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EGG HATCHING OF *PERIPHYLLUS CALIFORNIENSIS* (HEMIPTERA: APHIDIDAE) IN TWO MICROHABITATS WITH DIFFERENT BUDBURST PHENOLOGIES

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ABSTRACT

Egg hatching of the maple aphid, *Periphyllus californiensis* Shinji, was observed on saplings of *Acer amoenum* Carriere in two microhabitats, i.e., the understory of a maple stand (a shaded site) and an open area in a nursery (a sunny site), over a 2-year period. Buds of *A. amoenum* opened earlier at the shaded site than at the sunny site and eggs of *P. californiensis* also hatched a little earlier at the shaded site. To test whether oviposition timing or microhabitat characteristics affected the timing of egg hatching, eggs were collected during four periods in December to observe egg hatching in the laboratory. Hatching occurred earlier at the shaded site than at the sunny site only for eggs laid in early December. The duration of egg hatching was shorter for eggs laid earlier compared with those laid later. The duration of the egg stage (estimated as the median oviposition date to the median egg hatching date) was negatively correlated with the time when the eggs were laid. These results suggest that differences in timing of egg hatching between habitats may be affected by the microhabitat and date of oviposition.

Key Words: oviposition, egg duration, host plant phenology, synchrony

RESUMEN

La eclosión de huevos del áfido arce, *Periphyllus californiensis* Shinji, fue observada en renuevos de *Acer amoenum* Carriere en dos micro hábitares, o sea, la parte abajo de los árboles de arce (un sitio con sombra) y una área abierta de un vivero (un sitio con sol), durante un período de 2 años. Los brotes de *A. amoenum* abrieron mas temprano en el sitio con sombra que en el sitio bajo el sol y los huevos de *P. californiensis* también escllosionaron un poco mas temprano en el sitio de sombra. Para probar si el tiempo de la oviposición o las características del micro hábitares afectaron el tiempo de la eclosión de los huevos, se recolectaron huevos durante cuatro períodos en el mes de diciembre para observar la eclosión de huevos en el laboratorio. La eclosión fue mas temprana en el sitio de sombra que en el sitio bajo el sol solamente para los huevos colocados durante el inicio del mes de diciembre. La duración de la eclosión de huevos fue mas corta para los huevos puestos tempranamente que en comparación con los huevos puestos mas tarde. La duración del estadio de huevo (calculado de la fecha mediana de oviposición hasta la fecha mediana de la eclosión de huevos) fue negativamente correlacionada con el tiempo cuando los huevos fueron puestos. Estos resultados sugieren que las diferencias en el tiempo de la eclosión de huevos entre los hábitares puede ser afectados por el micro hábitat y la fecha de la oviposición.

Insect performance is strongly influenced by the environments in which the insects and their host plants grow. In forests, the environment around a plant may vary both temporally and spatially (Bazzaz 1979). The phenology of dormancy, leaf emergence, and leaf senescence of trees of the upper layer may result in seasonal changes in the quality and quantity of sunlight reaching different regions of the forest floor, e.g., forest edges, gaps, understory, and open areas next to forests (Denslow et al. 1990; Uemura 1994; Gill et al. 1998; Seiwa 1998; Kato & Komiyama 2002). These differences in quality and quantity of sunlight within the forest may result

in variable temperature, humidity, food quality, and predation by natural enemies, and may consequently influence the development, growth, survival, and abundance of insects (Rausher 1979; Lowman 1992; Shure & Wilson 1993; Dudt & Shure 1994; Louda & Rodman 1996; Bergman 1999; McDonald et al. 1999).

Host plant phenology, including the timing of budburst and leaf senescence, may be affected by environmental conditions; for example, by exposure to sun or shade (Furuta 1990; Lowman 1992; Seiwa 1999). This is particularly important in the early spring when synchrony between the time of egg hatching and the budburst plays an important role

in the performance and population growth of insects (Dixon 1976; Holliday 1977; Wint 1983; Watt & McFarlane 1991; Hunter 1992; Akimoto & Yamaguchi 1994; Quiring 1994; Lawrence et al. 1997; Van Dongen et al. 1997; Martel & Kause 2002).

The maple aphid, *Periphyllus californiensis* Shinji, dwells on maple trees year-round. In the early spring, stem mothers (fundatrix), the first parthenogenetic generation appearing from fertilized eggs (Miyazaki 1987), hatch from overwintering eggs and give rise to one or more winged or wingless spring generations by parthenogenesis. This aphid feeds on growing buds, leaves, shoots, and the inflorescence in spring. As leaves expand, the soluble nitrogen concentration in the phloem declines, and aestivating dimorphs are produced. In the summer, aestivating dimorphs remain as first instars, mostly on leaves, until autumn when they resume growth and become wingless adults as the food quality improves once again. In spring and autumn, winged females disperse among maple trees (Furuta 1987). In spring and autumn, the performance of the maple aphid is closely attuned to the budburst and leaf senescence phenology of its host trees. In spring, the numbers of stem mothers and their survival rates are higher on early-budding trees than on late-budding trees (Furuta 1987). Therefore, reproduction of stem mothers is mostly observed on early-budding trees, and their winged progeny disperse to late-budding trees where they reproduce in turn (Furuta et al. 1984). In autumn, the population increases first on early-senescing trees, and the winged female progeny of the aestivating dimorphs then disperse to late-senescing trees on which they then reproduce. As a result, oviparae are produced earlier on early-senescing trees than on late-senescing trees (Furuta 1986). The budburst and leaf senescence phenology of the maple tree, *Acer palmatum*, is influenced by the light conditions experienced by the trees (Furuta 1990). Environmental differences in exposure to sun and shade may thus affect development of the egg stage of the maple aphid, and the host tree phenology may also affect the reproductive schedules of the autumnal population and subsequent egg hatching.

In this study, the egg hatching of *P. californiensis* was studied on *Acer amoenum* Carriere saplings in two microhabitats with different light conditions and microclimates, i.e., the understory of a maple stand (a shaded site) and an open area in a nursery (a sunny site) over a 2-year period. Two questions were examined. First, do microclimatic differences between sites cause differences in the timing of egg hatching between microhabitats? Second, does the timing of oviposition have an effect on the timing of egg hatching?

MATERIALS AND METHODS

The study was conducted from spring 1997 until spring 2000 in the Forest Experimental Sta-

tion at Tanashi (35°N; 139°E; 60 m elev.), situated in Nishitokyo-shi, Tokyo, Japan. Two study sites, a maple stand understory and an open area in a nursery, were selected in order to observe the phenology of the egg hatching of *P. californiensis* and the budburst of *A. amoenum*. The maple stand was shaded by the trunks and branches of overstory trees in winter and early spring (hereafter called the 'shaded site'). The nursery was in an open field with no shading (hereafter called the 'sunny site'). The two study sites were separated by about 100 m.

Egg Hatching and Budburst in the Field

Potted saplings, 15-40 cm high, of *A. amoenum* from the same provenance randomly placed in either the sunny or shaded site from the spring of 1997 were used for observing the budburst phenology. At the sunny site, 28 and 19 saplings were observed, while 25 and 12 saplings were observed at the shaded site in 1999 and 2000, respectively. Budburst (defined as the time when leaves first become visible from opening buds) was monitored every 2-3 days from the beginning of February in both years. The median date of budburst was determined from counts of all buds on all saplings. The cumulative percentage of budbursts was estimated by averaging the accumulated percentage of budbursts across all saplings.

In autumn 1998, only saplings at the shaded site had established natural maple aphid colonies. In order to permit observation of egg hatching at both study sites, fourth instar-adult oviparae and males collected from *Acer* spp. in the field were artificially placed onto saplings at both sites on December 11, 1998.

Eggs laid by oviparae in autumn 1999 were observed in 2000. Adult oviparae were observed on saplings at the sunny and shaded sites at the beginning and the end of December 1999, respectively. In spring 2000, all hatched stem mothers were removed after each observation. Observations were made every other day beginning in February and ending in April in both years.

Unlike other studies that indicated high overwintering mortality of aphid eggs (Leather et al. 1995; Wade & Leather 2002), no obvious mortality of eggs was observed in this study. Since larval syrphids are the primary predators of the maple aphid in spring at the study sites, the eggs of syrphids were regularly removed from the study saplings whenever they were found in order to prevent predation of newly-hatched aphids.

Effect of Microhabitat and Oviposition Period

Oviparae were collected from maple trees in the field during four periods in 1999 on December 1-2, 7-10, 15-18, and 23-27. These oviparae were maintained in the lab on four to eight 15-30-cm-

high saplings of *A. amoenum* growing in the shade. Eggs were collected from these oviparae over short periods in the laboratory to minimize the effects of host plants or environments on the oviparae. On the last day of each period, all oviparae were removed, and the saplings with eggs were transferred to the field where they were placed in either the sunny or shaded site. Egg hatching was then recorded every 2 days during spring 2000, and all hatching stem mothers were removed during each observation.

Data Transformation and Statistical Analysis

Most statistical analyses in this study were performed with SYSTAT (version 8, SPSS, Chicago, IL, USA). The means and variation of the timing of egg hatching were compared between study sites by *t*-test and *F*-test (Elliott 1971), respectively. Patterns of egg hatching were compared by plotting regression lines of logit-transformed proportion of eggs hatched against degree-days within each study site. Differences between slopes and elevations of the regression lines were compared (Zar 1999). Slopes were compared first, and elevations were only analyzed when slopes showed significant differences. Degree-days were calculated by the Sine method (Frazer & Gilbert 1976; Pruess 1983; Raworth 1994) and were accumulated above 4.58°C from 1 February 2000 (Wang & Furuta 2002). Daily minimum and maximum temperatures were obtained from the Forest Experimental Station at Tanashi. Weekly maximum and minimum temperatures at the sunny and shaded sites were recorded by hanging a maximum/minimum thermometer about 40 cm above the ground on the north side of a wooden box from February to the beginning of April 2000. The relationships between these weekly maximum or minimum temperature data within each study site (*y*) and weekly maximum or minimum temperature data obtained from the Tanashi Experimental Station (*x*) were calculated by linear regression. Then, the daily temperature data from the Tanashi Experimental Station were applied to the equations to obtain estimated daily maximum and minimum temperatures for each study site.

RESULTS

Egg Hatching and Budburst in the Field

Egg hatching at the shaded site occurred earlier than that at the sunny site in both years (Fig. 1). Egg hatching occurred about 10 and 6 days earlier at the shaded site in 1999 and 2000, respectively ($t = 19.339$, $df = 783$, $P < 0.001$; $t = 9.408$, $df = 823$, $P < 0.001$), but variation in time of egg hatch between sites was the same in both years (in 1999: $F_{434/349} = 1.107$, $P > 0.05$; in 2000: $F_{38/785} = 1.474$, $P > 0.05$).

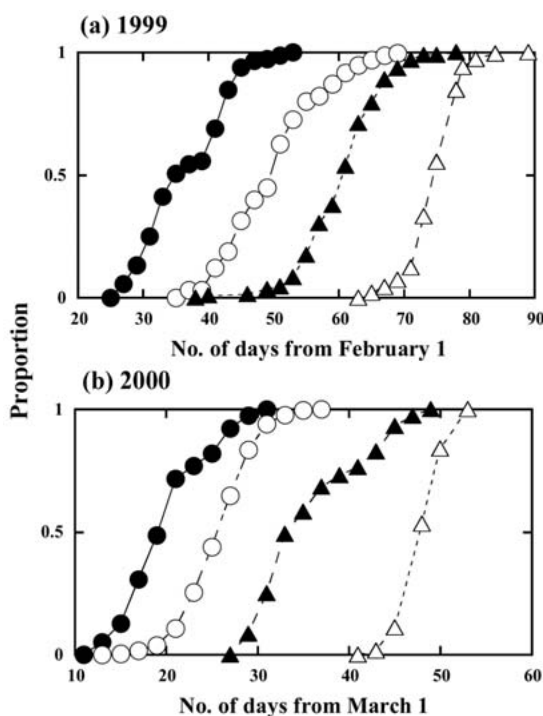


Figure 1. Proportion of eggs hatched (circles) and buds burst (triangles) in the sun (open) and shade (solid) against time in (a) 1999 and (b) 2000.

The median dates of budburst were about 14 and 13 days earlier at the shaded site than at the sunny site in 1999 and 2000, respectively. The degree of synchrony between egg hatching and budburst varied between sites and years. At the shaded site, budburst began when 56% and 97% of the eggs had hatched in 1999 and 2000, respectively. At the sunny site, budburst began when 97% and 100% of the eggs had hatched in 1999 and 2000, respectively. The interval between the date when the first egg hatched and the date of the first budburst at the shaded site was 13 and 16 days in 1999 and 2000, respectively. At the sunny site, the interval was 28 days in both years. The interval between the median dates of egg hatching and budburst at the shaded site was 26 and 16 days in 1999 and 2000, respectively, and 24 and 21 days at the sunny site.

Effect of Microhabitat and Oviposition Period

The timing of egg hatching varied between sites and among oviposition times (by two-way ANOVA: Site, $F_{1/721} = 5.312$, $P < 0.05$; Time, $F_{3/721} = 7.218$, $P < 0.001$). Between sites within each oviposition period, eggs laid on December 7-10 began to hatch 6 days earlier at the shaded site than at the sunny site. There were no differences between sites for eggs laid in other periods. The median

date of egg hatching was 4 days earlier at the shaded site than at the sunny site for eggs laid on December 1-2 and 15-18 (Table 1). The variation in the timing of egg hatching between sites differed for eggs laid on December 7-10 ($F_{105/110} = 1.620, P < 0.05$). Patterns of egg hatching between sites had significantly different slopes for eggs laid on December 1-2 and 7-10, and similar slopes but significantly different elevations for eggs deposited during the other two periods (Fig. 2, Table 1).

When oviposition periods were compared within sites, eggs laid on December 1-2 began to hatch about 8-14 days later than those laid on December 7-27. The duration of egg hatching (calculated as the number of days from when the first to the last eggs hatched) was shortest for eggs laid on December 1-2 (23-25 days), and longest for eggs laid on December 23-27 (39-41 days). The median duration of the egg stage (calculated as the number of days from the median oviposition date to the median egg hatching date) was negatively correlated with the date of oviposition (correlation coefficient $r = -0.982, n = 8, P < 0.001$). The longest egg stage duration was 109-113 days for those laid on December 1-2, and the shortest was 86 days for those laid on December 23-27. When patterns of egg hatching were compared within each study site, only the eggs laid on December 7-10 and 23-27 hatched at the shaded site revealed the same regression lines, as did eggs laid on December 15-18 and 23-27 hatched at the sunny site (Table 1).

DISCUSSION

Eggs at the understory site hatched a little earlier and tended to require fewer thermal units for egg development than those at the open site. Differences in patterns of egg hatching between sites tended to be larger for eggs laid earlier in December than those laid later. Egg diapause termination can be affected by two thermal features, the length of the lower temperature exposure and the actual temperatures eggs experience (Leather et al. 1995). Therefore, it is possible that greater extremes of temperature in the open site compared with the understory site may have influenced the thermal conditions for egg diapause termination (Tauber & Tauber 1976; Day 1984; Tauber et al. 1986; Fisher et al. 1994; Wang & Furuta 2002), and the speed of egg development during the post-diapause stage (Augspurger & Bartlett 2003), which generated differences in the timing of egg hatching between sites. Furthermore, differences in microclimates between sites might be larger when the deciduous canopy is still closed than they are after overstory trees lose their leaves (Gill et al. 1998; Kato & Komiyama 2002). The last tree shorter than 2 m high to shed its leaves at the shaded site did so by December 21, 1999 (Wang 2002). Therefore, differences between sites may have decreased over time in December and have resulted in larger environmental differences between sites for eggs laid early in December than for those laid later.

TABLE 1. TIME AND PATTERNS OF EGG HATCHING AT THE SUNNY AND SHADED SITES FOR FOUR SPECIFIC OVIPOSITION PERIODS IN DECEMBER. PATTERNS OF EGG HATCHING WERE EXPRESSED WITH REGRESSION LINES PLOTTING LOGIT-TRANSFORMED PROPORTION EGGS HATCHED AGAINST DEGREE-DAYS ABOVE 4.58°C FROM FEBRUARY 1, 2000 AND COMPARED BY TUKEY'S TEST.

Oviposition period	N	Egg hatching		Regression equation	r ²	Between	
		Period	Median date			Sites*	Periods*
Dec 1-2							
Shaded	35	Mar 7-29	Mar 19	y = -10.2 + 0.0662 x	0.954		
Sunny	50	Mar 7-31	Mar 23	y = -9.91 + 0.0501 x	0.976		
Dec 7-10							
Shaded	105	Feb 22-Mar 29	Mar 21	y = -6.03 + 0.0384 x	0.960		dE
Sunny	110	Feb 28-Mar 31	Mar 19	y = -10.0 + 0.0564 x	0.991		
Dec 15-18							
Shaded	118	Feb 22-Mar 31	Mar 15	y = -5.72 + 0.0410 x	0.974	a	dF
Sunny	153	Feb 22-Mar 31	Mar 19	y = -6.96 + 0.0401 x	0.996	a	G
Dec 23-27							
Shaded	94	Feb 22-Mar 31	Mar 19	y = -6.33 + 0.0419 x	0.992	b	EF
Sunny	64	Feb 22-Apr 2	Mar 19	y = -6.03 + 0.0376 x	0.975	b	G

*Test results from all regression lines by Tukey's test. Only those between sites within periods and among periods within sites are shown. Slopes and elevations of values with the same capital letters do not differ. Slopes of values with the same small letters do not differ, but the elevations differ. Slopes of values without the same letters differ.

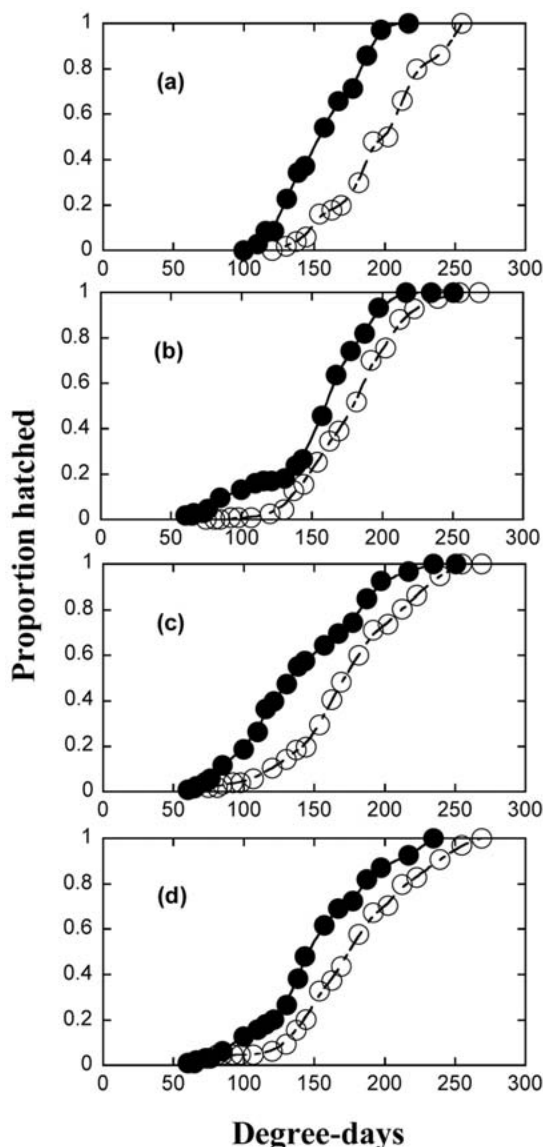


Figure 2. Proportion of eggs hatched in the sun (open) and shade (solid) for eggs laid during (a) December 1-2, (b) 7-10, (c) 15-18, and (d) 23-27 against degree-days accumulated above 4.58°C from February 1.

The duration of the egg stage was longer for eggs laid earlier in December than for those laid later. In a laboratory study (Wang & Furuta 2002), eggs of *P. californiensis* deposited earlier in December also exhibited delayed hatching compared to those deposited later. The period from December 7-18, 1999, in this study seemed to be the critical oviposition period for the timing of egg hatching. In the Tokyo region, the temperature gradually decreases in December, and day length is shortest between December 16 and 26 (Japan

Weather Association 1997). Because higher temperatures and changing day length have been implicated in the production of eggs with more-intensive diapause, i.e., entering a longer diapause, for some insects (Tauber et al. 1986; Masaki 1996), it is possible that oviparae might be stimulated by the higher temperatures and longer day lengths in early December thus producing eggs with more-intensive diapause than those produced later in the winter. In addition to the direct effects of microhabitats and oviposition times on eggs examined in this study, determining other potential factors which might have affected egg conditions through oviparae, e.g., genetic variation (Komatsu & Akimoto 1995), maternal effects (Mousseau 1991; Bradford & Roff 1993; Cherrill 2000; Roff & Bradford 2000; Denlinger 2002), and host plant quality (Hunter & McNeil 1997), may require further detailed investigations.

The duration of egg hatching was shorter and its onset was about 1-2 weeks later for eggs laid on December 1-2 than for those laid later. Fewer eggs were used in the experiment on December 1-2 as oviparae could only be found on early-senescent trees in small numbers. Therefore, eggs laid on December 1-2 may reflect the hatching pattern for those laid on early-senescent trees. After December 1-2, oviparae became increasingly abundant on both early- and late-senescent trees and were collected on both kinds of trees. Eggs laid during the period December 7-27 may represent a combination of both late- and early-hatching eggs, and this would be consistent with a longer period of egg hatching for this cohort.

Acer palmatum growing in the shade tends to break buds earlier and enter senescence later than those in full sun (Furuta 1990). Saplings of *Acer saccharum* are known to break buds earlier and enter senescence later in the understory than in gaps (Augsburger et al. 2003), and the results of the present study are consistent in this regard. Changes in a plant's phenology in different light environments may result from understory trees avoiding canopy shade in order to maximize net carbon gain (Uemura 1994). Because aphids are sap-sucking insects, the soluble nitrogen in the sap is critical for their growth (Dixon 1998). The maple aphid can only feed and grow on developing buds until leaf expansion is complete. They produce normal winged or wingless offspring when food quality is high, and aestivating dimorphs when food quality declines (Hashimoto & Furuta 1988). In spring, most stem mothers are found on early-budding trees, and their progeny, which develop into winged adults, disperse to late-budding trees and reproduce there (Furuta 1987). When food quality becomes poor, only dimorphs are produced. These aestivating first instars will aestivate on leaves for several months until leaf senescence begins in autumn. Autumnal populations build up earlier on early-senescent

ing trees than on late-senescent trees, and winged individuals maturing on early-senescent trees can also colonize and reproduce on late-senescent trees. This results in the earlier appearance of oviparae on early-senescent trees than on late-senescent trees. Thus the entire life cycle of the maple aphid is driven by the host plant phenology, including the production of oviparae and eggs.

Egg hatching of the maple aphid occurs earlier than the budburst. This phenomenon has also been observed in the gall-forming aphid *Hormaphis hamamelidis* which hatches in advance of the budburst (Rehill & Schultz 2002). In the early spring, stem mothers of the maple aphid can stay on the bud scales before bud growth begins, but they will not molt to second instars until the buds start to swell (Furuta 1990). Because stem mothers can survive starvation conditions for a time (Wang 2002), hatching earlier than bud swelling may permit immediate initiation of growth when suitable food becomes available, although it also incurs the cost of a longer period of exposure to natural enemies (Price et al. 1980). In addition, early hatching increases the chance that multiple generations can be completed on both early-budding and other late-budding trees. Thus the highest potential fitness will be obtained by stem mothers hatching early on early-budding trees.

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