Environmental factors that determine the seasonal onset and termination of reproduction in seed-sucking bugs (Heteroptera) in Japan

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Abstract

The onset and termination of reproductive seasons in insects are determined by various environmental factors under natural conditions. These factors will be reviewed in seed-feeding heteropterans that have winter adult diapause in Japan. Most species use photoperiod to time the induction of adult diapause and therefore the termination of reproduction in autumn. In some species, however, temperature or the quality of food are also used as seasonal cues. For initiation of reproduction in spring, a temperature increase above the lower thermal threshold for postdiapause development is essential. The appearance of host plant seeds primarily determines the onset of reproduction in *Dybowskyia reticulata*, and the photoperiod plays a definitive role in *Cletus punctiger*. However, the proximate factors that determine the onset of reproduction in spring have not been examined as intensively as those for the termination of reproduction in autumn.

Key words: Heteroptera; adult diapause; photoperiod; temperature; food

INTRODUCTION

Many heteropterans that feed on plant seeds are known to be serious agricultural pests, and most of them overwinter as diapause adults (Schaefer and Panizzi, 2000). Effective manipulation of a pest insect requires an understanding of the ecophysiological mechanisms that underlie the seasonal life cycle of the species (Tauber et al., 1986). Most insects have evolved the ability to receive environmental cues that signal the upcoming seasonal changes, and they respond to these cues by entering diapause, which prepares them for adverse conditions. In species that have an adult winter diapause, the reproductive season terminates with the induction of diapause in autumn. Of all the physical factors that change seasonally, photoperiod is the most regular, and therefore provides the most reliable cue. However, other factors, such as temperature, quality and quantity of food, density, and moisture, are also responsible in some species (Danilevskii, 1961; Tauber et al., 1986; Danks, 1987).

In species that have an adult winter diapause, the

reproductive season begins after completion of postdiapause development in spring. Although photoperiod is the major factor for the induction and maintenance of winter diapause in autumn, most species lose their sensitivity to the photoperiod before the end of winter. In most of these species, postdiapause development begins without a specific stimulus when the temperature exceeds the lower threshold in spring, and photoperiod plays no role in the onset of morphogenesis and reproduction after overwintering (Tauber et al., 1986). However, a few species respond to the long-day conditions in spring (e.g., Masaki and Oyama, 1963; Tauber and Tauber, 1975; see Tauber et al., 1986). Moreover, a supply of a specific food is needed for postdiapause reproduction in some species with an adult diapause, especially carnivores (e.g., Hodek, 1970; Tauber and Tauber, 1973).

In this review, I will summarize the proximate factors that determine the seasonal onset and termination of reproduction under natural conditions in seed-sucking bugs with a winter adult diapause living in Japan.

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Table 1. Environmental factors that determine the induction of winter adult diapause in seed-sucking bugs in Japan

Species	Factors	References
<i>Riptortus clavatus</i>	Photoperiod	Kidokoro (1978) Numata and Hidaka (1982) Kikuchi and Kobayashi (1984) Ito (1985) Kobayashi and Numata (1993, 1995)
<i>Halyomorpha halys</i>	Photoperiod	Watanabe (1980) Niva and Takeda (2003)
<i>Eysarcoris aeneus</i>	Photoperiod	Yanagi (1980)
<i>Eysarcoris ventralis</i>	Photoperiod	Noda and Ishii (1981)
<i>Eysarcoris lewisi</i>	Photoperiod	Hori and Kimura (1993)
<i>Plautia crossota stali</i>	Photoperiod	Yanagi and Hagihara (1980) Kotaki and Yagi (1987) Numata and Kobayashi (1994)
<i>Piezodorus hybneri</i>	Photoperiod	Kikuchi and Kobayashi (1984) Higuchi (1994) Ito (1988, 1989)
<i>Cletus punctiger</i>	Photoperiod	Nakamura and Numata (1997a)
<i>Aelia feberi</i>	Photoperiod	Musolin and Numata (2003a)
<i>Nezara viridula</i>	Photoperiod	Nakamura and Numata (unpublished)
<i>Dolycoris baccarum</i>	Photoperiod	Nakamura and Numata (1998)
<i>Dybowskyia reticulata</i>	Photoperiod, Temperature	Nakamura and Numata (1999)
<i>Graphosoma rubrolineatum</i>	Photoperiod, Temperature	Numata and Yamamoto (1990)
<i>Eurydema rugosum</i>	Photoperiod, Food	Ikeda-Kikue and Numata (2001)

INDUCTION OF ADULT DIAPAUSE

Photoperiod

Table 1 summarizes the environmental factors that determine induction of the winter adult diapause in seed-sucking bugs in Japan. Most seed-sucking bugs with an adult winter diapause use the photoperiod for the induction of diapause; this was first shown by Hodek (1968) in *Pyrrhocoris apterus* (L.) (Pyrrhocoridae) in central Bohemia. Like *P. apterus*, *Riptortus clavatus* (Thunberg) (Alydidae) shows a long-day photoperiodic response for the induction of adult diapause. Short-day conditions in the nymphal stage induce diapause, although sensitivity to the photoperiod continues after adult emergence (Numata and Hidaka, 1982). In the range between 20 and 30°C, the effect of temperature was slight around the critical daylength of about 13.5 h in *R. clavatus* in Kyoto (35.0°N) (Kobayashi and Numata, 1993, 1995). In this species, therefore, diapause is probably induced in the same season, whether it is warm or cool in autumn. Geographical clines in the critical daylength for the induction of winter diapause have been shown in many insects, i.e., populations at

higher latitudes have longer critical daylengths than those at lower latitudes (Danilevskii, 1961; Tauber et al., 1986; Danks, 1987). Such clines have been shown in some seed-sucking bugs in Japan also. In *R. clavatus*, the critical daylength at 25°C is between 13 and 14 h in populations of Kagoshima, Kumamoto, Kyoto, and Tsukuba (31.0–36.0°N), whereas it is between 14 and 15 h in Morioka (39.7°N) (Numata and Hidaka, 1982; Ito, 1985). In *Cletus punctiger* (Dallas) (Coreidae), the critical daylength at 25°C is about 12 h in Ishigaki (24.3°N), between 13 and 14 h in Fukuyama (34.5°N) and Tsukuba (36.0°N), and between 14 and 15 h in Shiroishi (38.0°N) (Ito, 1989). *Dolycoris baccarum* (L.) (Pentatomidae) in Osaka (34.7°N) has a critical daylength of between 13 and 14 h, whereas the critical daylength of the population in Tokoro, Hokkaido (44.1°N) is between 15 and 16 h at 25°C (Nakamura and Numata, unpublished). In *Graphosoma rubrolineatum* (Westwood) (Pentatomidae), although only some individuals show a long-day photoperiodic response, the critical daylength at 25°C is between 14 and 15 h in the population in Osaka and between 15 and 16 h in the population in Tokoro (Nakamura and Numata,

1999).

Many other species also show long-day photoperiodic responses, and the critical daylength at 25°C is also between 13 and 14 h in most species with a long-day photoperiodic response examined in central Japan between 34.0 and 37.0°N, e.g., *Halyomorpha halys* (Stål) (Pentatomidae) in Toyama (Watanabe, 1980), *Eysarcoris ventralis* (Westwood) (Pentatomidae) in Izumo (Noda and Ishii, 1981), and *Plautia crossota stali* Scott (Pentatomidae) in Tawaramoto, Nara Prefecture (Numata and Kobayashi, 1994). At higher altitudes, however, the critical daylength is slightly longer in *Eysarcoris aeneus* Scopoli and *P. c. stali* in Nagano Prefecture (Yanagi, 1980; Yanagi and Hagihara, 1980). In *Eysarcoris lewisi* (Distant) in Obihiro (42.9°N), the critical daylength at 25°C is between 15 and 15.5 h (Hori and Kimura, 1993), and in *Piezodorus hybneri* (Gmelin) (Pentatomidae) in Nishigoshi, Kumamoto Prefecture (32.9°N) it is slightly shorter than 13 h (Higuchi, 1994).

Aelia fieberi Scott (Pentatomidae) also shows a long-day photoperiodic response in Osaka, but the critical daylength is between 14.5 and 15 h at 25°C (Nakamura and Numata, 1997a). This longer critical daylength induces entry into diapause about one month earlier than in other species in the same region with critical daylengths of about 13.5 h. Nakamura and Numata (1997a) showed that in the field, adults of *A. fieberi* entered diapause in August. When eggs were placed outdoors in August and hatching nymphs were reared on wheat seeds, adults emerged in September and early October, and most of them overwintered. Therefore, the temperature after August is not the limiting factor preventing reproduction by *A. fieberi* in August. This species feeds on the seeds of grasses in Poaceae. Some seeding grasses were observed in the field from March to November, and these grasses were divided into two groups. In one group, seeds are produced in the spring and early summer, whereas the plants in the other group produce seeds in summer and autumn. When nymphs were reared in the laboratory on seeds of several grasses available in the field from spring to summer, they successfully emerged as adults. However, all of the nymphs died on seeds produced from summer to autumn. All suitable host species of grasses produce their seeds exclusively in the spring and early summer, and thus no suitable food

is available for *A. fieberi* in autumn. Poor food availability in autumn appears to be the ultimate factor determining diapause induction in August. In response to this selection pressure, *A. fieberi* has evolved a longer critical daylength for the induction of diapause (Nakamura and Numata, 1997a).

Nezara viridula (L.) (Pentatomidae) in Osaka also shows a long-day photoperiodic response for the induction of adult diapause, and the critical daylength falls into a narrow range of close to 12.5 h both at 20°C and at 25°C, suggesting that the photoperiod is the dominant factor in the induction of diapause under natural conditions (Musolin and Numata, 2003a). However, the critical daylength is shorter than that of many other species in central Japan (see above). Moreover, under near-critical photoperiods, a marked variation is shown in the incidence of diapause. In females under LD 12:12 at 25°C, for example, the incidence of diapause varied between 19 and 100% in three replicates (Musolin and Numata, 2003a). The distribution range of *N. viridula* expanded in Japan, and only recently reached Osaka (Kiritani et al., 1963; Musolin and Numata, 2003a). The shorter critical daylength along with a marked variation of the photoperiodic response within the near-critical range probably reflects a southern origin of the species. Because of the shorter critical daylength and great variation in the photoperiodic response, *N. viridula* produces a considerable amount of non-diapause adults in late autumn in Osaka. However, from the eggs laid by these adults do not develop into diapause adults before winter. Because this species can overwinter only as diapause adults, nymphs hatching from these late-season eggs die without producing offspring (Musolin and Numata, 2003b). Musolin and Numata (2003b) suggested that *N. viridula* is still incompletely adapted to the environmental conditions in Osaka, and they regard this inefficient late-season reproduction as the ecological cost of range expansion. To ensure a better adaptation to the new environmental conditions and complete establishment in the region, the local population of *N. viridula* will probably evolve a lengthening of the critical photoperiod, and, consequently, advance the timing of diapause induction.

Temperature

The function of temperature as a primary diapause-inducing stimulus has been shown for rela-

tively few temperate-zone species, however, modification of the photoperiodic responses by temperature has been shown in many species (Danilevskii, 1961; Tauber et al., 1986; Danks, 1987). Although a high temperature tends to prevent diapause in many long-day insects (Tauber et al., 1986), no distinct effect of temperature on the critical daylength has been shown in seed-sucking bugs in Japan. Temperature has little or no effect on the critical daylength for the induction of diapause in *R. clavatus* and *N. viridula*, as already mentioned (Kobayashi and Numata, 1993, 1995; Musolin and Numata, 2003a). In *E. aeneus*, however, when the laboratory temperature in the photophase was accidentally increased to 29°C, the critical daylength was shortened by 15–45 min from the value at constant 25°C (Yanagi, 1980).

In *Dybowskyia reticulata* (Dallas) (Pentatomidae) in Osaka, more than 80% of the adult females entered diapause at 25°C irrespective of the photoperiod. At 27.5°C, however, most adults raised under long-day conditions did not enter diapause, whereas those raised under short-day conditions did (Fig. 1). Therefore, *D. reticulata* shows a long-day photoperiodic response only at higher temperatures, and the threshold is between 25 and 27.5°C. Under outdoor conditions in a cool year, most adults of the first generation entered diapause in late July, although in a warmer year, oviposition was recorded in many females that emerged as adults from July to early August (Nakamura and Numata, 1998). In the Osaka population of *D. reticulata*, therefore, this dependence on temperature produces two alternative pathways in the life cycle, i.e., univoltine and bivoltine. *D. reticulata* feeds on the seeds of Apiaceae. In Osaka, these plants produce seeds only around early summer, and the seeds have dried up and fallen off the plants by autumn. Nakamura and Numata (1998) suggested, therefore, that *D. reticulata* produces a second generation only in warmer years, when production of two generations is possible in such a restricted period caused by dietary conditions.

G. rubrolineatum in Tokoro shows a similar temperature dependence for the induction of diapause to that of *D. reticulata* in Osaka: the higher the temperature, the greater the incidence of reproductive insects under long-day conditions (Nakamura and Numata, 1999). In *G. rubrolineatum* in Osaka, however, more than 50% of the adults entered dia-

Fig. 1. Effects of photoperiod and temperature on diapause induction in female adults of *Dybowskyia reticulata* in Osaka. Carrot seeds were supplied as food. Solid sectors represent the proportion of adults that did not lay eggs for 30 days. Adapted from Nakamura and Numata (1998).

pause even under long-day conditions at all temperatures between 20 and 30°C (Nakamura and Numata, 1999). As in *D. reticulata*, host plants of *G. rubrolineatum* are Apiaceae, the seeds of which occur only in a limited period in Osaka. Because of the absence of suitable food in later seasons, the Osaka population of *G. rubrolineatum* produces only a small proportion of nondiapause adults, even under long-day conditions at higher temperatures (Nakamura and Numata, 1999).

In *P. apterus* in central Bohemia, the exposure of adults to low temperatures (7.5–8°C) for only two days induced diapause in a portion of adults even under long-day conditions (Hodek, 1971a). Such an effect has not been examined in seed-sucking bugs in Japan.

Food

Nymphs of *Eurydema rugosum* Motschulsky (Pentatomidae) develop not only on seeds, but also on the leaves of crucifers, unlike the species discussed above. When reared on leaves, this species shows a long-day photoperiodic response. When seeds were given as food, however, most adults entered diapause even under long-day conditions, and all adults did so under short-day conditions (Fig. 2; Numata and Yamamoto, 1990). In this species, therefore, not only the photoperiod, but also the dietary conditions, play a critical role in the induction of diapause.

In fields in Tawaramoto, first generation adults of *E. rugosum* emerged from mid-June, and most entered diapause on brown mustard plants that bloomed in early spring, with all of the plants dying by early summer. On cultivated crucifers

such as radishes and cabbages, which have green leaves all year around, however, most adults of the first generation reproduced, and those of the second generation emerging in late summer entered diapause (Ikeda-Kikue and Numata, 2001). Therefore, diapause in *E. rugosum* is induced at different times of the year on different host plants, and thus the phenology of the host plants affects the life cycle of *E. rugosum*.

The status of the host plant affects the induction of diapause in many insects. In general, deficient or less nutritious diets enhance the tendency to enter diapause (Tauber et al., 1986; Danks, 1987). In *E. rugosum*, however, dietary conditions favoring diapause were not nutritionally inferior, because the survivorship and weight gain in the nymphal period were higher on seeds than on leaves (Numata and Yamamoto, 1990). Thus, in *E. rugosum*, the developmental state of the host plants functions as a signal to determine the induction of diapause. I regard this response to dietary conditions in *E. rugosum* as an adaptation to using host plants with different seasonal life cycles.

Fig. 2. Effects of photoperiod and food on diapause induction in female adults of *Eurydema rugosum* in Osaka at 25°C. Seeds or leaves of oilseed rape were supplied as food. Solid sectors represent the proportion of adults that had no vitellogenic oocytes or mature eggs 20 days after emergence. Adapted from Numata and Yamamoto (1990).

ONSET OF POSTDIAPAUSE REPRODUCTION

Photoperiod

It has been shown that diapause adults begin oviposition responding to long-day conditions in the laboratory in many species, e.g., *E. ventralis* (Noda and Ishii, 1981), *R. clavatus* (Numata and Hidaka, 1982), *P. c. stali* (Kotaki and Yagi, 1987), and *A. fieberi* (Nakamura and Numata, 1995). Under natural conditions, however, the species in which post-overwintering adults begin reproduction in response to the long-day conditions in spring are scarce (Tauber et al., 1986). In seed-sucking bugs, Hodek (1971b) first showed that adults of *P. apterus* in central Bohemia lose their sensitivity to photoperiod in winter. When diapause adults of *R. clavatus* were kept at a low temperature for a long period in the laboratory, or were overwintered in an outdoor cage, they began oviposition with no difference between the long-day and short-day conditions (Numata, 1987; Ito, 1988). Table 2 summarizes the environmental factors that determine the onset of reproduction after winter adult diapause in seed-sucking bugs in Japan. Ito (1988) transferred adults of *C. punctiger* after overwintering from an outdoor cage to the laboratory at 25°C in March and April. All adults began to lay eggs soon under long-day conditions, whereas under short-day conditions, the onset of oviposition was delayed, and less than 50% of females laid eggs. Of seed-sucking bugs in Japan, *C. punctiger* is the only species for which it has been shown that overwintering adults retain sensitivity to the photoperiod, and the long-day condition in spring is responsible for the onset of reproduction in the field.

Temperature

Although both the photoperiod and dietary con-

Table 2. Environmental factors that determine the onset of reproduction after winter adult diapause in seed-sucking bugs in Japan

Species	Factors	References
<i>Cletus punctiger</i>	Photoperiod	Ito (1988)
<i>Eurydema rugosum</i>	Temperature	Ikeda-Kikue and Numata (1992)
<i>Aelia fieberi</i>	Temperature	Nakamura and Numata (1995)
<i>Riptortus clavatus</i>	Food	Numata and Hidaka (1984)
<i>Dybowskyia reticulata</i>	Food	Nakamura and Numata (1997b)

ditions play a critical role in the induction of diapause in *E. rugosum* (see Fig. 2), adults collected in early April began to lay eggs similarly under four combinations of long-day and short-day conditions and two dietary conditions, i.e., seeds and leaves (Fig. 3; Ikeda-Kikue and Numata, 1992). After overwintering, in early April, the adults do not start reproducing, even though the host plants have already produced leaves. Moreover, the pre-oviposition period after transfer to the laboratory in mid-April depended on temperature; the median value was 3 days at 25°C, 5.5 days at 20°C, and 20 days at 15°C (Ikeda-Kikue and Numata, 1992). Therefore, photoperiod and diet do not play a role in the onset of reproduction in spring. Ikeda-Kikue and Numata (1992) suggested that in early April, *E. rugosum* has already terminated diapause and is in a state of postdiapause quiescence imposed by low temperature, and that reproduction in spring begins after the temperature rises above the lower thermal threshold for postdiapause development.

Nakamura and Numata (1995) collected adults of *A. fieberi* from late March to early April, and transferred them to a long-day or short-day conditions at 25°C on wheat seeds. The adults began to lay eggs much earlier than under natural conditions, with no difference between the two photoperiods. In late March and early April, seeds of suitable host plants of this species have already been produced in the field (Nakamura and Numata, 1997a). Therefore, an increase in temperature is also the only factor inducing reproduction in spring in *A. fieberi*.

Yanagi (1980) showed the importance of genetic factors in the onset of postdiapause reproduction in *E. aeneus*. He collected adults of this species from two localities in Nagano Prefecture, and kept them and their hybrids in a laboratory without a heating apparatus. The onset of oviposition after overwintering differed between the insects from Miyata and Hotaka by more than one month, even though the distance between these two localities is only about 65 km. Moreover, the hybrids between them began to lay eggs in an intermediate period with larger variation (Yanagi, 1980). Although it has not been shown that temperature is the only factor inducing reproduction in spring in *E. aeneus*, the effective cumulative temperature for postdiapause development may differ genetically between the two populations.

Fig. 3. Survival and oviposition in female adults of *Eurydema rugosum* collected from the field on 3–5 April and transferred to the laboratory at 20°C. Open and shaded areas represent the proportion of non-ovipositing and ovipositing females, respectively. Seeds or leaves of oilseed rape were supplied as food. Adapted from Ikeda-Kikue and Numata (1992).

Food

When adults of *R. clavatus* were transferred after overwintering from an outdoor cage to a laboratory at 25°C with soybean grains in February or April, they soon began to lay eggs under both long-day and short-day conditions (Ito, 1988). However, the adults of this species start to lay eggs in legume fields from late May in Kyoto, and this timing seems to be too late if oviposition is induced only when the temperature rises above the lower thermal threshold. Numata and Hidaka (1984) explained this delay by the absence of legume seeds in the field, because starvation suppresses postdiapause ovarian development. Such an effect by starvation was reported earlier in *P. apterus* (Hodková, 1982). Both in *R. clavatus* and *P. apterus*, the suppression of ovarian development does not result from the deficiency of nutritional reserves, but is actively controlled by an endocrine mechanism, because the application of a juvenile hormone analogue or denervation of the corpus allatum induced ovarian development in starved insects (Hodková, 1982; Numata and Hidaka, 1984). In these studies, however, diapause was terminated under long-day conditions in the laboratory, and the effect of dietary factors has not been examined in insects that had naturally overwintered.

Fig. 4. Survival and oviposition in female adults of *Dytiscus reticulatus* transferred from outdoor conditions to the laboratory at 25°C on 21 March. Open and shaded areas represent the proportion of non-ovipositing and ovipositing females, respectively. Arrows indicate the onset of supplying carrot seeds. Adapted from Nakamura and Numata (1997b).

Nakamura and Numata (1997b) transferred overwintering adults of *D. reticulatus* from an outdoor cage to long-day or short-day conditions at 25°C in March, and gave them carrot seeds as food. Under both photoperiods, about 40% of the females began to lay eggs within 30 days, with no difference between the two photoperiods (Fig. 4, left panels), although these conditions induced diapause in all females (see Fig. 1). However, the host plants of *D. reticulatus* produce seeds only in early summer in Osaka, and there is no food available in spring. Nakamura and Numata (1997b) kept some adults with only water for 45 days after transfer from an outdoor cage to laboratory conditions, and then supplied them with food. All females began to lay eggs about 10 days after the food was supplied under both the long-day and short-day conditions (Fig. 4, right panels). Thus, the long-day condition in spring plays no role, but the food supply plays an important role, in the onset of oviposition in the field in *D. reticulatus*. Starvation delayed reproduction, and synchronized the onset of oviposition in the population.

CONCLUSIONS

Seed-sucking bugs with winter adult diapause

most often use the photoperiod as the proximate factor that determines the induction of diapause and therefore the termination of reproduction in autumn under natural conditions, similar to other insects. The species that only use the photoperiodic cue enter diapause at the same time every year, and have inflexible life cycles, even though the critical daylength and the seasonal timing of diapause induction vary with species. In some species, however, temperature or the quality of food is also used as a seasonal cue. Due to the responses to such signals, these species show alternative pathways in their life cycles. This flexibility has probably evolved to synchronize the life cycle of the insect to that of its host plant. The effects of density and moisture have not been reported for either the onset or termination of reproduction in seed-sucking bugs.

Temperature above the lower thermal threshold for postdiapause morphogenesis is essential for initiating reproduction in spring in seed-sucking bugs, as in many other insects. The appearance of host plant seeds primarily determines the onset of reproduction in at least one species, *D. reticulatus* (Nakamura and Numata, 1997b), and probably in some other seed-sucking bugs. Moreover, the photoperiod plays a definitive role in *C. punctiger* (Ito, 1988). However, the proximate factors that determine the onset of reproduction in spring have not been examined as intensively as those for the termination of reproduction in autumn. Early studies of diapause showed clear effects of long-day conditions and low temperatures on the termination of diapause (e.g., Baker, 1935; Andrewartha, 1943; Muroga, 1951; McLeod and Beck, 1963). Therefore, long-day conditions and a temperature increase after exposure to low temperatures have been considered to play dominant roles in the initiation of postdiapause activities. However, as Tauber and Tauber (1976) pointed out as early as 28 years ago, these conditions do not play active roles in the initiation of postdiapause activities under natural conditions in most species. Extensive studies on the proximate factors that determine the onset of reproduction under natural conditions are needed to illustrate the common features among seed-sucking bugs.

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