

Reproductive Inactivity and Prolonged Developmental Time Induced by Seasonal Decline in Host Plant Quality in the Willow Leaf Beetle *Plagioderia versicolora* (Coleoptera: Chrysomelidae)

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ABSTRACT *Plagioderia versicolora* Laicharting (Coleoptera: Chrysomelidae) stops reproduction in mid-August at Ishikari, Hokkaido, Japan, despite the fact that the degree-days required for complete development predict an additional generation late in the season. We examined whether the life cycle of *P. versicolora* was constrained by the seasonal decline in quality of its host plant, *Salix sachalinensis* Fr. Schmidt (Salicaceae). *P. versicolora* was maintained for three successive generations throughout a season under constant laboratory conditions and fed host leaves obtained from the field site. Larval and adult performance declined in the generations that were produced later in the season. Developmental time in the last generation was significantly longer than in the first generation, although larval survivorship did not differ significantly between generations. Preoviposition periods were significantly longer and the number of eggs laid from the first oviposition to the 10th day of oviposition was significantly fewer in the last two generations compared with the first generation. In addition, reproductively inactive females that laid no eggs were significantly more frequent in the last two generations. This reproductive inactivity in female adults in late generations may be caused by diapause, which can prevent *P. versicolora* from producing an additional generation on poor-quality host plants. However, the physiological condition of the reproductively inactive females was different from that induced by short photoperiod in diapausing females because feeding was observed in the former females but not in the latter ones.

KEY WORDS seasonal decline in host quality, reproduction, diapause, Chrysomelidae, *Plagioderia versicolora*

HOST PLANT QUALITY IS a key determinant of the fitness of herbivorous insects. Components of host plant quality, such as levels of carbon, nitrogen, and defensive metabolites, positively or negatively affect the performance of herbivorous insects, including survivorship, development time, and fecundity (Scriber and Slansky 1981, Bernays and Chapman 1994, Schoonhoven et al. 1998, Awmack and Leather 2002). Natural selection will favor strategies of herbivorous insects to use host plants on which they perform best. For example, host preference for high-quality host plants has been detected in many insect species (Thompson 1988, Craig et al. 1989, Ohgushi 1992, 1998, Nylin and Janz 1993, Bernays and Chapman 1994, Schoonhoven et al. 1998, Yamaga and Ohgushi 1999, Craig and Ohgushi 2002).

In the temperate zone, in general, the suitability of a host plant for herbivorous insects declines late in the season (Feeny 1970, Hough and Pimentel 1978, Bernays and Chapman 1994, Schoonhoven et al. 1998,

Awmack and Leather 2002). For example, in the classic study of Feeny (1970), water and protein content of oak leaves decreased and tannins accumulated over the course of the summer. In the winter moth, *Operophtera brumata*, the mean fresh weight of fourth-instar larvae reared on oak leaves late in the season was lower than that of larvae reared on leaves early in the season. In this situation, natural selection would favor a strategy that prevents herbivorous insects from using poor-quality hosts in the late season. In fact, most insect herbivores on oak leaves concentrated their feeding in the early spring and might retain univoltine life cycles because of the decline in leaf quality in summer (Feeny 1970). In this case, it would be advantageous for these insects to enter diapause or quiescence without producing an additional generation (Tauber et al. 1986, Danks 1987). If the insects produce an additional generation, most or all offspring would not survive to reach a critical (diapause) stage before winter.

Seasonal declines in host quality may also interact with photoperiodic and temperature responses to influence diapause rather than act in isolation (Tauber et al. 1986). In the tortricid moth *Choristoneura rosa-*

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ceana, photoperiodic induction of diapause was enhanced when the larvae fed on unsuitable host species or on low-quality artificial diet instead of a suitable host or on high-quality diet (Hunter and McNeil 1997). Enhanced induction of diapause has also been reported in the Colorado potato beetle, *Leptinotarsa decemlineata*, when fed on physiologically aged rather than young or mature potato leaves (de Wilde et al. 1969). Such enhanced induction of diapause on poor quality hosts in late season avoids the risks of producing an additional generation.

To our knowledge, however, only a few studies have evaluated the effect of seasonal decline in host plant quality on the performance and life cycles of herbivorous insects (de Wilde et al. 1969, Tauber et al. 1986, Ohgushi 1996). In this study, we evaluated the effect of seasonal decline in quality of willow leaves on the performance and life cycle of a willow leaf beetle, *Plagioderma versicolora* Laicharting (Coleoptera: Chrysomelidae) in successive generations under a constant laboratory condition.

P. versicolora is a common herbivorous insect on willows and uses *Salix sachalinensis* Fr. Schmidt (Salicaceae) as a host in Hokkaido, Japan (Ishihara et al. 1999). *P. versicolora* adults stop reproducing in mid-August at Ishikari, Hokkaido (Ishihara et al. 1999). Ishihara and Hayashi (2000) interpreted this to mean that these adults are entering reproductive diapause for overwintering (Ishihara and Hayashi 2000). However, the threshold temperature and degree-days required for a complete development of *P. versicolora* predicted that these adult females could still produce an additional generation in mid-August (M.I., unpublished data). Furthermore, leaves of *S. sachalinensis* are available until late September. Why does *P. versicolora* finish reproduction in mid-August despite the fact that an additional generation can be produced? Is the reproductive season of *P. versicolora* constrained by a seasonal decline in host quality? To answer this question, we tested the following predictions: (1) the performance of *P. versicolora* declines late in the season and (2) the proportion of adults entering diapause or quiescence increases so as to avoid using poor quality hosts in the late season. In addition, if enhanced induction of diapause was observed late in the season, the diapause may have different physiological characteristics from diapause directly induced by short photoperiod. We examined whether there was a difference in physiology between diapause induced by short photoperiod and by seasonal decline in host quality.

Materials and Methods

Study Insect. The willow leaf beetle *P. versicolora* is distributed over wide areas of Asia, Europe, and north Africa (Kimoto and Takizawa 1994). Both adults and larvae feed exclusively on willow leaves.

Field collections were conducted along the Ishikari River (43° N, 141° E; Ishikari, Hokkaido, Japan). At this study site, six willow species (*Salix miyabeana* Seemen, *S. sachalinensis* Fr. Schm, *S. integra* Thunb,

S. subfragilis Anders, *S. hultenii* Floderus, and *S. pet-susu* Kimura) are present (Ishihara et al. 1999). *P. versicolora* is a common herbivore on the willows, but the abundance of adults and egg clutches varies among willow species (Ishihara et al. 1999). Most adults and egg clutches are found on *S. sachalinensis*, which is the second most abundant willow species (Ishihara et al. 1999). However, *P. versicolora* larvae can feed on all willow species at Ishikari except for *S. subfragilis* (M.I., unpublished data).

At Ishikari, *P. versicolora* shows a bivoltine life cycle (Ishihara et al. 1999). *S. sachalinensis* flowers from mid-April to early May. Budbreak occurs in May after flowering, and leaf expansion and shoot elongation continue until mid-July. Overwintered adults start laying egg clutches on willow leaves in early June. The clutch size varies from 1 to 37 eggs (average: 15). The hatched larvae feed in groups of related individuals but in most cases mature (third instar) larvae feed solitarily. Pupation occurs on leaves after the third instar. First-generation adults emerge starting in mid-July and produce the second generation. The second-generation larvae grow on mature leaves from mid-July to August, and the adults emerge in August when host leaves start turning color from green to yellow. The threshold temperature and degree-days required for the complete development of *P. versicolora* are 12°C and 149 DD, respectively, which predict that the adults could produce a third generation in mid-August (Ishihara, M. I., unpublished data). However, these adults do not reproduce and disappear from host trees to overwinter by early September, when most leaves start senescing.

In addition to the second-generation adults, some first-generation adults, especially those that emerge late, may overwinter without reproducing (Ishihara 2000). *P. versicolora* adults enter diapause to overwinter (Hood 1940, Ishihara 2000, Ishihara and Hayashi 2000). Laboratory experiments were conducted in incubators at the Institute of Low Temperature Science, Hokkaido University (Sapporo, Hokkaido, Japan), located 15 km southwest of the Ishikari field site.

Comparison Between Generations Under Constant Laboratory Conditions. We examined the effects of seasonal decline in host plant quality on the performance of *P. versicolora* by comparing traits among generations under constant laboratory conditions. Forty pairs of *P. versicolora* adults of the overwintering generation were collected on 2–6 June 1997 at Ishikari. Adult sex was determined by morphological differences. Each mating pair was introduced into a petri dish containing moist filter papers and *S. sachalinensis* leaves. Petri dishes were maintained at 20°C, 16:8 (L:D) h. All leaf material was obtained fresh from ≈5 young clones at Ishikari and was replaced by new material from different clones every 2 d. The same clones were rarely used twice as a source of leaf material. We checked leaves daily for eggs. When leaves were found to have egg clutches, we recorded the clutch sizes and each clutch was immediately transferred to another empty petri dish. These eggs were defined as first generation and maintained until

adult emergence, using the same procedure by which their parents had been maintained.

When the first-generation adults emerged, they were immediately paired, but sib-pairing was avoided. Each mating pair was maintained in a petri dish containing leaves at 20°C, 16:8 (L:D) h. The preoviposition period was determined when the females laid the first egg clutch. We continued to count egg clutch sizes until the 10th day after the first oviposition. Because *P. versicolora* adults can survive for 3 mo, use of the number of eggs laid during a short period rather than lifetime fecundity should be a better measure of the effects of seasonal decline in host quality on reproduction. The females that laid no eggs within 30 d of emergence were defined as reproductively inactive. The egg clutches laid were coded according to pedigree and used to produce the next generation. We did not manipulate clutch size because it did not affect larval performance (Spearman rank correlation of clutch size and larval survivorship: second generation, $n = 23$, $r_s = 0.035$, $P = 0.8683$; third generation, $n = 34$, $r_s = -0.0002$, $P = 0.9993$; clutch size and developmental time: second generation, $n = 23$, $r_s = 0.134$, $P = 0.5290$; third generation, $n = 34$, $r_s = -0.135$, $P = 0.4387$).

In this way, *P. versicolora* was maintained for three generations throughout the season from June to September 1997 under constant laboratory conditions at 20°C, 16:8 (L:D) h. In this case, the quality of the host leaves as food could not be regarded as uniform. Because the host leaves were obtained from the field site, the change in the quality of host leaves would reflect the seasonal decline in quality in the field. In the second and third generations, the developmental time was determined as the period from oviposition to adult emergence. The survivorship per clutch from oviposition to adult emergence was also recorded. In the first generation, we did not record the larval survivorship and developmental time. The adults in the first, second, and third generations were maintained 2–22 July, 19 July to 30 August, and 24 August to 20 September, respectively. The larvae in the second and third generations were maintained 30 June to 4 August and 5 August to 21 September, respectively.

Comparison Between Long and Short Photoperiods. If enhanced induction of diapause was observed in the late season, the diapause may have different physiological characteristics from that directly induced by short photoperiod. We examined whether there was a difference in physiological characteristics between diapause induced by short photoperiod and that induced by seasonal decline in host quality in the second generation.

Egg clutches laid by the first-generation females were divided into two groups. Each group was maintained at 20°C and a photoperiodic condition of either 16:8 (L:D) h (long photoperiod) or 10:14 (L:D) h (short photoperiod). We recorded egg laid by females until the 30th day after emergence. Thirty days after emergence (28–30 September), we also recorded whether adults fed on leaves. In general, diapausing insects show low metabolic activity and reduced be-

havioral activity (Tauber et al. 1986, Danks 1987). When adults did not feed, we considered them to be diapausing. This experiment can distinguish the effect of host plant quality from that of photoperiod on the reproduction of *P. versicolora*.

Statistics. The proportion of reproductively inactive females was compared among generations by a Tukey-type multiple comparison test for proportions followed by a χ^2 test (Zar 1996) and between photoperiods by a Fisher exact test. In the comparison between photoperiods, the proportion of nonfeeding reproductively inactive pairs was also compared by a Fisher exact test. In the reproductively active females that laid at least one egg clutch, the preoviposition period and total number of eggs laid during 10 d after the first oviposition were analyzed by one-factor analysis of variance (ANOVA) after \log_{10} -transformation to normalize the variance, where generation was a main effect. The larval developmental time was analyzed by a two-factor nested ANOVA after \log_{10} -transformation, where generation and sex were completely crossed as main fixed effects and family groups were nested in generations. These means were compared between generations by Tukey-Kramer tests. The larval survivorships were compared between generations by a Mann-Whitney's *U* test because the distribution of the data were biased from normality.

Results

Adult Performance. Significant effects of generation were found on the proportion of reproductively inactive females ($\chi^2 = 28.251$; $df = 2$; $P < 0.0001$), preoviposition period ($F = 18.656$; $df = 2,66$; $P < 0.0001$), and the total number of eggs laid by reproductively active females ($F = 7.519$; $df = 2,66$; $P < 0.0011$). The proportion of reproductively inactive females increased significantly from the first generation to the second generation, but there was not a significant difference between the second and the third generations (Fig. 1). Although the adults laid eggs, the preoviposition periods in the second and third generations were significantly longer than in the first generation (Fig. 2). The total number of eggs laid by the reproductively active second- and third-generation females until the 10th day after the first oviposition were significantly less than the number laid by reproductively active first-generation females (Fig. 3). There were no significant differences in the preoviposition period and total number of eggs between the second and third generations (Figs. 2 and 3). The egg clutch size did not significantly differ among generations ($F = 0.647$; $df = 2,164$; $P = 0.5250$).

Larval Performance. Larval survivorship did not differ significantly between the second and third generations (Mann-Whitney's *U* = 207.500, $P = 0.2996$). The developmental time in the third generation was significantly longer than in the second generation (Fig. 4). There were no significant differences between sexes within the same generation (Fig. 4). Two-factor nested ANOVA on the \log_{10} -transformed data indicated significant generation and family ef-

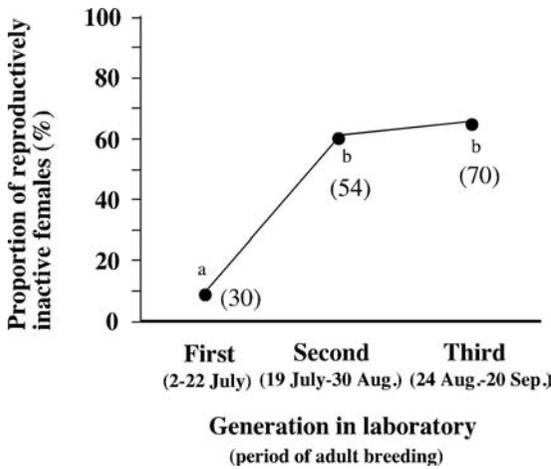


Fig. 1. Proportion of reproductively inactive females that laid no eggs over three generations under constant laboratory conditions at 20°C, 16:8 (L:D) h. Only the quality of host leaves as food could not be regarded as a constant condition because they were collected fresh from the field site. Comparisons with different letters indicate significant differences (Tukey-type multiple comparison test for proportions, $P < 0.05$). Sample sizes are given in parentheses.

fects but no sex effect or generation \times sex interaction (Table 1).

Difference in Adult Characters Between Short and Long Photoperiods. None of the females ($n = 51$) laid eggs under 10:14 (L:D) h, but 38.9% of females ($n = 54$) laid at least one egg clutch under 16:8 (L:D) h (the second generation in Fig. 1; Fisher exact test, $P <$

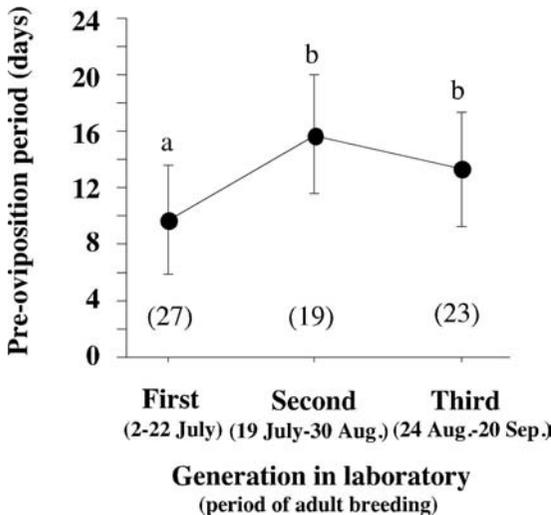


Fig. 2. Preoviposition period over three generations under constant laboratory conditions at 20°C, 16:8 (L:D) h. Only the quality of host leaves as food could not be regarded as a constant condition because they were collected fresh from the field site. Data represent mean \pm SD. Comparisons with different letters indicate significant differences (Tukey-Kramer tests, $P < 0.05$). Sample sizes are given in parentheses.

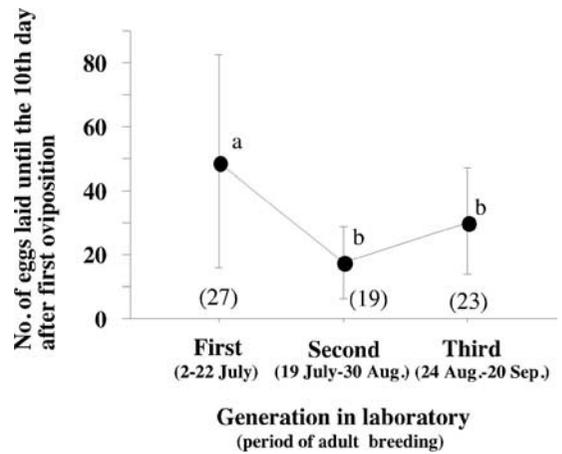


Fig. 3. Number of eggs laid by reproductively active females until the 10th day after the first oviposition over three generations under constant laboratory conditions at 20°C, 16:8 (L:D) h. Only the quality of host leaves as food could not be regarded as a constant condition because they were collected fresh from the field site. Data represent mean \pm SD. Comparisons with different letters indicate significant differences (Tukey-Kramer tests, $P < 0.05$). Sample sizes are given in parentheses.

0.0001). No pairs kept at 10:14 (L:D) h fed on leaves, whereas >90% fed on leaves under 16:8 (L:D) h (Fisher exact test, $P < 0.0001$). This result showed the physiological difference in reproductively inactive adults induced by the long and short photoperiods.

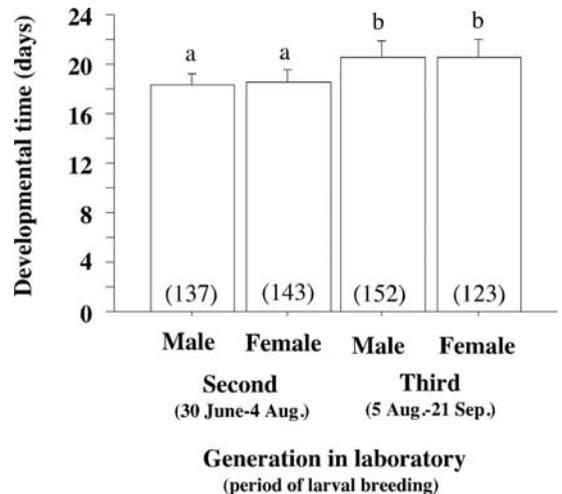


Fig. 4. Developmental time from oviposition to adult emergence between the second and third generations under constant laboratory conditions at 20°C, 16:8 (L:D) h. Only the quality of host leaves as food could not be regarded as a constant condition because they were collected fresh from the field site. Bars represent mean \pm SD. Comparisons with different letters indicate significant differences (Tukey-Kramer tests, $P < 0.05$). Sample sizes are given in parentheses.

Discussion

Seasonal Decline in Performance of *P. versicolora*.

Our laboratory experiments showed seasonal decline in the performance of *P. versicolora* through generations. Although there was no significant difference in larval survivorship between generations, longer developmental time and higher proportion of reproductively inactive females occurred in late generations. In many insects, developmental time is one of the most important life history traits for seasonal adaptations (Roff 1980, Tauber et al. 1986, Masaki and Walker 1987). In particular, a prolonged developmental time late in the season may prevent *P. versicolora* from completing its life cycle by the end of season. In addition, according to the slow growth/high mortality hypothesis (Feeny 1976, Clancy and Price 1987, Häggström and Larsson 1995), insects developing later in the season suffer higher mortality because of enemies owing to the longer period spent in vulnerable larval stages compared with conspecifics early in the season. Furthermore, the female reproductive inactivity induced in late generations would directly affect their fitness. Reduced fecundity in such females would undoubtedly decrease their fitness. Although female adults could lay eggs, the total number of eggs laid late in the season was significantly fewer than that laid early in the season. The prolonged preoviposition period late in the season may also decrease opportunities for oviposition before the end of the season.

What caused the decline in the performance of *P. versicolora* in the late generations? Two possibilities could be considered. One possibility is circannual rhythm. If the physiology of *P. versicolora* follows a circannual rhythm, adult and larval performances associated with this rhythm may show seasonal change even under constant environmental conditions. To test this possibility, a control treatment (nonsenescent leaves in the late generations) must be added to our experiment. Unfortunately, we could not do this experiment because of the difficulty in obtaining nonsenescent leaves in the late season, because willows are deciduous trees. However, we regard a physiological circannual rhythm as unlikely because, except for the pupation rhythm of the varied carpet beetle, *Anthrenus verbasci* (Nisimura and Numata 2001), no evidence for this has been reported in insects.

The other possibility is that a seasonal decline in host leaf quality caused the decline in performance, because all environmental conditions except for host leaves were constant in this experiment. Willow leaves used for this experiment were obtained from the field site. In the temperate zone, in general, the suitability of host plants for herbivorous insects declines in the late season because of a decrease in nutritional components, such as nitrogen, carbohydrates, and lipids, or an increase in defensive compounds, such as alkaloids, terpenes, tannins, and lignins (Feeny 1970, Hough and Pimentel 1978, Bernays and Chapman 1994, Schoonhoven et al. 1998, Awmack and Leather 2002).

Table 1. Results of two-factor nested ANOVA of developmental time (\log_{10} -transformed) of *P. versicolora*

Source	df	SS	F	P
Generation	1	0.222	556.581	0.0001
Sex	1	0.001	1.852	0.1741
Family (generation)	30	0.122	10.213	0.0001
Generation \times sex	1	0.0001	0.342	0.5591
Residual	521	0.208		

In the study site, leaf expansion of *S. sachalinensis* occurs in the beginning of May. Vigorous leaf expansion lasts 1 mo, and most leaves emerge by mid-July. The host leaves provided to the first-generation adults and second-generation larvae that were maintained during July were soft and not fully expanded. In contrast, host leaves used for the later generations that were maintained after July were mature, and the number of leaves that had fallen because of senescence increased after July. In addition to leaf senescence, leaf damage by herbivores accumulated greatly after July. Such leaves are more likely to be tough and qualitatively poor. In the 2004 study, which was independent of this study, we recorded the leaf toughness and water and nitrogen contents of *S. sachalinensis* from May to September in the study site. The leaf toughness increased and water and nitrogen contents decreased through the season (M. I., unpublished data). Such a seasonal decline in leaf quality has also been reported in another Japanese willow species, *S. miyabeana* (Kudo 2003). The seasonal decline in adult performance observed in this experiment was also synchronized with the seasonal variation in the oviposition pattern of *P. versicolora* females in the field. Oviposition in the field decreased in early August and was no longer observed in late August (Ishihara et al. 1999). Thus, the seasonal decline in leaf quality of *S. sachalinensis* is the most likely cause of the decline in the performance of *P. versicolora*.

Reproductive Diapause Induced by Seasonal Decline in Host Plant Quality. Reproductive inactivity in female adults in late generations in the laboratory may be caused by diapause that was induced by the seasonal decline in host quality rather than reproductive quiescence induced by nutrient deficiency in mature old leaves. This is because most of the female beetles not only showed egg resorption but also survived for 6 mo at 5°C (M. I., unpublished data). However, the physiological condition of the reproductively inactive females was different from that of diapausing females that was induced by short photoperiod because feeding was observed in the former females but not in the latter ones. Therefore, the female adults that do not reproduce might be undergoing summer diapause rather than reproductive diapause for overwintering. Similar evidence has been reported in the herbivorous lady beetle, *Epilachna niponica*. Thistle leaves damaged by conspecific feeding increased the proportion of reproductively inactive female adults showing egg resorption and thus prolonged longevity as a result of reproductive diapause (Ohgushi and Sawada 1985).

These females that had resorbed eggs resumed oviposition when fed fresh intact leaves (Ohgushi 1996).

Our prediction from the threshold temperature and degree-days required for the complete development of *P. versicolora* assumed that *P. versicolora* could produce an additional generation in mid-August (M. I., unpublished data). Leaves of *S. sachalinensis* are also available until late September. However, producing an additional generation in the late season should incur reduced fitness because of the low performance on low quality hosts in late season. Diapause induced by deteriorating host quality can prevent *P. versicolora* from producing offspring. In the field, *P. versicolora* finished oviposition by late August, after which time low larval and adult performances were shown to occur in this experiment. For insects, predicting seasonal change in host quality by using environmental cues such as temperature might be difficult. This is because there may be large year-to-year variation in seasonal changes in host quality. Furthermore, host quality might not necessarily synchronize with temperature because many factors, such as rainfall, soil quality, herbivory, and disturbance, affect host quality. In such situations, a strategy that uses two different environmental factors, host plant quality and day length, as diapause-inducing cues is likely to be adaptive. If seasonal decline in host quality begins early in the season and high temperature is maintained, using the change in host plant quality as a diapause-inducing cue is adaptive because *P. versicolora* can stop reproduction before host quality declines later in the season. In contrast, if the seasonal decline begins late in the season, using the change in day length rather than that in host quality as the cue is adaptive because daylength is a more reliable cue which will ensure that *P. versicolora* of entering diapause before winter.

The cues associated with diapause in insects have received considerable attention. However, most studies have concentrated on the roles of photoperiod and temperature as primary cues responsible for diapause induction or termination (Tauber et al. 1986, Danks 1987). Other environmental factors, such as humidity (Wardhaugh 1986, Lenga et al. 1993) or food quality (de Wilde et al. 1969, Nagasaka 1992, Lenga et al. 1993, Hunter and McNeil 1997), have received limited attention. Nonetheless, food has been shown to be a major factor regulating diapause for a few insect species (Tauber et al. 1986). In some cases, food quality interacts with photoperiod and temperature responses to influence diapause instead of acting in isolation (Tauber et al. 1986). Such evidence coupled with our results indicates that seasonal decline in host plant quality can play a dominant role in inducing diapause in herbivorous insects.

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