Effects of Temperature on Development, Longevity and Reproduction of the Soybean Aphid, *Aphis glycines* (Homoptera: Aphididae)¹

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The soybean aphid, *Aphis glycines* MATSUMURA, is distributed in tropical and subtropical regions such as Southeast Asia and parts of Africa as well as temperate zones such as northern China and Japan (WANG et al., 1962; KOBAYASHI et al., 1972; SINGH and van EMDEN, 1979; HILL, 1987; HIRANO and FUJII, 1993). *A. glycines* is an important pest of the soybean plant (WANG et al., 1962; KOGAN and TURNIPSEED, 1987), causing not only direct damage by feeding but also indirect damage from its heavy secretion of honeydew on the plants, which serves as a growing medium for sooty mold fungus. *A. glycines* is also an important vector of viral diseases (IWAKI, 1979; TAKAHASHI et al., 1980).

Although *A. glycines* has long been known as a soybean pest, few studies have been carried out on the mechanism involved in its population fluctuations. It is necessary to clarify the demographic parameters and ecological characteristics of *A. glycines* as a first step toward understanding the population dynamics of this species. The present report focuses on the developmental thresholds and rates, intrinsic rates of increase, and other pertinent demographic parameters for *A. glycines*.

MATERIALS AND METHODS

Fourth-instar nymphs of viviparous apterae (wingless form) were collected from soybean fields at

Tohoku National Agricultural Experiment Station, Morioka (39°42'N, 141°10'E) in July, 1994. These were reared until the adult stage, and allowed to larviposit for 4 days on soybean seedlings in the laboratory (27°C, 16L:8D photoperiod, and about 80–90% RH). For the purposes of this study, all nymphs produced during the 6-h period were assumed to be of uniform age. A cohort of 1 to 3 newly born nymphs was placed in each of four constant-temperature cabinets at 17, 22, 27, or 32°C, 16L:8D photoperiod, and about 80–90% RH. Within each temperature regime the cohort was reared on one soybean seedling, which was replaced every 5 to 7 days depending on rearing temperature.

Observations on nymphal development were conducted for 19–27 individuals per temperature, but mortality reduced this number in successive life stages. Daily survival rates of nymphs and developmental time to adult, all of which were viviparous apterae, were determined by checking each nymph every 24 h. When nymphs became adults, the new adults were reared singly on soybean seedlings at two temperature regimes (22 and 27°C). Progeny of these adults were removed daily and the numbers recorded. Longevity, time to first reproduction, and mortality were also recorded.

RESULTS AND DISCUSSION

Table 1 shows that the developmental time to adult decreased with increasing temperature, up to 27°C. At 32°C the developmental time increased, indicating that the developmental rate declined due to the high temperature. Survival rate from first-instar nymphs to adults at 32°C was also much lower than that at other temperatures. The linear regression of mean developmental rate per day (the reciprocal of developmental time to adult), Y , on temperature, X , was applied only to the range from 17 to 27°C, and the following equation was obtained: $Y = 0.0175X - 0.167$ ($r^2 = 1.00$, $p < 0.05$). The developmental zero estimated from this linear regression equation was 9.5°C. The number of degree-days needed to develop from the newly born nymph to the adult stage was 57.1, which was given by the reciprocal of the regression coefficient ($1/0.0175$).

The mean durations of reproductive period and adult longevity were significantly greater at 22°C than at 27°C (Table 2 and Fig. 1). Reproduction at 22°C ceased at a time when about 50% of the adult

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Table 1. Mean developmental time (days) and survival rate of immature stage of *A. glycines* apterae at four constant temperatures

Temp. (°C)	N	Mean developmental time to adult and 95% confidence interval		Survival rate of immature stage
17	26	7.8	7.5–8.0	0.81
22	23	4.5	4.2–4.8	0.91
27	27	3.3	3.1–3.5	0.89
32	19	3.8	3.6–4.1	0.58

Table 2. Reproductive life of viviparous apterae at two constant temperatures

Temp. (°C)	N	Mean age at first reproduction $\pm$ SE (days)	Mean reproductive period $\pm$ SE (days)	Mean adult longevity $\pm$ SE (days)
22	20	5.2 ^a $\pm$ 0.1	9.6 ^b $\pm$ 0.9	13.5 ^c $\pm$ 1.4
27	20	3.9 $\pm$ 0.1	6.5 $\pm$ 0.7	7.9 $\pm$ 0.8

^a There was a significant difference between the two temperature regimes (*t*-test, $p = 0.001$).

^{b,c} There were significant differences between the two temperature regimes (MANN-WHITNEY *U*-test, ^b $p = 0.003$, ^c $p = 0.005$).

Fig. 1. Age-specific survivorship (l_x , ■) and fecundity (m_x , ●) patterns for *A. glycines* apterae at two constant temperatures.

aphids were still alive (Fig. 1). The gross fecundity, which represents the lifetime production of offspring by a female, was significantly higher at 22°C than at 27°C (Table 3). These results indicate that *A. glycines*

had a higher gross fecundity at 22°C because of the longer reproductive period, and that adult longevity at 22°C is not a major factor affecting the gross fecundity because most of the offspring are produced early in the adult's lifetime.

The finite rate of increase (λ) and intrinsic rate of increase (r_m) were higher at 27°C than at 22°C (Table 3). The time needed for first reproduction was significantly shorter at 27°C than at 22°C (Table 2 and Fig. 1). The mean daily fecundity (m_x) peaked earlier and more rapidly and declined more rapidly at 27°C than at 22°C. The peak of m_x was higher at 27°C than at 22°C (Fig. 1). When reproduction ceased at 27°C, only about 13% of the adults were still alive (Fig. 1). The higher r_m at 27°C appears to be due to earlier first reproduction and the greater proportion of the offspring produced early in the adult's lifetime, compared with those at 22°C.

The foxglove aphid, *Aulacorthum solani* (KALTENBACH), is also a common pest of soybean plants in East Asian countries, such as China, Korea and Japan (KOGAN and TURNIPSEED, 1987). The developmental zero and effective cumulative temperature for completion of the nymphal stage of *A. solani* are 3.2°C and 159.1 degree-days, respectively (KAZINO, 1971). When the two linear regressions of mean developmental rate of *A. glycines* and *A. solani* per day on temperature were extrapolated, the point of intersection was found to be 13°C. The two linear regres-

Table 3. Gross fecundity and intrinsic rate of increase for *A. glycines* apterae at two constant temperatures

Temp. (°C)	Gross fecundity (nymphs per female)		Finite rate of increase per day ^a (λ)		Intrinsic rate of increase ^c (r_m)
	Mean	SE (<i>N</i>)	Mean	95% confidence interval (<i>N</i>) ^b	
22	60.3 ^d	5.2 (20)	1.561	1.225–1.897 (22)	0.445
27	45.0	4.8 (20)	1.704	1.280–2.128 (24)	0.533

^a Values were estimated by the method of LENSKI and SERVICE F"-method (1982).

^b Numbers are different from those shown in Table 1 because one individual at 22°C and three individuals at 27°C were lost during the adult stage due to inappropriate handling during the course of rearing.

^c The value was obtained by $r_m = \ln(\lambda)$.

^d There was a significant difference between the two temperature regimes (MANN-WHITNEY *U*-test, $p = 0.012$).

sions indicate that when temperature conditions are greater than 13°C, the developmental rate of *A. glycines* is faster than that of *A. solani*.

The gross fecundity of *A. glycines* at 22°C and that of apterae of *A. solani* at 23°C were 60.3 (Table 3) and 58.1 nymphs (OKADA and NAKASUJI, 1980), respectively. The intrinsic rate of increase of *A. glycines* at 22°C (Table 3) was much higher than that of *A. solani* at 23°C (0.21) (OKADA and NAKASUJI, 1980) because the developmental rate of *A. glycines* was faster than that of *A. solani*. *Aphis glycines* appears to be adapted to conditions of higher atmospheric temperature in terms of r_m , compared with *A. solani*.

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