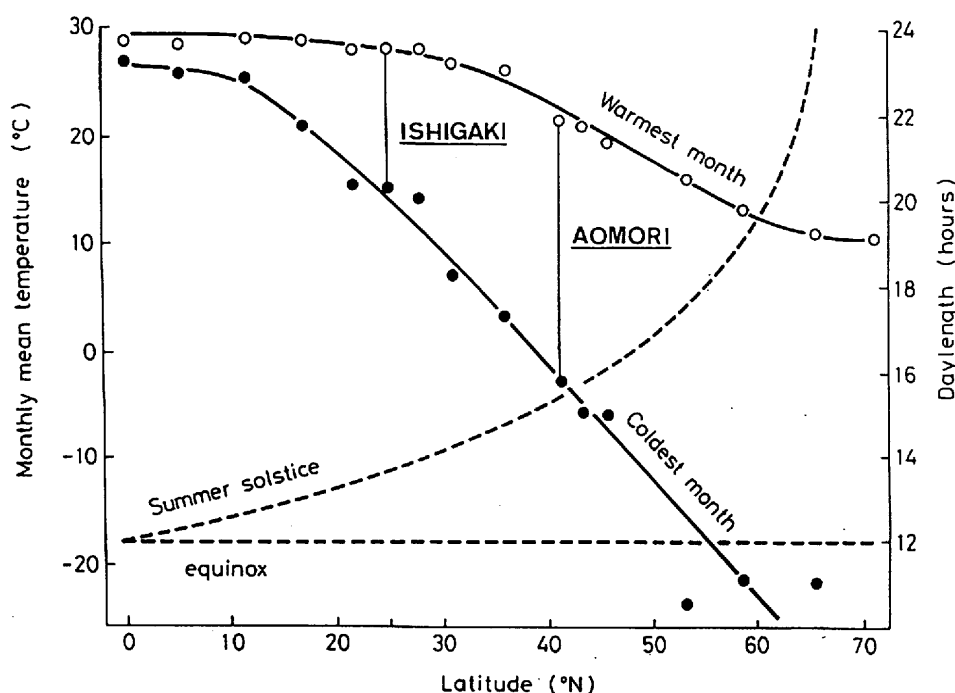


Fig. 1. The latitudinal gradients of temperatures and daylengths (time from sunrise to sunset) along the eastern periphery of Eurasia including the Japanese Islands. Data are drawn from Tokyo Astronomical Observatory (1989).

northern bivoltine population than in the southern trivoltine population (Takeda, 1996).

Interestingly, clines of both categories occur in *Chilo suppressalis*. The larval diapause becomes more intense from north to south within its bivoltine area, while the diapause intensity is lowest in the southern trivoltine populations (restricted to an area in Shikoku), intermediate in the bivoltine populations and highest in the northern univoltine populations (Kishino, 1974).

Why do these clines differ along similar climatic gradients? What selective factors establish these clinal patterns?

#### Correlation between diapause incidence and intensity

A clue to solve the above questions has been obtained from experiments with a subtropical population of the ground cricket *Dianemobius fascipes* collected from the subtropical island Ishigaki situated at about 24°N. I separated 13 groups of crickets with different diapause intensities (as measured by the duration of the egg stage at 26°C) in the 2nd laboratory generation, and determined the hatching distributions of their progeny. These eggs were highly variable in the incidence and intensity of diapause, and the two diapause parameters are significantly correlated with each other (Fig. 3).

I have been selecting strains for different durations of the diapause egg stage in this ground cricket for 15

years under short days at 25–26°C. During this long course of selection, the diapause incidence and intensity varied from generation to generation in several lines kept under different selection pressures (Masaki, 1996; details will be published elsewhere). Therefore, a long series of paired data on diapause intensity and incidence is now available. In Fig. 4 are plotted percentages of diapause eggs against means of the diapause egg stage in the three lines selected for egg stages of about 8, 15 and 22 weeks for 38, 26 and 21 generations, respectively. The correlation between the two diapause parameters is again significant.

#### Diapause propensity and threshold response

A hypothesis to explain the observed correlation between the incidence and intensity of diapause can be derived from a threshold response model. Falconer (1981) proposed a model of this sort for analyzing polygenic systems controlling a continuous variable underlying discontinuous phenotypes (e.g., diapause/nondiapause, short-winged/long-winged). He called this variable liability. Roff (1988) successfully applied a similar model for analyzing wing polymorphism in crickets. I made the premises that the physiological trait underlying the process determining diapause (called here 'diapause propensity' for convenience) varies quantitatively and that the final expression of diapause is controlled by a threshold response, i.e. there is a threshold propensity for the phenotypic

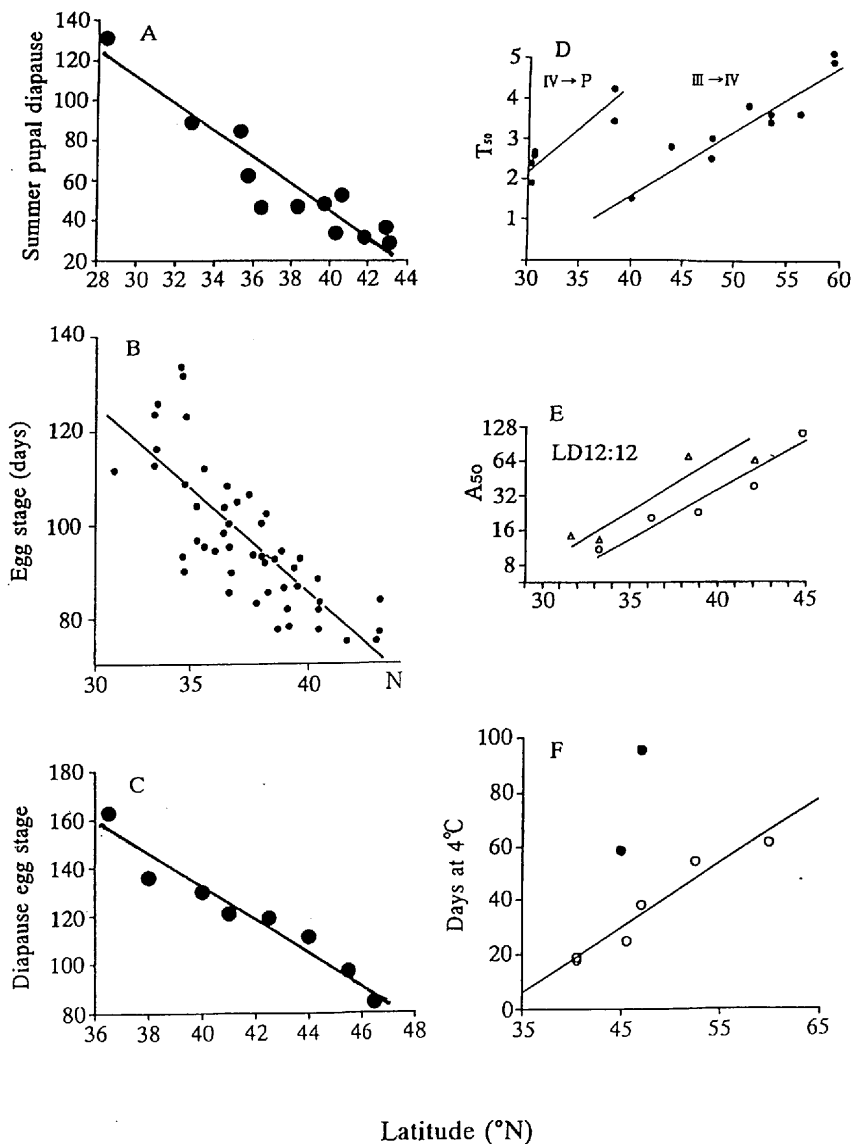


Fig. 2. Examples of latitudinal clines in diapause intensity. A: Duration of summer diapause at 26°C in *Mamestra brassicae* (Masaki, 1956, modified). B: Egg stage at 25°C in *Teleogryllus emma* (Masaki, 1965). C: Diapause duration of eggs at 25°C in the *Diabrotica virgifera* species group (Krysan, 1982). D: Number of long-day cycles ( $T_{50}$ ) required for diapause termination in the 3rd and 4th larval stages in *Wyeomyia smithii* (Bradshaw & Lounibos, 1977). E: Duration of reproductive diapause ( $A_{50}$ , days) in LD12:12 h at 15°C in *Drosophila auraria* (circles) and *D. triauraria* (triangles) (Kimura, 1988, courtesy of Blackwell Science Ltd.). F: Days of chilling for 50% termination of diapause under LD10:14 h in *Tetranychus urticae*. Closed circles represent samples from high altitudes (Koveos *et al.*, 1993, courtesy of Blackwell Science Ltd.).

manifestation of diapause (Fig. 5).

Individuals with propensities higher than this threshold enter diapause while those with lower propensities do not. Diapause propensity might be related to activities of enzymes, hormones, other physiologically active molecules or DNA ultimately coding them. The left half of Fig. 5 shows the distribution of diapause propensity in four hypothetical insect populations. When the propensity distribution crosses the threshold, the population shows a bimodal distribution in the phenotype of developmental pattern, compris-

ing nondiapause and diapause groups, as shown in the right graphs. The top pair of graphs depicts a univoltine case. The lower three pairs represent polyphenic populations in which diapause and nondiapause phenotypes coexist in various proportions.

#### A hypothesis to explain reversed clines

Based on the correlation between the incidence and intensity of diapause described above, the occurrence of two contrasting latitudinal clines in diapause intensity can be explained as illustrated in Fig. 6.

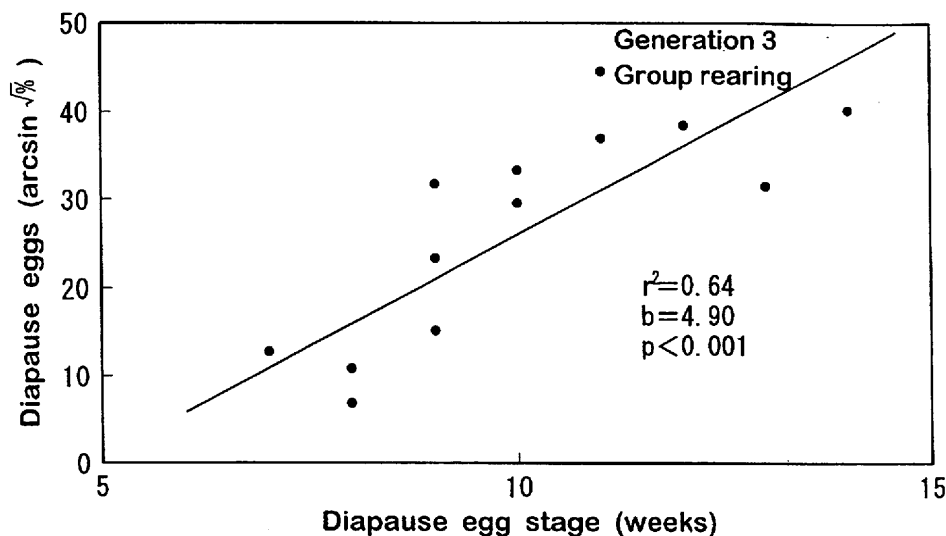


Fig. 3. Correlation between the incidence and intensity of egg diapause at 26°C in the progeny of 13 groups of the subtropical ground cricket *Dianemobius fascipes* separated by the duration of diapause egg stage.

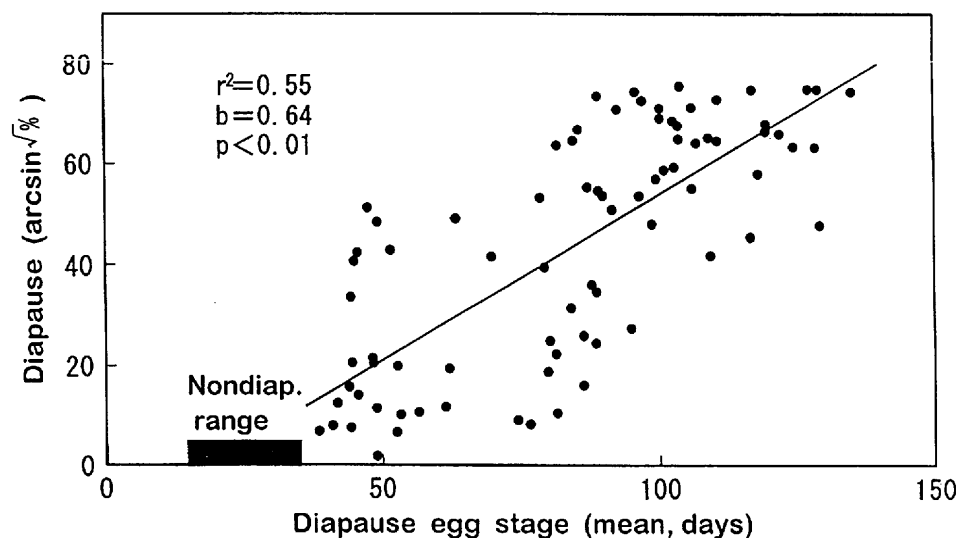


Fig. 4. Correlation between the incidence and intensity of egg diapause at 26°C in three lines of *D. fascipes* selected for egg stages of about 8, 15 and 22 weeks through 39, 26 and 21 generations, respectively. See Masaki (1996) for the time course of the responses to selection.

The right panel in this figure represents a diapause intensity cline decreasing northward, commonly found in univoltine species. The arrows indicate the direction of selection pressure. In the north, selection for a deeper diapause is not strong, because the cool autumn and consistently cold winter decrease the risk of untimely emergence from diapause. On the other hand, the short growing season requires prompt resumption of development as soon as effective heat becomes available in the spring. Therefore, natural selection would favour a less intense diapause. In the south, the selection pressures would tend to intensify diapause, because the risk of untimely hatch would be higher than that of developmental failure during

the long summer. Similar reasoning is feasible for the overwintering generation of multivoltine species within the area where the same number of annual generations is maintained. In the case of summer diapause, the intensity is simply proportional to the summer length.

The left panel in Fig. 6 illustrates how a cline of diapause intensity increasing northward might be established as observed in species with variable voltinism. In such species, both diapause and nondiapause phenotypes can occur. If the nondiapause phenotype has a higher fitness than the diapause phenotype under certain conditions, for example, long-day and high-temperature conditions, selection for nondiapause

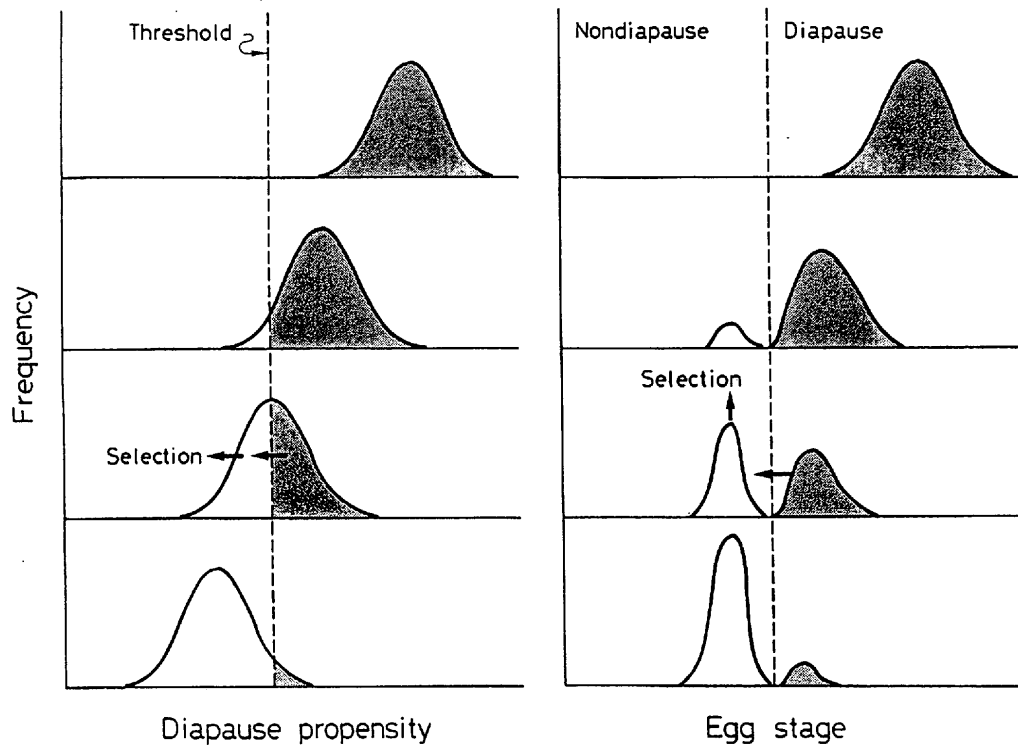


Fig. 5. A threshold response model to explain correlation between diapause intensity and incidence. If selection acts to enhance nondiapausing development as indicated by the upward arrow in the third graph in the right column, the distribution of diapause propensity moves left as shown by the horizontal arrows in the left graph. For further explanation see text.

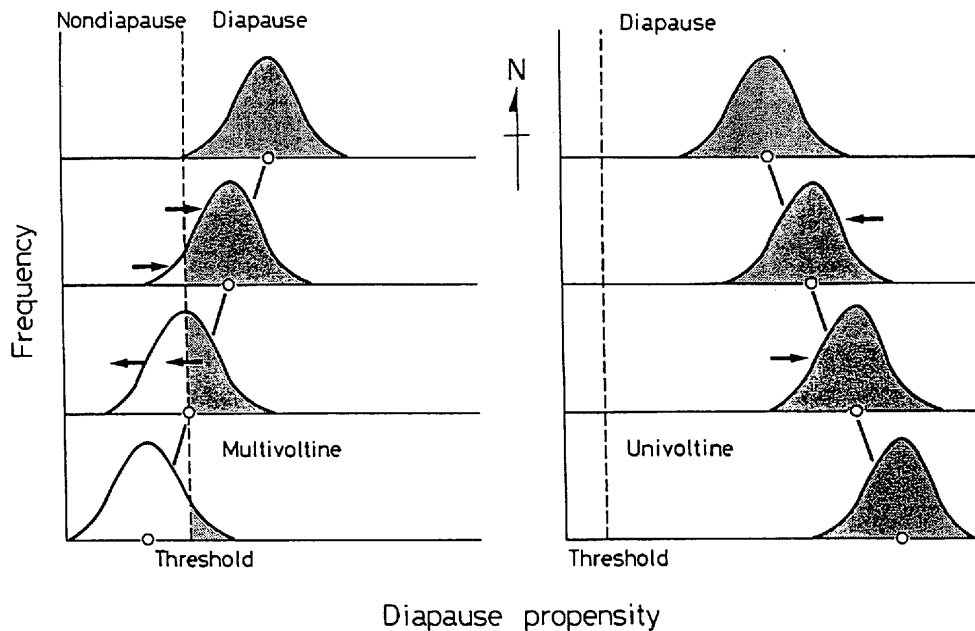


Fig. 6. Threshold response models for the formation of diapause-intensity clines with latitudinal tendencies contrary to each other. Arrows indicate directions of selection pressure increasing northward in the second graph and southward in the third graph. For further explanation see text.

should necessarily be associated with selection for a lower diapause propensity. The distribution of diapause propensity should be determined by the balance between the forces of selection for nondiapausing and

diapause.

Multivoltine species can switch between diapause and nondiapausing phenotypes in response to seasonal cues such as daylength and temperature. This requires

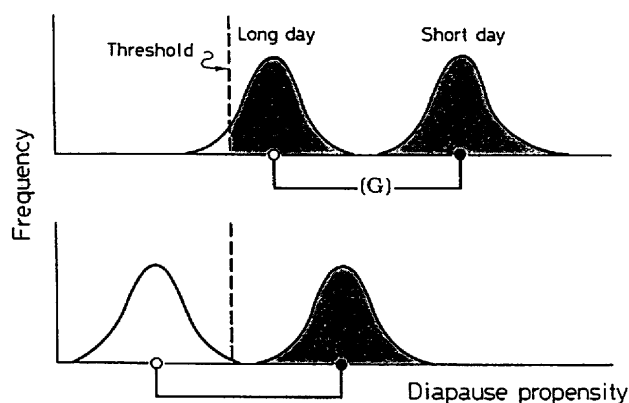


Fig. 7. Threshold response models for the photoperiodic shift of distribution of diapause propensity. *G* shows the magnitude of shift and also the genetic correlation between short-day and long-day distribution of diapause propensity.

two further assumptions in order to understand the latitudinal clines ascending northward. First, the diapause propensity shifts in response to a seasonal cue such as daylength (Fig. 7). Second, the shift of diapause propensity in one environment is linked genetically with the propensity in another, for example, different photoperiodic and thermal conditions. If such a correlation exists, selection for nondiapause under long days would result in a reduction in diapause intensity under short days. However, the magnitude of the shift of diapause propensity itself may become a target of selection. Such selection might be involved in the increasing diapause intensity southward within the bivoltine area of *C. suppressalis* and in other similar cases.

### Mimicking Photoperiodic Clines by Phenotypical Plasticity

#### *Clines in critical photoperiod (CP)*

Now, we shall turn to the second problem, photoperiodic cline, or the latitudinal variation in CP for diapause induction. In Fig. 8A are reproduced the diapause responses to photoperiod in 4 local populations of *Acronycta rumicis* (Danilevskii, 1961). This is the first and most beautiful demonstration of the latitudinal photoperiodic adaptation. CP for the induction of diapause varies regularly with the original latitude. Following Danilevskii, many workers found similar variations in different species of insects in different parts of the world. Some examples are given in Fig. 9. Most species of insects and mites show latitudinal clines in CP in parallel to the increasing summer daylength and the shortening growing season northward.

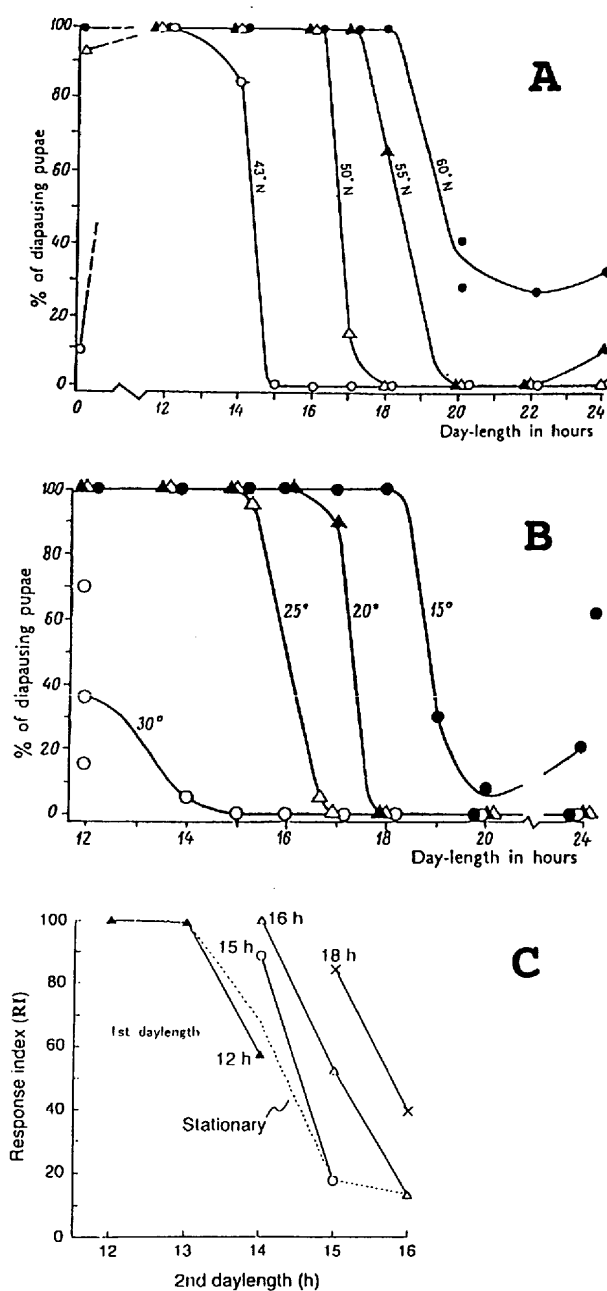


Fig. 8. Phenotypic variations in critical photoperiod mimicking latitudinal clines. A: Latitudinal cline of CP in *A. rumicis* (Danilevskii, 1961). B: Variation of CP with temperature in *A. rumicis* (Danilevskii, 1961). C: Shift of CP caused by the photoperiod of the early larval life in *M. brassicae*. Response index (see text) is plotted as a function of the photoperiod in the later stages (Kimura & Masaki, 1998).

The tendencies are similar in all these examples, reflecting the general selection pressure imposed by the latitudinal gradients. However, there may be considerable differences among different species or different geographical areas in the slope of regression line as exemplified by the lower right two panels in

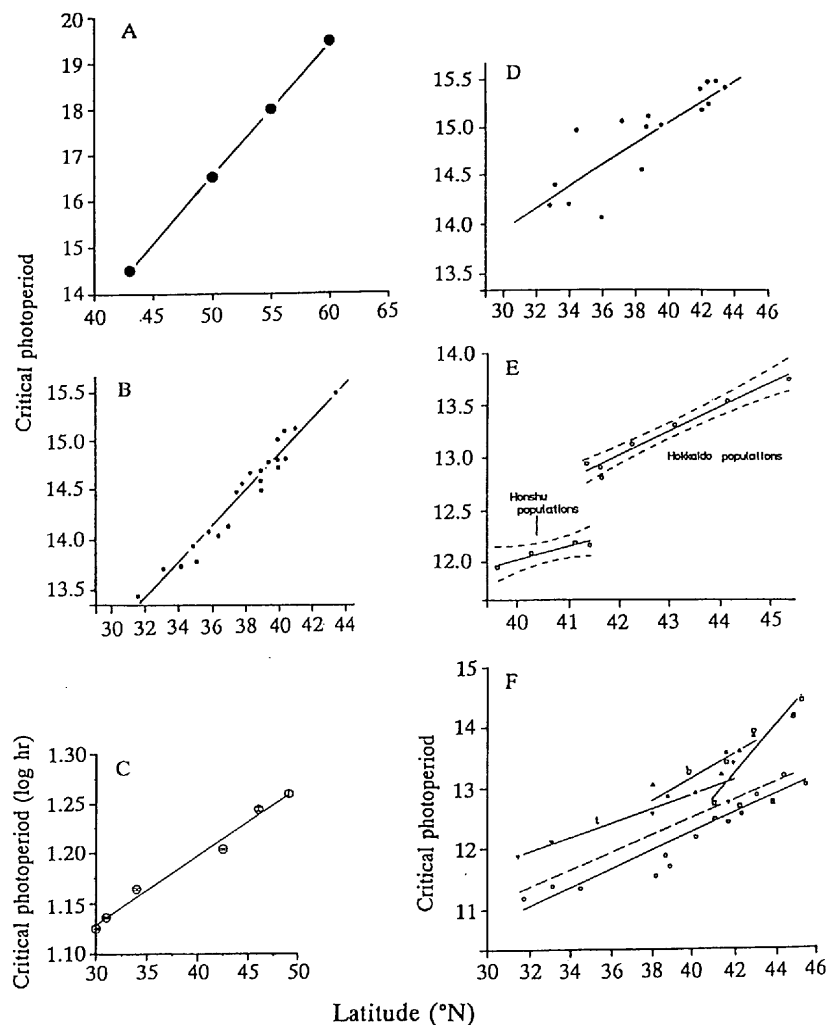


Fig. 9. Examples of latitudinal clines in the critical photoperiod for diapause induction. A: *Acronycta rumicis* in Russia (Danilevskii, 1961). B: *Chilo suppressalis* in Japan (Kishino, 1974, courtesy of Japanese Society of Applied Entomology and Zoology). C: *Wyeomia smithii* in North America (Hard *et al.*, 1993). D: *Cydia pomonella* in North America (Riedl & Croft, 1978, courtesy of The Entomological Society of Canada). E: *Drosophila lacertosa* in Japan (Ichijo, 1986). F: *Drosophila auraria* complex in Japan. Broken line shows daylength at the date when daily mean temperature falls to 15°C (Kimura & Bessho, 1993, courtesy of Academic Press Ltd.).

Fig. 9. If more examples of photoperiodic clines are extensively collected and carefully compared, we can get deeper insight into the mode of natural selection on CP.

#### Adaptive role of phenotypic plasticity in CP

Although CP generally varies with latitude within the same species, it may also be subject to phenotypic modification in response to environmental cues such as temperature and food quality (see the reviews referred to in Introduction). This is most beautifully demonstrated for the first time also in *Acronycta rumicis* (Danilevskii, 1961; Fig. 8B). The CP changes regularly with temperature in a way similar to its change with latitude, i.e. CP becomes longer as either temperature decreases or latitude increases, although

this thermal effect varies from species to species.

As temperature generally decreases northward, this well-known phenotypic response might expand the latitudinal range of adaptation of a given genotype as schematically illustrated in Fig. 10 (Masaki, 1961). The three ascending lines in this graph represent the latitudinal gradients of the daylength at the summer solstice, local CP, and shortest daylength at the end of the growing season, respectively. A local population with a CP shown by the closed circle A cannot expand beyond the latitudinal range indicated by the horizontal line a below the latitudinal axis, because the CP should be between the longest and shortest daylength in the growing season. The actual range of adaptation should be narrower than this, because allowance should be made for the process of diapause induction.

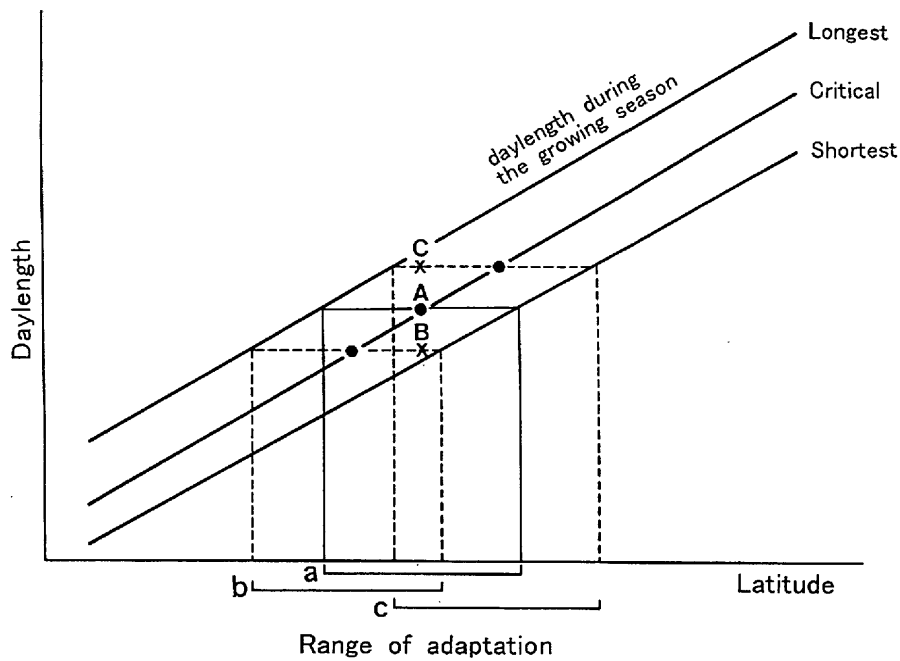


Fig. 10. Scheme showing the possible range of adaptation by a given genotype with a critical photoperiod A and the consequences of phenotypic shifts from A to B and C. The possible ranges of adaptation are indicated by the lines a, b, and c. For further explanation see text (Masaki, 1961, modified).

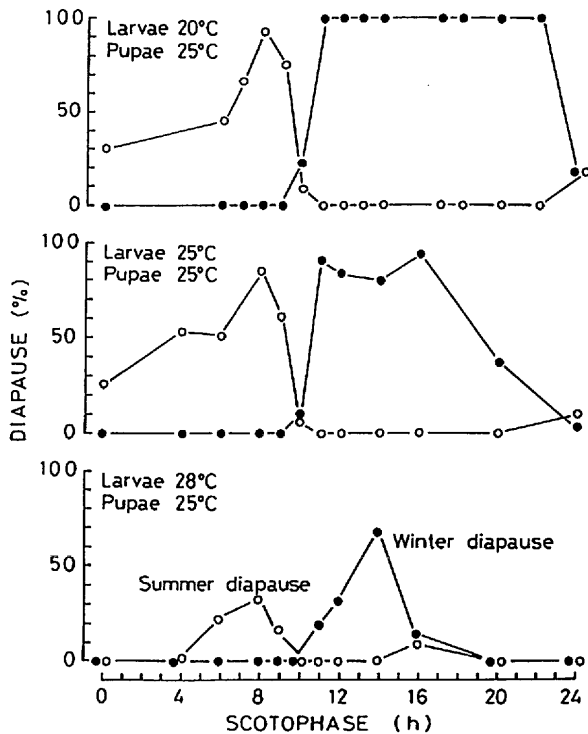


Fig. 11. Effects of photoperiod and temperature on the developmental pattern in pupae of *Mamestra brassicae* (Furunishi *et al.*, 1982). Summer diapause and winter diapause can be distinguished by their different durations and thermal requirements for termination (Masaki, 1956).

If the CP is shortened by high temperature to the cross B, the range of adaptation extends accordingly to lower latitudes as given by the line b. By the same token, the possible consequence of an increased critical photoperiod by low temperature as indicated by the cross C is a shift of the range of adaptation northward. These phenotypic variations may give a higher probability than otherwise to survive latitudinal migration and to respond to natural selection in a new environment. Therefore, a phenotypic response of this kind may facilitate the establishment of a photoperiodic cline.

*Photoperiodic response in Mamestra brassicae*

Recently, another environmental factor has been found simulating a photoperiodic cline in *Mamestra brassicae* (Kimura & Masaki, 1998). The pupae of this moth take one of three different developmental pathways, short summer diapause, nondiapause or long winter diapause, depending on the photoperiod during the larval stage (Furunishi *et al.*, 1982). As in many other species of arthropods, the diapause response depends mainly on scotophase rather than photophase length. The ranges of scotophase inducing winter diapause and summer diapause are clearly separated; the winter diapause occurs under a long scotophase and the summer diapause under a short scotophase (Fig. 11). Nondiapause pupae are most common under intermediate photoperiodic condi-



tions. Therefore, under the naturally decreasing day-lengths from early summer to autumn, the developmental pattern of the pupae changes progressively from summer diapause to nondiapause and then to winter diapause (Kimura & Masaki, 1998). In terms of the induction of winter diapause, this species is a long-day insect.

Although the winter and summer types of diapause would seem to differ only in intensity, they are discontinuous phenotypes, being separated by the nondiapause form in the photoperiodic response. The winter diapause and summer diapause show a clear difference in the thermal relations to their completion (Masaki, 1956) and also in the ecdysteroid titre, the prothoracicotrophic hormone activity and the sensitivity of prothoracic glands to this brain hormone (Endo *et al.*, 1997). In this noctuid moth, therefore, there are two thresholds in diapause propensity for determining the three different developmental patterns, one dividing between summer diapause and nondiapause and the other between nondiapause and winter diapause (Kimura & Masaki, 1998).

#### *Response to change in photoperiod*

Effects of photoperiodic shift have been studied by many workers as comprehensively reviewed by Zaslavski (1988). In many species of insects, experiments of this type were performed mainly to determine the stage sensitive to photoperiod. Some species, however, showed characteristic responses to photoperiodic change that could not be explained by the simple additive effects of different stationary photoperiods given at different stages of development. In some cases, the photoperiodic induction or termination of diapause is assumed to include two-step reactions requiring two different ranges of photoperiod. In other cases, responses to relative changes, either decrease or increase in photoperiod, are suggested.

However, the responses of *M. brassicae* could not be understood by either of these models, when larvae were exposed to photoperiods ranging from 10 to 18 h during the first 7 days and then transferred to those from 12 to 16 h (Kimura & Masaki, 1998). The direction of photoperiodic change alone did not determine the response. The two-step response model was also rejected, because diapause could be controlled perfectly by stationary photoperiods (Fig. 10). These results suggested a previously unknown effect of change in photoperiod on the seasonal and latitudinal adaptations of this insect as given below.

#### *Early photoperiod is involved in CP plasticity*

To express the complicated photoperiodic response in *M. brassicae* in a simpler way, a 'response index' is used. This index is based on the assumption of quantitative change of diapause propensity (=overwintering liability in Kimura & Masaki [1998]) combined with two thresholds, one between summer diapause and nondiapause and the other between nondiapause and winter diapause as mentioned above. To compute the response index, scores of 0, 0.5 and 1 are given to summer diapause, nondiapause and winter diapause, respectively, because these developmental patterns occur successively with the advent of season in this order and also with systematically increased photoperiod in the laboratory: summer diapause in early summer or long days, nondiapause in mid to late summer or intermediate days and winter diapause in late summer to autumn or short days. The photoperiodic response can be expressed as a single curve by using the response index, which sums the percentages of the three types of pupae multiplied by the respective scores. If all pupae enter winter diapause, the response index will be 100. If all pupae enter summer diapause, the response index will be 0. Therefore, this index varies between 0 and 100 like the percentage diapause in many other insects so that CP can be defined by a response index of 50 representing the mid point between the long-day and short-day values of diapause propensity (see Fig. 8 in Kimura & Masaki, 1998).

In Fig. 8C are plotted the response indexes as a function of the second daylength after transfer. Although available data are still scanty, these curves seem to represent parts of the response curves with different CPs. The photoperiod in the early stage of development would modify the CP for programming the seasonal development in the later stage. This phenotypic variation in CP somewhat resembles the temperature effect as observed in *A. rumicis* (Fig. 8B). A long daylength in the early stage of development in *M. brassicae* and a low temperature in *A. rumicis* similarly tend to increase their CPs. A short daylength and a high temperature may exert opposite effects.

So far as I am aware, the phenotypic adjustment of CP by the photoperiodic conditions early in larval development has not been known previously.

#### **Concluding Remarks**

The recent success of molecular genetic studies of circadian clocks in *Drosophila melanogaster* (Chen *et*

*al.*, 1998; Rutila *et al.*, 1998) might stimulate this line of approach to the photoperiodic clock which occupies a pivotal position in seasonal adaptation. If one can open the black box enclosing the photoperiodic clock, it would certainly be a big break-through to our understanding of the seasonal adaptation in insects.

However, the insects show tremendous diversity in their way of life. Their diapause behaviours including the photoperiodic programming are no exceptions. Even when the responses look very similar, the similarity might be a result of convergent evolution but with very different physiological backgrounds. This supposition comes from the fact that, in the evolutionary history of insects, diapause and hence its photoperiodic programming originated many times independently in different taxonomic groups (e.g., Masaki, 1996).

Under such circumstances, geographical variations in diapause and photoperiodism might provide a rich resource for understanding the evolutionary process of seasonal adaptation. Latitudinal and altitudinal gradients in environmental conditions occur all over the earth's surface, so that insect populations are exposed to gradually shifting seasonal conditions while expanding their distribution. Also, they have experienced global climate change through geological time and now encounter an unprecedentedly rapid change of climate.

Established clines are the results of adaptation to the environment changing in space and time. By analyzing them, we may infer the evolutionary responses of insects to future climate changes. We might find clues to the origin of diapause and photoperiodism, which are no less important than biochemical and molecular dissection of the photoperiodic clock for further understanding of seasonal adaptation in insects.

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### References

- Beck, S. D. 1980. *Insect Photoperiodism*, 2nd ed. Academic Press, New York.
- Bradshaw, W. E. & Lounibos, L. P. 1977. Evolution of dormancy and its photoperiodic control in pitcher-plant mosquitoes. *Evolution*, **31**: 546–567.
- Chen, Y., Hunter-Ensor, M., Schotland, P. & Sehgal, A. 1998. Alternations of *per* RNA in noncoding regions affect periodicity of circadian behavioral rhythms. *Journal of Biological Rhythms*, **13**: 364–379.
- Danilevskii, A. S. 1961. Fotoperiodizm i Sezonnoe Razvitiye Nasekomykh. Izdatelstvo Leningradskogo Universiteta, Leningrad. (In Russian.)
- Danks, H. V. 1987. *Insect Dormancy: An Ecological Perspective*. Biological Survey of Canada (Terrestrial Arthropods), Ottawa.
- Endo, K., Fujimoto, Y., Kondo, M., Yamanaka, A., Watanabe, M., Weihua, K. & Kumagai, K. 1977. Stage-dependent changes of the prothoracicotropic hormone (PTTH) activity of brain extracts and of the PTTH sensitivity of the prothoracic glands in the cabbage armyworm, *Mamestra brassicae*, before and during winter and estival pupal diapause. *Zoological Science*, **14**: 127–133.
- Falconer, D. S. 1981. *Introduction to Quantitative Genetics*, 2nd ed. Longman, New York.
- Furunishi, S., Masaki, S., Hashimoto, Y. & Suzuki, M. 1982. Diapause response to photoperiod and night interruption in *Mamestra brassicae* (Lepidoptera: Noctuidae). *Applied Entomology and Zoology*, **17**: 398–409.
- Hard, J. J., Bradshaw, W. E. & Holzapfel, C. M. 1993. The genetic basis of photoperiodism and its evolutionary divergence among populations of the pitcher-plant mosquito, *Wyeomyia smithii*. *American Naturalist*, **142**: 457–473.
- Holtzer, T. O., Bradley, J. R. & Rabb, R. L. 1976. Geographic and genetic variation in time required for emergence of diapausing *Heliothis zea*. *Annals of the Entomological Society of America*, **69**: 261–265.
- Ichijo, N. 1986. Distinctive cline of critical photoperiod in the reproductive diapause of *Drosophila lacertosa*. *Evolution*, **40**: 418–421.
- Kimura, M. T. 1988. Interspecific and geographic variation of diapause intensity and seasonal adaptation in the *Drosophila auraria* species complex (Diptera: Drosophilidae). *Functional Ecology*, **2**: 177–183.
- Kimura, M. T. & Bessho, A. 1993. The influence of gene flow on latitudinal clines of photoperiodic adult diapause in the *Drosophila auraria* species-complex. *Biological Journal of the Linnean Society*, **48**: 335–341.
- Kimura, Y. & Masaki, S. 1998. Diapause programming with variable critical daylength under changing photoperiodic conditions in *Mamestra brassicae* (Lepidoptera: Noctuidae). *Entomological Science*, **1**: 467–475.
- Kishino, K. 1974. Ecological studies on the local characteristics of the seasonal development in the rice stem borer *Chilo suppressalis* Walker. *Bulletin of Tohoku Agricultural Station*, **47**: 13–114.
- Koveos, D. S., Kroon, A. & Veerman, A. 1993. Geographic variation of diapause intensity in the spider mite *Tetranychus*

- chus urticae*. *Physiological Entomology*, **18**: 50–56.
- Krysan, J. L. 1982. Diapause in the Nearctic species of the *virgifera* group of *Diabrotica*: evidence for tropical origin and temperate adaptations. *Annals of the Entomological Society of America*, **75**: 136–142.
- Krysan, J. L., Branson, T. F. & Castro, G. D. 1977. Diapause in *Diabrotica virgifera* (Coleoptera: Chrysomelidae): a comparison of eggs from temperate and subtropical climates. *Entomologia Experimentalis et Applicata*, **22**: 81–89.
- Masaki, S. 1956. The local variation in the diapause pattern of the cabbage moth, *Barathra brassicae* Linné, with special reference to the aestival diapause (Lepidoptera: Noctuidae). *Bulletin of Faculty of Agriculture, Mie University*, **13**: 29–46.
- Masaki, S. 1961. Geographic variation of diapause in insects. *Bulletin of Faculty of Agriculture, Hirosaki University*, **7**: 66–98.
- Masaki, S. 1965. Geographic variation in the intrinsic incubation period: a physiological cline in the Emma field cricket (Orthoptera: Gryllidae: *Teleogryllus*). *Bulletin of Faculty of Agriculture, Hirosaki University*, **11**: 59–90.
- Masaki, S. 1996. Geographical variation of life cycle in crickets (Ensifera: Grylloidea). *European Journal of Entomology*, **93**: 281–302.
- Riedl, H. & Croft, B. A. 1978. The effects of photoperiod and effective temperatures on the seasonal phenology of the codling moth (Lepidoptera: Tortricidae). *The Canadian Entomologist*, **110**: 455–470.
- Roff, D. A. 1986. The evolution of wing dimorphism in insects. *Evolution*, **40**: 1009–1020.
- Rutia, J. E., Maltseva, O. & Rosbash, M. 1998. The *tim<sup>SL</sup>* mutant affects a restricted portion of the *Drosophila melanogaster* circadian cycle. *Journal of Biological Rhythms*, **13**: 380–392.
- Saunders, D. V. 1982. *Insect Clocks*, 2nd ed. Pergamon Press, Oxford.
- Tauber, M. J., Tauber, C. A. & Masaki, S. 1986. *Seasonal Adaptations of Insects*. Oxford Univ. Press, New York.
- Takeda, M. 1996. Photoperiodic induction, maintenance and termination of winter diapause in two geographic ecotypes of the rice stem maggot, *Chlorops oryzae* Matsumura (Diptera: Chloropidae). *Applied Entomology and Zoology*, **31**: 379–388.
- Tokyo Astronomical Observatory. 1989. *Rikanenpyou*. (1989 edition.) Maruzenn, Tokyo.
- Watson, T. F., Crowder, L. A. & Langston, D. T. 1974. Geographical variation of diapause termination of the pink bollworm. *Environmental Entomology*, **3**: 933–934.
- Zaslavski, V. A. 1988. *Insect Development: Photoperiodic and Temperature Control*. (English edition.) Springer-Verlag, Berlin.

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