

Research Article

Host plant preference and life table of *Brevicoryne brassicae* (Hemiptera: Aphididae)

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Abstract: The antibiosis, host preference in free-choice situation, and digestive enzyme activity of Brevicoryne brassicae L. (Hemiptera: Aphididae) were evaluated in the laboratory (25 \pm 1 °C, 60 \pm 5% R. H. with a 14-h day) on nine host plants: broccoli, canola (leaf, flower, and pod), cauliflower, kohlrabi, radish, red cabbage and white cabbage. The antibiosis test was based on life table parameters and the experiment started with 50 replicates for each host plant using clip cages. The immature survival varied from 34% on red cabbage to 78% on cauliflower. The viviparous aphids reared on rapeseed (flower) had the highest GRR and R_0 values, and those on red cabbage had the lowest GRR and R_0 values. Also, aphids reared on rapeseed (flower) had significantly higher $r_{\rm m}$ value. The lowest $r_{\rm m}$ value was obtained when individuals fed upon red cabbage. In host preference experiment, rapeseed (leaf) attracted the significantly higher number of adults as opposed to radish, which attracted the lower number of adults. Females who came from nymphs reared on rapeseed (flower) were heavier than other hosts. The growth index of nymphs varied from 0.035 to 0.103, with the minimum on red cabbage and the maximum on cauliflower. The amylolytic activity in adults was higher on rapeseed (flower) and the lowest on red cabbage. In addition, the highest and lowest proteolytic activity was on rapeseed (flower) and red cabbage, respectively. The results of this study indicated that red cabbage was an unsuitable host for feeding of B. brassicae.

Keywords: *Brassica* plants, digestive enzymes activity, life table parameters, plant resistance, the cabbage aphid.

Introduction

Brevicoryne brassicae L. (Hemiptera: Aphididae), the cabbage aphid, is one of the most destructive pests, causing damage at all growth stages of brassica plants directly by sucking and indirectly by secreting honeydew (Mirmohammadi *et al.*, 2009; Bashir *et al.*,

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* Corresponding author, e-mail: razmjou@uma.ac.ir Received: 20 March 2018, Accepted: 9 December 2018 Published online: 17 April 2019 2013). Cabbage aphid is also known to be the vectors of various plant viruses (Dáder *et al.*, 2017). Chemical insecticides are the primary tactic used to control the aphids (Tawfiq et al., 2010; Ali and Zedan, 2015). However, insecticide resistance and toxicity problems for human and environment caused by continuous insecticides usage have stimulated studies exploring alternative methods to control of insect pests (Foster *et al.*, 2007; Saldo and Szpyrka, 2009). The study of the effects of various host plants on life table parameters and digestive physiology of pest

can contribute to developing new control strategies such as producing plants with endogenous resistance and integrated pest management programs.

Feeding preference and performance of insects were reported to be affected by For several factors. many ectotherms, temperature and food are the primary environmental factors affecting growth and developmental rates (Ramalho et al., 2015; Borzoui et al., 2017). Plants contain all the nutrients insect herbivores require, although the amounts and ratios of macronutrients can be highly variable (Lee et al., 2004). The selection of host plant species relies on primary metabolites associated with the physiological conditions of the host plant, as well as, on the detection of secondary plant substances (Francis et al., 2001). However, insect herbivores are not always able to forage and choose between host plants. Dietary restriction in the form of intake of low-quality dietary macronutrients produces a higher mortality, as shown, for example, by recent observations in studies on aphids (Özgökçe and Athhan, 2005; Razmjou et al., 2006; Goldasteh et al., 2012; Araujo et al., 2016).

A life table is a convenient and fundamental method for summarizing the mortality, survival, development, age structure and fecundity of a population of animals. Using a life table, one can compare the growth potential of an insect on different host plants, under controlled environmental conditions (Razmjou et al., 2006; Modarres-Najafabadi et al., 2014; Borzoui et al., 2016). Ulusoy and Ölmez-Bayhan, (2006) investigated the biology of B. brassicae on leaves of six Brassica species and demonstrated that cabbage, cauliflower, and broccoli were susceptible host plants for the cabbage aphid. In contrast, rapeseed, turnip, and mustard showed resistance to the pest. Bashir et al.. (2013)studied the effect oftexture/morphology of host plants on the biology of B. brassicae and reported that Cauliflower is a suitable host for the development and feeding of this pest. Aziz et al., (2016) evaluated the effect of different Brassica vegetables on biology and demographic parameters of B. brassicae and reported a significantly higher intrinsic rate of increase (r_m) and finite rate of increase (λ) on China cabbage followed by Broccoli and Cabbage.

Although cited studies have dealt with biology and life table parameters of B. brassicae, results have been variable, and issues such as the relationship between life history and digestive physiology of insect have not been examined. For example, it is not known whether nitrogen content of leaves that the insects feed during their lifespan are important determinants of survival and offspring production. Such information, which takes into account the age structure of the population, is requisite to creating baseline population growth models. Our objectives were to examine the effect of seven brassicaceous host plants on the physiological and biological traits of cabbage aphid.

Materials and Methods

Plants

The seeds of various host plants including broccoli, canola (leaf, flower, and pod), cauliflower, kohlrabi, radish, red cabbage and white cabbage were obtained from the Plant and Seed Improvement Research Institute, Karai, Iran.

The plants grown were carried out at 25 ± 5 °C with a natural photoperiod in a greenhouse, and they were irrigated as needed. Plants that individually planted in plastic pots (19cm in diameter by 21cm in depth) filled with a suitable mixture of soil (2: 1: 1 field soil, sand, and animal manure, respectively) were used for the experiments. When *Brassica* plants reached the six-leaf stage, the experiments were started. For rapeseed-flower and rapeseed-pod hosts, the plants were used in the reproductive stage. The pots were arranged in a randomized complete block design and protected by muslin (50 meshes) to prevent insect attack.

Insects

A colony of *B. brassicae* used in the experiment was originally obtained from Kohlrabi fields in Ardabil (Iran), on Jun 2016. Stock culture was initiated on Chinese cabbage sown in plastic pots inside a growth chamber under experimental conditions $(25 \pm 1 \, ^{\circ}\text{C}, 60 \pm 5\% \, \text{relative humidity}$ with a 14h day length). Every 2 weeks, 10-15 aphids were transferred from an infested Chinese cabbage to a healthy Chinese cabbage to maintain the colony. After colonization for more than ten months, apterous virginoparous aphids were used for the experiments.

Bioassays

Experiments were conducted in a growth chamber at 25 ± 1 °C, 60 ± 1 % relative humidity with a 14 h day length during the morning and afternoon mid-May to mid-July 2017.

Antibiosis experiment A single young apterous female (within 24 h) from the stock colony was transferred onto each leaf caged with a Petri dish (6cm in diameter by 1cm in depth). The Petri dishes were attached to leaves by clips. Females were allowed to produce nymphs for 12h; after that, the adult aphid and all nymphs except for one nymph were removed from the cages. Individual nymphs were daily monitored to assess their developmental time and survival. After the immature became an adult, the duration of prereproductive, reproductive, post-reproductive time and adult longevity, as well as the reproduction of females, were daily recorded. During the reproductive period, all offspring were removed from the caged plant. Observations were continued until all females died. Experiments were started with 50 replicates for each host plant, but only the individuals that survived to adulthood were nymph included in calculations of development time.

Host preference experiment In order to determine the host preference of *B. brassicae* in a free-choice situation, plants that planted in

plastic pans (40 cm in diameter by 15cm in depth) filled with a suitable mixture of soil (2: 1: 1 field soil, sand, and animal manure, respectively) were used for this experiment. The pots were arranged in a randomized complete block design and protected by muslin (50 meshes) to prevent insect attack. When Brassica plants reached the VI stage, the experiments were started. One hundred apterous females were randomly collected from the rearing chambers and starved for 2h. Aphids were released on a filter paper (11cm in diameter) placed at the center of the circle of plants. The number of apterous females on each plant was counted and recorded after 24h. This experiment was replicated five times.

Mass of females One hundred apterous females (within 24 h) came from nymphs reared on *Brassica* plants were randomly collected and weighed. This experiment was replicated five times.

Population growth index When *Brassica* plants reached the VI stage, caged hosts were infested with twenty 1^{st} instar nymphs (within 24h) per experimental cage. All the aphids remained on the upside of the leaves throughout the duration of the experiment. Population growth was measured in terms of the number of nymphs that became adults and the time is taken to reach the adult stage using the following formula (Saxena *et al.*, 1974; Carey, 1993): GI = l_x/T ; where l_x = survival rate of nymphs, T = duration of the nymphal period. This experiment was replicated five times.

Enzyme activity in aphids Chemicals

Substrates, buffers and reagents were purchased from Sigma Chemical Co. (St. Louis, USA).

Enzyme preparation The apterous female aphids (within 24-48h) fed on each *Brassica* plant were water rinsed and ice chilled for dissection in distilled water at 4 °C. The body of aphids was drilled in pre-cooled distilled

water and homogenized on ice using a precooled homogenizer (Teflon pestle). The extracts were subsequently centrifuged (Eppendorf Microcentrifuge 5415 R, Eppendorf Co., USA) at 15,000g for 15min at 4 °C and the resulting supernatant was used as the enzyme source.

Amylolytic activity The dinitrosalicylic acid (DNS) method (Bernfeld, 1955) was used to assay the digestive amylolytic activity of B. brassicae adults fed on various Brassica plants. In brief, 20µl of enzyme extract from 100 individuals along with 40µl of 1% soluble starch as substrate and 500µl of ice-cold 20 mM Tris-HCl buffer (pH 8.0; data not shown) containing 0.1mM CaCl₂ was incubated at 37 °C for 30min and reducing sugars formed was determined. The reaction was stopped by adding 100mL of DNS and heating in boiling water for 10min. The absorbance was read at 540nm after cooling on ice. Amylolytic activity was expressed as µg of producing maltose per individual. Blanks, in which enzyme extract was added after DNS, were prepared for each assay. This experiment was replicated five times.

Proteolytic activity The general proteolytic activity of B. brassicae adults fed on various Brassica plants was assayed by azocasein digestion method (Gatehouse et al., 1999; Elpidina et al., 2001). Azocasein (1.5% w/v) dissolved in 50 mM acetate buffer (pH 6.0; data not shown) was used as substrate. In brief, 50µl of enzyme extract from 100 individuals was incubated with 80µl of azocasein at 37 °C. The reaction was stopped 50min later by adding 100µl of 30% trichloroacetic acid (TCA). Precipitation was caused by cooling at 4 °C for 30min and the reaction mixture was centrifuged at 15000 g for 10min. At the end, 100µl of the supernatant was added to the equal amount of 2 M NaOH and the absorbance was read at 440nm. Blanks, in which TCA was added before the substrate, were prepared for each assay. This experiment was replicated five times.

Experimental design and statistical analysis

The development time, immature survival rate and adult fecundity were used to the calculation of life table parameters. Calculations were made for age-specific survival rate (l_x) and age-specific fecundity (m_x) of B. brassicae on various Brassica plants based on the method of Carey, (1993). Estimates were made for the intrinsic rate of natural increase (r_m) for B. brassicae on various Brassica plants (Birch, 1948). The other parameter obtained from the life table was the gross reproductive rate (GRR), net reproductive rate (R_0) , intrinsic rate of increase $(r_{\rm m})$, finite rate of increase (λ) , mean generation time (T), and doubling time (DT), which was calculated as described by Birch, (1948) and Southwood and Henderson, (2000).

The duration of life stages of aphids, reproduction, the mass of females, growth index and physiological parameters were compared between the eight Brassica plants and one-way analysis of variance was done in Tukey's HSD test (0.05%) using SAS 9.2 software (PROC GLM; SAS Institute, 2009). Differences in r_m , R_0 , T, DT, and λ values were tested for significance using the Jackknife procedure (Maia et al., 2000). Jackknife pseudo-values computed for life parameters on eight Brassica plants were analyzed by one-way ANOVA and the means were compared using Tukey's test (0.05%) using SAS 9.2 software. Correlation analysis of the life table parameters, population growth index and feeding efficacy and enzyme activities of B. brassicae fed on various Brassica plants with the nitrogen content of host plants was performed using SPSS 16.0.

Results

Growth and reproductive capacity

Nymphal period and adult longevity of *B. brassicae* on the various host plants is given in Table 1. Nymphs reared on cauliflower (7.72 days) developed significantly faster than those on any other host plants. In

contrast, the individuals reared on radish (10.71 days) had a significantly longer nymphal period. The longevity of females was also different on *Brassica* plants tested. The record for female longevity was longest when *B. brassicae* was reared on rapeseed (flower) (15.38 days) and were shortest when it was reared on red cabbage (4.94 days).

Most females began to reproduce nymphs after 24h of emergence. Various host plants significantly affected fecundity of *B. brassicae*

(Table 1). The data revealed that the highest fecundity was recorded for female developed from nymphs reared on rapeseed (flower) (60.13 nymphs), while the lowest was on red cabbage (7.00 nymphs). Also, the mean number of nymphs produced per female per day on rapeseed (flower) (3.91 nymphs) was significantly higher than that of nymphs on the other *Brassica* plants (Table 1). In most cases, the reproduction periods were smaller than adult longevity.

Table 1 Developmental time, adult longevity, mean number of nymphs, and fecundity of *Brevicoryne brassicae* reared on *Brassicae* plants.

Broccoli 64 8.72 ± 0.22 bc 11.19 ± 0.35 b 2.64 ± 0.07 e $30.00 \pm$ Cauliflower 78 7.72 ± 0.17 c 14.20 ± 0.40 a 3.15 ± 0.04 bcd $44.70 \pm$ Kohlrabi 56 8.93 ± 0.26 b 8.11 ± 0.26 c 2.92 ± 0.09 d $24.10 \pm$ Radish 48 10.71 ± 0.34 a 6.79 ± 0.33 c 2.29 ± 0.08 f $15.92 \pm$ Rapeseed (flower) 74 8.00 ± 0.17 bc 15.38 ± 0.34 a 3.91 ± 0.03 a $60.13 \pm$ Rapeseed (leaf) 72 8.33 ± 0.17 bc 15.28 ± 0.35 a 3.30 ± 0.04 b $50.89 \pm$ Rapeseed (pod) 62 8.61 ± 0.20 bc 12.52 ± 0.43 b 3.23 ± 0.04 bc $40.32 \pm$	g/female
Kohlrabi 56 8.93 ± 0.26 b 8.11 ± 0.26 c 2.92 ± 0.09 d 24.10 ± 0.00 Radish 48 10.71 ± 0.34 a 6.79 ± 0.33 c 2.29 ± 0.08 f 15.92 ± 0.00 Rapeseed (flower) 74 8.00 ± 0.17 bc 15.38 ± 0.34 a 3.91 ± 0.03 a 60.13 ± 0.00 Rapeseed (leaf) 72 8.33 ± 0.17 bc 15.28 ± 0.35 a 3.30 ± 0.04 b 50.89 ± 0.00	1.50 de
Radish 48 10.71 ± 0.34 a 6.79 ± 0.33 c 2.29 ± 0.08 f $15.92 \pm$ Rapeseed (flower) 74 8.00 ± 0.17 bc 15.38 ± 0.34 a 3.91 ± 0.03 a $60.13 \pm$ Rapeseed (leaf) 72 8.33 ± 0.17 bc 15.28 ± 0.35 a 3.30 ± 0.04 b $50.89 \pm$	1.35 bc
Rapeseed (flower) 74 8.00 ± 0.17 bc 15.38 ± 0.34 a 3.91 ± 0.03 a 60.13 ± 0.04 b 72 8.33 ± 0.17 bc 15.28 ± 0.35 a 3.30 ± 0.04 b 50.89 ± 0.04 b	1.40 e
Rapeseed (leaf) 72 8.33 ± 0.17 bc 15.28 ± 0.35 a 3.30 ± 0.04 b $50.89 \pm$	1.10 f
	1.45 a
Rapeseed (pod) 62 8.61 ± 0.20 bc 12.52 ± 0.43 b 3.23 ± 0.04 bc 40.32 ± 0.04	1.66 b
	1.34 c
Red cabbage 34 10.12 ± 0.51 a 4.94 ± 0.36 d 1.40 ± 0.06 g 7.00 ± 0.06 g	0.67 g
White cabbage 68 8.62 ± 0.20 bc 11.09 ± 0.25 b 2.99 ± 0.06 cd $33.47 \pm$	1.30 d
df 8, 269 8, 269 8, 269 8, 269	
F 14.64 93.89 114.76 122.41	
P < 0.01 < 0.01 < 0.01	

The means followed by different letters in the same column are significantly different (Turkey's test, P < 0.05).

The age-specific survival rate (l_x) and age-specific fecundity rate (m_x) of *B. brassicae* on *Brassica* plants tested is presented in Fig. 1 and 2. The l_x of aphid started to drop earlier on radish and red cabbage in comparing with other hosts (Fig. 1). The width of the m_x peak, i.e., the fecundity period, was narrower on red cabbage than on other hosts (Fig. 2).

Life tables on various host plants

The gross reproductive rate (GRR), net reproductive rate (R_0) , intrinsic rate of

increase $(r_{\rm m})$, finite rate of increase (λ) , mean generation time (T), and doubling time (DT) were calculated for B. brassicae populations on Brassica plants tested (Table 2). The viviparous apterae reared on rapeseed (flower) (73.08 female/female) had the highest GRR value, and those on red cabbage (12.62 female/female) had the lowest GRR value. The R_0 was highest when B. brassicae was reared on rapeseed (flower) (60.13 female/female) and were shortest when it was reared on red cabbage (7.00 female/female).

¹ The n value shows the sample size for each parameter.

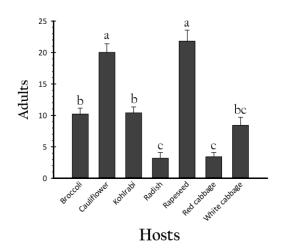


Figure 1 Age-specific survival rate of *Brevicoryne* brassicae caged on different *Brassica* plants.

The $r_{\rm m}$ values ranged from 0.33 to 0.16 female progenies per female per day on Brassica plants tested. Aphids reared on rapeseed (flower) had significantly higher $r_{\rm m}$ value. The lowest $r_{\rm m}$ value was obtained when individuals fed upon red cabbage. The variations in the finite rate of increase (λ) were similar to the intrinsic rate of increase, and the former parameter was significantly influenced by Brassica plants tested. The mean generation time (T) was lowest for B. brassicae reared on cauliflower (11.80 days), mainly because of the shorter developmental period. The time required for doubling the population (DT) was shorter on rapeseed (flower) (2.09 days).

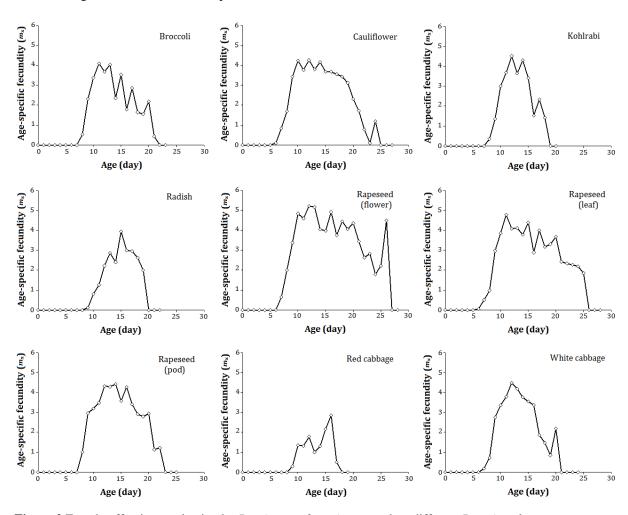


Figure 2 Female offspring production by Brevicoryne brassicae caged on different Brassica plants.

Table 2 Life table parameters of *Brevicoryne brassicae* reared on *Brassica* plants.

Brassica plants	n^1	GRR	R_0	$r_{ m m}$	λ	T	DT
Broccoli	64	34.43 ± 1.57 d	$30.00 \pm 1.49 de$	0.28 ± 0.03 cd	1.32 ± 0.05 cd	12.25 ± 0.21 b	2.50 ± 0.04 cd
Cauliflower	78	50.17 ± 1.96 bc	44.74 ± 1.36 bc	$0.32 \pm 0.05 a$	$1.38\pm0.07~a$	$11.80 \pm 0.22 \ b$	2.15 ± 0.04 e
Kohlrabi	56	$29.59 \pm 1.27 de$	$24.07 \pm 1.39 e$	$0.27\pm0.03~d$	$1.30\pm0.07~\textrm{d}$	$11.93 \pm 0.26 b$	$2.60\pm0.06~c$
Radish	48	24.31 ± 1.51 e	$15.92 \pm 1.09 \text{ f}$	$0.20\pm0.05~e$	$1.22\pm0.06~e$	12.63 ± 0.40 a	$3.41 \pm 0.09 \ b$
Rapeseed (flower)	74	73.08 ± 2.33 a	$60.13 \pm 1.45 \text{ a}$	$0.33 \pm 0.05 \ a$	1.39 ± 0.07 a	$12.38 \pm 0.23 \ b$	2.09 ± 0.04 e
Rapeseed (leaf)	72	57.68 ± 1.69 b	$50.89 \pm 1.66 \text{ b}$	$0.31 \pm 0.05~ab$	$1.36\pm0.06~ab$	12.65 ± 0.26 ab	$2.23 \pm 0.04 de$
Rapeseed (pod)	62	$46.00 \pm 1.49 c$	40.32 ± 1.34 c	$0.29\pm0.04~bc$	$1.34\pm0.06~bc$	12.54 ± 0.21 ab	2.35 ± 0.04 cde
Red cabbage	34	$12.62 \pm 1.00 \mathrm{f}$	$7.00\pm0.67~g$	$0.16\pm0.08~f$	$1.17\pm0.09~\mathrm{f}$	$12.04 \pm 0.44 \ b$	$4.27 \pm 0.24 \ a$
White cabbage	68	$36.73 \pm 1.72 d$	$3.47 \pm 1.30 \ d$	$0.29\pm0.04~bc$	$1.34 \pm 0.05 \ bc$	12.00 ± 0.17	$2.37 \pm 0.04~cde$
df		8, 269	8, 269	8, 269	8, 269	8, 269	8, 269
F		95.30	122.41	85.60	81.77	4.15	85.82
P		< 0.01	< 0.01	< 0.01	< 0.01	< 0.01	< 0.01

The means followed by different letters in the same column are significantly different (Turkey's test, P < 0.05).

Host preference in free-choice situation

The number of adult aphids attracted to various host plants showed that there was a significant difference among *Brassica* plants ($F_{6,28} = 38.97$; P < 0.01). In 24h, rapeseed (leaf) (21.8 aphids) attracted the significantly higher number of *B. brassicae* aphids as opposed to radish (3.2 aphids), which attracted the lower number of aphids (Fig. 3).

Mass of females

The results of females' weight of *B. brassicae* on different *Brassica* plants are shown in Table 3. The females which came from nymphs reared on rapeseed (flower) were heavier (108.68mg) than those reared on any other hosts. By contrast, the lowest mass of *B. brassicae* females was seen in the insects that came from nymphs reared on red cabbage (37.22mg).

Population growth index

The growth index of nymphs varied from 0.035 to 0.103, with the minimum on red cabbage and the maximum on cauliflower (Table 3).

Midgut enzymes activity on various host plants

Amylolytic Activity The amylolytic activity of the adults of *B. brassicae* on various host plants is given in Fig. 4. Tested *Brassica* plants significantly affected digestive α -amylase activity in this insect ($F_{8, 18} = 27.64$; P < 0.01). The amylolytic activity in females was higher on rapeseed (flower) (0.107 mU/min/individual) than on other hosts. However, amylolytic activity was the lowest when the insects were reared on red cabbage (0.034 mU/min/individual).

General proteolytic Activity The general proteolytic activity of the adults of *B. brassicae* on various host plants is given in Fig. 4. Tested *Brassica* plants also affected digestive proteolytic activity in this insect ($F_{8,18} = 6.02$; P = 0.008). The females reared on rapeseed (flower) (0.0083 OD/min/individual) demonstrated the highest level of proteolytic activity, whereas the lowest activity was in the females reared on red cabbage (0.0024 OD/min/individual).

¹ The n value shows the sample size for each parameter.

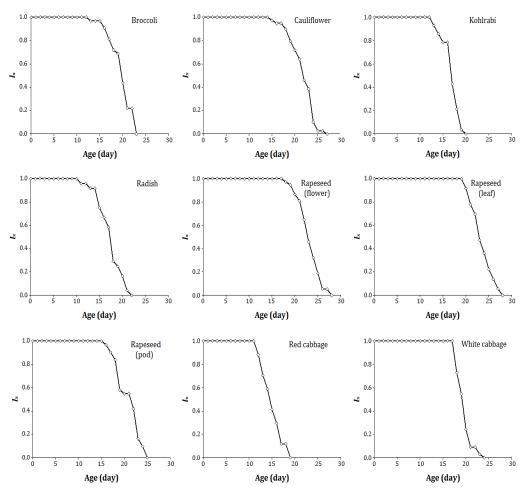


Figure 3 The number (mean \pm SE) of *Brevicoryne brassicae* apterous adults (n = 5) selecting different *Brassica* plants after 24h.

Table 3 Mass of females and growth index of Brevicoryne brassicae reared on Brassica plants.

Brassica plants	n^1	Mass of females (mg)	n	Growth index
Broccoli	5	52.56 ± 46 d	64	0.075 ± 0.002 d
Cauliflower	5	$96.48 \pm 0.63 \text{ b}$	78	0.103 ± 0.002 a
Kohlrabi	5	$46.38 \pm 0.58 e$	56	0.064 ± 0.002 e
Radish	5	45.34 ± 0.63 e	48	$0.046 \pm 0.001 \text{ f}$
Rapeseed (flower)	5	$108.68 \pm 1.28 \ a$	74	$0.094 \pm 0.002 \text{ ab}$
Rapeseed (leaf)	5	$94.06 \pm 0.68 \ b$	72	$0.088 \pm 0.002 \ bc$
Rapeseed (pod)	5	74.40 ± 0.61 c	62	$0.073 \pm 0.002 de$
Red cabbage	5	$37.22 \pm 0.59 \text{ f}$	34	$0.035 \pm 0.001 \text{ g}$
White cabbage	5	$53.62 \pm 0.73 d$	68	$0.080 \pm 0.002 \text{ cd}$
df		8, 36		8, 269
F		133.52		101.64
P		< 0.01		< 0.01

The means followed by different letters in the same column are significantly different (Turkey's test, P < 0.05). The n value shows the sample size for each parameter.

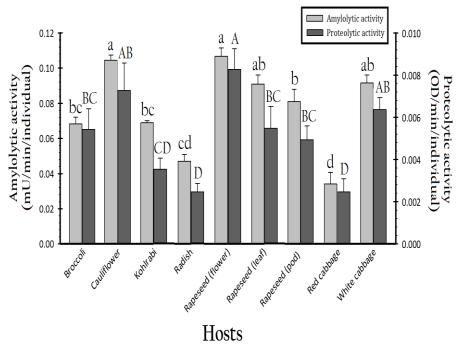


Figure 4 Mean (\pm SE) amylolytic and proteolytic activity (n = 5) in the gut extract of *Brevicoryne brassicae* adults reared on different *Brassica* plants.

Discussion

Quality of host plant affected both development and reproduction among individual B. brassicae in this study. Feeding on radish and rapeseed, as unsuitable hosts, was improved performance in B. brassicae as compared to other hosts. Nymphs developed slower on these hosts, suggesting that those had not relatively optimal nutrition and/or higher concentration of secondary metabolites. Cole, (1996) showed that increased concentrations of 2phenylethylglucosinolate in Brassica species cause the resistance of plants to B. brassicae.

In the present study, females reared on red cabbage showed substantially reduced longevity and were not able to produce significant numbers of nymphs. Probably, quality of host plant plays a decisive role in reproduction of *B. brassicae*. Ulusoy and Olmez-Bayhan, (2006) reported that female longevity of *B. brassicae* varied between 6.2 days on turnip and 21.8 days on cauliflower. Ellis and Farrell, (1995) reported that different fecundity of *B. brassicae* on host plants can be attributed to differences in

the levels of resistance or sensitivity of the plants.

In this study, the decreased age-specific survival rate (l_x) of *B. brassicae* on red cabbage and radish may be because of lower nutritional quality and the presence of inhibitors, as a more appropriate food usually increases survival rate (Goławska *et al.*, 2012; Borzoui *et al.*, 2017), as observed for the nymphal period of *B. brassicae* on both rapeseed (flower).

The low immature survival, low female longevity, and reduced reproduction of *B. brassicae* on red cabbage and radish observed in the present study may possibly be attributed to the presence of antibiosis in these hosts. Munthali and Tshegofatso, (2014) reported that the chemical contents of the sap and physical characteristics of plants affect development rate, survival, and the reproductive potential of *B. brassicae*.

The R_0 and $r_{\rm m}$, both of which are important indicators of the combined effect of host plant on development, survivorship, and reproduction of aphids, were lowest on red cabbage. The lower values of those parameters on red

cabbage were mainly due to longer development time, a later peak in reproduction, low daily nymph production, and low total fecundity. The results regarding the R_0 and $r_{\rm m}$ of B. brassicae did not agree with those achieved by Ulusoy and Olmez-Bayhan, (2006) on different *Brassica* plants. Such discrepancy might be attributed to genetic variation in populations, variation in quality of tested hosts, and variations in experimental conditions and cultivars used for the feeding of this pest. Population DT was longer for aphids reared on red cabbage than for those reared on rapeseed (flower) and cauliflower, due to the lower $r_{\rm m}$ on this plant. We believe that the differences in life parameters of B. brassicae experimental plants can be attributed to differences in the nutritional quality and the differences in the physiology and biochemical structure of the host plants tested.

In the antixenosis experiment, radish and red cabbage were host plants with the statistically lower number of females than the number of females found on the susceptible checks 24h after aphid release, indicating a strong antixenotic effect of these plants to B. brassicae. Factors responsible antixenotic in these plants against B. brassicae remain unknown. Several factors of plants including plant architecture, chemical structure, the color of leaf, and secondary metabolites probably cause host preference of B. brassicae. Diaz-Montano et al., (2006) reported that a strong less host preference may result in a reduction of antibiosis parameters.

Growth index and body weight is an important fitness indicator of population dynamics of insects (Liu et al., 2004; Hosseininejad et al., 2015). According to results of this study, growth index of individuals reared on red cabbage was also reduced and aphids were smaller at maturity than individuals reared on other host plants; suggesting that the quality of host plant have the main effect on the fitness of *B. brassicae*.

This study is the first attempt to characterize digestive α -amylase and general protease activity of *B. brassicae* in response to feeding

on various host plants. Both amylolytic and proteolytic activity was detected in the gut of B. brassicae adults as reported for other aphids (Cristofoletti et al., 2003; Pyati et al., 2011; Darvishzadeh et al., 2014). Also, α-amylase and protease differentially expressed between aphids grown on various host plants. Higher gut amylolytic and proteolytic activity in rapeseed (flower) and cauliflower-reared insects as compared to those reared on radish and red cabbage, i.e., the gut enzymes level was proportional to the quality of the host plans. This supports earlier observations that quality of food is the main factor that has a direct effect on digestive enzymes activity responsible for providing energy and nutrition to the growing insects (Sivakumar et al., 2006; Borzoui et al., 2018). In this case, the differences obtained in digestive enzyme activity may be due to the different concentrations of enzyme inhibitors, especially lectins (Cole, 1997; Napoleão et al., 2012; Kumar et al., 2012).

In conclusion, resistant plants play a key role in IPM programs. Therefore, identification of resistant plants is the first step in the development of an IPM program. According to results obtained in this study, rapeseed and cauliflower appeared to be the most favorable hosts for B. brassicae among the host plants tested. Also, we found a close and positive association between quality of the host plant suitability and the enzyme's activity. These findings might provide useful information for mass producing B. brassicae prey, in insectaries or under laboratory conditions, for release in augmentative biological control programs. However, additional studies are required on the chemical composition of the sap and the performance of B. brassicae on different host plants in the field, and the effect of the plants tested on the effectiveness of the natural enemies of this pest.

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ترجیح میزبانی و جدول زندگی شته مومی کلم (Hemiptera: Aphididae) ترجیح میزبانی و جدول

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چکیده آنتیبیوزی، ترجیح میزبانی در وضعیت انتخابی و فعالیت آنزیمهای گوارشی Brevicoryne brassicae L. (Hemiptera: Aphididae) روی میزبانهای مختلف کلمیان شامل تربیعه، کلزا (برگ، گل و غلاف)، کلم بروکلی، کلم سفید، کلم قرمز، کلم قمری و گل کلم در شرایط آزمایشگاهی (دمای ۱ \pm ۲۵ درجه سلسیوس، رطوبت نسبی $\Delta \pm \delta$ و دوره نوری ۱۴ ساعت روشنایی و ۱۰ ساعت تاریکی) بررسی شد. آزمایش آنتیبیوزی براساس آمارههای جدول زندگی انجام و آزمایش با ۵۰ تکرار برای هر میزبان با استفاده از قفس برگی شروع شد. بقای مراحل نابالغ از ۳۴ درصد روی کلم قرمز تا ۷۸ درصد روی گل کلم متغیر بود. شتههای پرورش یافته روی کلزا (گل) بالاترین مقدار R0 و R0 را داشتند و افراد پرورش یافته روی کلم قرمز کمترین مقادیر GRR و GRR را داشتند. همچنین، مقدار $r_{
m m}$ برای شتههای پرورش یافته روی کلزا (گل) بهطور معنیcداری بالاتر بود. کمترین مقدار $r_{
m m}$ وقتی بهدست آمد که افراد روی کلم قرمز تغذیه کردند. در آزمایش ترجیح میزبانی، کلزا (برگ) بهطور معنی داری تعداد بیشتری از بالغین را نسبت به تربچه جذب کرد. مادههایی که از پورههای پرورش یافته روی کلزا (گل) آمده بودند، نسبت به سایر میزبانها وزن بیشتری داشتند. نرخ رشد شتهها از ۰/۰۳۵ تا ۰/۱۰۳ متغیر بود که بیشترین روی گل کلم و کمترین روی کلم قرمز بود. بالاترین فعالیت آمیلولیتیک در بالغین پرورش یافته روی کلزا (گل) و پایین ترین آن روی کلم قرمز بود. همچنین، بالاترین و پایین ترین فعالیت پروتئولیتیک بهترتیب روی کلزا (گل) و کلم قرمز بود. نتایج این مطالعه نشان داد که کلم قرمز میزبان نامناسب برای شته مومی کلم میباشد.

واژگان کلیدی: گیاه چلیپائیان، فعالیت آنزیمهای هضم، آمارههای جدول زندگی، مقاومت گیاهان، شته مومی کلم