Life table and demographic parameters of mustard aphid, *Lipaphis erysimi* (Kaltenbach) (Hemiptera: Aphididae) on five brassicaceous host crops

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Abstract: *Brassica* plants play a significant economic role, as they are cultivated as vegetables, oilseed sources, condiments and, forages. Emerging insect pest outbreaks threaten the production of cole crops. The mustard aphid, *Lipaphis erysimi* (Hemiptera: Aphididae), is a perpetual annual threat to the cultivation of cole crops in India. The construction of a life table is a fundamental requisite for designing management practices; hence, the life table of *L. erysimi* was studied on five brassicaceous host plants. The results show that the total nymphal duration was shortest on mustard (5.82±1.10 days), whereas it took 8.80±0.89 days on broccoli. Similarly, the most prolonged and shortest oviposition period was recorded on mustard (6.81±0.44 days) and broccoli (4.25±2.59 days), respectively. The *GGE biplot* analysis shows that cabbage was the most preferred host, whereas broccoli was the least preferred by *L. erysimi*. The intrinsic rate of increase (r) of *L. erysimi* was lowest on broccoli (0.21) and highest on mustard (0.35). Similarly, the net reproductive rate (R_0) was highest on mustard (28.52±0.37) and lowest on broccoli (12.52±0.21). The age-stage-specific survival rate (S_{xj}) of an adult was maximum on cauliflower (0.84), and the highest age-stage life expectancy (e_{xj}) of *L. erysimi* at age zero (e_0) was 12.84 days observed on cauliflower. Age-stage reproductive value (V_{xj}) at the age zero (V_0) was 1.42 on mustard. The population was doubled every 1.98±0.008 days on mustard compared to 3.30±0.025 days on broccoli. The data shows that mustard was the most preferred host for *L. erysimi*, and broccoli was the least preferred or comparatively resistant.

Keywords: Brassica hosts; Broccoli; Intrinsic rate of increase; *Lipaphis erysimi*; two-sex life table.

Introduction

Cole crops are one of the most abundantly consumed vegetables worldwide. It belongs to the genus *Brassica* of the family Brassicaceae. The Brassica vegetables, *viz.*, broccoli, Brussels sprouts, cabbage, cauliflower, collard greens, kale, and turnips, are economically significant due to their nutrition and health-promoting substances to humans. In India, the cole crops are mainly grown during winter, and the country ranks second in producing cauliflowers and cabbage[1,2]. The production of cole crops is constantly threatened by emerging insect pests and diseases, whose incidence has increased in recent years. About 50 insects are known to cause significant economic damage to *Brassica* hosts. Among these, aphids, members of the order Hemiptera, are one of the world's most notorious pests of *Brassica* crops primarily visible at the flowering stage affecting the crop yield severely every year up to 65- 96% [3,4]. The mustard aphid, *Lipaphis erysimi* (Hemiptera: Aphididae), is a specialist aphid species on *Brassica* hosts, which poses a serious threat to their cultivation, including cabbage, cauliflower, and rapeseed-mustard in India[5,6]. The *L. erysimi* cause direct plant damage by sucking phloem sap and indirect damage by releasing honeydew, which later serves as a medium for fungal growth, restricting the photosynthetic activity and respiration in plants[7,8,9].

In India, *L. erysimi* typically infests crops between the months of December and March. The *Brassica* coenospecies lack genetic resistance to aphids or have it restricted to a few wild accessions[10]. It compels growers to protect the yield losses from insect pests by applying synthetic insecticides. In addition, to easy availability and application, and immediate knock-down effect on insects, the farmers typically prefer chemical insecticides to control pests in less developed and developing nations[11]. The application of insecticides is associated with various problems like resistance, resurgence, and residues to the ecosystem and humans. There is an urgent need for alternative management techniques. Knowledge of any insect pest's biological, reproductive, and population parameters is crucial for formulating effective and sustainable pest management strategies[12].

The development and stability of insects are significantly influenced by the species and quality of host plants, and the variety of host plants can also affect the population dynamics of insect pests[13]. Comparison of the life table factors is the most helpful technique for investigating the role of host plants on the fitness of insect pests. For this purpose, researchers frequently use demographic variables[14]. Here in the present study, we hypothesized that studying the life table parameters helps understand the biological response of *L. erysimi* on different brassica cultivars and helps formulate suitable management practices.

MATERIALS AND METHODS

Growing of plants for life table analysis

The seeds of cauliflower (*Brassica oleracea* L. var. *botrytis*) cv. Pusa Snowball 16, cabbage (*Brassica oleracea* L.) cv. Pusa hybrid 81, broccoli (*Brassica oleracea* L. var. *italica*) cv. Local variety, mustard (*Brassica napus* L.) cv. Local variety and knol khol (*Brassica oleracea* L. var. *gongylodes*) cv. Local variety were sown in raised nursery beds of 5 m (L) × 1 m (W) × 0.15 m (H). Three to four-leaved plants were transplanted in a protected net house (1.5× 2 m). The plants were watered once a week and the recommended fertilizers were ensured (At the rate of 100 kg N, 60 kg P and 80 kg K per hectare).

Rearing of mustard aphid, *L. erysimi*

The mustard aphid, *L. erysimi* adults were collected from a cauliflower crop (Experimental field of Division of Entomology, ICAR- IARI, New Delhi) and carried to the laboratory. The collected aphids were released on the respective brassicaceous host plants and reared for a single generation (host conditioning) to avoid the effect of the previous host before studying the life table parameters. All experiments were undertaken in a growth chamber set at 25- 26 ^{o}C, 60- 65 % RH, and 16: 8 (L: D) h photoperiod.

Observations

The leaves of each of the five cole crops, which were at the 10-12 leaf stage, were taken off and cut into small leaf disc with diameters ranging from 1.5 to 3 cm. These leaf discs were then placed inside Petri dishes (9 cm- diameter and 1.5 cm- height). To keep the host leaves turgid for longer, moistened filter paper was provided in Petri dishes. An adult female, identified by its bigger size and prominent cornicles, was chosen from the laboratory culture and delicately placed on a leaf disc of each cole crop using a triple zero brush. Each Petri plate was then examined at 12-hour intervals to monitor potential oviposition by adult females. During each observation, strict measures were taken to ensure that only one first-instar nymph remained, with all other nymphs and adult females being removed. The young instar nymphs (n= 30) were daily provided with the respective cole crops until their natural demise, while various biological parameters, including nymphal duration, adult longevity, pre- and post-oviposition periods, and fecundity, were meticulously documented.

Statistical analysis

For *GGE Biplot* analysis, R studio software was used, using *GGEModel* or *gge* program. The graphs are two ways, and the Principal Component Analysis (PCA) consists of the first principal component (PC1) and the second principal component (PC2) contributions to the total sum of squares in GGE biplots. In GGE Biplot analysis, ten biological properties of *L. erysimi* reared on 5 hosts were evaluated. In this study, the host plants were accepted as the genotype, and the biological characters were examined as the environment[15,16,17]. Since biological properties are considered an environment, GGE Biplot analysis has been created to determine which biological properties are better in which host plant, the state of the relationships between biological properties, and the effect of the host plants on life properties.

The age-stage, two-sex life table can eliminate many inherent errors of female-based life tables. The pest's life table was constructed using 'TWOSEX-MS Chart' software[18,19]. According to the age-stage, two-sex life table principle and method[20], the following demographic parameters were calculated, and the age-stage, two-sex life tables of *L. erysimi* on the five brassicaceous host was established. In addition, the age-stage, two-sex life table was also constructed using the 'TWOSEX-MS Chart', eliminating many of the inherent errors of female-based life tables. According to the age-stage, two-sex life table principle, and method[20], the following parameters *viz.*, Age-stage-specific survival rates (S_{xj}) $=\frac{n_{xj}}{n_{01}}$; Age-specific survival rate (l_x) $= \sum_{j=1}^{m} S_{xj}$; Age-stage-specific fecundity (f_{xj}); Age-specific fecundity (m_x) $= \frac{\sum_{j=1}^{m} S_{xj} f_{xj}}{\sum_{j=1}^{m} S_{xj}}$; Age-specific maternity (l_x*m_x); Age-stage-specific life expectancy (e_{xj}) $=\sum_{j=1}^{m} \sum_{j=1}^{m} S_{ij}$; Age-stage-specific reproductive value (V_{xj}) $=\frac{e^{-r(x+1)}}{S_{xj}} \sum_{i=x}^{n} e^{-r(i+1)} \sum_{j=y}^{m} S_{ij} f_{ij}$; Intrinsic rate of increase (r)- $\sum_{x=0}^{\infty} e^{-r(x+1)} l_x m_x = 1$; Finite rate of increase (λ)= e^r; Net reproductive rate (R_0)=

$\sum_{x=0}^{\infty} l_x \ m_x$; Mean generation time (T)= $\frac{l_n \ R_0}{r}$ were studied. The biological and reproductive data were analyzed by one-way analysis of variance (ANOVA), followed by a comparison of the means with least significant difference (LSD) test at a = 0.05 using the online statistical software WASP- Web Agri Stat Package 2.0. The means, standard errors, and variances of the population parameters were arrived at by bootstrapping technique (100,000 repetitions). Sigma **plot 14.5** was used to create graphs.

Results and Discussion

The life cycle of mustard aphid, *L. erysimi* on brassicaceous vegetables under laboratory conditions

The mustard aphid, *L. erysimi* completed its life cycle on all the selected host crops with four instars, and the duration of each instar varied among the tested brassicaceous crops (Table 1). The total nymphal period of *L. erysimi* on brassica vegetables was in the ascending order on mustard (5.82±1.10 days) < cauliflower (6.65±1.37 days) < cabbage (7.90±0.89 days) < knol khol (8.12±1.27 days) < broccoli (8.80±0.89 days). The *L. erysimi* had varied oviposition periods on tested crops (Table 1). Several authors reported similar results earlier [21,22,23,24]. Interestingly the developmental period of each instar (nymph I- IV) of *L. erysimi* on different brassica hosts varied significantly. The varietal effect might have attributed to longer or shorter nymphal duration. Further, we believe that the differences in total developmental time can be attributed to the differences in nutritional quality among the host plants and in the host plant physiology and biochemical constituents like glucosinolates, total phenols and ortho-dihydroxy phenols[25].

The most prolonged oviposition period was recorded on mustard (6.81±0.44 days) and the lowest on broccoli (4.25±2.59 days). However, *L. erysimi* had a statistically similar oviposition period on cabbage (6.00±1.86 days) and cauliflower (6.04±2.62 days), respectively. The maximum mean fecundity of *L. erysimi* was observed on mustard (33.95±2.09 nymphs/ female) and cabbage (32.45±14.03 nymphs/ female), whereas the lowest fecundity was observed on broccoli (15.65±10.57 nymphs/ female). Adult longevity (days) and fecundity (nymphs/female) are crucial characteristics determining insect injury potential and population dynamics in the field[26]. The longevity of adults was comparatively lower in the present study compared to the findings of earlier workers [27,21,28,23]. The experimentation under the controlled conditions (growth chamber) and varietal changes might have contributed to the shorter longevity of adults on all the tested crops[29]. Moreover, variations in the biochemical composition of host plants, specifically in the levels of anthocyanins or myrosinase present in brassica host leaves, are responsible for differences in their sensitivity and resistance to insects[30,31,32].

The biotic potential of *L. erysimi* on brassica vegetables was in the ascending order as follows broccoli (2.33×10^{27}) < knol khol (8.65×10^{35}) < cabbage (2.27×10^{38}) < cauliflower (2.86×10^{38}) < mustard (1.36×10^{43}). The life cycle duration of *L. erysimi* was non-significant on the tested brassica crops. The total life cycle was in ascending order on mustard (12.95±2.38 days) < cauliflower (13.65±2.48 days) < broccoli (13.90±2.55 days) < knol khol (14.00±1.27days) < cabbage (14.38±2.20 days). Based on GGE Biplot Analysis, the effects of tested hosts on the aphid's life cycle parameters are shown in Figures 1 and 2. In this study, 86.35 % of the variation was explained by the first two principal components (PCs), where the principal component (PC1) explains 71.39, and PC2 explains 14.96 % of the total variation. GGE Biplot analysis was used to select the most favourable host for the aphid based on the results of this work and graphically shown in Figure 1. The hosts in the same direction and the same circle showed that they have values close to each other (Figure 2). In other words, cabbage and mustard were the most suitable hosts for almost all biological characteristics examined for each stage. However, Genç and Saran[33], observed that cauliflower was the most preferable host for *P. xylostella*. The analysis was performed for the first time against the pest.

Population growth parameters of *L. erysimi* on five brassicaceous host plants

The population or demographic parameters are significant in predicting population dynamics and formulating management strategies. The intrinsic rate of increase (r) is the number of females produced per female/day (Table 2). The analysis of the bootstrapping values showed that r was significantly ($P < 0.0001$) varied among the tested brassica crops. The results showed that the r value of *L. erysimi* on brassica vegetables was in the ascending order for broccoli (0.21±0.0015) < knol khol (0.23±0.015) < cabbage (0.28±0.0013) < cauliflower (0.31±0.013) < mustard (0.35±0.0014). The r value encompasses numerous factors, including fecundity, survival, and generation time, providing a comprehensive measure of an insect's physiological attributes in terms of its ability to multiply. It serves as a highly suitable metric for assessing the performance of an insect on various host plants and gauging the resistance of those host plants[14,19,25]. The highest finite rate of increase (λ) was recorded on mustard (1.42±0.0019) and the lowest on broccoli (1.23±0.0018; $P < 0.0001$). The net reproductive rate (R_0) is the total females produced per female/generation; highest R_0 value was recorded on mustard (28.52±0.37), followed by cabbage (25.96±0.36), cauliflower (25.24±0.32), knol khol (13.2±0.19) and broccoli (12.52±0.21; P < 0.0001). The high value of R_0 on mustard is a reflection of high r values. Gross Reproduction Rate (GRR) is the probable proportion of offspring that becomes female; the ascending order of GRR on brassica crops was as follows knol khol (24.54±0.036) < broccoli (27.58±0.025) < cabbage (44.68±0.028) < cauliflower (49.85±0.035) < mustard (50.78±0.029; $P < 0.0001$). The combined effects of the biological characteristics are reflected in the population parameters (r, R_0, GRR, T, and DT) of *L. erysimi*. According to the findings of this study, mustard aphids raised on broccoli have the lowest intrinsic rate of increase (r, 0.21), finite rate of increase (λ, 1.23), and net reproductive rate (R_0, 12.52). Lower r and R_0 values of aphids on any host plant indicate the lower suitability of hosts for population growth[34,35]. As in this study, other researchers have reported that feeding on different host plants affects the population growth of *L. erysimi*[36,37,38,30].

Mean generation time (T) is one of the important parameters indicating an average interval between an individual's birth and its offspring's birth. It was longest on broccoli (12.05±0.32 days), followed by cabbage (11.60±0.24 days), knol khol (11.42±0.19 days), cauliflower (10.45±0.44 days), and mustard (9.59±0.31 days; $P < 0.0001$). The Doubling Time (DT) was lowest on mustard (1.98±0.008 days), followed by cauliflower (2.24±0.010 days), cabbage (2.47±0.012 days), knol khol (3.07±0.021 days), and broccoli (3.30±0.025 days; $P < 0.0001$). Aphid performance on host plants can be influenced by various parameters, including the physico-morphic characteristics, biochemical content, and nutritional value of the host plant[30,39]. The biochemical contents/ parameter levels in the *Brassica* vegetables we used may differ, and our results may reflect this variability[40]. The lowest intrinsic rate of increase and highest mean generation time and doubling time of *L. erysimi* on broccoli may also be attributed to higher antibiosis characteristics in this *Brassica* vegetable[37].

Life table parameters of *L. erysimi* on five brassicaceous host plants under laboratory conditions

a. Age-stage-specific survival rate (S_{xj}) of *L. erysimi* on five brassicaceous host plants

S_{xj} of *L. erysimi* on five brassicaceous host plants has been shown in Fig. 3. The values varied across developmental stages, and the survival curves overlapped, which can be attributed to the fact that different individuals grow at different rates. The lowest S_{xj} of stage N_1 was observed on cauliflower (0.92), whereas on other brassica hosts, it was 1. During the adult stage, the maximum S_{xj} was observed on cauliflower (0.84) and the lowest on broccoli (0.60).

b. Population survival rate and fecundity

Figure 4 shows the influence of brassicaceous hosts on the survival rate and fecundity of *L. erysimi*: l_x, f_x and $l_x.m_x$ showed a downward trend with increasing age. The estimated values showed that the death of the last adult (female) occurred on 18, 17, 20, 16, and 17 days, respectively on broccoli, cabbage, cauliflower, knol khol, and mustard. The results showed that the maximum f_x value (7.4) was recorded on mustard on the 15th day. Whereas, the lowest f_x value (4.4) was recorded on the 10th day of broccoli. Similarly, $l_x.m_x$ reached its maximum value on mustard (4.28), followed by cauliflower (4.20) on the 8th and 9th day, respectively.

c. Life expectancy

The value of e_{xj} showed a downward trend in all the brassicaceous hosts studied under laboratory conditions. The maximum life expectancy of 12.84 and 12.56 days, respectively, was observed at age zero ($e_{0,\ 1}$) on cauliflower and cabbage (Fig. 5). The value of e_{xj} was lowest on cauliflower, indicating faster development, while the e_{xj} was highest on broccoli, indicating slower development on the host.

d. Reproductive value

The V_{xj} of the *L. erysimi* reared on the five brassicaceous hosts at the age zero ($V_{0, 1}$) was 1.23 (broccoli), 1.32 (cabbage), 1.36 (cauliflower), 1.25 (knol khol) and 1.42 (mustard) which were close to λ (Fig 6). With the advancement of age, the V_{xj} curve showed an upward trend, and the highest value on each host was 12.83 (cauliflower), 12.74 (mustard), broccoli (11.84), 11.82 (knol khol), and 11.61 (cabbage) at 8^{th}, 8^{th}, 10^{th}, 8^{th}, and 9^{th} days, respectively. The female adults had the highest V_{xj} on cauliflower.

e. Age-specific life expectancy and reproductive value

The age-specific life expectancy (e_x) estimates the time individuals of age *x* are expected to live (Fig. 7). The expected longevity of *L. erysimi* at age zero (e_0) was in ascending order as follows: knol khol (11.60 days) < broccoli (11.88 days) < mustard (11.96 days) < cabbage (12.56 days) < cauliflower (12.84 days). In all the tested crops, the results showed that as the age advanced, the chances of survival decreased. The age-specific reproductive value (v_x) indicates the contribution of individuals from age *x* to the future population (Fig 8). The results showed that as reproduction begins, the curve for the reproductive value increases rapidly. The peak of the v_x curve was the highest on cabbage (16.56 d^{-1} on 9D), followed by mustard (12.50 d^{-1} on 8D), cauliflower (12.13 d^{-1} on 9D), broccoli (11.60 d^{-1} on 10D) and knol khol (10.85 d^{-1} on 9D). In the past, numerous researchers have endeavored to examine demographic parameters of *L. erysimi* on selected hosts[21,37,38]. Nevertheless, upon thorough review, it becomes evident that none of these studies have provided a comprehensive account of the survival rates, life expectancy, and reproductive values of *L. erysimi* graphically at different age intervals, particularly in the context of significant brassicaceous vegetables.

Conclusion

The varying life cycles of *L. erysimi* on mustard and broccoli signify the respective susceptibility and resistance of these host plants to the insect. These findings offer valuable insights for the development of effective cultural management strategies. By considering demographic parameters such as life expectancy and reproductive value, we can better plan management approaches, including the strategic deployment of bioagents and the judicious use of biopesticides or chemical insecticides.

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Author contributions

SSS conceptualized, and designed the experiments; KMC conducted experiments and wrote the manuscript, to which VKP assisted. SSS, SC and PKS reviewed the manuscript.

Conflict of interest

The authors declare that they have no conflict of interest.

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Fig. 1. The effects of different host plants on the biological properties of aphid based on GGE biplot graph

Fig. 2. GGE biplot graph shows the ideal host plants for aphid

Fig. 3. Age-stage-specific survival rate (S_{xj}) of *L. erysimi* on five brassicaceous host plants under laboratory conditions. *A- broccoli, B- cabbage, C- cauliflower, D- knol khol, E- mustard*

Fig. 4. The age-specific survival rate (l_x), female age-specific fecundity (f_x), and age-specific maternity ($l_x.m_x$) of *L. erysimi* on five brassicaceous host plants under laboratory conditions.

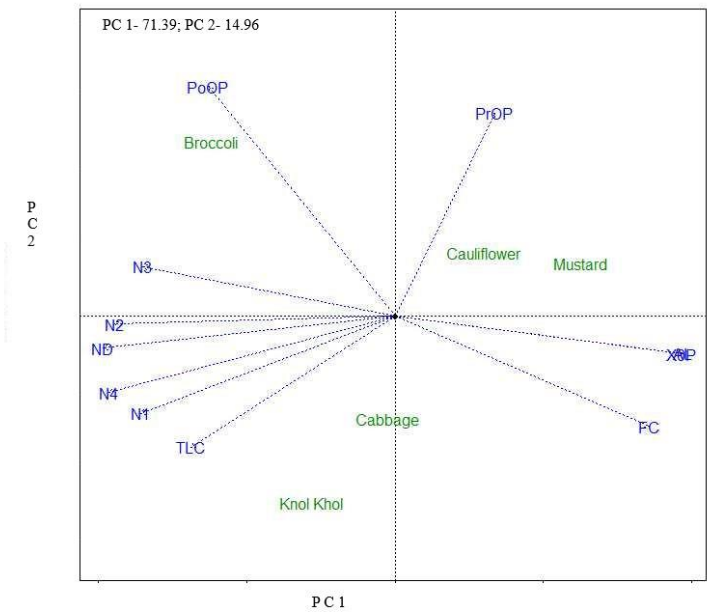
(A- broccoli, B- cabbage, C- cauliflower, D- knol khol, E- mustard)

Fig. 5. Age-stage life expectancy (e_{xj}) of *L. erysimi* on five brassicaceous host plants under laboratory conditions *(A- broccoli, B- cabbage, C- cauliflower, D- knol khol, E- mustard)*

Fig. 6. Age-stage reproductive value (v_{xj}) of *L. erysimi* on five brassicaceous host plants under laboratory conditions *(A- broccoli, B- cabbage, C- cauliflower, D- knol khol, E- mustard)*

Fig. 7. Age-specific life expectancy (e_x) of *L. erysimi* on five brassicaceous host plants under laboratory conditions

Fig. 8. Reproductive value (v_x) of *L. erysimi* on five brassicaceous host plants under laboratory conditions



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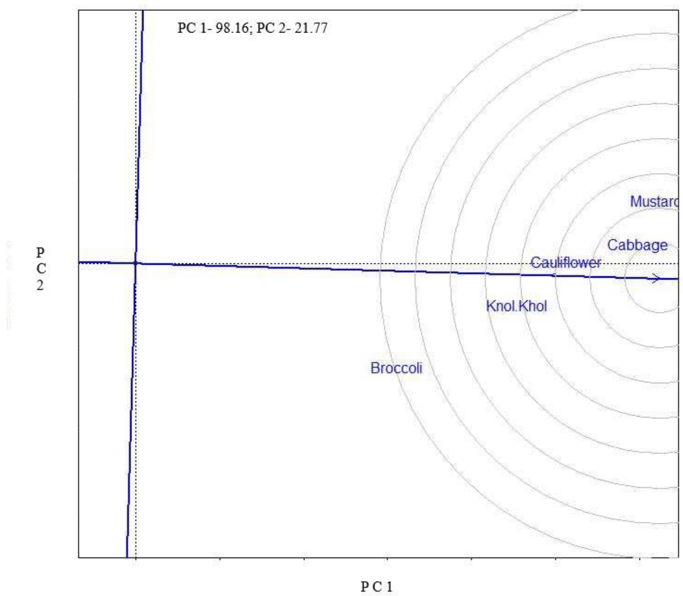

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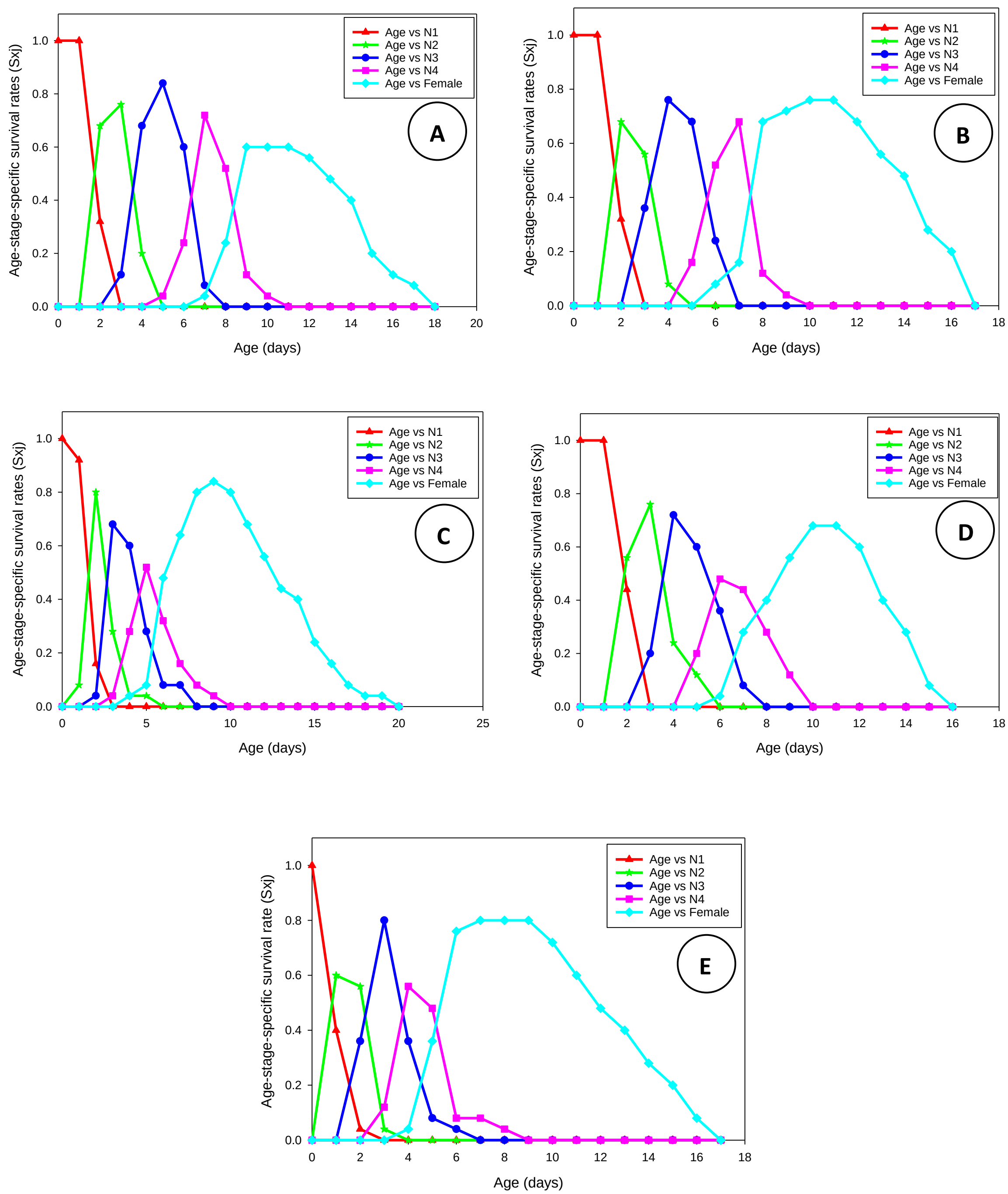
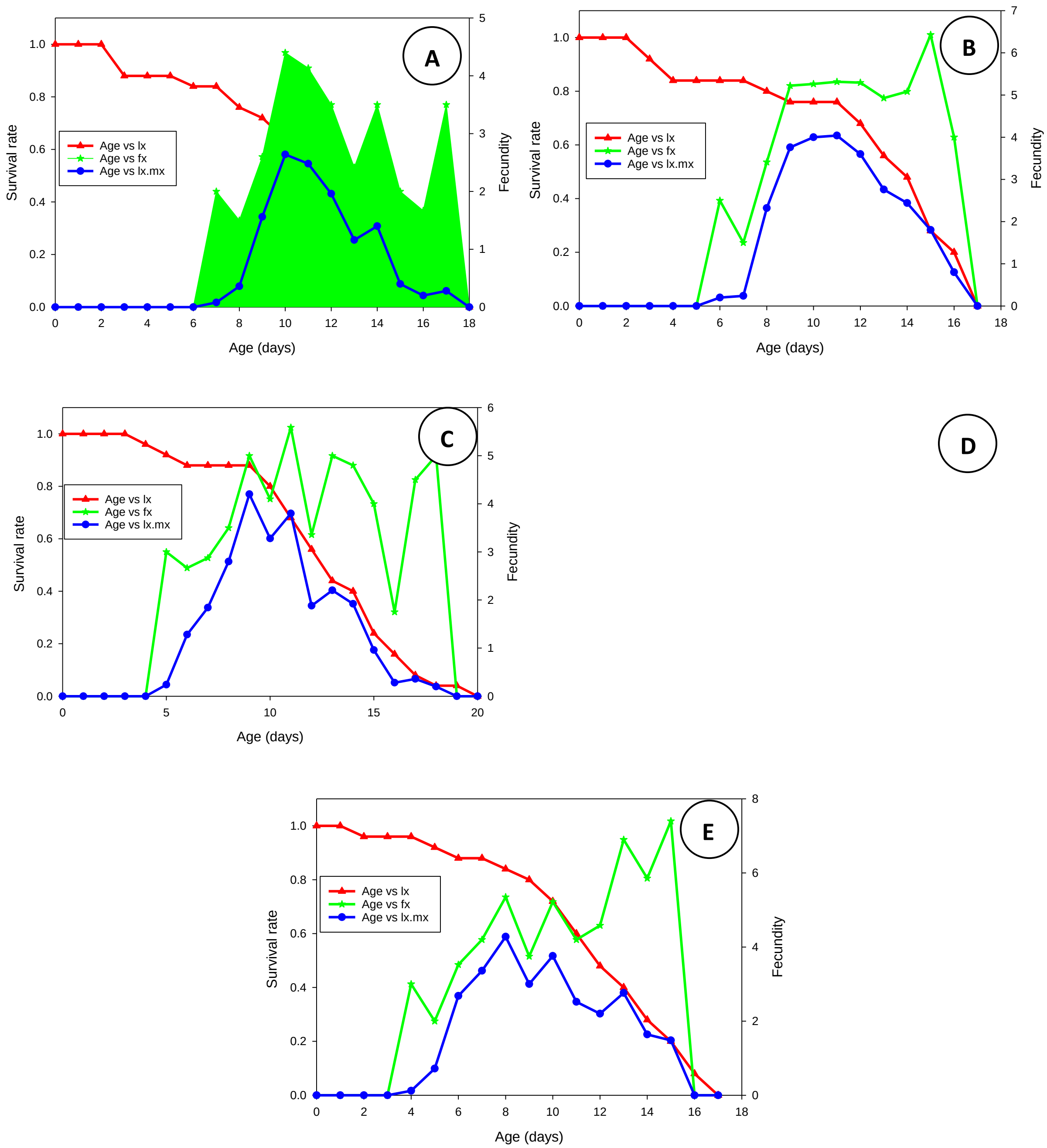


Fig. 3. Age-stage-specific survival rate (S_{xj}) of *L. erysimi* on five brassicaceous host plants under laboratory conditions. A- broccoli, B- cabbage, C- cauliflower, D- knol khol, E- mustard



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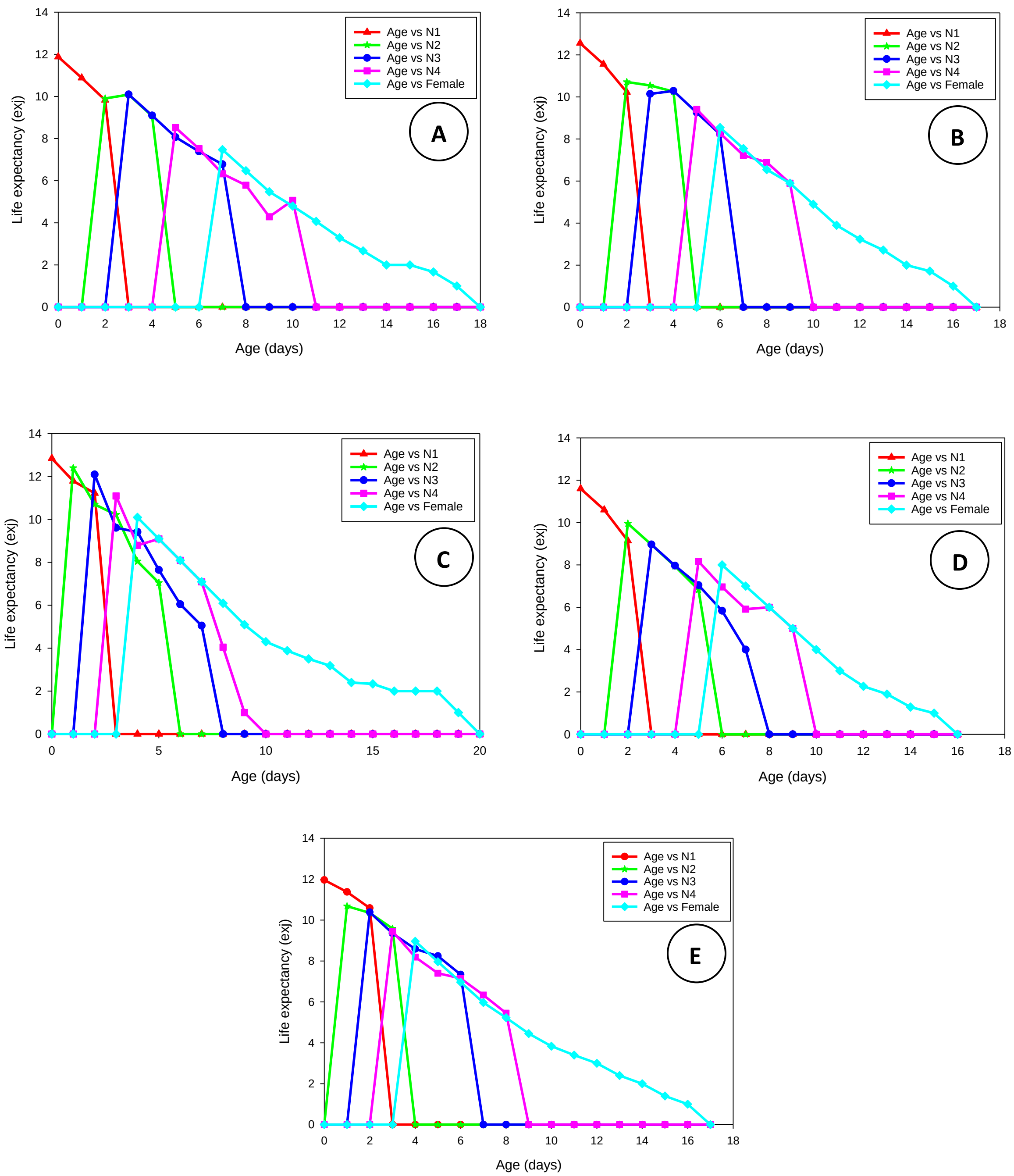

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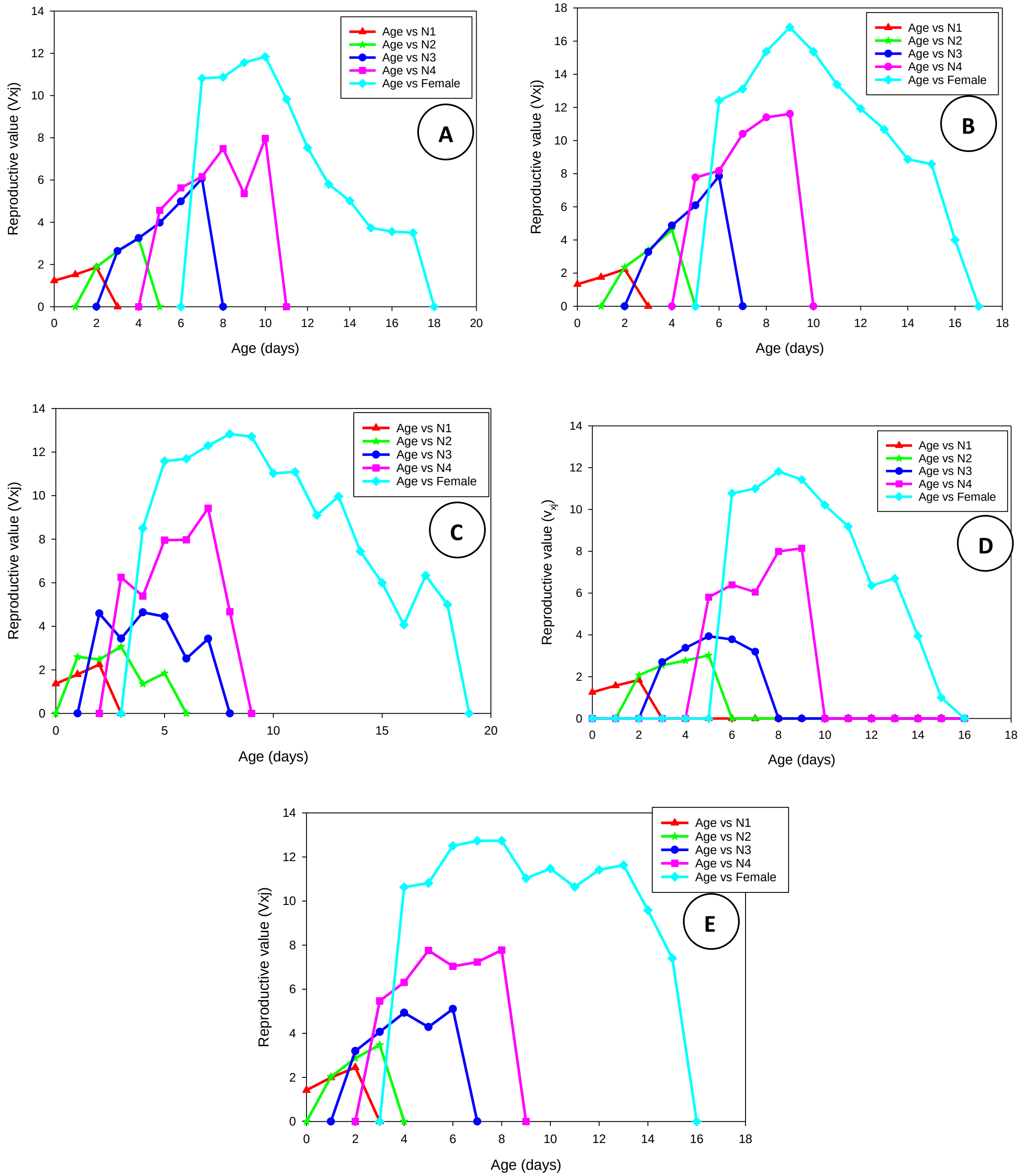
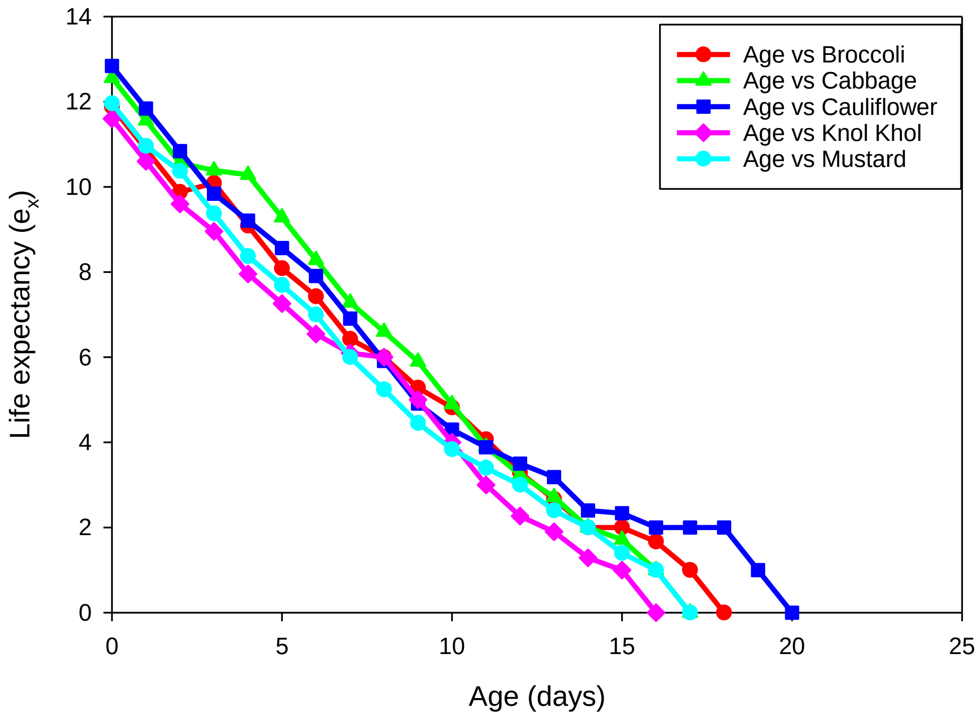


Fig. 6. Age-stage reproductive value (v_{xj}) of *L. erysimi* on five brassicaceous host plants under laboratory conditions (A- broccoli, B- cabbage, C- cauliflower, D- knol khol, E- mustard)



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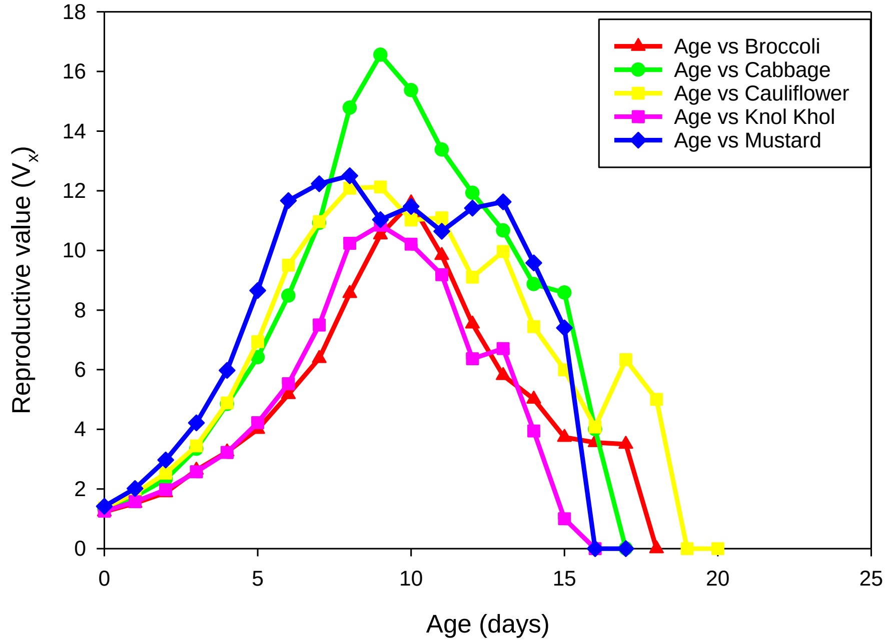

Fig. 8. Reproductive value (v_x) of *L. erysimi* on five brassicaceous host plants under laboratory conditions

Table 1. Biological and reproductive parameters of mustard aphid, *Lipaphis erysimi* (mean±SE) on different brassicaceous hosts under laboratory conditions

	Broccoli	**Cabbage**	**Cauliflower**	**Knol Khol**	**Mustard**	***F cal; F prob***
I instar	2.35±0.49ab	2.33±0.48ab	2.09±0.51b	2.41±0.51a	1.50±0.60c	10.974; 0.0001
II instar	1.80±0.52a	1.38±0.50b	1.26±0.54b	1.71±0.59a	1.23±0.41b	5.256; 0.001
III instar	2.65±0.59a	2.38±0.50ab	1.74±0.86c	2.00±0.71bc	1.68±0.65c	8.038; 0.0001
IV instar	2.00±0.56a	1.81±0.60ab	1.57±0.51bc	2.00±0.79a	1.41±0.59c	3.866;0.006
Nymphal duration	8.80±0.89a	7.90±0.89b	6.65±1.37c	8.12±1.27b	5.82±1.10d	24.09; 0.0001
Adult longevity	5.10±2.63b	6.48±2.32ab	7.00±2.66a	5.88±1.36ab	7.14±2.40a	2.632; 0.039
Pre-oviposition period	0.35±0.49	0.35±0.49	0.43±0.51	0.17±0.38	0.33±12.99	NS
Post-oviposition period	0.59±0.71	0.25±0.44	0.30±0.47	0.22±0.43	0.25±0.58	NS
Oviposition period	4.25±2.59c	6.00±1.86ab	6.04±2.62ab	5.00±1.71bc	6.81±0.44a	4.044; 0.004
Total life cycle	13.90±2.55	14.38±2.20	13.65±2.48	14.00±1.27	12.95±2.38	NS
Fecundity	15.65±10.57c	32.45±14.03a	27.44±13.68ab	23.90±9.19b	33.95±2.09a	7.148; 0.0001
Biotic potential	2.33×10^{27}	2.27×10^{38}	2.86×10^{38}	8.65×10^{35}	1.36×10^{43}	-

Means followed by different letters in the same row are significantly different (n=30)

Table 2. Demographic parameters of *Lipaphis erysimi* (Mean ± SE) on five brassicaceous host plants.

Demographic parameters	Broccoli	Cabbage	Cauliflower	Knol Khol	Mustard	*F cal; F Prob*
Intrinsic rate of increase (*r*)	0.21±0.0015e	0.28±0.0013c	0.31±0.013b	0.23±0.015d	0.35±0.0014a	1751.74; *<0.0001*
Finite rate of increase (λ)	1.23±0.0018e	1.32±0.0017c	1.36±0.0018b	1.25±0.0019d	1.42±0.0019a	1779.38; *<0.0001*
Net reproductive rate (R_0)	12.52±0.21e	25.96±0.36b	25.24±0.32c	13.2±0.19d	28.52±0.37a	647.19; *<0.0001*
Gross reproduction rate (*GRR*)	27.58±0.025d	44.68±0.028c	49.85±0.035b	24.54±0.036e	50.78±0.029a	1504.29; *<0.0001*
Mean generation time (*T*)	12.05±0.32a	11.60±0.24b	10.45±0.44d	11.42±0.19c	9.59±0.31e	1063.14; *<0.0001*
Doubling time (*DT*)	3.30±0.025a	2.47±0.012c	2.24±0.010d	3.07±0.021b	1.98±0.008e	1175.46; <0.0001

Means followed by different letters in the same column are significantly different; Standard errors were estimated by using 100,000 bootstrap resampling