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Original article

Effects of different host plants on population fitness of pea aphid (*Acyrthosiphon pisum*)

Ning Lv [a], Qiao-Yan Yang [a], Chun-Chun Li [a], Ting-Wei Zhang [a], Shahbaz Ali [a,b], Chang-Zhong Liu [a,*], Islem Abid [c], Mohamed Ragab AbdelGawwad [d]

[a] Biocontrol Engineering Laboratory of Crop Diseases and Pests of Gansu Province, College of Plant Protection, Gansu Agricultural University, Lanzhou 730070, China
[b] Department of Agricultural Engineering, Khwaja Fareed University of Engineering and Information Technology, Rahim Yar Khan, Punjab, Pakistan
[c] Botany and Microbiology Department, Science College, King Saud University, Riyadh, Saudi Arabia
[d] Genetics and Bioengineering, Faculty of Engineering and Natural Sciences, International University of Sarajevo, 71210 Sarajevo, Bosnia and Herzegovina

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ABSTRACT

Background: Host plants not only provide and living places and energy materials for insects, but also influence insect population parameters and population fitness.
Methods: This study examined the influence of various host plant species on the fitness of pea aphid (*Acyrthosiphon pisum*). The biological parameters and population parameters of pea aphid on 6 different host plants (*Vicia fabae*, *Pisum sativum*, *Medicago sativa*, *Trifolium pratense*, *Onobrychis viciaefolia* and *Melilotus officinalis*) were observed and counted by ecological experiments, which were carried out in a control chamber.
Results: The results showed that the developmental duration of 1st and 2nd instar nymphs of pea aphids on *T. pratense* and *P. sativum* was significantly prolonged, whereas that of 3rd and 4th instar nymphs on *O. viciaefolia* and *M. officinalis* was significantly shortened. Compared with the pea aphid on the *V. faba*, the longevity of adults on *M. officinalis* and *P. sativum* was significantly prolonged, but only the generation time on *P. sativum* was significantly prolonged. Moreover, the survival rate of nymphs was significantly lower on *O. viciaefolia* and *M. sativa* than on others. Net reproductive rate and mean generation time on *V. faba* were significantly higher than in other host plants. The intrinsic rate of increase (r_m) and finite rate of increase (λ) of pea aphid feeding of *A. pisum* on *P. sativum* and *O. viciaefolia* decreased. However, those on the double population time on *P. sativum* and *O. viciaefolia* were significantly higher than the others.
Conclusion: The findings will clarify the population fitness of pea aphids on different hosts and guide the rational distribution of different host plants, and provide new references for aphid control strategies.

1. Introduction

Aphids is an important kind of pest with piercing-sucking mouthparts, which can reduce crop yields by invading plant tissues and absorbing phloem sieve components. This results in stunted plant development and low growth. At the same time, aphids can spread plant virus diseases, causing infection and severe damage to crops. In addition, honeydew secreted by aphids not only affects the photosynthesis of plants, but also causes soot diseases of the plant (Gong et al. 2014, Patrick et al. 2018, Nalam et al. 2018). The pea aphid (Hemiptera: Aphididae), scientifically known as *Acyrthosiphon pisum* Harris, is a major pest across the world because it feeds on many different kinds of leguminous plants (Peccoud et al. 2009b, De Geyter et al. 2011, Peccoud et al. 2015). When introduced into a suitable host field, pea aphids can rapidly increase population size due to their parthenogenetic system and short generation time, resulting in significant economic losses. Furthermore, pea aphids are capable of spreading more than 30 plant viruses, such as pea streak virus, red clover vein mosaic virus, and bean yellow mosaic virus, which can be transmitted through aphids (Peccoud et al. 2009a, Goławska and Łukasik 2012,

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* Corresponding author at: Biocontrol Engineering Laboratory of Crop Diseases and Pests of Gansu Province, College of Plant Protection, Gansu Agricultural University, Lanzhou 730070, China.

E-mail address: lvn@gsau.edu.cn (N. Lv).

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Congdon et al. 2017). Consequently, serious production losses occurred the destruction of alfalfa fields by pea aphids caused an average annual loss of 60 million US dollars in the United States (Harmon et al. 2009), and an annual economic loss of about 10%-30% in Northwest China (He et al. 2005).

Insect populations are affected by biotic and abiotic factors, including host plants, temperature, carbon dioxide, and concentration (Sun et al., 2016). Both plants and the insects that feed on plants are engaged in a strong competition for their own survival (Tesfaye et al., 2021). Host plants have created a wide variety of unique, poisonous, and insect-repelling compounds that serve as organic defenses against herbivorous insects (Li et al. 2017). These plants can synthesize a variety of secondary metabolites, such as phenolic compounds, phenols, saponins, flavonoids, and alkaloids (Heidel-Fischer and Vogel 2015). Secondary metabolites can repel phytophagous insects or have antifeedant, toxic and regulatory activities by increasing oxidative stress in insect tissues, thus affecting insect physiology (Woźniak et al. 2019, Goławska and Łukasik 2012). To maintain homeostasis, aphids have evolved complex adaptive mechanisms, such as detoxification enzymes against host plants' defense (Heiko and Celorio-Mancera, 2014)Li et al. 2020). Activities of insect detoxification enzymes (Pei et al. 2010), such as glutathione S-transferases (GSTs), cytochrome P450 (CYP450s), and carboxylesterases (CarEs), protect aphids under stress (Heidel-Fischer and Vogel 2015, Amezian et al. 2021). Changes in biochemical and morphological characteristics associated with plant defense have a significant affect on the expression of plants resistance to insect pests (Sharma et al. 2016b). In the last few years, the emergence of the global greenhouse effect, the frequent occurrence of extreme climates, and the incorrect use of chemical fertilizers and insecticides in agriculture have led to the significant expansion of the aphid population (Sharma et al. 2016a, Chen et al. 2019).

Climate change has increased the impact of irregular weather conditions, such as low and erratic precipitation, which can lead to drought stress and increase pest population density, adversely affecting crop production (Sharma et al. 2016a, Chen et al. 2019). Sap-sucking insects are among the most significant economic pests of crops and cause substantial damage to agricultural production all over the world (Nguyen et al., 2017). Globally, farmers consider pea aphids a more serious economic pest than defoliators. These aphids cause extensive plants damage by feeding, honeydew production, and transmission of the virus. As a result, a variety of synthetic pesticides are still employed to manage agricultural pests. Such a method has seriously endangered the health of farmers, animals, and food consumers while also greatly increasing environmental pollution and pesticide resistance. Hence, the identification of aphid-resistant cultivars is critical to agricultural production. The hypothesis behind this research is that the natural defense of different host plants will affect the performance of pea aphids. As a result, the study aimed to evaluate how various host plant species affect the population fitness of pea aphids and to identify its ecological phenotypes on different hosts. This study serves as a basis for further research on the interactions between pea aphids and host plant species.

2. Materials and Methods

2.1. Aphids culture

Pea aphids were collected from the alfalfa experimental field of Gansu Agricultural University in Lanzhou, China (36.03°N, 103.40°E). The parthenogenesis of one pea aphid led to the establishment of a single asexual line, which was used for further tested materials. The aphid populations were cultured on broad bean *Vicia fabae* under a 16-h ligh:8-h dark photoperiod at 22 ± 1 ℃ with 70–80% relative humidity in the laboratory. Aphid cultures were maintained for at least 3 generations before being used in the experiment.

2.2. Host plants

The experiment involved six host plants, including broad bean *Vicia fabae* (primary host plant), pea (*Pisum sativum*), alfalfa (*Medicago sativa*), clover (*Trifolium pratense*), red bean grass (*Onobrychis viciaefolia*) and melilotus (*Melilotus officinalis*). All host plants were used for further experiments in the laboratory to study the effects of different host plants on the population fitness of pea aphids. The experimental populations of different host plants of pea aphids were established in the laboratory with six host plants of at least 3 generations and then used in the experiment.

2.3. Effects of different plants on the growth and reproduction of pea aphid

To investigate how different host plants impact the growth, development, and fecundity of pea aphids, the experiment utilized detached leaves-feeding method. This involved placing fresh and clean leaves on a piece of filter paper in a Petri dish (10 cm). The petioles of leaves were wrapped with absorbent cotton balls, and sufficient ddH_2O was added to keep the cotton ball and filter paper wet. Then one aphid was put into a Petri dish within 6 h after birth and fed on the leaves of the corresponding six plant species. The Petri dishes were placed in an artificial climate box (RZX, Ningbo Jiangnan Co. Ltd., Ningbo, China) with a temperature of 22 ± 1 °C, 70–80% relative humidity, and a 16-h ligh:8-h dark photoperiod. The fresh leaves were added every 3 days. A total of aboat 50 aphids were used per plant. The number of dead aphids, the molting time, and frequency was observed and recorded every 12 h, and the molting dander was picked out with camel brush. Each nymph was counted every day until the death of the adult aphids. The biological parameters of pea aphids on six host plants were calculated, such as nymph survival rate, nymph developmental duration, aphid mortality, adult fecundity, and adult longevity.

2.4. Statistical analysis

The biological parameters (developmental duration, adult longevity, and generation time) of a single aphid were used as a biological replicate for statistical analysis. 17 aphids were randomized into one group, and each group was established as a biological replicate for statistical analysis of the time-dependent life table and nymph survival rate. The experiment was repeated three times. Population parameters of different host plants were calculated as: Net reproductive rate: $R_0 = \sum l_x m_x$; Mean generation time: $T = \sum x l_x m_x / \sum l_x m_x$; Intrinsic rate of increase: $r_m = \ln R_0 / T$; Finite rate of increase: $\lambda = e^{rm}$; Population doubling time: $Dt = \ln 2 / r_m$; where x is a time interval in days, l_x denotes the survival probability of female during the period of x, and m_x indicates the average numbers of new nymphs during the period of x (Gou et al.2021, Govindan and Hutchison 2020). Excel 2019 was used for data sorting, and Sigmaplot 12 (Systat Software Inc., San Jose, CA, USA) was used to draw diagrams. Statistical analysis was performed using IBM SPSS Statistics version 20.0 (SPSS 20.0) (IBM, Armonk, NY, USA). Tukey' S HSD was used in the variance analysis (ANOVA) to indicate significant differences among different treatments. Nymphal survival data was performed arcsine transformation and then analyzed with one-way ANOVA.

3. Results

3.1. Effects of different host plants on the developmental duration of pea aphid

Six host plants have different effects on the development duration of the pea aphid. The development duration of the 1st instar nymph of pea aphid on the *T. pratense* was the longest, which was significantly different from the other five hosts (Fig. 1A, $F_{(5,\ 300)} = 11.027$, $P < 0.001$). The developmental duration of the 2nd instar nymph was significantly shorter on *M. officinalis* than that of *P. sativum* (Fig. 1B, $F_{(5,\ 300)} = 6.014$, $P < 0.001$). The nymph developmental time of the 3rd and 4th instar pea aphids was the same in the six host plants. The development duration of pea aphid on *O. viciaefolia* was obviously longer than that of *V. faba, P. sativum*, and on *T. pretense* (Fig. 1C, $F_{(5,\ 300)} = 9.891$, $P < 0.001$; Fig. 1D, $F_{(5,\ 300)} = 2.991$, $P < 0.05$).

3.2. The survival rate of pea aphid nymph on different host plants

The survival rate of pea aphid nymph was the highest on the *T. pretense*, compared with other host plants. There was no significant difference in the survival rates of pea aphid nymphs fed on *M. officinalis*, *T. pratense*, *P. sativum*, and V. *faba*. However, the nymph survival rates fed on *O. viciaefolia* and *M. sativa* had no statistically significant difference but had a significant difference when fed on other plants (Fig. 2, $F_{(5,\ 12)} = 43.185$, $P < 0.001$).

3.3. Effects of different host plants on the adult longevity and generation time of pea aphid

The adult longevity of pea aphids on *M. officinalis* and *P. sativum* was longer than that of the other four host plants (Fig. 3A, $F_{(5,\ 300)} = 210.435$, $P < 0.001$). However, the effect of host plants on the generation duration of pea aphids differed from that of adult longevity. The generation time of pea aphid on *T. pratense* was the shortest, which was significantly different from that of the *P. sativum* and *M. officinalis*, but had no significant difference with that of the other three host plants (Fig. 3B, $F_{(5,\ 300)} = 30.12$, $P < 0.001$).

3.4. Effects of different host plants on the survival curve of pea aphid

The nymph survival and survival rate of pea aphids were different in all host plants. The nymph survival on *P. sativum* and *M. officinalis* were significantly lower than that on *V. faba* (Fig. 4). The survival curve of pea aphid on *V. faba* was significantly different from that of the other five host plants (log-rank test,

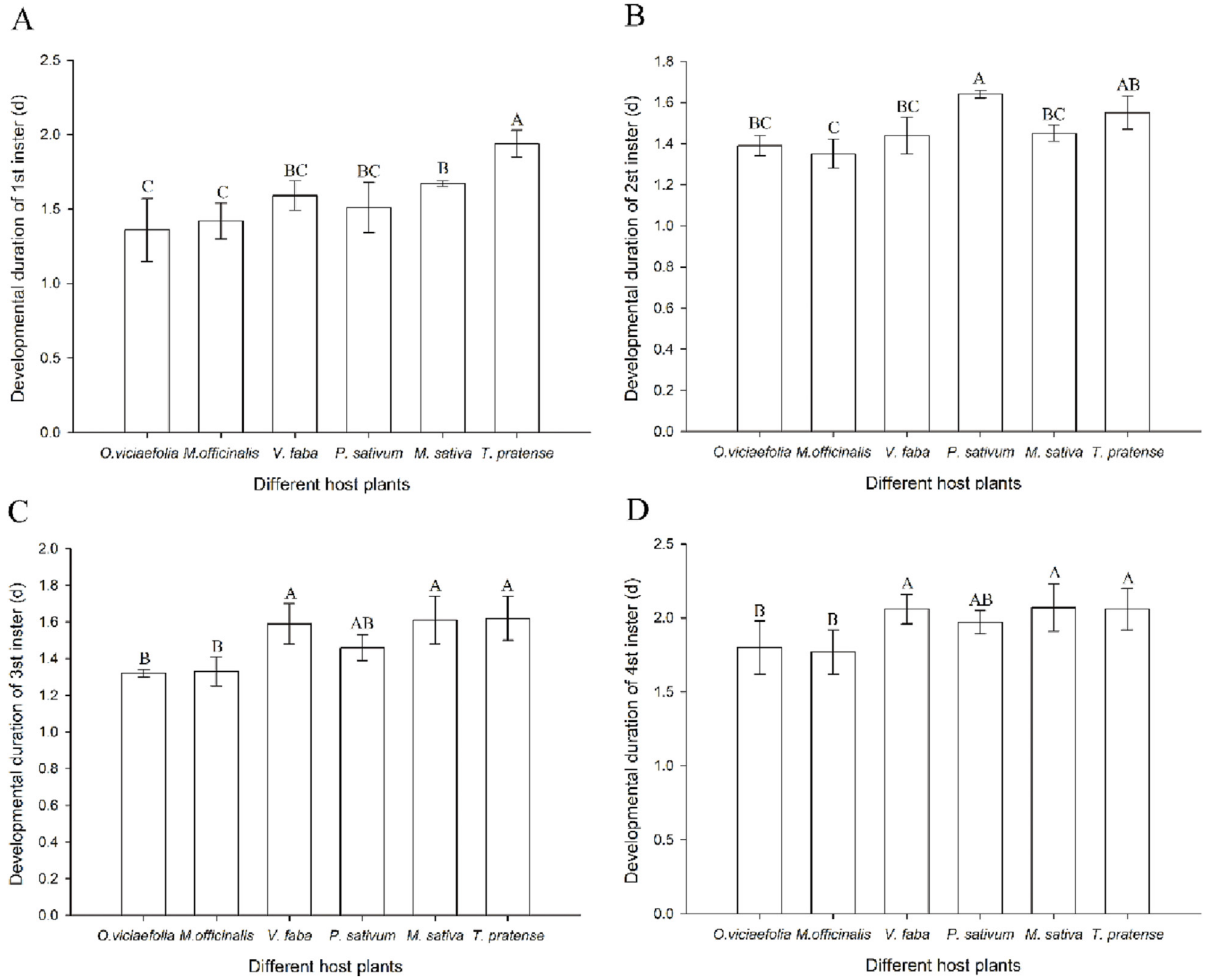

Fig. 1. Effects of different host plants on the developmental duration of pea aphid**.** (A) developmental duration of 1st instar; (B) developmental duration of 2nd instar; (C) developmental duration of 3rd instar; (D) developmental duration of 4th instar; The bars displayed mean ± SE, different letters above the bars indicate significant differences ($P \leq 0.05$).

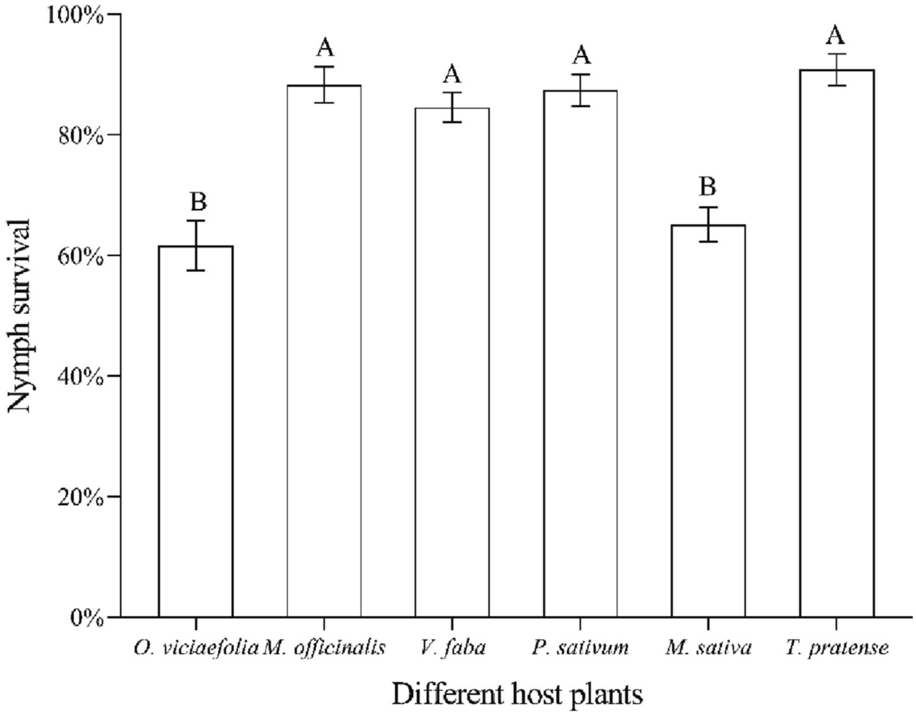

Fig. 2. Effects of different host plants on the nymph survival of pea aphid. Nymphal survival data were performed arcsine transformation and then were analyzed with one-way ANOVA. The bars displayed mean ± SE, different letters above the bars indicate significant differences ($P \leq 0.05$).

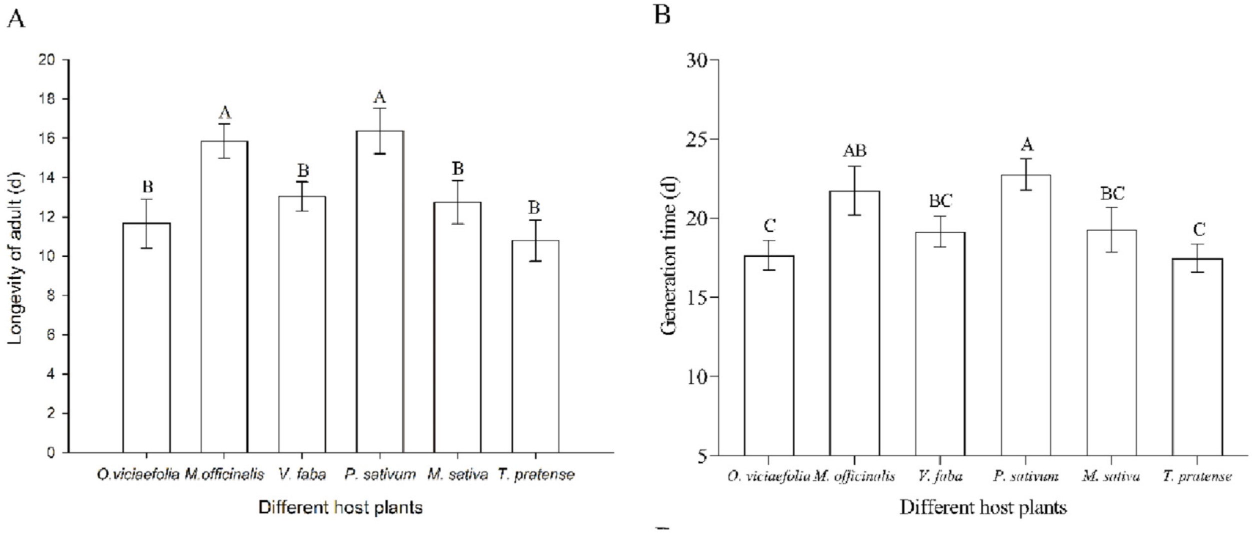

Fig. 3. Effects of different host plants on the longevity of adult and generation time of pea aphid. (A) longevity of adult; (B) generation time; The bars displayed mean ± SE, different letters above the bars indicate significant differences ($P \leq 0.05$).

O. viciaefolia vs *V. faba*: $\chi^2 = 23.98$, $P < 0.001$; *M. officinalis* vs *V. faba*: $\chi^2 = 19.54$, $P < 0.001$; *P. sativum* vs *V. faba*: $\chi^2 = 18.54$, $P < 0.001$; *M. sativa* vs *V. faba*: $\chi^2 = 23.12$, $P < 0.001$; *T. pratense* vs *V. faba*: $\chi^2 = 15.61$, $P < 0.001$). However, the survival curves of pea aphids on five host plants (except for *V. faba*) were not significantly different from each other, indicating that the population fitness costs of different hosts were different.

3.5. Effects of different host plants on population parameters of pea aphid

Host plants showed significant effects on the population parameters of pea aphids. The population characteristics of pea aphids differed significantly across the six host plants examined. The highest net reproduction rate and mean generation time were seen in aphids feeding on *V. faba*, which was statistically distinct from the other plants. However, the least net reproductive rate and mean generation time of aphids occurred on *O. viciaefolia* and *M. officinalis*, respectively (Fig. 5A, $F_{(5,\ 12)} = 22.465$, $P < 0.001$; Fig. 5B, $F_{(5,\ 12)} = 7.863$, $P < 0.002$). The intrinsic rate of increase of aphids fed on *P. sativum* was the highest and showed no significant difference compared with the populations fed on *V. faba*, *T. pratense*, and *M. officinalis*. However, they were significantly different from those that fed on *O. viciaefolia* and *M. sativa* (Fig. 5C, $F_{(5,\ 12)} = 21.421$, $P < 0.001$). The highest doubling time occurred on aphids fed on *M. sativa*. There was no significant

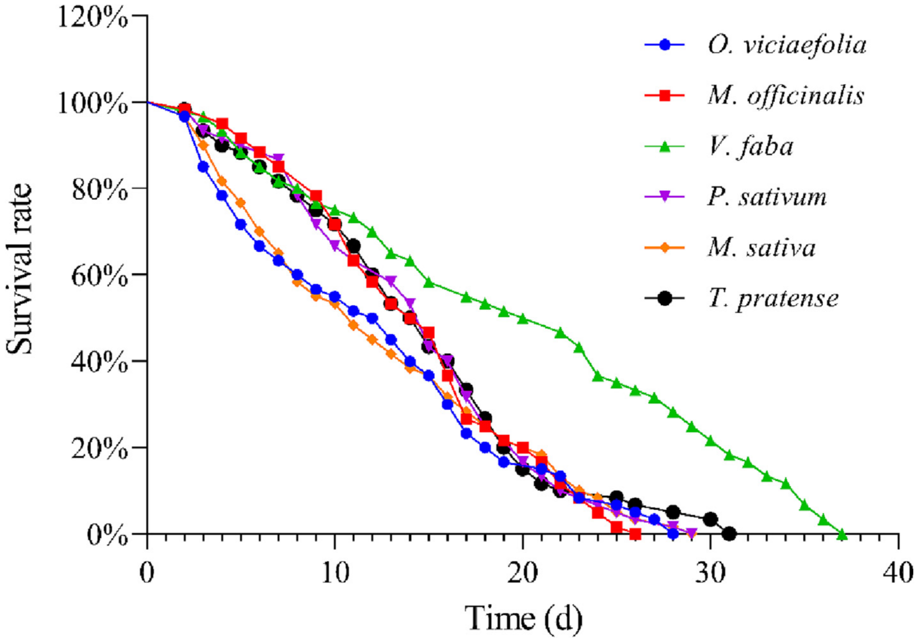

Fig. 4. Effects of different host plants on survival rate of pea aphid. Survival rate datum of pea aphid were analyzed with log-rank test.

difference compared with the population fed on *O. viciaefolia*. However, the doubling time significantly deferred among the populations fed on *V. faba, T. pratense, M. officinalis*, and *P. sativum* (Fig. 5D, $F_{(5,\ 12)} = 21.2$, $P < 0.001$). The highest finite rate of increase also occurred in the population fed on *P. sativum*, which was significantly different from the population fed on *V. faba, M. sativa*, and *O. viciaefolia* (Fig. 5E, $F_{(5,\ 12)} = 13.424$, $P < 0.001$).

4. Discussion

Aphids are sap-sucking insect pests, causing economic loss to crops (Nalam et al. 2018). Aphids have evolved complex adaptive mechanisms, such as the defense of detoxification enzymes against host plants (Elzinga and Jander 2013, Will and Vilcinskas 2015, Kaloshian and Walling 2016, Van and Torsten 2016). The global greenhouse effect, frequent occurrences of harsh weather, improper use of chemical fertilizers and pesticides in agriculture, and other factors have all contributed to the recent considerable increase in the aphid population (Sharma et al. 2016a, Chen et al. 2019). On the other hand, several defense mechanisms in plants were developed at the same time. These defense mechanisms included anti-xenobiotic factors, which have a negative impact on the fecundity, survival, growth, and development of aphids (Nalam et al. 2018). Host plants affect not only the quality of nutrition provided to insects but also their interactions, thus affecting insects' biological characteristics and population parameters.

In the present study, all six host plants had different effects on the developmental duration of pea aphids. Among the tested host plants, the 1st instar nymphs had the most extended developmental duration on the *T. pratense*. The developmental duration of the 2nd instar nymph on *M. officinalis* was significantly shorter than that of on *P. sativum*. All six host plants showed the same effect on the developmental duration of the 3rd and 4th instar nymphs. The developmental duration of pea aphid on *O. viciaefolia* was significantly longer than that of on *V. faba, P. sativum*, and *T. pretense*. It implies that the pea aphid has a certain adaptability to host plants. Our research reveals that different host plants can affect the plasticity of aphids in host utilization, which is supported by relevant references (Balog and Schmitz 2013, Barman et al. 2017, Mehrparvar et al. 2019). According to research carried out by Tesfaye (2013), pea aphids are more attracted to field peas than broad beans. The reason for the opposite results of the two experiments may be that the experimental environmental conditions and host plant species are different. The present study was conducted under laboratory conditions with six different host plants, while the research of Tesfaye was conducted under field conditions with four legume crops. Furthermore, the maternal effect is a critical determinant of aphid fitness, which suggests that the performance of offspring is the result of the mother's experience. Because aphids have overlapping telescopic generations, it can be expected that there will be a a significant maternal effect in subsequent offspring generations. Eliminate any biases brought on by the existence of maternal effects, aphids may need to be monitored throughout many generations in novel habitats (Olivares-Donoso et al. 2007, Tariq et al. 2010, Chung et al. 2013). In this study, different host plant had different affects on the nymph survival and survival rate of pea aphids nymphs. The nymph survivals on *P. sativum* and *M. officinalis* were significantly lower than that on *V. faba*. The adult longevity of pea aphids on *M. officinalis* and *P. sativum* was significantly longer than that of the other four host plants.

The chemical composition of host plants can be modified due to stress, which can positively or negatively impact the aphid's performance or, in some cases, have no effect. The nutritional conditions and secondary metabolites of host plants will influence the biological parameters of insects. The compositions of the plant epicuticle have been proven to promote the feeding of pea aphids. The relationship between the quality of host plant and the reproductive performance of aphid has also been verified in pea aphids, which provide better nutrients of *V. faba* can help pea aphids that produce more offspring. Furthermore, *V. faba* can provide a better plant surface for all aphid host races that are more conducive to aphid growth and reproduction (Friedemann et al. 2015). In this study, the pea aphid raised on fava beans had a higher net reproductive rate and mean generation time, which was more favorable for the growth of the pea aphid population than the other five host plants. Moreover, plants are known to contain secondary metabo-

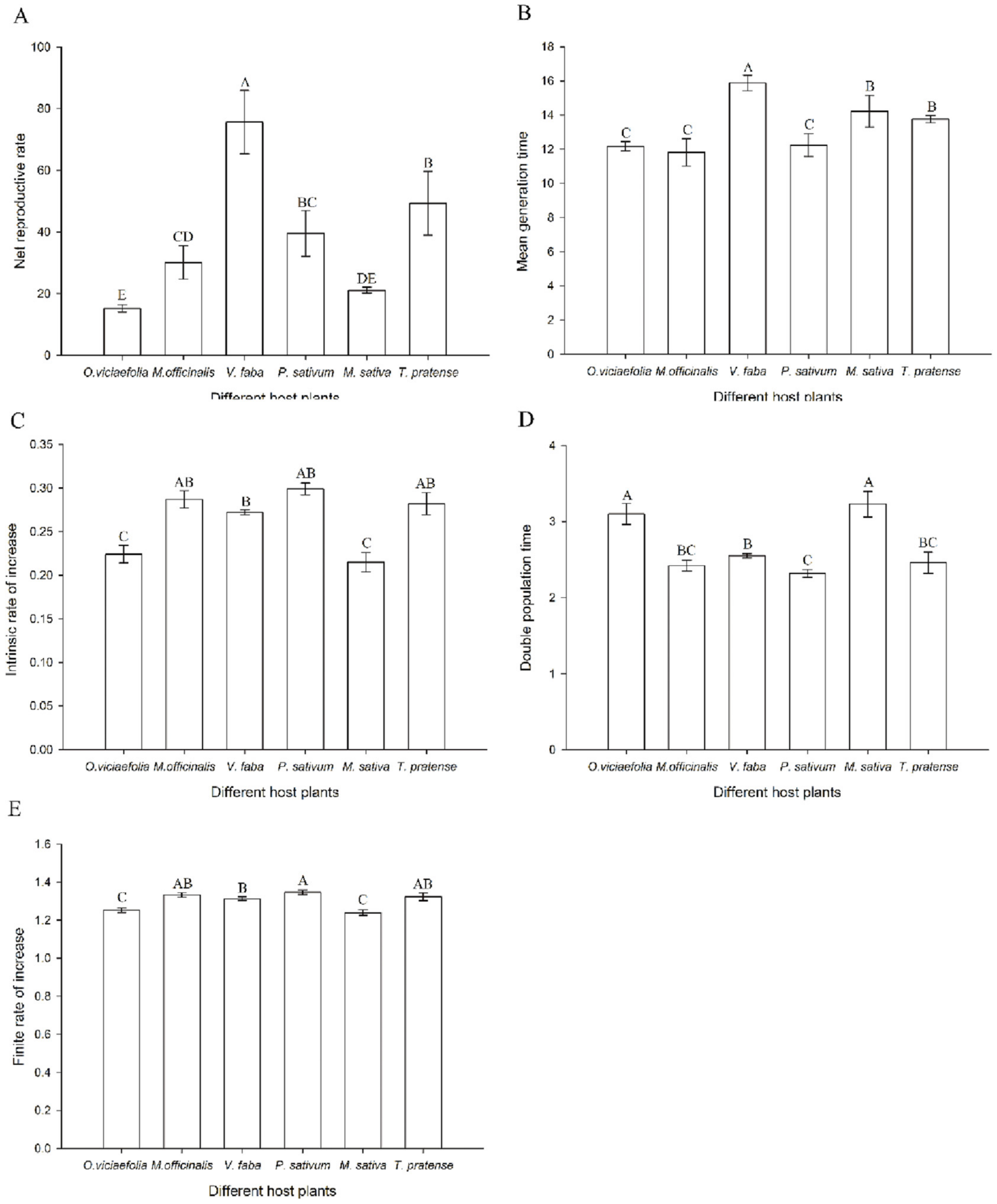

Fig. 5. Effects of different host plants on population parameters of pea aphid. (A) net reproductive rate; (B) mean generation time; (C) intrinsic rate of increase; (D) double population time; (E) finite rate of increase; The bars displayed mean ± SE, different letters above the bars indicate significant differences ($P \leq 0.05$).

lites that are capable of affecting the survival of aphids (Balog and Schmitz 2013, Barman et al. 2017, Mehrparvar et al. 2019). This demonstrates that various host plants may have varied effects on the functioning of pea aphids due to differing chemical compositions. The dynamics of herbivore populations may be significantly impacted by changes in the physical and chemical makeup of hosts (Lee and Lee 2013, Kuczyk et al. 2021). This affects the formation and growth of aphids on cucumber and watermelon plants (Moran 1981). Plants' secondary metabolites, known as "plant protectants", can influence both the biological and phenotypic traits of aphids. The secondary metabolites associated with plant resistance mainly include indirection (phenolic compounds) and end-products (flavonoids, lignin, and isoflavones) (Wu et al. 2021). This indicates that compared with other host plants, *P. sativum* and *M. officinalis* may contain secondary metabolites that inhibit growth and development. Although our current research did not involve the effect of host plant secondary metabolites on the growth, development and population parameters of pea aphids. Literature research shows significant differences in the metabolic fingerprints of four leguminous species (*M. sativa, T. pratense, P. sativum* and *V. faba*) studied before aphid infestation, which is related to the performance of the aphid (Sanchez-Arcos et al. 2019).

The life table parameter values (R_0, r_m, and λ) can reflect the ability of the insect population to proliferate and forecast future trends in population rise (Gou et al. 2021). The greatest net reproduction rate and mean generation time were found in the *V. faba* species in the current investigation. The susceptibility of the *V. faba* to pea aphids may be due to the lack of noxious compounds or secondary metabolites in the plant, although it exhibited a poor net reproductive rate. The population parameters of pea aphids on different host plants can provide a reference for the reasonable planting layout of six different plants or have a certain significance for selecting artificial restoration plants in grassland and for the rational distribution of crops in the interlaced areas of agriculture and animal husbandry.

The population adaptability of insects was affected by many factors, such as insect symbiotic bacteria, Bacterial symbiosis can also affect the adaptability of insect populations, and it plays an important role in the interaction between insects and hosts (Weinert et al. 2015). Symbiosis can affect the fitness of the hosts by reducing the density of symbiont (Scott et al. 2022), and *Cardinium* can increase the female yield by increasing maternal adaptability and egg size, thus improving fertilization rate and offspring adaptability (Katlav et al. 2022). In this study, Pea aphids on different host plants have different reproductive capacity, We will study and analyze the correlation between pea aphid and obligate endosymbionts *Buchnera* to to better explain the effects of host plants on the adaptability of insects.

5. Conclusions

Host plants are critical for the aphid growth and development. Compared with the other host plant, Pea aphid was more conducive to development and reproduction feeding on *V. faba*, while pea aphid was least conducive to reproduction feeding on *O. viciaefolia*, reproduction of pea aphid feeding on the other host plants was between *V. faba* and *O. viciaefolia*. Pea aphid exhibits different fintness on different host plants, which will provide theoretical basis for the prevention and control of pea aphids by the rational utilization of crop layout, and it provide reference for the selection of legumes in artificial restoration of degraded grassland.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jksus.2023.102764.

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