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## Identification of generalist and specialist phenotypes of the peach-potato aphid *Myzus persicae* (Insecta : Hemiptera : Aphididae) in agroecosystem of northeast India

Basant K. Agarwala\* and Parna Bhadra

Ecology and Biodiversity Laboratories, Department of Zoology, Tripura University, Suryamaninagar 799 022, India

**Different phenotypes of the peach-potato aphid, *Myzus persicae*, with prominent differences in ecological and biological performances were identified on mustard, eggplants and potato plants in the agroecosystem of Tripura, north east India. Asexual clones of *M. persicae* on mustard plants were consistently light green in colour and their adults were heavier than the greenish yellow to light pink coloured aphids of this species that occurred on eggplants and potato plants in the same geographical area. Life history traits, like population growth rate, carrying capacity of respective plants, mean relative growth rate, intrinsic rate of increase and net reproductive rates differed between the three plant species. Differences in life history traits persisted in reciprocal host plant transfer experiments; aphid clones from mustard plants when transferred to eggplants and potato plants did not survive but those from the latter two plant species survived and colonized well on mustard plants. Results showed that *M. persicae* in the agro-ecosystem of Tripura consisted of at least two distinct phenotypes, the ‘specialist’ phenotypes from mustard plants and the ‘generalist’ phenotypes from eggplants and potato plants. These results may have significant implications for designing crop-specific measures for the management of *M. persicae*.**

**Keywords:** Population diversity, life history traits, *Myzus persicae*, crop plants, northeast India.

AMONG insects, aphids are well known for exhibiting polymorphism, polyphenism (seasonal variations), and phenotypic plasticity in response to environmental variables including host plants<sup>1-3</sup>. Occurrence of asexual reproduction by parthenogenesis and viviparity in spring and summer months followed by sexual reproduction during winter have made these phytophagous insects to breed profusely with wide range of adaptations to different host plants<sup>3</sup>. The prevalent polyphenism and plasticity in different traits in aphids have often proved difficult to correctly identify species that are morphologically similar but show different reaction norms (differences in physiological, ecological, biological, or behavioural performances) on different host plants of agroecosystems<sup>4</sup>.

\*For correspondence. (e-mail: bagarwala00@gmail.com)

Worldwide, host-adapted races, also called biotypes, phenotypic plasticity, and cryptic species have been reported in aphids, like *Aphis gossypii* Glover, *Aphis fabae* Scopoli, *Myzus persicae* (Sulzer) and *Sitobion miscanthi* (Takahashi) based on their reaction norms<sup>5-9</sup> and/or genetic differences<sup>10</sup>. In addition, intraspecific generalist and specialist morphs or genotypes adapted to a wide range of unrelated and specialized food plants respectively, have also been reported from different geographical regions<sup>5,8-11</sup>.

The green peach-potato aphid, *Myzus persicae*, is of Asian origin like its primary host, *Prunus persica* (L.), but has become a world-wide pest of many food crops, especially vegetables like potato, tomato, eggplants and kale crops<sup>12</sup>, and a vector of many plant diseases<sup>13</sup>. In India, the species is known to live by asexual reproduction on 244 species of secondary hosts belonging to 56 plant families<sup>14</sup>. In Tripura (23.50°N, 91.25°E), located in south-west part of northeast India, *M. persicae* populations regularly infest potato and eggplants (Solanaceae) and mustard (Brassicaceae) crops<sup>15</sup>. Wingless aphids on mustard plants, *Brassica campestris* (L.), were mostly light green, and form colonies on both sides of young leaves and apical twigs (Figure 1 a). In contrast, aphids on potato, *Solanum tuberosum* L., and eggplants, *Solanum melongena* L., were greenish yellow to light pink, and formed colonies majorly on lower surface of young and older leaves (Figure 1 b). Host plant-based specializations in phenotypic and genotypic variants of *M. persicae* have been determined in several parts of the world<sup>11,16,17</sup> but none were recorded from India or south Asia despite being a native of Asian countries and a major pest of crops of Solanaceae and Brassicaceae<sup>18,19</sup>.

Potato, eggplants and mustard are the principal vegetable food of majority of the people of northeast India and,



**Figure 1.** Colour difference recorded in phenotypes of *Myzus persicae* on different plant species in field: *a*, light green aphids colonizing upper surface of a leaf of mustard plant; *b*, greenish yellow to light pink aphids colonizing the under surface of a leaf of eggplant.

therefore, these crops are widely cultivated in tropical and subtropical climates of plains, valleys and hills of this region<sup>20</sup>. It was predicted that the differences recorded in life colour and colonization behaviour of different asexual lineages of *M. persicae* on three different host environments of potato, eggplants and mustard crops in the fields of Tripura might also show differences in their ecological and biological fitness. It was tested in multiple clonal lineages of *M. persicae* reared on three host plants by examining their ecological (growth) and biological (developmental and reproductive) performances, the determinants of Darwinian's fitness of phytophagous insects in selection of their host plants<sup>21-23</sup>. Aphids from three crop hosts were also subjected to reciprocal host transfer experiments to record the effect of a new host environment on their performances<sup>6,7,22,24</sup>.

Three plant species were raised in open nursery till early vegetative stage (2-3 leaf stage) and then ten plants of each species were planted individually in clay pots (20 cm diameter) and were held in water trays on benches illuminated with photo-synthetically active radiation lamps in a greenhouse (temperature:  $24 \pm 1^\circ\text{C}$ , RH: 65%, photoperiod: 16:8L:D). Individual plants were infested at random with a single fourth instar apterous aphid collected from fields of respective plant species. These were allowed to grow, reproduce and increase in numbers to raise the stock culture. Aphid cultures of individual potted plants were confined in nylon net cages. All aphids produced from a single mother on a plant by this practice consisted of same genotype and, thus, constituted a clone. As a result, several independent aphid clones of different lineages were produced on three plant species. For testing the ecological and biological performances, fourth instar aphids chosen randomly from the respective plant species of the stock culture were placed singly on apical leaves of another set of 18-20 day-old pot grown plants of corresponding species ( $n = 10$  replicates) in a rearing cabinet (Sheldon, USA) maintained under similar environmental conditions as in the greenhouse. This method allowed achieving several sister clones of mixed origins of *M. persicae* on each of the three plant species. Aphids on each plant were monitored by frequent observations to record the following parameters after Agarwala and Ray Choudhury<sup>22</sup>.

For ecological performance, maximum population size representing the carrying capacity of the host plant, which is the maximum aphids that can be supported by a growing plant under a set condition ( $K$ ), population growth rate denoting increase in number of aphids per day per plant (GR), and the time ( $T_k$ ) taken to reach  $K$  value were determined for each clone of the three plant species. For biological performance, birth weight (BW) of nymphs within 12 h of laying by a mother aphid, adult weight (AW) at the final molt, developmental time from the time of birth till the final molting to adult (D), generation time from the time of birth to first reproduction by

the female (G), reproductive duration (RD), total fecundity (F), adult longevity (AL), and mean relative growth rate, denoting gain in weight per day by progeny relative to their mother (MRGR) were recorded for individual aphids of different clones from the three plant species. Also, net reproductive rate ( $R_0$ ), representing the multiplication rate of an aphid of a clone per generation, was determined using the equation

$$R_0 = \sum_0^{\alpha} l_x \cdot m_x,$$

where  $l_x$  is the proportion of aphids surviving, and  $m_x$  is the number of aphids born per mother during its reproductive duration. Intrinsic rate of increase ( $R_{max}$ ), a measure of rate of increase of a population under controlled conditions, was determined using the formula<sup>4,22,23</sup>

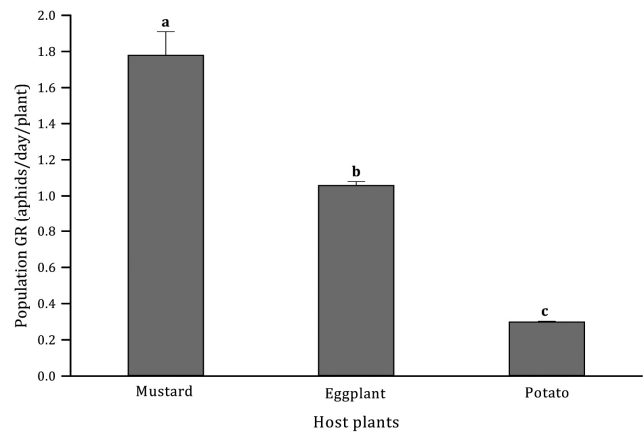
$$R_{max} = \frac{\log_e(R_0)}{G},$$

Aphid clones of the potato, eggplants and mustard were subjected to reciprocal transfers of host plants to record the colonization success, which is the ability of individual aphid to survive and reproduce in a new food environment, on the transferred hosts<sup>4,22</sup>. Individual 0–12 h old nymphs were collected from the stock culture and released one per potted plant of similar age of the field host species (control) and the laboratory host species (treatment). These were allowed to settle and produce nymphs in the first generation. If successful, second and third generations were produced. Three experiments (hereafter denoted as ‘Exp.’), I, II and III, each with three treatments, including a control were set up simultaneously using parental clones of *M. persicae* from their respective host plant species. In experiment I, *M. persicae* were transferred individually from eggplants (Ep) (control) to its conspecific plants, potato (Pt) and mustard (Ms) plants (treatments 1, 2 and 3); in experiment II, aphids were transferred from the potato (control) to its conspecific plants, eggplants and mustard plants (treatments 1, 2 and 3); and in experiment III, aphids were transferred from the mustard (control) to its conspecific plants, eggplant and potato (treatments 1, 2 and 3). Twenty replicates each were used in all the three. Thus, 60 replicates were used in each of the three experiments. Aphids that either failed to develop to the adult stage in the first generation or failed to produce second or third generation progeny were considered unsuccessful.

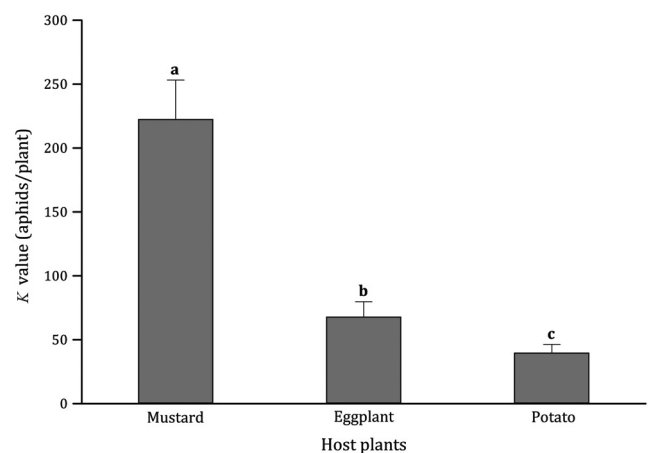
Data on the third generation aphids, where available, were used to compare the results. This was done to allow sufficient time to aphids for acclimatization in the laboratory rearing conditions. All weights in this study were taken using Mettler Toledo microbalance (model AT20) with a precision of 2  $\mu$ g. All ecological and biological

parameters that were measured from the wingless aphids of *M. persicae* met the criteria of normality and equal variance. These were compared by analysis of variance (ANOVA) for three plant species followed by post-hoc Tukey’s multiple comparison test, and by two-tailed Student’s *t*-test for two plant species. Colonization successes of *M. persicae* clones between treatment and control plants in the host-transfer experiments were compared by  $\chi^2$  test. Origin 7 ([www.originlab.com](http://www.originlab.com)) was used for data analysis.

Among three plant species, aphids showed faster population GR (mean  $\pm$  SE = 1.78  $\pm$  0.13 aphids/day/plant) on mustard clones than those from eggplants (mean  $\pm$  SE = 1.06  $\pm$  0.20 aphids/day/plant) and potato (mean  $\pm$  SE = 0.30  $\pm$  0.002 aphid/day/plant) (ANOVA: *F* value = 14.59, *df* = 2, 27, *P* < 0.001) (Figure 2). Between two *Solanum* species, aphid population GR was slower on potato plants than on eggplants (*t* value = 5.83, *df* = 18,



**Figure 2.** Mean values of population GR recorded in *M. persicae* clones reared on mustard, eggplants and potato plants under laboratory conditions. Different letters accompanying error bars denote significant differences by Tukey’s multiple comparison tests following ANOVA.



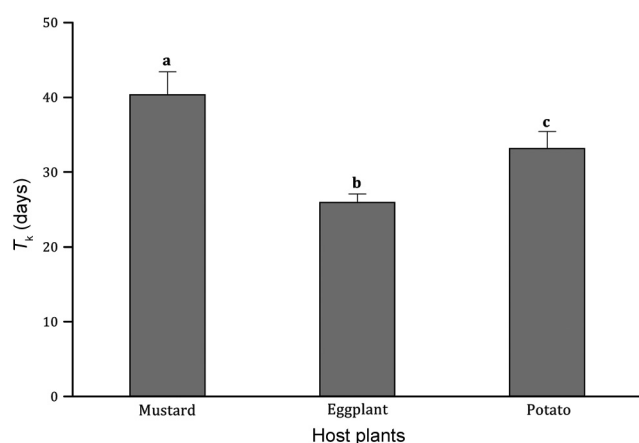
**Figure 3.** Mean values of carrying capacity (*K*) recorded in *M. persicae* clones reared on mustard, eggplants and potato plants under laboratory conditions.

## RESEARCH COMMUNICATIONS

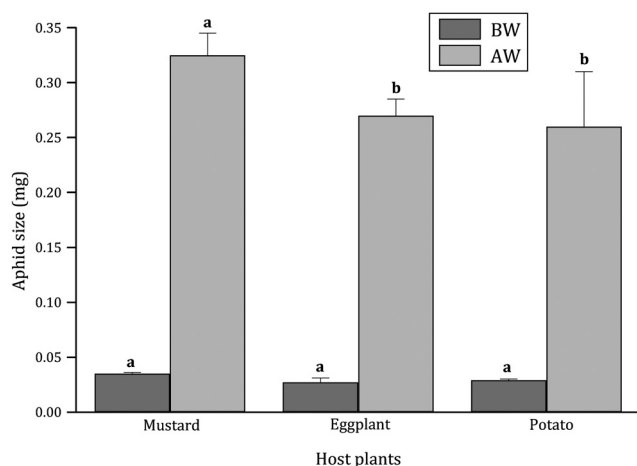
$P < 0.01$ ). Mustard plants supported higher number of aphids per plant ( $K$ ), 3.28 times and 5.60 times higher than that of eggplants and potato plants respectively (ANOVA:  $F$  value = 26.32,  $df = 2, 27, P < 0.001$ ) (Figure 3). Average time taken ( $T_k$ ) by aphid clones to achieve the  $K$  values on the respective plant species was longer on mustard than on eggplants and potato (ANOVA:  $F$  value = 10.23,  $df = 2, 27, P < 0.001$ ) (Figure 4). Mean weights of aphids at birth (BW) on the three plant species did not differ significantly (ANOVA:  $F$  value = 3.29,  $df = 2, 27, P = 0.052$ , NS), but weight of adult aphids (AW) on mustard plants was 1.25 times more than that reared on two species of *Solanum* plants (ANOVA:  $F$  value = 8.98,  $df = 2, 27, P < 0.001$ ) (Figure 5). Newly born aphids of mustard clones developed significantly faster into adults (D: mean  $\pm$  SE =  $8.0 \pm 0.211$  days) than that on *Solanum* hosts (eggplants =  $9.0 \pm 0.27$  days; potato =  $8.75 \pm 0.86$  days) (ANOVA:  $F$  value = 4.55,  $df = 2,$

27,  $P = 0.019$ ) (Figure 6) but these aphids did not show significant difference in their generation time on the three plant species (G: mean  $\pm$  SE: mustard =  $9.60 \pm 0.37$ ; eggplants =  $9.80 \pm 0.79$ ; potato =  $10.05 \pm 0.27$ ; ANOVA:  $F$  value = 0.555,  $df = 2, 27, P = 0.58$ ). Individual *M. persicae* that developed on mustard plants gained significantly more weight per day relative to their mother (MRGR: mean  $\pm$  SE =  $0.23 \pm 0.004$  mg aphids/mg of mother/day) than clones that developed on *Solanum* hosts (mean  $\pm$  SE: potato clones =  $0.11 \pm 0.01$  mg aphids/mg of mother/day; eggplant clones =  $0.10 \pm 0.004$  mg aphids/mg of mother/day) (ANOVA:  $F$  value = 1.95,  $df = 2, 27, P = 0.016$ ) (Figure 7). MRGR of *M. persicae* did not differ significantly between the two *Solanum* hosts ( $t$  value = 0.22,  $df = 18, P = 0.09$ ).

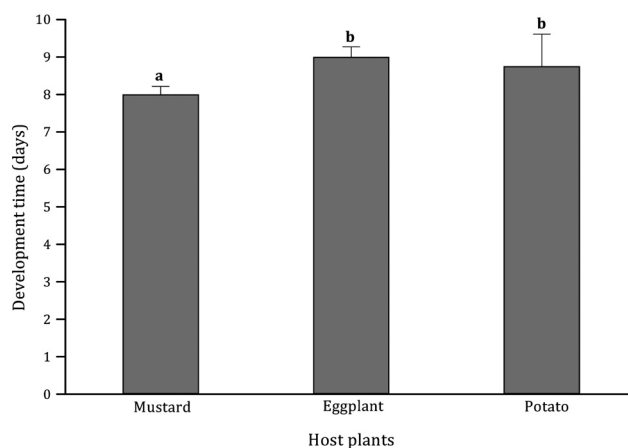
Aphids of mustard clones showed higher total fecundity (mean  $\pm$  SE =  $38.40 \pm 5.19$  aphids), higher  $R_{max}$  (mean  $\pm$  SE =  $4.30 \pm 0.01$  aphids/mother/day), and higher  $R_0$



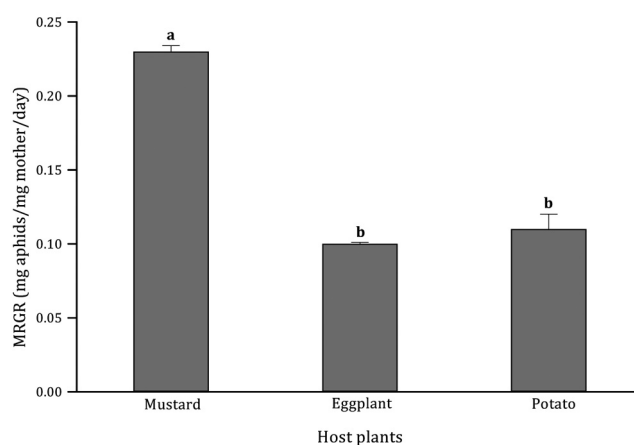
**Figure 4.** Mean values of time taken to reach the  $K$  value ( $T_k$ ) recorded in *M. persicae* clones reared on mustard, eggplants and potato plants under laboratory conditions.



**Figure 5.** Mean values recorded in the size by fresh weight (mg) of *M. persicae* clones at birth (BW) and at final molting (AW) when reared on mustard, eggplants and potato plants under laboratory conditions.



**Figure 6.** Mean values of development time (D) recorded in *M. persicae* clones reared on mustard, eggplants and potato plants under laboratory conditions.



**Figure 7.** Mean values of mean relative growth rate (MRGR) recorded in *M. persicae* clones reared on mustard, eggplants and potato plants under laboratory conditions.

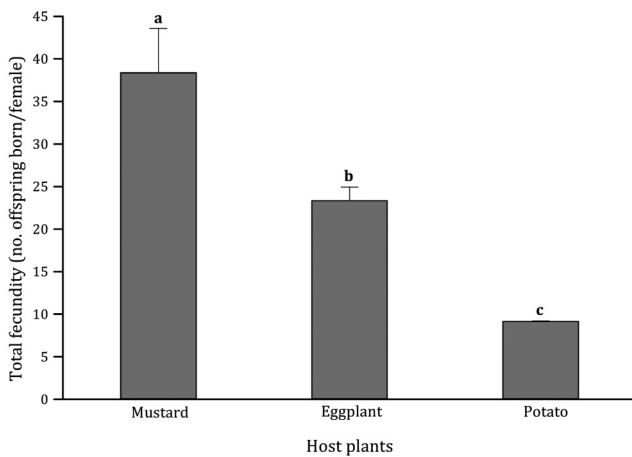
(mean  $\pm$  SE =  $40.98 \pm 1.23$ ) in comparison to aphid clones of potato or eggplants ( $F$ : mean  $\pm$  SE: potato =  $9.20 \pm 0.489$  aphids, eggplants =  $23.40 \pm 1.54$  aphids, Figure 8;  $R_{max}$ : mean  $\pm$  SE: potato =  $1.43 \pm 0.013$  aphids/mother/day, eggplants =  $2.58 \pm 0.008$  aphids/mother/day, Figure 9;  $R_0$ : mean  $\pm$  SE: potato =  $8.19 \pm 1.08$  aphids, eggplants =  $22.85 \pm 1.39$  aphids, Figure 10).  $R_0$  of the mustard clones was higher by about 1.8 times and 5 times than the numbers of progeny produced by clones of eggplant and potato respectively.

Table 1 presents the results of success rates of colonization by *M. persicae* clones in the three experiments of host transfers. The transfer of aphids from eggplants (Ep) and potato (Pt) (control) to mustard (Ms) (treatment) (experiments I-3 and II-3) showed that aphids from 70% and 90% of the eggplant and potato clones respectively, formed viable colonies on mustard plants in the third

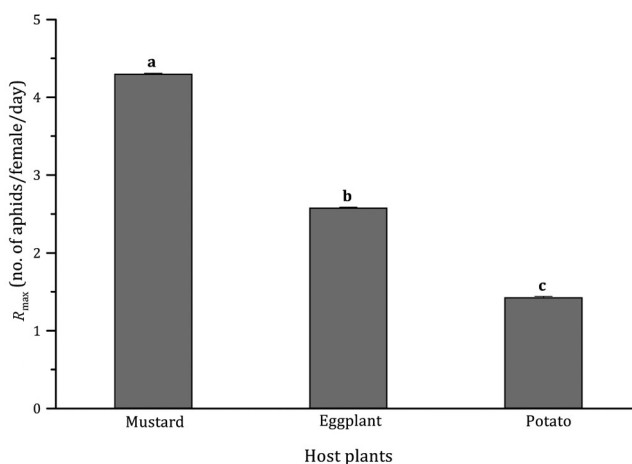
generation. This was almost similar to the success rates of *M. persicae* clones on their respective conspecific hosts: eggplants (80% in the third generation) and potato (90% in the third generation). However, aphids of both eggplants and potato clones performed poorly even in the first generation and none of the transferred aphids survived in the third generation (Table 1). In contrast, aphid transfer from mustard (control) to solanaceous plants (treatments) (experiments III-2 and III-3) in the first generation showed 80% and 40% success rates of colonization on eggplants and potato plants respectively; these declined to 50% and 20% respectively, in the second generation, and to 10% and 5% respectively, in the third generation (Table 1). Thus, the transfers of aphids from mustard plants to eggplants and potato plants were less successful in the first and second generations and nearly perished in the third generation (experiments III-2, III-3).

Life colour of the mustard clones remained light green and those from eggplants and potato plants showed greenish yellow to light pink, and no overlap occurred when transferred to non-native plants in the reciprocal host transfer experiments.

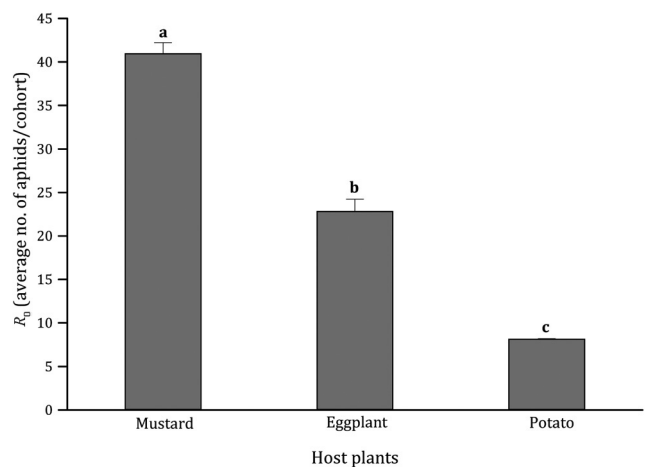
This study has revealed that *M. persicae* in the agroecosystem of Tripura, northeast India, consists of divergent asexual populations in relation to their food plants. Populations from mustard plants were heavier and showed conspicuous differences in fitness traits, like population GR,  $K$  value,  $T_k$ , AW, MRGR,  $D$ , total fecundity,  $R_{max}$  and  $R_0$  in comparison to those from eggplants and potato plants. Also, in reciprocal host transfer experiments, aphids from the mustard host nearly failed to survive on solanaceous plants but those from eggplants and potato hosts survived well on mustard plants but not reciprocal hosts. Results clearly suggest that asexual clones of *M. persicae* from mustard host behaved significantly different than those from the two *Solanum* hosts.



**Figure 8.** Mean values of total fecundity recorded in *M. persicae* clones reared on mustard, eggplants and potato plants under laboratory conditions.



**Figure 9.** Mean values of intrinsic rate of increase ( $R_{max}$ ) recorded in *M. persicae* clones reared on mustard, eggplants and potato plants under laboratory conditions.



**Figure 10.** Mean values of net reproductive rate ( $R_0$ ) recorded in *M. persicae* clones reared on mustard, eggplants and potato plants under laboratory conditions.

**Table 1.** Success rate of colonization by *M. persicae* clones on field host and on transferred plants in the laboratory in three successive generations denoted by 1st gen., 2nd gen. and 3rd gen. respectively

Experiment	Aphid clones		Percentage of successful colonization		
	Field host (control)	Laboratory host (treatments)	1st gen (n)	2nd gen (n)	3rd gen (n)
	I	Ep	Ep Pt Ms	90 (18) 30 (6) 90 (18)	90 (18) 0 (0) 80 (16)
II	Pt	Pt Ep Ms	100 (20) 20 (4) 100 (20)	90 (18) 10 (2) 90 (16)	90 (18) 0 (0) 90 (18)
III	Ms	Ms Ep Pt	100 (20) 80 (16) 40 (8)	100 (20) 50 (10) 20 (4)	100 (20) 10 (2) 5 (1)

Values within parentheses indicate the number of plants on which the transferred aphids formed viable colonies. Ep = Eggplant, Pt = Potato plant, Ms = Mustard plant.

However, aphids from eggplants showed significantly greater fitness in terms of higher GR, K, total fecundity,  $R_{max}$  and  $R_0$  than aphids from potato plants in the agroecosystem of Tripura. These results suggest that aphids that infested mustard plants (Brassicaceae) appear to be ‘specialists’ in ecological and biological performances whereas those from eggplants and potato plants (Solana-ceae) show polymorphism of ‘generalist’ aphids.

Presence of different phenotypes in sympatric populations of *M. persicae* on different cultivated host plants in the tropical agroecosystem of Tripura is the first record of occurrence of polymorphism in apterous viviparous female morph in this species from northeast India and south Asia<sup>14,18</sup>. Distinct phenotypes and genotypes of *M. persicae* have been recorded from different parts of the world under diverse conditions and from different host plants, both wild and cultivated<sup>5,17,23,25,26</sup>. The recorded differences in phenotypes, based on differences in genotypes, are from the secondary host plants of diverse plant families which vary from region to region<sup>27,28</sup>. Apterous viviparous female morph of aphids, which is the colonizer of food plants, appears to undergo constant changes in its structures and functions in order to adapt to variable conditions of host environments including presence of allelochemicals which profoundly influence the selection process of host plant<sup>28,29</sup>. The generalist and specialist clones of *M. persicae* from Chile, South America, Europe and Australia were reported<sup>5,9,11,26</sup>; generalist genotypes live on optimal as well as suboptimal hosts without compromising their life history fitness, that is,  $R_{max}$  of suboptimal hosts significantly improved when transferred to optimal hosts and decreased in reciprocal transfers. In contrast, specialist genotypes performed at fixed level only on optimal host. It is argued that higher reproductive rates coupled with greater abundance of secondary host plants in warmer conditions permit asexual aphids to accumulate mutations over short time and

these affect growth and reproduction<sup>28</sup> and is the major cause of clonal diversity within sympatric populations<sup>6,23</sup>.

This view is vindicated by Ramsey *et al.*<sup>28</sup> who identified 2423 novel genes specific to *M. persicae* from a large collection of aphids from different geographical regions and found high polymorphism in nucleotide sequence tags. The present and some previous studies from Tripura<sup>2,5,8,19,26,27</sup> bring out that discrimination in host plant utilization in asexual lineages of *M. persicae* and other aphid species appears to be a common phenomenon and, therefore, requires a focussed approach in understanding aphid–food plant relationship and management of aphid populations on specific host plants<sup>2,4,7,22</sup>.

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