

Effects of Five Host Plant Species on the Life History and Population Growth Parameters of *Myzus persicae* (Hemiptera: Aphididae)

Feng Hong,^{1,2} Hong-Liang Han,² Po Pu,^{2,3} Dong Wei,^{2,*} Jia Wang,² and Yinghong Liu^{2,4}

¹College of Agriculture, Xinyang Agriculture and Forestry University, Xinyang 464000, China, ²Chongqing Key Laboratory of Entomology and Pest Control Engineering, College of Plant Protection, Southwest University, Chongqing 400715, China, ³Sichuan Plant Protection Station, Chengdu 610041, China, and ⁴Corresponding author, e-mail: yhliu@swu.edu.cn

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Abstract

The green peach aphid, *Myzus persicae* Sulzer (Hemiptera: Aphididae), is an important agricultural pest with a wide range of host plants. To study effects of host species on the life history traits of *M. persicae*, aphids were individually reared on five host plants: *Brassica campestris* L. (Brassicales: Brassicaceae), *Capsicum annuum* L. (Tubiflorae: Solanaceae), *Nicotiana tabacum* L. (Tubiflorae: Solanaceae), *Raphanus sativus* L. (Brassicales: Brassicaceae), and *Vicia faba* L. (Rosales: Leguminosae). TWOSEX-MSchart software was used for the statistical analysis according to the age-stage, two-sex life table theory. The results showed that the shortest preadult stage and adult/total prereproductive period of *M. persicae* were 6.48, 0.19, and 6.67 d on *V. faba*, respectively. While the adult and total longevity of *M. persicae* on *R. sativus* (25.00 and 31.62 d) and *N. tabacum* (24.40 and 30.56 d) were significantly longer than that on the other three hosts, as was the reproductive period. The fecundity of *M. persicae* on *R. sativus* (80.83 nymphs per female), *N. tabacum* (71.72 nymphs per female), and *V. faba* (70.39 nymphs per female) was also greater than that on *B. campestris* and *C. annuum*. It was demonstrated that *V. faba*, *R. sativus*, and *N. tabacum* were more suitable plants for the growth of *M. persicae* exhibiting a shorter preadult stage, longer longevity, and greater fecundity than the remaining two species, as confirmed by the higher intrinsic rate of increase and net reproductive rate.

Key words: *Myzus persicae*, host species, life table, population characteristics

Ecological patterns may often be determined by the physiological constraints of interacting organisms (Singer 2001). One of the most important factors affecting the fitness of insect herbivores is the quality of the host plant. Compounds from host plants, such as carbon, nitrogen, and defense metabolites, directly affect the potential and achieved herbivore fecundity, and the responses of insect herbivores to changes in host plant quality vary within and between feeding guilds (Awmack and Leather 2002, Hosseini et al. 2019). Polyphagous herbivores are particularly challenged, as feeding on different plant species can result in differences in life history traits (Ojala et al. 2005). It is estimated that 15% of crop yield worldwide is lost to herbivore pests in spite of plant breeding and pest control efforts (Van Der Meijden 2015). However, plant diversity also promotes herbivore suppression through movement patterns, host associations, and predation promises a potential alternative to pesticide-intensive monoculture crop production (Letourneau et al. 2011). The fitness of a pest population is represented by its damage capacity to the host plant. That fitness can be properly evaluated using a life table, as it provides an integrated and comprehensive

description of the survival, development, and reproduction of a population (Tuan et al. 2016).

The life table is a powerful and necessary tool for analyzing and understanding the effect of external factors and host plants on the growth, survival, reproduction, and intrinsic rate of increase of insect populations (Chi and Su 2006). A life table study is fundamental for population ecology research and provides a complete description of the survivorship, development, stage differentiation, and reproduction of a population as well as basic population growth parameters (Hu et al. 2010, Yousaf et al. 2018). Using a life table, population projections can be made by means of computer simulations (Chi 1990). Life tables have been used in a variety of studies related to population ecology, such as the effect of temperature on population growth of *Hyalopterus pruni* Geoffroy (Hemiptera: Aphididae) (Atlihan and Chi 2008), climate change/global warming studies (Kanle Satishchandra et al. 2019), host plant resistance on *Lipaphis erysimi* Kaltentbach (Hemiptera: Aphididae) (Qayyum et al. 2018), and harvesting theory (Yu et al. 2018).

As an economically important pest, the green peach aphid, *Myzus persicae* Sulzer (Hemiptera: Aphididae), attacks over 400 species in

more than 50 plant families, including Solanaceae, Cruciferae, and Leguminosae (Weber 1985, Tang et al. 2019). Its polyphagy is attributed to its ecological and phenotypic plasticity and physiological adaptability to a large array of primary and secondary compounds from diverse host species. To quantitatively analyze the effect of different host plants on the life history of *M. persicae*, we constructed several life tables of *M. persicae* using the age-stage, two-sex life table theory. The current study provides a comprehensive insight into the host preference of *M. persicae*. Our findings can be used for developing targeted strategies for prevention of the green peach aphid.

Materials and Methods

Aphid and Host Plant Culture

Adult *M. persicae* samples were collected from *Nicotiana tabacum* L. (Tubiflorae: Solanaceae) plants in Chongqing, China, and then maintained on the same host species in a climate incubator at $23 \pm 1^\circ\text{C}$, $50 \pm 5\%$ RH, and a photoperiod of 16:8 (L:D) h. Five host plants commonly found in Chongqing were used for this study, including rapeseed [*Brassica campestris* L. (Brassicales: Brassicaceae)], pepper [*Capsicum annuum* L. (Tubiflorae: Solanaceae)], tobacco (*N. tabacum*), radish [*Raphanus sativus* L. (Brassicales: Brassicaceae)], and faba bean [*Vicia faba* L. (Rosales: Leguminosae)]. All tested plants were grown in growth chambers with Pindstrup substrate as media and were watered as required.

Life Table Construction

For the life table study, more than 100 *M. persicae* adults were transferred onto tobacco leaves. After 12 h, newborn nymphs were individually transferred to the leaf discs (2 cm of diameter) of five host plants. The leaf disc was placed upside down on a water-saturated sponge pad in a plastic dish (8.5 cm of diameter, and 1.5 cm of height). A piece of filter paper with a hole (2 cm of diameter at the center) was placed onto the leaf disc to form a water fence. The molting and reproduction of *M. persicae* were observed and recorded every 12 h until all aphids were dead. All studies were carried out in climate incubators (MLR-351H, Panasonic, Matsuyama, Japan) at $23 \pm 1^\circ\text{C}$, $70 \pm 5\%$ RH, and a photoperiod of 16:8 (L:D) h (Tang et al. 2017).

Statistical Analysis

TWOSEX-Mschart software was used for analysis of the life history based on the age-stage, two-sex life table theory (Chi and Liu 1985).

The means of developmental periods for each stage and total longevity of *M. persicae* reared on different host plants were calculated as well as the age-stage-specific survival rate (s_{xj}). s_{xj} represents the probability that a newborn aphid will survive to age x and stage j . The age-stage life expectancy (e_{xj}) was also calculated, which is defined as the length of duration or time that a green peach aphid of x and j is predicted to live (Chi and Su 2006).

$$e_{xj} = \sum_{i=x}^{\infty} \sum_{y=j}^k s'_{iy}$$

where s'_{iy} represents the probability that individuals of age = x and stage = j will survive to age = i and stage = y .

Additionally, the means of prereproductive period and female fecundity were also calculated. The adult prereproductive period (APRP) was defined as the duration of time from the emergence of the adult female to its initial reproduction, and the total prereproductive period (TPRP) was the total duration of time from the beginning of the life table study to the female's initial reproduction. After that, we calculated the reproductive value (v_{xj}) to evaluate the contribution of an individual at age x in stage j to the future population (Rostami et al. 2018).

$$v_{xj} = \frac{e^{r(x+1)}}{s_{xj}} \sum_{i=x}^{\infty} e^{-r(i+1)} \sum_{y=j}^k s'_{iy} f_{iy}$$

The population parameters (R_0 , net reproductive rate; r , intrinsic rate of increase; λ , finite rate of increase; and T , the mean generation time) of *M. persicae* on different host plants were estimated accordingly. R_0 is defined as the total offspring produced by an individual during its life span. r is the rate at which a population increases in size without density-dependent forces. λ indicates the number of times the population multiplies in a unit of time. T is the time required for a population to increase its size by R_0 -fold in the stable age distribution (Akköprü et al. 2015). These parameters were calculated as:

$$R_0 = \sum_{x=0}^{\infty} l_x m_x,$$

$$\sum_{x=0}^{\infty} e^{-r(x+1)} l_x m_x = 1,$$

Table 1. Effect of host plants on the development of *Myzus persicae*

Statistics	Host species									
	<i>Vicia faba</i>		<i>Capsicum annuum</i>		<i>Raphanus sativus</i>		<i>Nicotiana tabacum</i>		<i>Brassica campestris</i>	
	<i>n</i>	Mean \pm SE	<i>n</i>	Mean \pm SE	<i>n</i>	Mean \pm SE	<i>n</i>	Mean \pm SE	<i>n</i>	Mean \pm SE
Preadult duration (d)	116	6.48 \pm 0.04c	118	6.44 \pm 0.06c	120	6.62 \pm 0.05b	117	6.77 \pm 0.08b	116	7.54 \pm 0.11a
First instar (d)	120	1.70 \pm 0.03c	120	1.80 \pm 0.03b	120	1.61 \pm 0.03d	120	1.78 \pm 0.03bc	120	2.34 \pm 0.05a
Second instar (d)	119	1.42 \pm 0.02d	120	1.50 \pm 0.03bc	120	1.55 \pm 0.03b	120	1.42 \pm 0.03cd	116	1.78 \pm 0.07a
Third instar (d)	118	1.57 \pm 0.02a	120	1.42 \pm 0.03b	120	1.57 \pm 0.02a	119	1.63 \pm 0.03a	116	1.63 \pm 0.05a
Fourth instar (d)	116	1.79 \pm 0.03b	118	1.71 \pm 0.03b	120	1.89 \pm 0.02a	117	1.97 \pm 0.05a	116	1.81 \pm 0.09ab
Adult longevity (d)	116	17.66 \pm 0.62b	118	15.37 \pm 0.82c	120	25.00 \pm 0.56a	117	24.40 \pm 0.81a	116	17.80 \pm 0.71b
Total longevity (d)	120	23.51 \pm 0.68bc	120	21.55 \pm 0.83c	120	31.62 \pm 0.56a	120	30.56 \pm 0.85a	120	24.69 \pm 0.75b

Means in the same row followed by different letters are significantly different ($P < 0.05$) using bootstrap test.

$$\lambda = e^r,$$

$$T = \frac{\ln R_0}{r}.$$

The means and standard errors of the developmental time, longevity, fecundity, and population parameters were estimated using the bootstrap technique. To reduce the variability of the results, we used 200,000 bootstrap replications in this study. The differences among

the five host treatments were analyzed by the paired bootstrap test with a P value of less than 0.05.

Results

Effect of Host Species on the Development of *M. persicae*

The durations of the four nymph stages for the aphids fed with five plant species all differed significantly from each other (Table 1). The preadult durations for *M. persicae* reared on *B. campestris*,

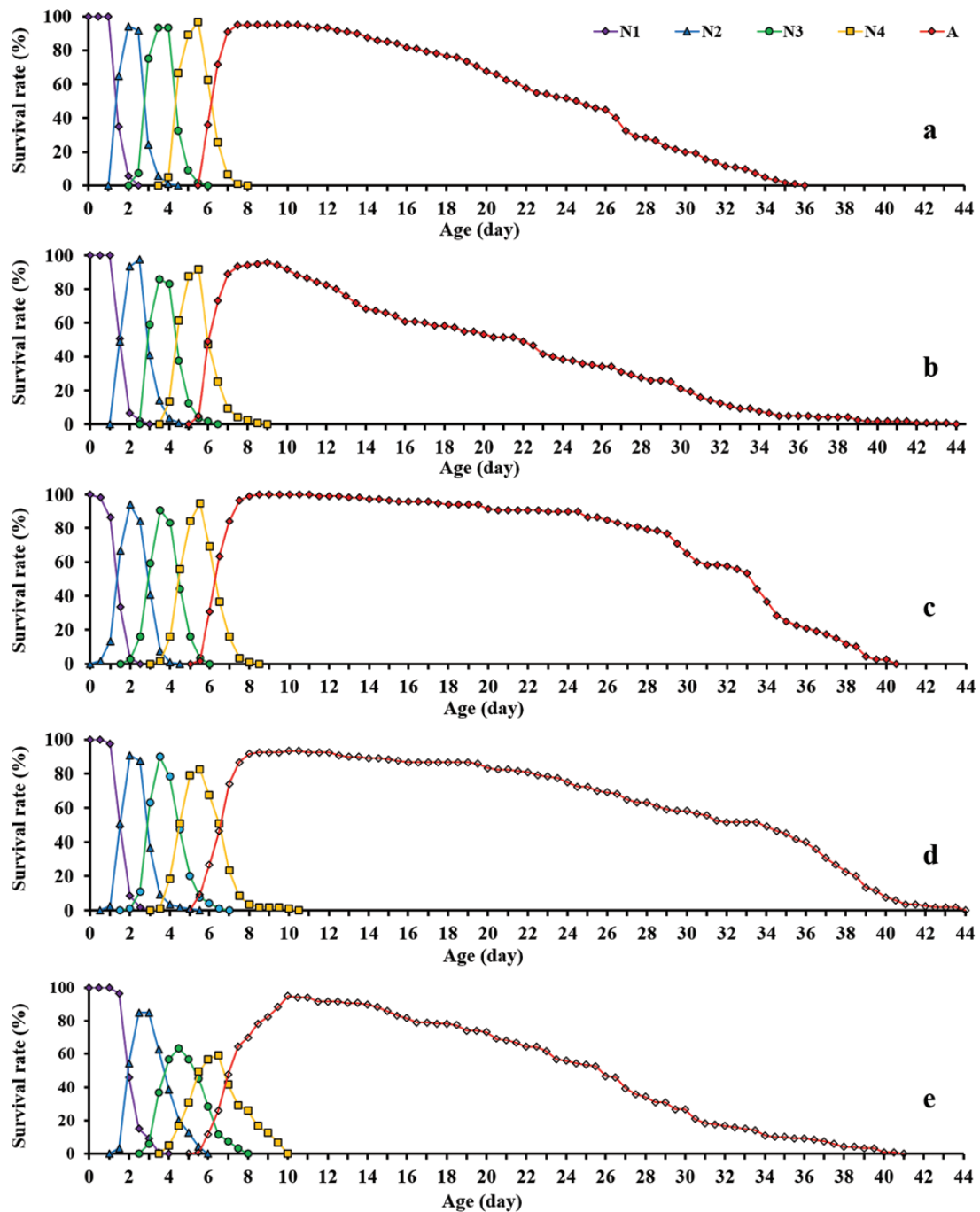


Fig. 1. The age-stage-specific survival rate (s_{x_i}) of *Myzus persicae* on five different host plants. N1, first instar nymph, purple curve; N2, second instar nymph, blue curve; N3, third instar nymph, green curve; N4, fourth instar nymph, yellow curve; A, adult aphid, red curve. Each panel represents *Vicia faba* (a), *Capsicum annuum* (b), *Raphanus sativus* (c), *Nicotiana tabacum* (d), *Brassica campestris* (e), respectively.

C. annuum, *N. tabacum*, *R. sativus*, and *V. faba* were 7.54 ± 0.11 , 6.44 ± 0.06 , 6.77 ± 0.08 , 6.62 ± 0.05 , and 6.48 ± 0.04 d, respectively. The shortest preadult durations were observed on *C. annuum* and *V. faba*, and the curves of the age-stage-specific survival rate (s_{xj}) showed that the survival rates of mature aphids on *C. annuum* and *B. campestris* were lower than those on *N. tabacum* and *R. sativus* (Fig. 1; Supp Fig. 1 [online only]). The adult longevity and total longevity of the aphids reared on *C. annuum* and *B. campestris* were also significantly shorter than those reared on *N. tabacum* and *R. sativus*. The age-stage life expectancy (e_{xj}) showed the same trend

(Fig. 2; Supp Fig. 2 [online only]). The life expectancy of the new born nymph at age = 0 and stage = 1 (e_{01} value) was exactly the mean longevity of 21.55 ± 0.83 d on *C. annuum*, 23.51 ± 0.68 d on *V. faba*, 24.69 ± 0.75 d on *B. campestris*, 30.56 ± 0.85 d on *N. tabacum*, and 31.62 ± 0.56 d on *R. sativus*, respectively (Table 1).

Effect of Host Species on the Fecundity of *M. persicae*

Means of TPRP and APRP of *M. persicae* reared on different host plants also differed significantly (Table 2). Mature aphids and

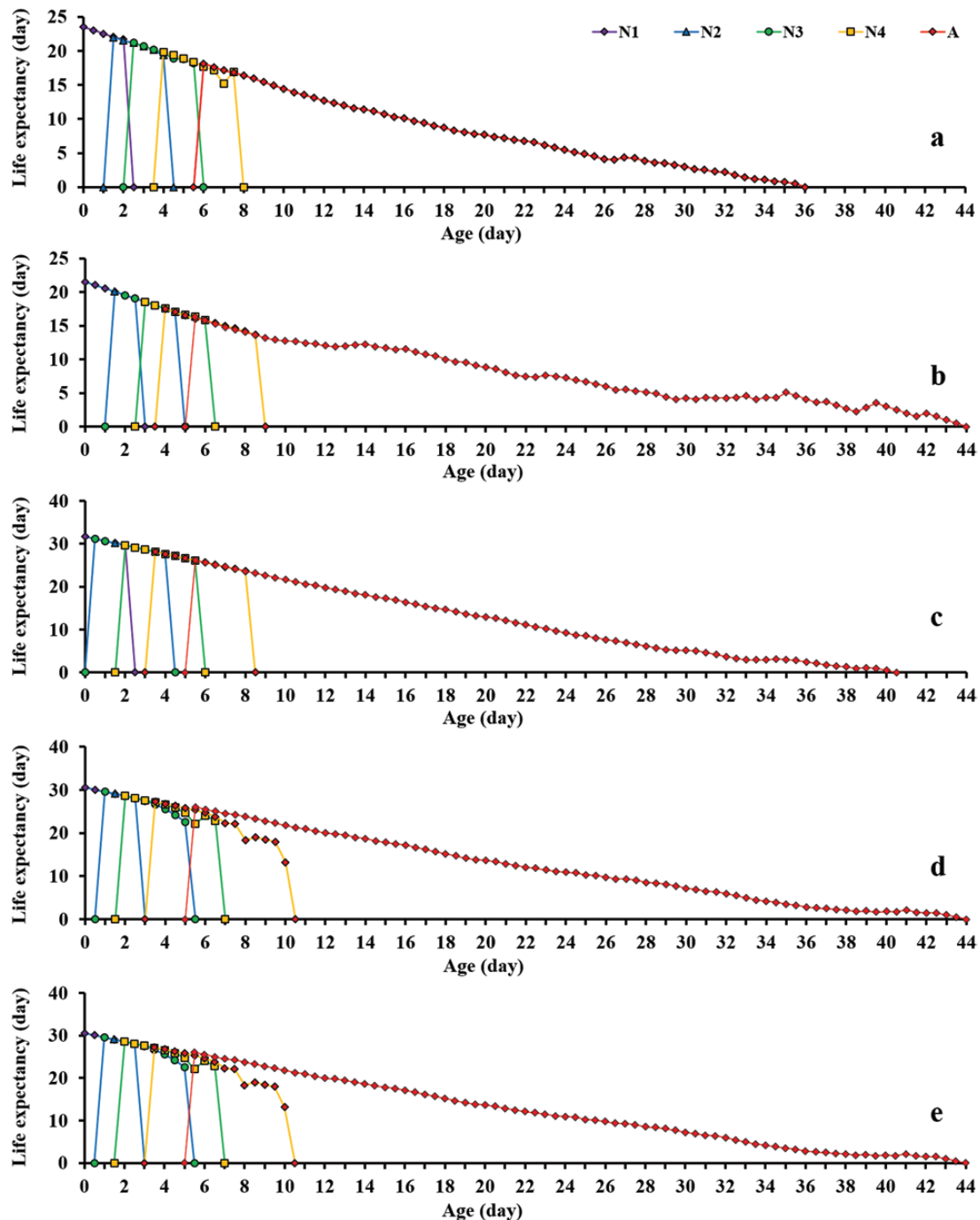


Fig. 2. The age-stage-specific life expectancy (e_{xj}) of *Myzus persicae* on five different host plants. N1, first instar nymph, purple curve; N2, second instar nymph, blue curve; N3, third instar nymph, green curve; N4, fourth instar nymph, yellow curve; A, adult aphid, red curve. Each panel represents *Vicia faba* (a), *Capsicum annuum* (b), *Raphanus sativus* (c), *Nicotiana tabacum* (d), *Brassica campestris* (e), respectively.

Table 2. Effect of host plants on the fecundity (nymphs per female) of *Myzus persicae*

Statistics	Host species									
	<i>Vicia faba</i>		<i>Capsicum annuum</i>		<i>Raphanus sativus</i>		<i>Nicotiana tabacum</i>		<i>Brassica campestris</i>	
	<i>n</i>	Mean ± SE	<i>n</i>	Mean ± SE	<i>n</i>	Mean ± SE	<i>n</i>	Mean ± SE	<i>n</i>	Mean ± SE
APRP (d) ^a	114	0.19 ± 0.03c	116	0.61 ± 0.04a	120	0.41 ± 0.03b	112	0.64 ± 0.07a	115	0.44 ± 0.08ab
TPRP (d) ^b	114	6.67 ± 0.05d	116	7.04 ± 0.08c	120	7.03 ± 0.06c	112	7.37 ± 0.09b	115	7.99 ± 0.13a
Reproductive period (d)	114	12.96 ± 0.36c	116	11.05 ± 0.59d	120	18.30 ± 0.43a	112	14.03 ± 0.34b	115	12.26 ± 0.44cd
Fecundity (nymphs per female)	114	70.39 ± 2.26b	116	47.05 ± 2.54d	120	80.83 ± 2.09a	112	71.72 ± 2.12b	115	53.71 ± 2.23c

Means in the same row followed by different letters are significantly different ($P < 0.05$) using bootstrap test.

^aAPRP = adult prereproductive period.

^bTPRP = total prereproductive period.

newborn aphids on *V. faba* both took the least time to produce offspring (APRP = 0.19 ± 0.03 d and TPRP = 6.67 ± 0.05 d), whereas the greatest APRP and TPRP were, respectively, observed in newborn aphids on *C. annuum* (APRP = 0.61 ± 0.04 d) and mature aphids on *B. campestris* (TPRP = 7.99 ± 0.13 d). Conversely, the reproductive period of *M. persicae* on *C. annuum* and *B. campestris* was shortest. Upon comparison of aphids' fecundity on different host species, we found that the mean nymph-laying per female on *C. annuum* and *B. campestris* was also significantly lower than on the other three host plants. There were no significant differences among the v_{xj} of the *M. persicae* females reared on various host species, but the curves for aphids on *C. annuum* and *B. campestris* showed lower peaks than the others (Fig. 3; Supp Fig. 3 [online only]), which further supported the weak fecundities of the two host populations.

Life Table Parameters

Table 3 presents the age-stage, two-sex life table parameters of *M. persicae* reared on different host species, all of which showed significant differences among these populations. Aphids on *V. faba* exhibited the highest intrinsic rate ($r = 0.3831 \pm 0.0037$ d⁻¹) and finite rate of increase ($\lambda = 1.4669 \pm 0.0054$ d⁻¹), and the shortest mean generation time ($T = 11.0139 \pm 0.0842$ d). Correspondingly, the aphids on *B. campestris* exhibited the lowest r (0.3207 ± 0.0052 d⁻¹) and λ (1.3781 ± 0.0072 d⁻¹), and the longest T (12.3146 ± 0.1360 d). The largest net reproductive rate R_0 was detected in aphids on *R. sativus* (80.8317 ± 2.0886 offspring per individual), while aphids on *C. annuum* and *B. campestris* produced the least total offspring (46.2691 ± 2.5565 offspring per individual for *C. annuum*, and 51.9251 ± 2.3313 offspring per individual for *B. campestris*) during their life spans.

Discussion

The parameter r (intrinsic rate of increase) is regarded as a useful concept in demographic analyses of insect populations (Birch 1948). This parameter (r) summarizes the physiological qualities of an animal relative to its capacity of increase and is often used to compare the fitness of populations across diverse climatic and food-related conditions (Tsai and Wang 2001, Saeed et al. 2010). The r values for *M. persicae* were reported as 0.160 – 0.256 d⁻¹ a decade ago on solanaceous and cruciferous vegetables and crops (Boughton et al. 2006, Chi and Su 2006, Davis et al. 2006, Ribeiro et al. 2006), which is significantly lower than in the present study. This might be attributed to the enhanced adaptability of *M. persicae* to a complex

environment. Life history theory is based on the assumption that evolution is constrained by trade-offs among different traits that contribute to fitness, and life history costs play a central role in explaining the evolution of resistance (Carriere et al. 1994). Fitness costs include reduced survival, increased developmental time, and reduced fecundity (Sayyed et al. 2008). Therefore, the stronger the adaptability, the lower the fitness cost, and the higher the r value.

The age at first nymph-laying is critical for r value calculation. If fecundity remains the same, early reproduction will be associated with a high r value (Huang and Chi 2012). Both the APRP and TPRP of *M. persicae* on *V. faba* were shortest, resulting in the highest r value of increase, which is consistent with the aforementioned theory. Conversely, the two statistics, APRP and TPRP do not represent the actual beginning of reproduction, and thus their effects on the r value should not be overemphasized (Jha et al. 2012). Barlow (1962) found that offspring produced after peak fecundity have little influence on the r value of the population when the fecundity rate is more or less sharply defined in time. Therefore, the number of offspring produced by aphids on the five host species before peak fecundity was analyzed and indicated the same r value order. It does not necessarily follow that the higher the r value is, the more successful the species will be.

Most species exist in saturated environments and abundance fluctuates in response to changes in the conditions of survival and growth as a result of changes in factors such as weather (Cole 1954). One can examine the potential importance of life history parameters in adapting to perturbations by determining the effect of change in the life history parameters on the net reproductive rate R_0 . In our study, aphids reared on *R. sativus* exhibited a higher R_0 than that on the other plant species, while the aphids on *C. annuum* and *B. campestris* performed poorly. To determine the effective factors, correlation analyses were carried out with a correlation coefficient equal to 0.05 between R_0 and the means of each developmental period, reproductive period, female fecundity, age-stage-specific survival rate s_{xj} , and the female age-stage-specific fecundity $f_{x,j, \text{female}}$. With the exception of reproductive period, s_{xj} , and female fecundity, the remainder of the indices showed no significant correlation with R_0 value. Female fecundities showed a similar tendency as the R_0 value, as preadult survival rates of the *M. persicae* females on the five host plants were quite similar in terms of the equation $R_0 = s_{\alpha} \cdot F$, where s_{α} represents the preadult survival rate and F is the mean female fecundity. However, the female age-stage-specific fecundity $f_{x,j, \text{female}}$ was not found to be closely related to the R_0 value, which indicated that the net reproductive rate of a population is associated with the adult number and the total offspring but not the adult age or the daily

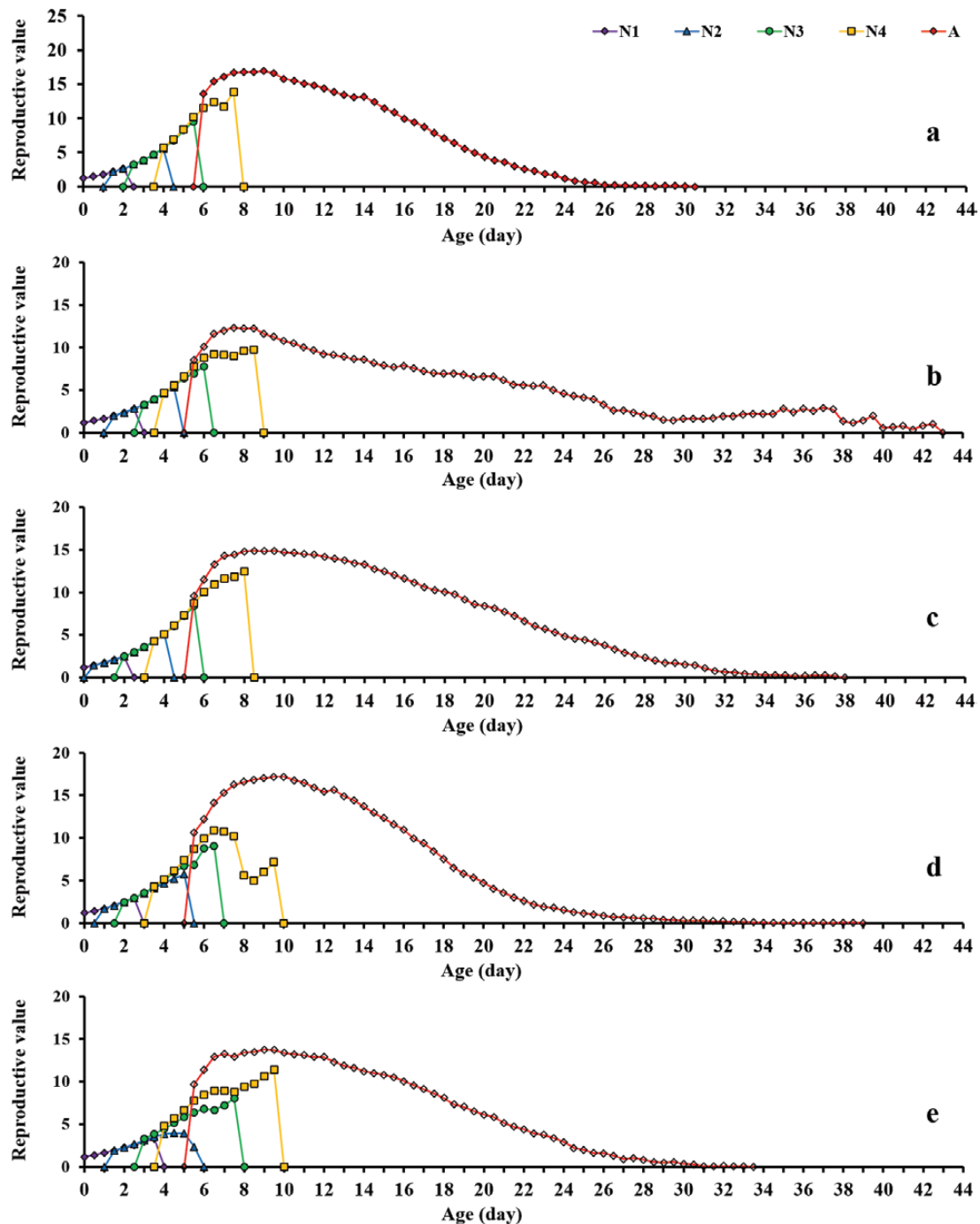


Fig. 3. The age-stage-specific reproductive value (v_{xj}) of *Myzus persicae* on five different host plants. N1, first instar nymph, purple curve; N2, second instar nymph, blue curve; N3, third instar nymph, green curve; N4, fourth instar nymph, yellow curve; A, adult aphid, red curve. Each panel represents *Vicia faba* (a), *Capsicum annuum* (b), *Raphanus sativus* (c), *Nicotiana tabacum* (d), *Brassica campestris* (e), respectively.

fecundity. Though the reproductive period and s_{xj} of the aphids on *V. faba* were both lower than those on *N. tabacum*, the R_0 value for *M. persicae* on *V. faba* was similar to that on *N. tabacum*. Nitrogen application rates are known to affect the individual size, survival, and r value of several species of rice pest (Jahn et al. 2005). It was concluded that the nitrogen-rich legumes improved the fertility of the parasitic aphid and further affected the population development.

In conclusion, *V. faba*, *R. sativus*, and *N. tabacum* constituted more suitable host plants for *M. persicae* and were associated with a shorter preadult stage, longer longevity, and stronger fecundity

in comparison to the remaining species. Furthermore, the intrinsic rate r of the aphids was also significantly higher on *V. faba*, which depended on their ages at first nymph-laying and the number of offspring produced before peak fecundity. Another important life history parameter, R_0 was found to be higher in aphids reared on *R. sativus* than that on the other plant species, proving that the adult number was more meaningful to the population growth of *M. persicae* than the adult age. Laboratory colonies of *M. persicae* are necessary for experimental study of its biology, behavior, and insect-virus interactions. In our study, *R. sativus* was proved to be the

Table 3. Life table parameters of *Myzus persicae* on five different host plants

Statistics	Host species				
	<i>Vicia faba</i>	<i>Capsicum annuum</i>	<i>Raphanus sativus</i>	<i>Nicotiana tabacum</i>	<i>Brassica campestris</i>
	<i>n</i>	<i>n</i>	<i>n</i>	<i>n</i>	<i>n</i>
r (d^{-1})	120	120	120	120	120
λ (d^{-1})	0.3831 ± 0.0037a	0.3422 ± 0.0045c	0.3616 ± 0.0034b	0.3595 ± 0.0045b	0.3207 ± 0.0052d
R_0 (offspring per individual)	1.4669 ± 0.0054a	1.4080 ± 0.0063c	1.4356 ± 0.0049b	1.4327 ± 0.0065b	1.3781 ± 0.0072d
T (d)	68.0439 ± 2.4674b	46.2691 ± 2.5565c	80.8317 ± 2.0886a	67.5278 ± 2.5226b	51.9251 ± 2.3313c
	120	120	120	120	120
	11.0139 ± 0.0842c	11.2025 ± 0.1346c	12.1484 ± 0.1041a	11.7156 ± 0.0890b	12.3146 ± 0.1360a

r = intrinsic rate of increase; λ = finite rate of increase; R_0 = net reproductive rate; T = mean generation time. Means in the same row followed by different letters are significantly different ($P < 0.05$) using bootstrap test.

most favorable cultivar for the green peach aphid in lab which exhibited the longest longevity and strongest fecundity. If mass-rearing of this species, *V. faba* will be the best choice because of the short prereproductive period and the strong fecundity.

Supplementary Data

Supplementary data are available at *Journal of Insect Science* online.

Figure S1. The age-specific survival rate (s_{xj}) of adult *Myzus persicae* on five different host plants. Purple curve, *Vicia faba*; blue curve, *Capsicum annuum*; green curve, *Raphanus sativus*; yellow curve, *Nicotiana tabacum*; red curve, *Brassica campestris*.

Figure S2. The age-specific life expectancy (e_{xj}) of adult *Myzus persicae* on five different host plants. Purple curve, *Vicia faba*; blue curve, *Capsicum annuum*; green curve, *Raphanus sativus*; yellow curve, *Nicotiana tabacum*; red curve, *Brassica campestris*.

Figure S3. The age-specific reproductive value (v_{xj}) of adult *Myzus persicae* on five different host plants. Purple curve, *Vicia faba*; blue curve, *Capsicum annuum*; green curve, *Raphanus sativus*; yellow curve, *Nicotiana tabacum*; red curve, *Brassica campestris*.

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