Effects of temperature on survival, development, and reproduction of *Aphis glycines* (Hemiptera: Aphididae) autumnal morphs

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**Abstract**

*Aphis glycines* Matsumura (Hemiptera: Aphididae) is a common pest in soybeans in China. Though the pest has been studied extensively for many yr, there is little information regarding life history traits of *A. glycines* autumnal morphs on buckthorn in autumn. Life tables were constructed of *A. glycines* gynoparae, males, and oviparae reared at 13, 18, 23, 28, and 33 °C with a photoperiod of 12:12 h (L:D). Our results showed that gynoparae nymphs of *A. glycines* could survive well at temperatures from 13 to 33 °C, but male and oviparae nymphs could not develop into adults at 33 °C. Development time of nymphal gynoparae, males, and oviparae all gradually decreased when temperatures increased from 13 to 28 °C. Adult longevity of gynoparae and virgin males also decreased gradually when temperatures increased from 13 to 28 °C. Fecundity of *A. glycines* gynoparae was the greatest at 23 °C, with a value of 15.87 ± 0.33 oviparae per gynoparae. Males and oviparae of *A. glycines* mated only at 13 and 18 °C in the laboratory. Oviparae fecundity at 18 °C was greater than at 13 °C. This study provides important information on survival, development, and reproduction of *A. glycines* autumnal morphs, which is useful for understanding the population dynamics and life cycle of *A. glycines* in autumn, and to study the ecological adaptability of *A. glycines* in autumn.

**Key Words:** *Aphis glycines*; autumnal morphs; temperature; life table

**Resumen**

*Aphis glycines* Matsumura (Hemiptera: Aphididae) es una plaga común en la soja en China. Aunque la plaga ha sido ampliamente estudiada durante muchos años, hay poca información sobre los rasgos de la historia de vida de las formas otoñales de *A. glycines* en espino amarillo en el otoño. Se construyeron tablas de vida de los gino-parae, machos y ovariparos de *A. glycines* criados a 13, 18, 23, 28, y 33 °C con un fotoperiodo de 12:12 h (L:D). Nuestros resultados mostraron que las ninfa-s gino-parae de *A. glycines* podían sobrevivir a temperaturas de 13 a los 33 °C, pero las ninfas masculinas y oviparaes no podrían desarrollarse en adultos a los 33 °C. El tiempo de desarrollo de la ninfa gino-parae, los machos y las ovariparos disminuyó gradualmente cuando las temperaturas aumentaron de 13 a 28 °C. La longevidad adulta de gino-parae y machos virgenes también disminuyó gradualmente cuando las temperaturas aumentaron de 13 a 28 °C. La fecundidad del gino-parae de *A. glycines* fue la mayor a 23 °C, con un valor de 15.83 ± 0.33 ovariparos por gino-parae. Los machos y las ovariparos de *A. glycines* se aparearon solo a 13 y 18 °C en el laboratorio. La fecundidad de las ovariparos a 18 °C fue mayor que la de 13 °C. Este estudio proporciona información importante sobre la sobrevivencia, el desarrollo y la reproducción de las formas otoñales de *A. glycines*, lo que es útil para comprender la dinámica de la población y el ciclo de vida de *A. glycines* y para estudiar la adaptabilidad ecológica de *A. glycines* en otoño.

**Palabras Claves:** *Aphis glycines*; morfosis otoñales; formas otoñales temperatura; tabla de vida

*Aphis glycines* Matsumura (Hemiptera: Aphididae) is an important pest in soybeans and is native to Asia (Liu & Zhao 2007). Since *A. glycines* invaded North America in 2000 (Hartman et al. 2001; Ragsdale et al. 2004), they have spread throughout the main soybean planting regions (Venette & Ragsdale 2004). They can damage soybean plants directly by feeding in addition to transmission of plant viruses (Hill et al. 2001). Additionally, black sooty mold fungus growing on honeydew produced by *A. glycines* may lead to inhibition of soybean photosynthesis (Liu & Zhao 2007).

In China, the life cycle of *A. glycines* is characterized as heteroecious and holocyclic (Wang et al. 1962). During spring, overwintering eggs on buckthorn (*Rhamnus* spp. [Rhamnaceae], the primary host) hatch and become fundatrices (wingless females). Their offspring undergo several generations, then winged viviparous females are produced which migrate to soybeans *Glycine max* (L.) Merr. (Fabaceae) where they reproduce parthenogenetically on this host throughout the summer. When temperatures decrease, d-lengths shorten and plants become senescent in autumn. At this time, winged gynoparae are produced on soybean plants and then migrate to *Rhamnus* spp. where they produce ovariparos. Similarly, winged males develop in soybean and migrate to *Rhamnus* spp. (buckthorn) where they mate with ovariparos, which lay overwintering eggs (Wang et al. 1962; Ragsdale et al. 2004; Wu et al. 2004).

Summer morphs of *A. glycines* (virginoparae) have been extensively studied with a wealth of research articles on their population dynamics (Liu et al. 2004; Fan et al. 2017), natural enemies (Costamagna & Landis 2006; Desneux et al. 2006; Dieckhoff & Heimpel 2010; Liu et al. 2012), host plants (Sun et al. 2015; Chen et al. 2017; Wang et al. 2019),

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economic thresholds (Ragsdale et al. 2007; McCarville et al. 2011), etc. However, there is only a limited number of studies dealing with autumnal morphs of *A. glycines*. Thus far, morphological characteristics of gynoparae, males, and oviparae have been identified (Takahashi et al. 1993; Voegtil et al. 2004; Tian et al. 2018); gynoparae and males may also be induced in the laboratory (Wang et al. 2014; Xu et al. 2015; Oka et al. 2018). Temperature is one of the most important factors that can affect development and reproduction of herbivorous insects. Effects of temperature on morphological traits, development, and reproduction of *A. glycines* gynoparae on *G. max* have been studied (Hirano et al. 1996; McCormack et al. 2004; Richardson et al. 2011; Xu et al. 2011). In the Harbin region, northeast China, gynoparae of *A. glycines* disappear gradually on soybeans in Sep (Fan et al. 2017), whereas gynoparae, males, and oviparae occur on buckthorn at that time. In this region, environmental temperatures fluctuate usually from daily lowest to highest (−10.4 °C to 31.4 °C) during Sep to Oct (2007–2014, Heilongjiang Meteorological Bureau, China). Many questions remain unanswered regarding their survival, development and reproduction on primary hosts when gynoparae, males and oviparae of *A. glycines* are subject to these fluctuating temperatures in autumn.

The life table is an important tool for the study of insect population dynamics. It can provide crucial information on life traits, including survivability, growth, development, and reproduction of insects (Chi 1988). The life table also is beneficial for studying the influence of different temperatures on ecological fitness of pests (Gao et al. 2013). Here we report on life table studies of survival, development, and reproduction of *A. glycines* autumnal morphs on their primary host, *Rhamnus davurica* Pallus (Rhamnaceae). This information is important for understanding the seasonal ecological adaptability of this pest in northeast China.

Materials and Methods

APHID SOURCE AND ITS PRIMARY HOST

In our study, 20 wingless virginoparae *A. glycines* were collected from a soybean field at Northeast Agricultural University, Harbin, Heilongjiang Province, northeast China (1.445333°E, 45.740000°N) in 2014. Only 1 individual adult was retained as the mother aphid to build a monoclone population resulting in greater fecundity and body size. The only aphids used in our study were the offspring of this single mother aphid. In this way, we could ensure the homology of individuals used in experiments. The colony was maintained on *G. max* (variety ‘Heinong 51’) in a growth chamber at 25 ± 1 °C, 70 ± 5% RH, and a 14:10 h (L:D) photoperiod with artificial light of 12,000 lx. Primary host leaves of *A. glycines* were collected from *R. davurica* in a garden at Northeast Agricultural University, where no insecticides were used.

Artificial Induction of *Aphis glycines* Autumnal Morphs

In this study, autumnal morphs of *A. glycines* gynoparae, males, and oviparae were successfully induced in the laboratory under low temperatures and a reduced photoperiod. Detached leaves of *G. max* (variety ‘Heinong 51’) were cut into 2.0 cm diam leaf discs using a hole-punch. Solid agar media were prepared in 45 mL, 4 cm × 4.5 cm (diam × height) glass beakers. Twenty wingless adult aphids (denoted as the G₀ cohort) were transferred from the stock colony onto soybean leaf discs with 1 aphid per disc and were reared at 20 ± 1 °C, a 10:14 h (L:D) photoperiod, and 70 ± 5% RH. Each adult was placed on the reverse side of a leaf disc adhered to the surface of the medium.

The beaker was then placed upside-down on a 5 cm diam Petri dish (Chen et al. 2017). Adults were checked daily and newly deposited nymphs were removed individually from beakers with a small brush. Nymphs deposited by generation G₀, aphids on d 1, 6, and 11 were denoted as G₁, and reared to adults using the leaf disc method above. Nymphs deposited by G₁ aphids on d 1, 6, and 11 were denoted as G₂, and also reared to adults using the same methods. Leaves and media were replaced every 5 to 7 d when old leaves became yellowish or upon observation of fungal growth (Tian et al. 2018). The first instar of *A. glycines* gynoparae were used for trials on nymphal development as mentioned in the following section, which were produced on d 6 by G₁ from that produced on the first d by G₀. The first instar of males were produced on day 11 by G₁ from that produced on d 11 by G₀. The first instar of oviparae produced by gynoparae adults also were used for the following trial.

Nymphal Development of *Aphis glycines* Autumnal Morphs

Life tables were constructed of autumnal morphs on their primary host, *R. davurica*, at 13, 18, 23, 28, and 33 ± 1 °C, 70 ± 5% RH, and a photoperiod of 12:12 h (L:D). The first instar of *A. glycines* gynoparae, males, and oviparae were placed in growth chambers using the aforementioned leaf disc method (Chen et al. 2017). Gynoparae and males were fed on soybean leaf discs, whereas oviparae were fed on *R. davurica* leaf discs. For each different temperature treatment, 23 to 50 nymphs were tested. Individual aphids were checked daily for ecdysis and survivorship. Leaves and media were replaced every 5 to 7 d when old leaves became yellowish or the media showed fungal growth.

Adult Longevity and Fecundity of *Aphis glycines* Autumnal Morphs

Adults of *A. glycines* gynoparae, males, and oviparae, reared from nymphs at 13 to 33 ± 1 °C were maintained in the same conditions as the immature aphids. All adults of the 3 autumnal morphs were reared on *R. davurica* leaves. Adult longevity was recorded daily until the death of each adult. Nymphs deposited by gynoparae were counted and removed daily.

Another group of artificially induced males and oviparae of *A. glycines* adult also were used in this trial. Each couple, males and oviparae, were placed together into 1 beaker to mate. Couples were maintained together until they mated for the first time. Once mated, males and oviparae were moved into separate beakers and reared individually. Longevity of these mated morphs were recorded daily. Eggs deposited by mated oviparae were counted and removed daily. Males and oviparae were reared on *R. davurica* leaves that also served as egg-laying substrate. Leaves and media were replaced every 5 to 7 d as mentioned earlier.

Life Table Parameters of *Aphis glycines* Gynoparae and Oviparae

The age-stage-specific survival rate (Sₓ) and age-stage-specific fecundity (fₓ) of gynoparae and mated oviparae were calculated from raw recording data. Intrinsic rate of increase (r) was calculated by bisection method from the Euler-Lotka equation: \( \sum_{x}^{\lambda} e^{-\lambda x} f_x = 1 \), with age indexed from 0 (Goodman 1982). Finite rate of increase (λ) was calculated as \( \lambda = e^r \). Net reproductive rate (R₀) was calculated as \( R_0 = \sum S_x f_x e^{-\lambda x} \). Mean generation time (T) was calculated as \( T = (\ln R_0)/r \), and defines the time necessary for a population size to increases to \( R_0 \)-fold at the stable stage distribution (Chi & Liu 1985; Chi 1988).
DATA ANALYSIS

Raw data of nymph duration, adult longevity, and fecundity of gynoparae and oviparae at different temperatures were calculated according to age-stage, Two-Sex Life Table Theory (Chi 1988). Differences in nymph duration and adult longevity of gynoparae, males, and oviparae, and fecundity among temperatures were analyzed using PROC general linear model (GLM) and Tukey’s honest significant difference (HSD) tests. Differences in adult longevity of mated males and oviparae and fecundity of mated oviparae between 13 and 18 °C were analyzed using a t-test with SAS 8.1 software (SAS 2000). To estimate the lower developmental temperature threshold and effective cumulative temperature for nymph development of A. glycines gynoparae, males, and oviparae, linear regression of the mean developmental rate y (the reciprocal of development time to adult) on temperature x was applied to each temperature from 13 °C to 28 °C (Murai 2000), and was performed with a general linear model.

Intrinsic rate of increase and finite rate of increase, mean generation time, and net reproduction rate of gynoparae and oviparae were calculated using the bootstrap technique (Efron & Tibshirani 1993) in the computer program TOWSEX-MSChart (Chi 2017). Because bootstrap analysis uses random resampling, a small number of replications will generate variable means and standard errors; thus, 200,000 bootstrap iterations were used to reduce the variability of the results. The differences among parameters at each temperature were analyzed by the paired bootstrap test (Efron & Tibshirani 1993).

Results

NYMPHAL DEVELOPMENT OF Aphis glycines AUTUMNAL MORPHS

There were significant differences in development time of nymphal A. glycines among different temperatures (gyoparae: \( F = 1,696.73 \); df = 4,157; \( P < 0.05 \); males: \( F = 1,100.07 \); df = 3,191; \( P < 0.05 \); oviparae: \( F = 191.70 \); df = 3,136; \( P < 0.05 \)). Generally nymphal gynoparae, males, and oviparae decreased gradually when temperatures increased from 13 °C to 28 °C (Table 1). At 33 °C, only nymphs of A. glycines gynoparae could develop into adults. At this temperature, nymphal development time was 6.96 ± 0.14 d. Lower temperature thresholds for nymphal development of gynoparae, males, and oviparae were estimated as 6.24, 2.85, and 3.87 °C, respectively; based on those temperatures, the effective cumulative developmental times of gynoparae, males, and oviparae from first instar to adult were estimated at 117.64, 185.19, and 212.77 degree-d, respectively (Table 2).

Adult longevity and fecundity of Aphis glycines Autuminal morphs

Survival time of gynoparae, males, and oviparae of A. glycines decreased gradually when temperatures increased from 13 to 33 °C. At 13 °C, survival time of gynoparae was the longest whereas a similar pattern was observed for autumnal morphs at 18 °C. At 23 and 28 °C, survival time of oviparae was the greatest, followed by gynoparae and males. However, at 33 °C, no autumnal morphs could survive more than 14 d (Fig. 1).

There were significant differences in adult longevity of A. glycines among different temperatures (gyoparae: \( F = 76.58 \); df = 4,157; \( P < 0.05 \); virgin males: \( F = 206.78 \); df = 3,191; \( P < 0.05 \); virgin oviparae: \( F = 9.21 \); df = 3,136; \( P < 0.05 \)). Adult longevity of gynoparae decreased gradually when temperatures increased from 13 to 33 °C (Table 3). Adult longevity of virgin males also decreased gradually when temperatures increased from 13 to 28 °C. There were no significant differences in adult longevity of virgin oviparae among 13, 18, and 23 °C, which were all longer than at 28 °C (Table 3). Males of A. glycines only mated with oviparae at 13 °C and 18 °C. Adult longevity of mated males and mated oviparae at 13 °C were significantly greater than at 18 °C (males: t = 2.79; \( P < 0.05 \); oviparae: t = 2.43; \( P < 0.05 \) (Table 3).

There were significant differences in fecundity of gynoparae at different temperatures (\( F = 203.49 \); df = 4,157; \( P < 0.05 \)). Gynoparae fecundity increased gradually when temperature increased from 13 to 23 °C, with the highest value of 15.87 ± 0.33 oviparae per gynoparae at 23 °C. Gynoparae fecundity decreased gradually when temperature increased from 28 to 33 °C (Table 4). Oviparae fecundity at 18 °C was

### Table 1. Nymphal development time (mean ± SE) of Aphis glycines gynoparae, males, and oviparae at different temperatures.

| Temperature (°C) | N | D          | N | D          | N | D          |
|------------------|---|------------|---|------------|---|------------|
| 13               | 50| 17.50 ± 0.12 a | 47| 18.55 ± 0.24 a | 23| 24.78 ± 0.87 a |
| 18               | 28| 10.00 ± 0.16 b | 49| 12.63 ± 0.10 b | 48| 13.73 ± 0.32 b |
| 23               | 31| 7.03 ± 0.11 c  | 49| 8.80 ± 0.11 c  | 25| 11.96 ± 0.52 c  |
| 28               | 26| 5.42 ± 0.13 d  | 50| 7.58 ± 0.10 d  | 44| 8.70 ± 0.30 d  |
| 33               | 27| 6.96 ± 0.14 c  | 50| 0           | 50| 0           |

Means within the same column followed by different letters were significantly different (\( P < 0.05 \); HSD test).

### Table 2. Lower threshold temperature and effective accumulated temperature for nymphal Aphis glycines gynoparae, males, and oviparae.

| Autumnal morph | Linear regression equations | Coefficient of determination (R²) | Lower threshold temperature (°C) | Effective accumulated temperature (degree-d) |
|----------------|-----------------------------|-----------------------------------|--------------------------------|---------------------------------------------|
| Gynoparae      | \( y = 0.0085x - 0.0530 \)  | 1.00*                             | 6.24                           | 117.65                                      |
| Male           | \( y = 0.0054x - 0.0154 \)  | 0.99*                             | 2.85                           | 185.19                                      |
| Oviparae       | \( y = 0.0047x - 0.0182 \)  | 0.97*                             | 3.87                           | 212.77                                      |

\( y = \) developmental rates, \( x = \) temperatures. An asterisk (*) denotes a significant difference at \( P < 0.05 \).
higher than at 13 °C ($t = 2.51; P < 0.05$). At 23, 28, and 33 °C, no males mated with oviparae (Table 4).

Gynoparae adults of *A. glycines* started to produce oviparae on d 5, 6, 9, and 17 at 28, 23, 18, and 13 °C, respectively (Fig. 2). Peak gynoparae reproduction occurred at d 1, 2, and 3, as well as the first d during reproductive periods at 23, 18, 13, and 28 °C, respectively. Oviparae adults of *A. glycines* started to produce eggs on d 14 and 19 at 18 °C and 13 °C, respectively (Fig. 2).

Table 3. Adult longevity (mean ± SE) of *Aphis glycines* gynoparae, males, and oviparae at different temperatures.

| Temperature (°C) | Gynoparae | Virgin males | Virgin oviparae | Mated males | Mated oviparae |
|-----------------|-----------|-------------|----------------|-------------|----------------|
|                 | N      | D       | N      | D       | N      | D       | N      | D       | N      | D       |
| 13               | 50     | 36.4 ± 1.8 a | 47     | 24.3 ± 0.9 a | 23     | 20.4 ± 1.8 a | 23     | 22.7 ± 1.0 * | 23     | 17.6 ± 1.3 * |
| 18               | 28     | 24.5 ± 2.1 b | 49     | 15.3 ± 0.9 b | 48     | 23.0 ± 1.3 a | 49     | 19.0 ± 0.8 | 38     | 14.4 ± 0.7 |
| 23               | 31     | 17.4 ± 1.4 c | 49     | 5.7 ± 0.2 c | 25     | 20.2 ± 1.5 a | 0      | 0          | 0      | 0          |
| 28               | 26     | 7.6 ± 0.6 d  | 50     | 3.1 ± 0.2 d  | 44     | 15.0 ± 0.7 b | 0      | 0          | 0      | 0          |
| 33               | 27     | 3.5 ± 0.3 d  | 0      | 0          | 0      | 0          | 0      | 0          | 0      | 0          |

*Mean adult longevity of gynoparae, virgin males, and virgin oviparae within the same column followed by different letters were significantly different ($P < 0.05$; HSD test). Differences in adult longevity only for each column group between 13 and 18 °C rows are marked with an asterisk (*) ($P < 0.05$; t-test).
Table 4. Mean fecundity ± SE of *Aphis glycines* gynoparae and oviparae on overwintering host, *Rhamnus davurica*, at different temperatures.

| Temperature °C | Gynoparae | Mated oviparae |
|----------------|-----------|----------------|
|                | N         | Fecundity a     | N         | Fecundity |
|                |           | (oviparae/gynoparae) |           | (eggs/oviparae) |
| 13             | 50        | 9.14 ± 0.15 c   | 23        | 1.30 ± 0.25* |
| 18             | 28        | 12.79 ± 0.41 b  | 38        | 2.16 ± 0.22  |
| 23             | 31        | 15.87 ± 0.33 a  | 0         | 0           |
| 28             | 26        | 11.81 ± 0.89 b  | 0         | 0           |
| 33             | 27        | 0 d             | 0         | 0           |

*Mean gynoparae fecundity (column) followed by different letters were significantly different (P < 0.05; HSD test). Differences in mean fecundity of mated oviparae between 13 and 18 °C are marked with an asterisk (*) (P < 0.05; t-test).

Table 5. Life table parameters (mean ± SE) of *Aphis glycines* gynoparae at different temperatures.

| Temperature °C | Intrinsic rate of increase r (d⁻¹) | Mean generation time T (d) | Finite rate of increase λ (d⁻¹) | Net reproductive rate R₀ (offspring) |
|----------------|------------------------------------|----------------------------|---------------------------------|------------------------------------|
| 13             | 0.1061 ± 0.0010 c                  | 20.85 ± 0.17 a             | 1.1112 ± 0.0011 c               | 9.14 ± 0.15 c                     |
| 18             | 0.2093 ± 0.0046 b                  | 12.01 ± 0.15 b             | 1.2328 ± 0.0057 b               | 12.34 ± 0.58 b                    |
| 23             | 0.3165 ± 0.0060 a                  | 8.73 ± 0.16 c              | 1.3723 ± 0.0082 a               | 15.87 ± 0.33 a                    |
| 28             | 0.3363 ± 0.0135 a                  | 7.34 ± 0.14 d              | 1.4000 ± 0.0189 a               | 11.81 ± 0.87 b                    |
| 33             | 0                                  | 0                          | 0                               | 0                                  |

*Means followed by different letters within the same column were significantly different (P < 0.05; paired bootstrap test).*

Fig. 2. Age-specific fecundity ($f_x$) of *Aphis glycines* gynoparae and oviparae on overwintering host, *Rhamnus davurica* at 13, 18, 23, and 28 °C.
the question remains whether lower temperatures are required for sexual maturation of A. glycines oviparae and males. Yoo et al. (2005) reported that oviparae could deposit 4.2 and 0.8 eggs on Rhamnus cathartica L. and Rhamnus alnifolia L’Her (both Rhamnaceae) at 20 °C, respectively. In our study, only 1 and 2 eggs were deposited by oviparae on R. davurica at 13 and 18 °C, respectively. But differences in egg deposition likely could be attributed to differences in hosts as well as experimental temperatures.

To avoid underestimating the value of life history traits in our study, further investigations should be conducted on autumnal morphs of A. glycines that are group-reared or reared on living plants with clip cages in the field. Our experiments focused on constant temperature in the laboratory, though environmental temperatures fluctuate sharply between d and night in the Harbin region. If such experiments could be conducted they would provide additional insight into actual circumstances that occur under field conditions.

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References Cited

Bale JS, Masters GJ, Hodkinson ID, Awmack C, Bezzemer TM, Brown VK, Butterfield J, Buse A, Coulson JC, Farrar I, Good JEG, Harrington R, Hartley S, Jones TH, Lindroth RL, Press MC, Symmoudis I, Watt AD, Whittaker JB. 2002. Herbivory in global climate change research: direct effects of rising temperature on insect herbivores. Global Change Biology 8: 1–16.

Chen XH, Fan YJ, Zhang W, Tian ZQ, Liu J, Zhao KJ. 2017. Soybean aphid, Aphis glycines (Homoptera: Aphiidae), developmental and reproductive capacity on white clover, Trifolium repens (Rosalae: Leguminosae), in northeast China. Applied Entomology and Zoology 52: 491–495.

Chi H. 1988. Life-table analysis incorporating both sexes and variable development rates among individuals. Environmental Entomology 17: 26–34.

Chi H. 2017. TWOSEX-MSChart: a computer program for the age-stage, two-sex life table analysis. http://140.120.197.173/ecology/prod02.htm (last accessed 11 Mar 2020).

Chi H, Liu H. 1985. Two new methods for the study of insect population ecology. Chi H. 2017. TWOSEX-MSChart: a computer program for the age-stage, two-sex life table analysis. http://140.120.197.173/ecology/prod02.htm (last accessed 11 Mar 2020).

Desneux N, O’Neil RJ, Yoo HJS. 2006. Suppression of population growth of the soybean aphid, Aphis glycines Matsunura, and its natural enemies in Harbin. Soybean Science 36: 104–107 (in Chinese with English abstract).

Gao GZ, Perkins LE, Zalucki MP, Lu ZZ, Ma JH. 2013. Effect of temperature on the biology of Acrhythsiphon gossypii Mordvilko (Homoptera: Aphiidae) on cotton. Journal of Pest Science 86: 167–172.

Goodman D. 1982. Optimal life histories, optimal notation, and the value of reproductive value. American Naturalist 119: 803–823.

Hartigan GL, Domier LL, Wax LM, Helm CG, Onstad DW, Shaw JT, Solter LF, Voegtlin DJ, D’Arcy CJ, Gray ME, Steffey KL, Isard SA, Orwick PL. 2001. Occurrence and distribution of Aphis glycines on soybeans in Illinois in 2000 and its potential control. Plant Health Progress. doi: 10.1094/PHP-2001-0205-01-HN

Hill JH, Alleman R, Hogg DB, Grau CR. 2001. First report of transmission of soybean mosaic virus and alfalfa mosaic virus by Aphis glycines in the New World. Plant Disease 85: 561. 3. dx.doi.org/10.1094/PDIS.2001.85.5.561C

Hirano K, Honda K, Miyai S. 1996. Effects of temperature on development, longevity and reproduction of the soybean aphid, Aphis glycines (Homoptera: Aphiidae). Applied Entomology and Zoology 31: 178–180.

Hoffmann AA, Sørensen JG, Leschke V. 2003. Adaptation of drosophila to temperature extremes: bringing together quantitative and molecular approaches. Journal of Thermal Biology 28: 175–216.

Liu J, Wu KM, Hopper KR, Zhao KJ. 2004. Population dynamics of Aphis glycines (Homoptera: Aphiidae) and its natural enemies in soybean in northern China. Annals of the Entomological Society of America 97: 235–239.

Liu J, Zhao KJ. 2007. Biology and control techniques of soybean aphid, Aphis glycines (Homoptera: Aphiidae). Chinese Bulletin of Entomology 44: 179–185 (in Chinese with English abstract).

Liu J, Xu WJ, Wang QY, Zhao KJ. 2012. Insect predators in northeast China and their impacts on Aphis glycines. Canadian Entomologist 144: 779–789.

MacCarville MT, Kanobe C, Macintosh GC, O’Neal M. 2011. What is the economic threshold of soybean aphids (Homoptera: Aphiidae) in enemy-free space? Journal of Economic Entomology 104: 845–852.

McCornack BP, Ragsdale DW, Venette RC. 2004. Demography of soybean aphid (Homoptera: Aphiidae) at summer temperatures. Journal of Economic Entomology 97: 854–861.

Murai T. 2000. Effect of temperature on development and reproduction of the onion thrips, Thrips tabaci Lindeman (Thysanoptera: Thripidae), on pollen and honey solution. Applied Entomology and Zoology 35: 499–504.

Oka Y, Kagami-Yashima C, Kagawa K, Sonoda S, Mural T. 2018. Clonal variation of sexual morph production in response to temperature and photoperiod in soybean aphid, Aphis glycines (Homoptera: Aphiidae). Applied Entomology and Zoology 53: 509–517.

Ragsdale DW, Voegtlin DJ, O’Neil RJ. 2004. Soybean aphid biology in North America. Annals of the Entomological Society of America 97: 204–208.

Ragsdale DW, McCornack BP, Venette RC, Potter BD, Macrae IV, Hodgson EW, O’Neal ME, Johnson KD, O’Neil RJ, DiFonzo CD, Hunt TE, Glogoza PA, Cullen EM. 2007. Economic threshold for soybean aphid (Homoptera: Aphiidae). Journal of Economic Entomology 100: 1258–1267.

SAS. 2000. SAS Institute, vers. 8.1. SAS Software, Cary, North Carolina, USA.

Sun WP, Hu ZF, Han LL, Sanda NB, Xuan YH, Zhao KJ. 2015. Discovery of a transgenic soybean, Glycine max (L.) Merr., that are group-reared or reared on living plants with clip cages in the field. Therodaphera cerasi (L.) and honey solution. Applied Entomology and Zoology 31: 178–180.

Takahashi S, Inaizumi M, Kawakami K. 1993. Life cycle of the soybean aphid, Aphis glycines Matsunura, in Japan. Japanese Journal of Applied Entomology and Zoology 37: 207–212.

Tian ZQ, Wang SJ, Bai B, Liu J, Zhao KJ. 2018. A morphological study on autumnal morphs of A. glycines Matsunura and its natural enemies in Harbin. Soybean Science 36: 104–107 (in Chinese with English abstract).

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| Temperature °C | Intrinsic rate of increase r (d⁻¹) | Mean generation time T (d) | Finite rate of increase λ (d⁻¹) | Net reproductive rate R₀ (egg) |
|---------------|-----------------------------------|--------------------------|--------------------------------|-------------------------------|
| 13            | 0.0080 ± 0.0059 b                 | 33.24 ± 3.3 a            | 1.0080 ± 0.0059 b               | 1.30 ± 0.24 b                 |
| 18            | 0.0340 ± 0.0044 a                 | 22.64 ± 0.77 b          | 1.0345 ± 0.0045 a              | 2.16 ± 0.22 a                 |

Means followed by different letters within the same column were significantly different (P < 0.05; paired bootstrap test).
Wang CL, Xiang NY, Zhang GS, Zhu HF. 1962. Studies on the soybean aphid, *Aphis glycines* Matsumura. Acta Entomologica Sinica 11: 31–44.

Wang L, Yang S, Zhao KJ, Liu J, Dai CC, Han LL, Zhang LQ. 2014. Effect of low temperature and photoperiod on soybean aphid forms from different geographical populations. Soybean Science 33: 228–231 (in Chinese with English abstract).

Wang SJ, Bai B, Gao B, Liu J. 2019. Comparing performance of *Aphis glycines* Matsumura fed on two novel hosts relative to *Glycine max* (L.) Merrill. Journal of Asia-Pacific Entomology 22: 975–981.

Wu Z, Schenk-Hamlin D, Zhan W, Ragsdale DW, Heimpel GE. 2004. The soybean aphid in China: a historical review. Annals of the Entomological Society of America 97: 209–218.

Xu L, Xu GQ, Liu PB, Chen Y, Wang XY, Zhao TH. 2011. Effects of temperature on development and reproduction of *Aphis glycines* Matsumura. Chinese Journal of Oil Crop Science 33: 189–192 (in Chinese with English abstract).

Xu L, Zhao JQ, Xu GQ, Zhong T, Zhao TH. 2015. Artificial induction of sexuales in *Aphis glycines* (Hemiptera: Aphididae). Chinese Bulletin of Entomology 52: 1429–1437 (in Chinese with English abstract).

Yoo HJS, O’Neil RJ, Voegtlin DJ, Graves WR. 2005. Host plant suitability of *Rhamnaceae* for soybean aphid (Homoptera: Aphididae). Annals of the Entomological Society of America 98: 926–930.

Yu M, Xing JJ, Yu HM. 2009. Air temperature change in Heilongjiang Province in recent 46 years. Journal of Natural Disasters 18: 158–164 (in Chinese with English abstract).

Zhou XJ, Wang FL, Wu YY, Na JH, Pan HS, Wang Y. 2013. Analysis of temperature change characteristics of Heilongjiang Province, northeast China and whole country in recent 60 years. Journal of Natural Disasters 22: 124–129 (in Chinese with English abstract).