


Induction of resistance against *Brevicoryne brassicae* by *Pseudomonas putida* and salicylic acid in canola

H. Khoshfarman-Borji¹, M. Pahlavan Yali¹  and M. Bozorg-Amirkalaei²

¹Department of Plant Protection, Faculty of Agriculture, Shahid Bahonar University, Iran and ²Department of Plant Protection, Faculty of Agricultural Sciences, University of Mohaghegh Ardabili, Iran

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Author for correspondence:

M. Pahlavan Yali, Email: pahlavanm@uk.ac.ir

Abstract

The cabbage aphid, *Brevicoryne brassicae* L. (Hem: Aphididae), is one of the most serious pests of canola worldwide. In this research, the effects of *Pseudomonas putida*, salicylic acid (SA), and integrated application of both inducers were studied on the resistance of canola to *B. brassicae*. In free-choice situation, the number of *B. brassicae* attracted on canola plants under treatments containing *P. putida* and SA was significantly lower compared to control plants. In the life table study, pre-adult survival, longevity, reproductive period, and fecundity of this aphid were lowest on plants treated with *P. putida* + SA. The net reproductive rate (R_0), intrinsic rate of population increase (r), and finite rate of increase (λ) of *B. brassicae* decreased significantly in the following order: control (47.19 offspring, 0.293 and 1.340 day⁻¹), *P. putida* (16.7 offspring, 0.238 and 1.269 day⁻¹), SA (6.37 offspring, 0.163 and 1.178 day⁻¹), and *P. putida* + SA (3.24 offspring, 0.112 and 1.119 day⁻¹). Moreover, the beneficial effect of the integrated application of *P. putida* and SA on plant growth parameters was significantly evident in our study. The highest values of glucosinolates, total phenol, and flavonoids were recorded in *P. putida* + SA treatment. We concluded that canola plants treated with *P. putida* + SA are more resistant to the cabbage aphid. These findings demonstrated that SA integrated with *P. putida* on canola plants act effectively for reducing the population of *B. brassicae* and can be used in integrated management programs of this pest.

Introduction

Canola, *Brassica napus* L. (family Brassicaceae), is one of the most important oilseed crops, constituting approximately 41% of the edible oil production in Iran (Fathi *et al.*, 2011). This crop attracts a wide range of pests from seedling establishment to seed development. The cabbage aphid, *Brevicoryne brassicae* (L.) (Hemiptera: Aphididae), is one of the most serious pests of brassicaceous crops worldwide (Bhatia and Verma, 1994; Blackman and Eastop, 2000; Elhamahmy *et al.*, 2016). It causes direct damage while probing plant tissues for nutrition, and increases its population quickly on infested plants because of its high reproductive capacity (McKinley, 1992), which may result in stunted growth and deformation of the plant (Bonnemaison, 1965; Oatman and Platner, 1969). In addition, it can also lead to indirect damage by transmitting plant pathogenic viruses such as cauliflower mosaic, cabbage ring spot virus, and *B. brassicae* virus (BrBV) (Broadbent, 1954; Blackman and Eastop, 2000; Ryabov, 2007). Growers rely on insecticide applications to control *B. brassicae* infestations (David and Gardiner, 1959). However, chemical control has negative effects on agroecosystems and can result in insect resistance to pesticides (Furk and Hines, 1993). These factors have led to increased interest in finding eco-friendly and inexpensive alternative approaches such as plant resistance for managing pests (Smith, 1989).

Plant resistance mechanisms against insects can be classified into antixenosis, antibiosis, and tolerance (Kogan and Ortman, 1978). Plant antixenosis negatively influences the processes of an insect's colonization, causing a reduced initial infestation level (Stowe *et al.*, 2000). Antixenosis, also referred to as non-preference, is based on morphological and/or chemical traits that make a plant unattractive to insects for feeding or oviposition (Painter, 1941; Kogan and Ortman, 1978). In fact, antixenosis causes unfavorable effects on insect behavior (Painter, 1951). Antibiosis manifests after a host plant has been attacked. This mechanism is defined as the negative efficacy of a plant on the biological parameters of an insect pest as a result of feeding activity on the resistant host plant. This type of resistance is mainly attributed to plant allelochemicals and results in smaller body size, lower survival, longer development time, and poor fecundity in insects (Smith, 2005). High levels of resistance in *Brassica fruticulosa* Cirillo to the cabbage aphid have been ascribed to a combination of antixenosis and antibiosis (Ellis and Farrell, 1995). The tolerance mechanisms include resource allocation patterns, plant architecture, and other traits that lessen the loss of biomass or yield under

herbivore injury (Stowe *et al.*, 2000). Therefore, the tolerance mechanism differs from antixenosis and antibiosis mechanisms in how it influences the insect–plant relationship (Teetes, 2007). Antibiosis and antixenosis resistance cause an insect response when the insect attempts to utilize the resistant plant for food, oviposition, or shelter (Teetes, 2007), while plant tolerance involves plant compensatory characteristics, and consequently, the plant can harbor large numbers of herbivores without interfering with the insect pest's physiology or behavior (Koch *et al.*, 2016).

One defense system that plants use to protect themselves against insects is induced resistance. The two most clearly defined forms of induced resistance are systemic acquired resistance (SAR) and induced systemic resistance (ISR), which can be distinguished on the basis of the nature of the elicitor and the regulatory pathways involved, as demonstrated in model plant systems (Pieterse *et al.*, 1996, 1998; Knoester *et al.*, 1999). SAR can be activated by exposing the plant to virulent and non-pathogenic microbes, or artificially with chemicals such as salicylic acid (SA) (Sticher *et al.*, 1997). SAR is characterized by the accumulation of SA and pathogenesis-related proteins (Pieterse *et al.*, 1996). ISR is described as systemic protection of a plant by an inducing factor when used to a single part of the plant (Kloepper *et al.*, 1992). ISR is potentiated by plant growth-promoting rhizobacteria (PGPR), of which the best examples are strains within several species of *Pseudomonas* that cause no evident damage to the root system of a plant (van Loon *et al.*, 1998). ISR relies on pathways regulated by jasmonate and ethylene (ET) (Pieterse *et al.*, 1998; Knoester *et al.*, 1999), but several examples of ISR are related to the production of siderophores or SA by PGPR strains (Maurhofer *et al.*, 1994; Leeman *et al.*, 1995; De Meyer and Höfte, 1997).

The application of PGPR (Zehnder *et al.*, 1997; Stout *et al.*, 2006; Zebelo *et al.*, 2016; Rashid and Chung, 2017) and plant growth regulators including SA (Peng *et al.*, 2004; Kawazu *et al.*, 2012) has been shown to induce resistance in plants to some pests. For example, PGPR has induced resistance in corn against corn earworm, *Helicoverpa zea* Hübner (Bong and Sikorowski, 1991), in cucumber to cucumber beetles, *Diabrotica undecimpunctata* Barber (Zehnder *et al.*, 1997), and in cotton against cotton bollworm, *Helicoverpa armigera* Hübner (Qingwen *et al.*, 1998). Moreover, resistance induced by SA has been found in tomato against *H. armigera* and *Macrosiphum euphorbiae* (Thomas) (Cooper *et al.*, 2004), and in chili pepper against *Frankliniella occidentalis* Pergande (Zheng *et al.*, 2019).

SA is one of the most important phytohormones that generates a wide range of metabolic and physiological responses in plants and regulates many aspects of plant growth and resistance against various stresses, including phloem-feeding herbivores (Raskin, 1992; Zhao *et al.*, 2009; Kawazu *et al.*, 2012). In addition, SA induces plant tolerance to various abiotic and biotic stresses (Horváth *et al.*, 2007; Kamel *et al.*, 2016). Elhamahmy *et al.* (2016) reported that the foliar application of SA (50 mg l⁻¹) was an effective elicitor to reduce the *B. brassicae* population on canola inflorescence and improve its yield.

PGPR can improve plant growth through the induction of phytohormones such as jasmonic acid (JA), SA, and ET in plants; increased nitrogen and phosphorus uptake; and the enhancement of iron nutrition through iron-chelating siderophores (Bowen and Rovira, 1999; Naeem *et al.*, 2018). Many PGPR are able to induce the defense mechanism in host plants through alterations in the secondary plant compounds, thereby enhancing the resistance

in plants against challenging pathogens and insect pests (Vidyasekaran *et al.*, 1997; Zehnder *et al.*, 1997; Murphy *et al.*, 2000; Ramamoorthy *et al.*, 2001; Mohana Sundaram *et al.*, 2006; Chung *et al.*, 2015). Several rhizobacteria prompt the SA-dependent SAR pathway by SA production at the root surface (Maurhofer *et al.*, 1994; De Meyer and Höfte, 1997), while other rhizobacteria trigger a distinct signaling pathway independent of SA (van Wees *et al.*, 1997; Pieterse and van Loon, 1999). PGPR was also reported to be involved in the ISR of many plants against aphids (Kempster *et al.*, 2002; Boughton *et al.*, 2006; Morkunas and Gabryś, 2011). The main mechanisms of these bacteria in the process of ISR upon insect infestation include elevated cell wall or apoplastic peroxidase activity, callose deposition, and H₂O₂ accumulation (Valenzuela-Soto *et al.*, 2010; Niu *et al.*, 2011; de Oliveira Araujo, 2015; Rahman *et al.*, 2015). *Pseudomonas putida* ATCC12633 (one of the most commonly used PGPR) colonizes the rhizosphere of plants in a mutualistic relationship, resulting in increased plant growth (Kloepper *et al.*, 1985; Cray *et al.*, 2013). Furthermore, *P. putida* can produce allelopathic compounds such as plant growth hormone indole-3-acetic acid (Barazani and Friedman, 2001) that can help or hinder plant growth depending on the compound, plant species, and concentration (Cray *et al.*, 2013).

The PGPR-mediated induced resistance in canola against *B. brassicae* resulted in the increased production of secondary metabolites including glucosinolates, total phenol, and flavonoids (Sattari Nasab *et al.*, 2018). Furthermore, War *et al.* (2014) reported induced resistance through the exogenous application of SA and JA in groundnut against *H. armigera* (Hübner) led to the higher levels of secondary metabolites (total phenol, condensed tannins, and total flavonoids). There are no reports regarding the efficiency of SA integrated with PGPR (*P. putida*) on secondary metabolites of canola, nor on the behavior/performance of the cabbage aphid. Therefore, the objective of the current study was to investigate the impact of applying integrated SA and *P. putida* in comparison with the application of each individually on the contents of glucosinolates, total phenol, and flavonoids in canola plants and the resultant effects on antixenosis, antibiosis, and plant growth parameters for managing *B. brassicae* on this crop.

Materials and methods

Plant sources

The seeds of tested canola plants (cv. Hayola 420) were acquired from Research, Education, Agriculture and Natural Resources of Kerman (Iran). They were surface-sterilized with sodium hypochlorite (0.02%) for 2 min, and afterward were rinsed completely in sterile distilled water. The plants were grown individually in 20 cm-diameter pots filled with a mixture of soil, sand, and manure (2:1:1), and were used for rearing the aphid when they reached the four-leaf stage. They were kept in a greenhouse (20–30°C, 60 ± 5% RH, and natural photoperiod).

Induction treatments

Treatments involved in this study were as follows: (1) the use of an aqueous solution of distilled water for control; (2) application of bacterial suspension containing *P. putida* ATCC12633 on canola seeds; (3) the spraying of solutions of SA on entire leaves of canola plants at 1 mM concentration; (4) integrated application of both treatments (*P. putida* + SA).

Insect rearing

The used aphids in the experiments were obtained from the aphid colony reared in the laboratory of the plant protection department of Shahid Bahonar University, Kerman, Iran, in September 2019 and transferred to the potted plants under the above-defined conditions. Aphids were reared on canola plants (cv. Hyola) for four generations before starting the experiments. To maintain a suitable aphid colony, some aphids were transferred from infested plants to new young plants every week. Generally, in this research, 1300 and 200 wingless aphids were considered to determine the behavior and performance of *B. brassicae*, respectively. To measure secondary metabolites, ten third-instar nymphs, and to determine plant growth parameters, 20 fourth-instar nymphs were taken from the stock culture and transferred to each canola plant potted ($N = 10$; at the four-leaf stage) inside cylindrical plastic cages (15 cm in diameter, 30 cm in height) to prevent escape or parasitism. These nymphs were allowed to feed on the canola leaves under corresponding treatments for 3 days (to measure secondary metabolites) and 10 days (to determine plant growth parameters) in rearing cages. Then the cages and the aphids in them were removed before experiments.

Preparation of *P. putida* and seed inoculation procedure

Pseudomonas putida (strain ATCC12633) applied for the experiment was acquired from IROST, Iran (Iranian Research Organization for Science and Technology) and then were stored until use in a glycerol/Luria–Bertani (LB) broth mixture at -80°C . To prepare bacterial inoculums, cells from the glycerol mix were transferred to LB medium (solid) and permitted to grow for 2 days. Bacteria were directly taken from these plates and incubated in a rotary shaker at 110 rpm for 48 h at room temperature ($28 \pm 2^{\circ}\text{C}$). Then, it was suspended in water, and bacterial concentration was estimated by measuring absorbance at 600 nm. For inoculation, canola seeds sterilized were dipped in bacterial suspensions ($\text{OD}_{600} \sim 1$) and incubated for 20 min at 28°C , with shaking (50 rpm). Gum arabic was used as an adhesive in the inoculation of seeds. The reliability of inoculation was confirmed by plate counting (CFU ml^{-1}) in *P. putida* treatment compared to control (without bacteria). Then seeds were air-dried at room temperature for 30 min, before planting in sterile soil. Autoclaving was used for soil sterilization.

Application of SA

SA was applied based on the method described by HeithIt *et al.* (2001) with slight modifications. SA solutions (Sigma-Aldrich, St. Louis, Missouri, USA) were provided by mixing this compound in a 0.1% (v/v) aqueous solution comprised of TWEEN® 20 (Sigma-Aldrich), as an emulsifier. Canola plants were sprayed with SA at a concentration of 1 mM nearly 30 days after sowing (fourth leaf stage). They were exposed to cabbage aphids 48 h after the application of SA.

Determination of secondary metabolites

Total glucosinolate content

Spectrophotometric assessment was carried out using methanolic extract prepared from the youngest infested canola leaves under different treatments by homogenizing 0.1 mg leaf in a 2 ml vial with 80% methanol. This homogenate was centrifuged at 3000

rpm for 4 min after being kept overnight at room temperature. The supernatant was gathered after centrifugation and made up to 2 ml with 80% methanol. A total of 100 μl of this extract was applied for evaluation. A total of 0.3 ml double-distilled water and 3 ml of 2 mM sodium tetrachloropalladate (58.8 mg sodium tetrachloropalladate + 170 μl concentrated HCl + 100 ml double-distilled water) was appended to it. After incubation at room temperature for 1 h, absorbance was read at 425 nm using a spectrophotometer (Mawlong *et al.*, 2017). A blank was set following the same procedure without the extract. This procedure was conducted in ten replicates. Total glucosinolates were calculated by putting the OD of each sample taken at 425 nm into the predicted formula $y = 0.9846x + 1.1344$.

Total phenol and flavonoid contents

The amount of total phenolic content in the youngest aphid-infested leaves of the canola plants under the studied treatments was determined based on the method described by Ronald and Laima (1999) for which a 0.1 mg sample of the leaf was milled in 95% ethanol and allowed to extract for 24–72 h. Then, to 1 ml of sample, 1.5 ml of 95% ethanol was appended and made up to a volume of 5 ml with distilled water. To this combination, 0.5 ml of 50% Folin's reagent and 1 ml of 5% sodium carbonate was added and vortexed. The mixture was reserved in the dark for 1 h. Afterward, the absorbance was measured at 725 nm using a spectrophotometer (Ronald and Laima, 1999). The concentration of total phenolic content was determined as mg of gallic acid equivalent using an equation obtained from the gallic acid calibration curve. This experiment was carried out in ten replicates.

Total flavonoid content in the youngest aphid-infested leaves of canola plant under the studied treatments was evaluated using the technique of Jia *et al.* (1999). A total of 500 μl sample was mixed with 5% sodium nitrite (75 μl), and thereafter the mixture was shaken and permitted to place for 5 min at room temperature. Afterward, the mixture was sequentially blended with 10% aluminum chloride (150 μl), 1 M NaOH (500 μl), and distilled water (275 μl). The absorbance was determined at 510 nm by a spectrophotometer. Calibration curve was prepared by quercetin at a concentration between 0.01 and 0.5 mg ml^{-1} . Quantification of total flavonoids was performed using a calibration curve of quercetin at concentrations between 0.01 and 0.5 mg ml^{-1} and expressed as mg quercetin equivalents per gram sample (QE mg g^{-1}). This estimation of total flavonoid content from extracts was conducted in ten replicates.

Data analysis of secondary metabolites

Data of determination of secondary metabolites were tested for significance using the one-way analysis of variance in SPSS for Windows, version 22.0 (SPSS, 2015). The differences among treatment means were compared using the Tukey test with $P = 0.05$.

Aphid behavior

A free choice test was carried out in a greenhouse ($20\text{--}30^{\circ}\text{C}$, $60 \pm 5\%$ RH, and natural photoperiod) using a completely randomized design. One seedling for each treatment was reared and kept randomly at the margin of a large clay pot (40 cm diameter \times 7 cm height). Seedlings were spaced equidistantly in a circular pattern. Then starved 130 motile wingless aphids (for 4 h) were released in the center of the pot on paper. Each pot was surrounded with a transparent plastic cylinder (40 cm in diameter and 30 cm in

height), the top of which was covered with fine mesh gauze to prevent escape or parasitism of the aphids. This procedure was conducted in ten replicates. Data were recorded after 24 and 48 h according to Wiseman *et al.* (1982) and Khan *et al.* (1989). Data were assessed for normality with the Kolmogorov–Smirnov test. Variables were evaluated using the one-way analysis of variance in SPSS version 22.0 (SPSS, 2015). The Tukey test was used for multiple comparisons (SPSS, 2015).

Aphid performance

This experiment was conducted using clip cages (6 cm diameter and 1.5 cm depth) established on the leaves of potted canola plants under studied treatments in a growth chamber ($25 \pm 1^\circ\text{C}$, $60 \pm 5\%$ RH, and 16L: 8D). Apterous adults of the cabbage aphid were placed individually on the lower surface of the same leaves for each plant. Therefore, each plant was considered a replicate, and a total of 50 clip cages were established on canola plants in each treatment. There was one clip cage containing one leaf on each plant (at four-leaf stage). A narrow foam ring had been glued to the cage margin to prevent damage of the leaf. After 24 h, aphid mother and all nymphs except one nymph were removed. Each cage was monitored daily until the maturity of the aphid to determine nymph development period and preadult survival of *B. brassicae* for each treatment. After maturity, daily observations were continued until each female aphid died. The numbers of nymphs produced per female aphid were calculated in each cage daily, and then all nymphs were removed from the cages.

The raw life-history data of all individuals of the cabbage aphid were analyzed by the TWOSEX-MSChart program (Chi, 2017) based on the age-stage, two-sex life table theory (Chi and Liu, 1985). The age-stage-specific survival rate (s_{xj}) (where x is the age and j is the stage), age-stage-specific fecundity (f_{xj}), age-specific survival rate (l_x), age-specific fecundity (m_x), and age-specific maternity ($l_x m_x$) were calculated from the daily records of the survival and fecundity of all individuals in the cohort. Furthermore, the fertility life table parameters including the intrinsic rate of natural increase (r), finite rate of increase (λ), net reproductive rate (R_0), mean generation time (T), and doubling time (DT) were evaluated. The intrinsic rate of increase was determined using the iterative bisection method from the Euler–Lotka formula with age indexed from 0 (Goodman, 1982)

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

The means and standard errors of life table parameters were estimated via the bootstrap technique (Efron and Tibshirani, 1993; Huang and Chi, 2012) with 100,000 resampling. The bootstrap technique is embedded in the computer program TWOSEX-MSChart. The paired bootstrap test was used to assess the differences between treatments.

Measurement of plant growth parameters

We measured the plant growth parameters such as fresh weight, dry weight, and chlorophyll content under the four abovementioned treatments, 10 days after the artificial infestation of seedlings to cabbage aphid. This experiment was carried out at ten replications for each treatment. To determine the fresh weight,

the roots of canola seedlings were washed in water to remove soil particles and then the seedlings were dried with tissue towels for about 10 min, and weighed on a microbalance. To determine dry weight, the seedlings were then dried at 60°C for 48 h, and weighed.

In addition, the amounts of chlorophyll a, b and total were measured based on the standard method proposed by Arnon (1967). Therefore, 1 g leaf sample was crushed with 5 ml acetone 80% in the porcelain mortar. Obtained extract was purified by filter paper. Remained leftovers in the mortar were completely washed by 10 ml of acetone and crossed from filter paper. Obtained samples were as entirely homogenized liquid to 10 ml volume. Then, the absorbance was measured at the wavelengths of 663 and 645 nm using a spectrophotometer. Chlorophyll a, b and total for each sample of treatments were determined following Gu *et al.* (2016):

$$\text{Chlorophyll a (mg g}^{-1} \text{ fw)} = (12.7 \times A663) - (2.59 \times A645)$$

$$\text{Chlorophyll b (mg g}^{-1} \text{ fw)} = (22.9 \times A645) - (4.7 \times A663)$$

$$\text{Chlorophyll total (mg g}^{-1} \text{ fw)} = (8.2 \times A663) + (20.2 \times A645)$$

where A663 and A645 are the absorbance evaluated from 663 and 645 nm, respectively.

Data were evaluated for normality with the Kolmogorov–Smirnov test and were analyzed by the one-way analysis. Then, multiple comparisons were done using the Tukey test (SPSS, 2015).

Results

Determination of some secondary metabolites

Total glucosinolate content

Our results showed that studied treatments significantly influenced the amount of total glucosinolate in aphid-infested leaves of canola ($F = 28.29$; $df = 3, 36$; $P < 0.0001$; table 1). The level of total glucosinolate in plants treated with *P. putida*, SA, and *P. putida* + SA was significantly higher than control plants (table 1).

Total phenol and flavonoid contents

The level of total phenol and flavonoid contents in aphid-infested leaves of canola varied significantly among different treatments ($F = 18.74$; $df = 3, 36$; $P < 0.0001$ and $F = 120.88$; $df = 3, 36$; $P < 0.0001$; respectively) (table 1). The highest and lowest amounts of these compounds were observed on the treatments of *P. putida* + SA and control, respectively. Furthermore, the total phenol and flavonoid contents under SA treatment were significantly higher than *P. putida* treatment (table 1).

Antixenosis test

There were significant differences in the number of aphids attracted to the canola plants under different treatments, 24 and 48 h after the release ($F = 15.93$; $df = 3, 36$; $P < 0.0001$ and $F = 24.57$; $df = 3, 36$; $P < 0.0001$; respectively) (table 2). After 24 and 48 h, the lowest number of aphids was recorded on *P. putida* + SA treatment (8.80 and 12.20; respectively) and the highest was observed on control (19.60 and 29.00; respectively). Moreover, the number of aphids on SA treatment did not differ significantly from the treatments of *P. putida* and *P. putida* + SA (table 2).

Table 1. The mean (\pm SE) amount of secondary metabolites in aphid-infested leaves of canola plants treated with *Pseudomonas putida* and salicylic acid (SA)

Treatment	Total GLs ($\mu\text{mol g}^{-1}$)	TPC (mg g^{-1} fw)	TFC (Abs mg^{-1})
Control	2.19 \pm 0.03b	10.79 \pm 0.21d	0.036 \pm 0.004d
<i>P. putida</i>	2.88 \pm 0.13a	11.70 \pm 0.16c	0.098 \pm 0.007c
SA	3.05 \pm 0.11a	12.70 \pm 0.20b	0.134 \pm 0.003b
SA + <i>P. putida</i>	3.28 \pm 0.11a	13.98 \pm 0.19a	0.173 \pm 0.005a

Total GLs, total glucosinolate, TPC, total phenolic content, TFC, total flavonoid content. Means followed by a different letter within a column are significantly different (Tukey's HSD test; $P < 0.05$), $N = 10$.

Antibiosis test

There was no significant difference in the nymph periods of *B. brassicae* among treatments (table 3). However, tested treatments significantly influenced longevity, reproductive period, and fecundity of this aphid (table 3). The values of these parameters under the treatments of *P. putida* + SA, SA, *P. putida*, and control increased, respectively, at 5% significance level (table 3). Furthermore, the lowest (0.64) and highest (0.84) pre-adult survival rates of this aphid were recorded on the treatments of *P. putida* + SA and control, respectively (table 3). The age-stage-specific survival rate (s_{xj}) represents the probability that a nymph of *B. brassicae* will survive to age x and stage j (fig. 1). The variable development rates among individuals in the cohort resulted in an overlapping of the stage-specific survivorship curves. The probability that a newborn nymph would survive to the adult stage was 0.84 on control, 0.80 on *P. putida*, 0.76 on SA, and 0.64 on *P. putida* + SA. Then survival declined gradually with increased age of the aphid. When all stages are pooled, the age-specific survival rate (l_x) gives a simplified overview of the survival history of the whole cohort (fig. 2). Death of the last female under the treatments of *P. putida* + SA, SA, *P. putida*, and control occurred at days of 15, 18, 20, and 28, respectively. The highest f_{x2} peak in the treatments of *P. putida* + SA, SA, *P. putida*, and control was 1.48, 2, 3.09, and 5.44, respectively. The age-specific fecundity (m_x) and the age-specific maternity (l_{xmx}) of *B. brassicae* are also shown in fig. 2. The highest peaks of m_x and l_{xmx} were recorded as 1.4 and 0.9 on *P. putida* + SA (at 9 day), 1.88 and 1.24 on SA (at 10 day), 3.03 and 2.3 on *P. putida* (at 11 day), and 5.07 and 4.26 on control (at 12 day). The age-stage life expectancy (e_{xj}) (where x is the age and j is the stage) shows the expected lifespan for an individual of age x and stage j (fig. 3). The life expectancies of *B. brassicae* at age zero (e_{01}) were 9.20, 11.52, 13.52, and 18.64 days, on the treatments of *P. putida* + SA, SA, *P. putida*, and control, respectively, and at the stage of aphid maturity, 5.18, 7.55, 9.81, and 15.07 days (fig. 3).

The population growth parameters of *B. brassicae* fed on control and treated plants with *P. putida* and SA are presented in table 4. The values of the net reproductive rate (R_0), the intrinsic rate of population increase (r), and finite rate of increase (λ) of the cabbage aphid decreased significantly in the following order: control (47.19 offspring, 0.293 and 1.340 day^{-1}), *P. putida* (16.7 offspring, 0.238 and 1.269 day^{-1}), SA (6.37 offspring, 0.163 and 1.178 day^{-1}), and *P. putida* + SA (3.24 offspring, 0.112¹ and 1.119 day^{-1}) (table 4).

In the current study, there were significant differences in the generation time (T) and the doubling time (DT) values of *B.*

Table 2. Mean (\pm SE) numbers of attracted *Brevicoryne brassicae* on canola plants treated with *Pseudomonas putida* and salicylic acid (SA) after 24 and 48 h

Treatment	24 h	48 h
Control	19.60 \pm 4.24a	29.00 \pm 6.46a
<i>P. putida</i>	14.40 \pm 4.08b	20.70 \pm 4.02b
SA	11.50 \pm 3.71bc	16.10 \pm 2.96bc
SA + <i>P. putida</i>	8.80 \pm 2.25c	12.20 \pm 4.26c

Means followed by a different letter within a column are significantly different (Tukey's HSD test; $P < 0.05$).

brassicae among the tested treatments (table 4). The doubling time (DT) was the longest (6.13 days) in *P. putida* + SA treatment and the shortest (2.36 days) in control (table 4).

Plant growth parameters

In this study, the analysis of plant growth parameters data indicated significant differences in the amounts of fresh weight ($F = 5.54$; $df = 3, 36$; $P < 0.0001$), dry weight ($F = 8.24$; $df = 3, 36$; $P < 0.0001$), chlorophyll a ($F = 21.38$; $df = 3, 36$; $P < 0.0001$), chlorophyll b ($F = 46.45$; $df = 3, 36$; $P < 0.0001$), and total chlorophyll ($F = 123.55$; $df = 3, 36$; $P < 0.0001$) (table 5).

The maximum fresh weight and dry weight were determined in *P. putida* + SA treatment (6.59 and 1.61 g plant^{-1} ; respectively) and the least in control (3.57 and 0.82 g; respectively) (table 5). The chlorophyll a content was the highest on *P. putida* + SA treatment (2.30 mg g^{-1} fresh weight) and the lowest on control (1.82 mg g^{-1} fresh weight) (table 5). Furthermore, chlorophyll b content under *P. putida* + SA treatment (4.13 mg g^{-1}) was calculated to be significantly higher compared to *P. putida* and control treatments (3.30 and 3.24 mg g^{-1} , respectively) (table 5). For all the tested treatments, the amount of total chlorophyll exhibited following pattern in a descending order: *P. putida* + SA, SA, *P. putida*, and control (6.46, 5.85, 5.32, and 5.09 mg g^{-1} , respectively) (table 5).

Discussion

In the current study, canola plants treated with *P. putida* and SA negatively affected the behavior and performance of the aphids compared with the untreated control plants. This research makes a new contribution to the knowledge of the efficiency of the integration of both inducers. Additionally, secondary metabolites including the glucosinolates, total phenol, and flavonoids in canola leaves increased significantly under treatments containing *P. putida* and SA. Therefore, these inducers can influence the levels of secondary metabolites in canola. In particular, their effects on the amounts of flavonoids and phenolics seem to be significantly additive. The activation of the secondary metabolism in plants, produced by the application of elicitors, incites a series of mechanisms involved in the synthesis of metabolites such as phenolic compounds (Díaz-Rivas *et al.*, 2018). SA elicitor regulates the actions of various enzymes such as polyphenol oxidase, peroxidase, which are the key components of induced plant defense against biotic and abiotic stresses (Hayat *et al.*, 2009; Zhao *et al.*, 2009; War *et al.*, 2011). Díaz-Rivas *et al.* (2018) have shown that SA elicitor could enhance the phenylalanine ammonia-lyase activity in salvilla, and this response promotes

Table 3. Mean (\pm SE) nymph period, adult longevity, reproductive period, and fecundity of *Brevicoryne brassicae* on canola plants treated with *Pseudomonas putida* and salicylic acid (SA)

Treatment	Nymph period (days)	Adult longevity (days)	Reproductive period (days)	Numbers of progeny female	Pre-adult survival
Control	8.38 \pm 0.17a	12.69 \pm 0.44a	10.66 \pm 0.33a	56.19 \pm 1.94a	0.84 \pm 0.05a
<i>P. putida</i>	8.25 \pm 0.22a	7.6 \pm 0.35b	6.6 \pm 0.34b	20.88 \pm 1.22b	0.8 \pm 0.56ab
SA	8.26 \pm 0.14a	5.55 \pm 0.34c	4.84 \pm 0.27c	8.39 \pm 0.56c	0.76 \pm 0.06ab
SA + <i>P. putida</i>	8.03 \pm 0.09a	4.16 \pm 0.23d	3.53 \pm 0.17d	5.06 \pm 0.26d	0.64 \pm 0.06b

Means within a column followed by different letters are significantly different according to the paired bootstrap test at 5% significance level.

the phenolic synthesis associated with the enhancement of the defense resistance of the plants. Two basic routes of the shikimic and malonic acid pathways are known in the biosynthesis of phenolic compounds (Díaz-Rivas *et al.*, 2018). SA not only regulates the components of its own signaling pathway, but also is involved in cross-talk with other pathways that mediate plant resistance (War *et al.*, 2011). On the other hand, PGPR acts as an effective elicitor for the key enzymes that provoke the biosynthesis of secondary metabolites in plants through the ISR mechanism (Chen *et al.*, 2000; van Loon and Glick, 2004). PGPR can stimulate the biosynthesis of JA in plants which acts as a transducer for elicitor signaling pathways, leads to the accumulation of secondary metabolites in plants (Mueller *et al.*, 1993). There is some evidence that PGPR and SA could be related to the production of secondary metabolites. For example, Meena *et al.* (2000) demonstrated that the foliar application of *Pseudomonas fluorescens* strain Pfl could enhance the phenolic compounds of peanut plants. In another study, the values of total phenol, flavonoids, and glucosinolates were significantly higher in aphid-infested leaves of canola plants treated with PGPR (foliar spraying) compared with untreated plants and results in increased resistance to cabbage aphid (Sattari Nasab *et al.*, 2018). The current research also showed that seed inoculation with PGPR is effective on these secondary metabolites and, consequently, the resistance to *B. brassicae*. Moreover, SA considerably enhanced the phytochemical contents (such as total phenolic and flavonoid) in Chinese cabbage plants (Thiruvengadam *et al.*, 2015) and sweet basil (Koca and Karaman, 2015). These findings were similar to the current results on canola. Similarly, there are several other reports regarding the positive effects of SA on increasing phenolic levels in *Brassica alboglabra* Bailey (Sun *et al.*, 2012) and *Lactuca Sativa* L. (Kim *et al.*, 2007). Moreover, it has been previously shown that SA treatment increases glucosinolates in *B. napus* (Kiddle *et al.*, 1994), *Brassica rapa* L. (Smetanska *et al.*, 2007), and *B. alboglabra* (Sun *et al.*, 2012). In this research, the total glucosinolates content in aphid-infested leaves was enhanced by the induction of SA alone or in combination with PGPR. The SA signaling pathway is activated to induce resistance in a number of plant species by aphid feeding (Moran *et al.*, 2002; Zhu-Salzman *et al.*, 2004; Coppola *et al.*, 2013).

The current findings from the antixenosis experiment showed the significant efficacy of the tested treatments on the number of aphids attracted to *B. napus*, as plants treated with *P. putida* + SA displayed strong antixenosis after 24 and 48 h. Furthermore, canola plants treated with SA or *P. putida* were less preferred by *B. brassicae* compared with the control plants, which could be related to the higher levels of secondary metabolites in canola leaves under these treatments. The isothiocyanates (catabolites of

the glucosinolates) are main components mediating host location for *B. brassicae* (Nottingham *et al.*, 1991). The variation in plant volatiles among canola plants under tested treatments has not been examined. Bruce and Pickett (2011) demonstrated that the perception of blends of plant volatiles plays a key role in host recognition, non-host avoidance, and subsequent behavioral responses. Based on their findings, the behavioral activity elicited by blends of volatiles is stronger than that elicited by individual compounds. In general, the difference in the number of aphids attracted could be attributed to variations in chemical compounds, olfactory, and tactile stimuli in host plants (Mohammadi Anaii *et al.*, 2018). Thiruveni *et al.* (2011) showed antixenotic resistance induced by the talc-based bioformulation of PGPR (*P. fluorescens* Pfl + *Beauveria bassiana* B2) against *Earias vittella* (Fabricius) moths. Oluwafemi *et al.* (2011) suggested that the application of methyl salicylate on maize would effectively repel leaf hoppers, *Cicadulina storeyi* China. Furthermore, Favaro *et al.* (2019) verified the antixenosis resistance in strawberry cultivars treated with SA against the two-spotted spider mite. This effect can be due to SAR that results from invader recognition accompanied by the induction of the synthesis of particular materials, such as chitinases and other hydrolytic enzymes, because of the elicitor action as an endogenous signal for triggering the plant defense response (Mandal *et al.*, 2008).

In the current research, some biological characteristics (such as preadult survival, reproduction period, and fecundity) and population growth parameters (such as R_0 , λ , and r) of *B. brassicae* were lowest on the *P. putida* + SA treatment, representing the minor suitability of canola plants treated with these compounds compared with the others for this aphid. A reduction in total fecundity of the aphid on *P. putida* and SA-treated plants compared with the control plants appeared to be the result of a reduction in the number of productive days. Since the intrinsic rate of natural increase (r) is a reflection of survival, fecundity, and generation time of the pest, it can be used as the most valuable index to evaluate pest performance under different conditions of the host plant (Carey, 1993; Southwood and Henderson, 2000). In the present study, the lower value of r of the cabbage aphid (0.112 day^{-1}) under the *P. putida* + SA treatment could be related to meager fecundity, the shorter reproductive period, and the lower survival rate of this aphid. Moreover, the poor performance of *B. brassicae* on plants treated with *P. putida* + SA was associated with the lower age-stage life expectancy (e_{xj}) of individuals on this treatment. Therefore, it can be concluded that *P. putida* + SA leads to antibiosis resistance in canola plants to *B. brassicae*. Phytohormones like SA are able to regulate symbiosis and mediate ISR prompted by useful microbes in the interactions between plants and non-pathogenic rhizosphere microbes (De Vleeschauwer and Höfte, 2009; Zamioudis and Pieterse, 2012).

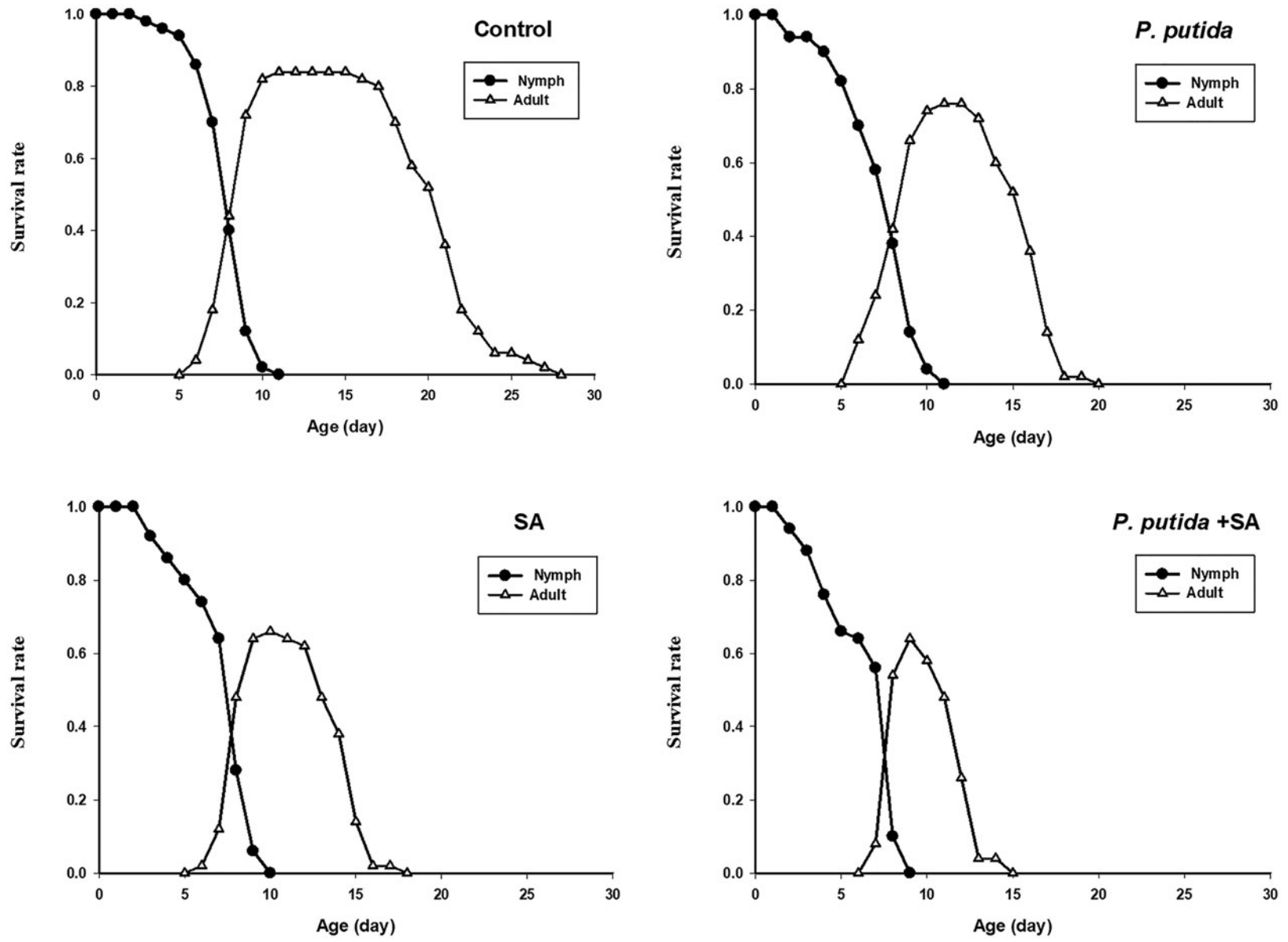


Figure 1. Age-stage specific survival rate (s_{ij}) of *Brevicoryne brassicae* on canola plants treated with *Pseudomonas putida* and salicylic acid (SA).

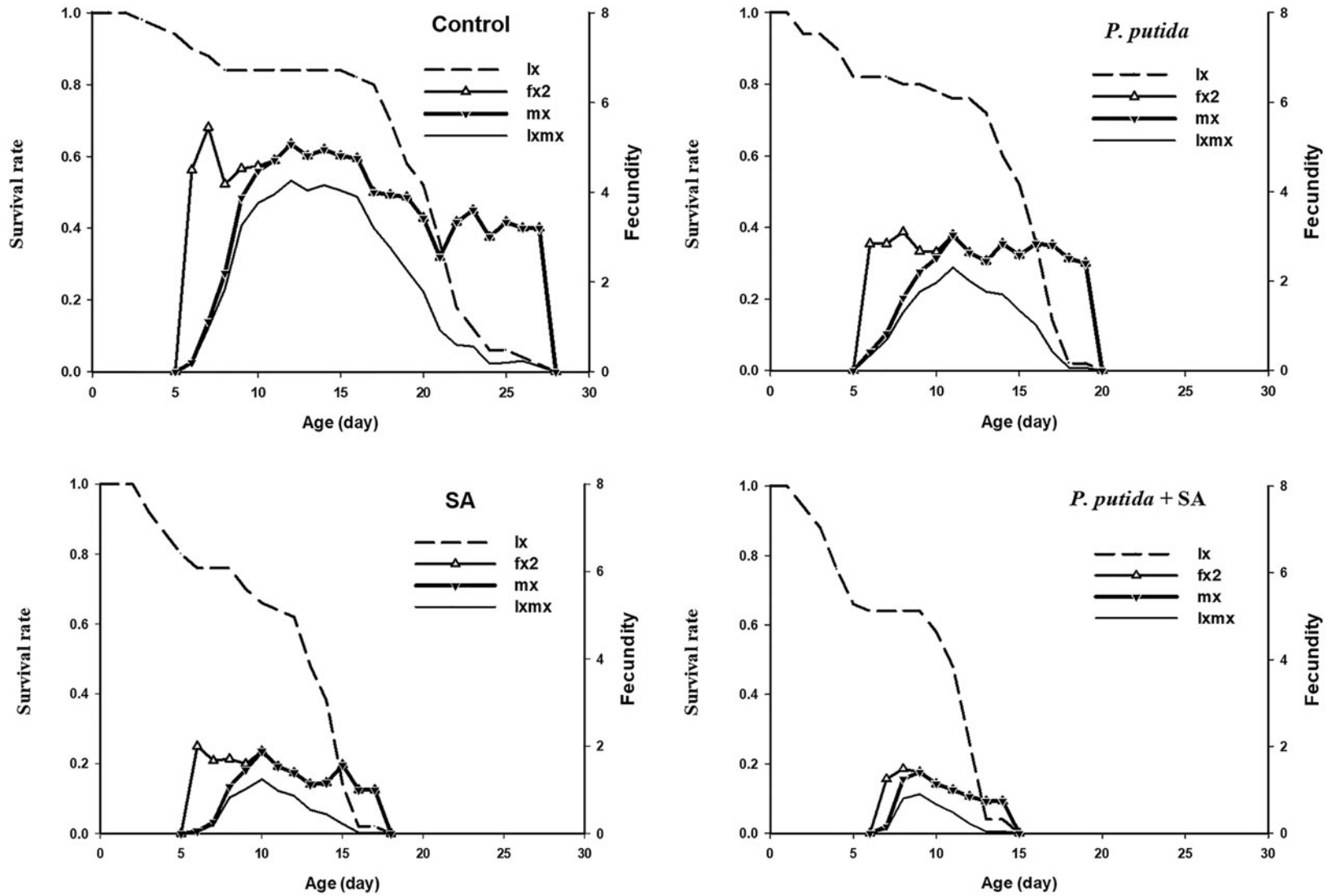


Figure 2. Age-specific survival rate (l_x), female age-specific fecundity (f_{x2}), age-specific fecundity (m_x), and age-specific maternity ($l_x m_x$) of *Brevicoryne brassicae* on canola plants treated with *Pseudomonas putida* and salicylic acid (SA).

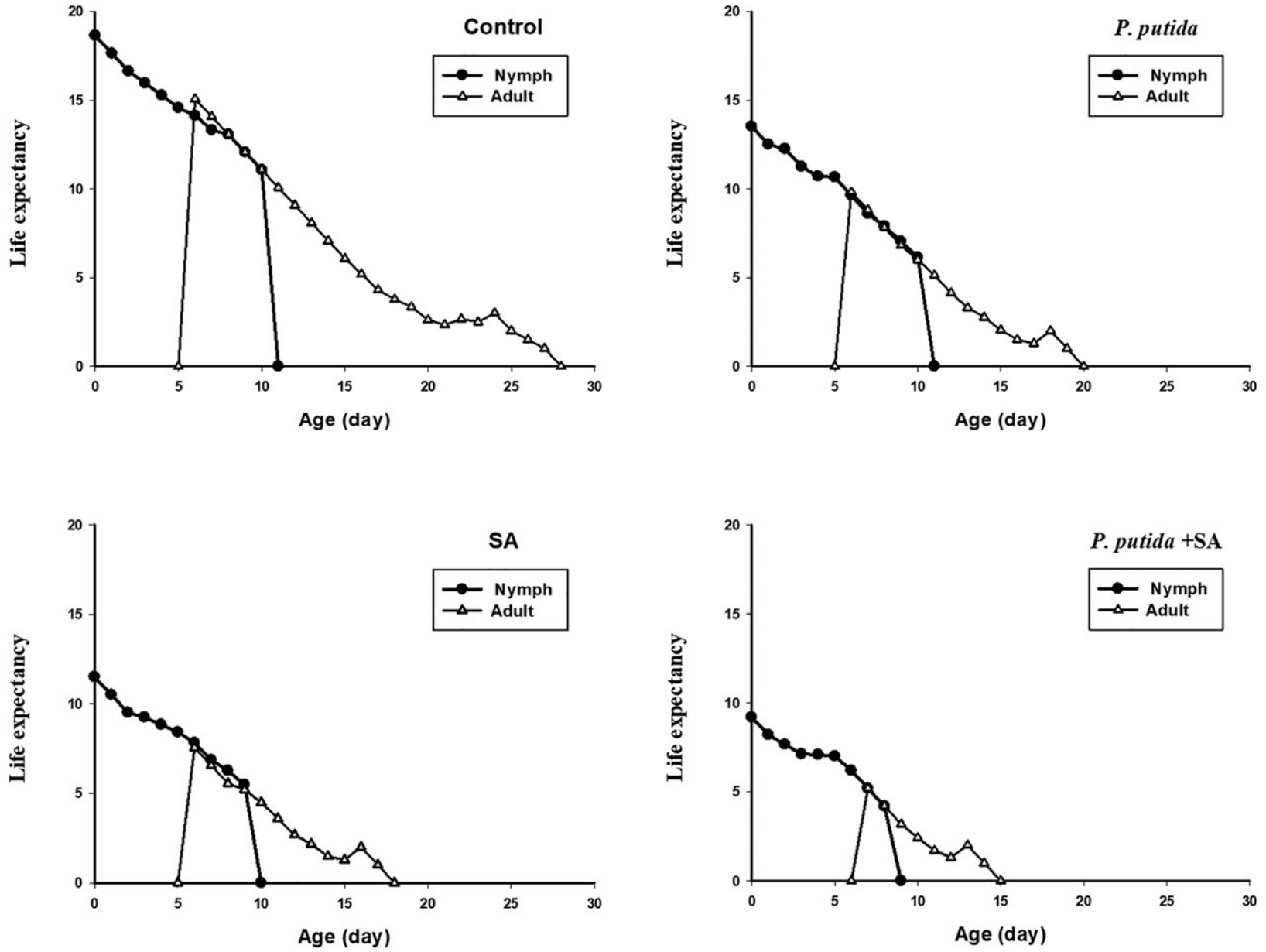


Figure 3. Age-stage specific life expectancy (e_{xy}) of *Brevicoryne brassicae* on canola plants treated with *Pseudomonas putida* and salicylic acid (SA).

Table 4. Mean (\pm SE) life table parameters of *Brevicoryne brassicae* L. on canola plants treated with *Pseudomonas putida* and salicylic acid (SA)

Treatment	R_0 (offspring)	r_m (day ⁻¹)	λ (day ⁻¹)	T (days)	DT (days)
Control	47.19 \pm 3.34a	0.293 \pm 0.007a	1.340 \pm 0.009a	13.13 \pm 0.19a	2.36 \pm 6.04d
<i>P. putida</i>	16.70 \pm 1.53b	0.238 \pm 0.009b	1.269 \pm 0.012b	11.78 \pm 0.24b	2.90 \pm 0.12c
SA	6.37 \pm 0.66c	0.163 \pm 0.009c	1.178 \pm 0.010c	11.27 \pm 0.20b	4.22 \pm 0.25b
SA + <i>P. putida</i>	3.24 \pm 0.38d	0.112 \pm 0.011d	1.119 \pm 0.012d	10.39 \pm 0.12c	6.13 \pm 0.69a

R_0 = net reproductive rate, r_m = intrinsic rate of increase, λ = finite rate of increase, T = mean generation time, and DT = doubling time. Means within a column followed by different letters are significantly different according to the paired bootstrap test at 5% significance level.

Table 5. The mean (\pm SE) fresh weight, dry weight, and chlorophyll content of *Brevicoryne brassicae* L. on canola plants treated with *Pseudomonas putida* and salicylic acid (SA)

Treatment	Fresh weight (g plant ⁻¹)	Dry weight (g plant ⁻¹)	Chlorophyll a (mg.g ⁻¹ fw)	Chlorophyll b (mg.g ⁻¹ fw)	Total chlorophyll (mg.g ⁻¹ fw)
Control	3.57 \pm 0.16b	0.82 \pm 0.77c	1.82 \pm 0.02c	3.24 \pm 0.03c	5.09 \pm 0.03d
<i>P. putida</i>	4.75 \pm 0.50ab	1.11 \pm 0.12bc	1.99 \pm 0.04b	3.30 \pm 0.05c	5.32 \pm 0.06c
SA	4.90 \pm 0.58ab	1.43 \pm 0.13ab	2.13 \pm 0.05ab	3.70 \pm 0.06b	5.85 \pm 0.06b
SA + <i>P. putida</i>	6.59 \pm 0.65a	1.61 \pm 0.13a	2.30 \pm 0.04a	4.13 \pm 0.07a	6.46 \pm 0.05a

Means followed by a different letter within a column are significantly different (Tukey's HSD test; $P < 0.05$).

Similarly, some PGPR-induced biochemical alterations prompt ISR in plants against herbivorous insects (Rajendran *et al.*, 2007; van de Mortel *et al.*, 2012; Wielkopolan and Obrepalska-Stepelowska, 2016; Zebelo *et al.*, 2016). Fahimi *et al.* (2014) showed that the application of *P. fluorescens* strains UTPF68 and PF169 on cucumber led to a decrease in the average number of progeny produced by *A. gossypii* adults. In the current life table study, it was found that when *B. brassicae* is reared on canola plants treated with *P. putida* alone, its performance is decreased compared with the control, but increased compared with the SA and *P. putida* + SA treatments, which implies that treatments containing SA were more effective in reducing pest infestation than *P. putida*. Several studies have documented that SA decreased the population of some aphid species (Pettersson *et al.*, 1994; Elhamahmy *et al.*, 2016). Field experiments have shown that methyl salicylate decreases the density of *Rhopalosiphum padi* L. (Hemiptera, Aphididae) in wheat (Pettersson *et al.*, 1994). Elhamahmy *et al.* (2016) concluded that the foliar application of SA on canola plant results in decreased *B. brassicae* L. population. Similarly, Thakur *et al.* (2016) indicated that the foliar application of SA was effective on the mustard aphid, *Lipaphis erysimi* Kalt, through positive modulation in the activities of defense proteins. In another study, the artificial induction of SA-dependent defenses has been shown to reduce population growth of the potato aphid, *M. euphorbiae* (Thomas) on tomato (Cooper *et al.*, 2004). Also, the exogenous application of SA enhanced the resistance of wild rice plants to the brown planthopper, *Nilaparvata lugens* (Stål) (Guo *et al.*, 2018). Those findings were consistent with the current ones, when *B. brassicae* fed on canola plants treated with SA. However, the current study achieved a new discovery regarding the application of integrated SA and *P. putida*, that were led to lower population growth of this aphid. It seems that in the current study, the lower performance of the cabbage aphid on canola plants treated with *P. putida* + SA could be due to the decreased

quality of the plant, which was caused by increasing the levels of secondary metabolites such as glucosinolates, total phenol, and flavonoids in canola leaves. Earlier reports indicated a significant negative relationship between the glucosinolates contents of *Brassica* species and the invasion of some aphids feeding on them (Labana *et al.*, 1983; Malik *et al.*, 1983). The glucosinolate content of brassicaceous crops can be altered as a systemic response to plant signaling molecules such as SA (Kiddle *et al.*, 1994). Moreover, phenolics are biologically effective secondary metabolites, negatively impacting the development, reproduction, and population growth parameters of aphids (Wójcicka, 2010). These effects were clear in the current research. Negative correlations between phenolic compounds presence in host plant and aphid populations have been demonstrated for some aphid species such as *Metoplophium dirhodum* (Walker) (Havličková, 1995), *Schizaphis graminum* (Rondani), *Diuraphis noxia* Kurdjumov (Sandström *et al.*, 2000), *Sitobion avenae* (Fabricius) (Czerniewicz *et al.*, 2017), and *Myzocallis coryli* Goetze (Gantner *et al.*, 2019). According to Taiz and Zeiger (2002), flavonoid compounds can mediate plant growth and defense response against insects and microbes. Kuśnierczyk *et al.* (2008) demonstrated that a wide range of defense responses in *Arabidopsis thaliana* (L.) Heynhold to *B. brassicae* attack is dependent upon SA signaling. Activation of the SA pathway can be a general mechanism of antibiosis or aphid repellence in resistant host plants, with limited effectiveness in susceptible ones (Hardie *et al.*, 1994; Morkunas and Gabryś, 2011).

The current research indicated that the application of treatments containing SA and *P. putida* compared with the control resulted in the enhancement of plant growth parameters. Also, Cakmakci *et al.* (2007) reported the significant effects of PGPR on plant growth parameters like plant height, leaf area, and shoot fresh weight in spinach and wheat. Cheng *et al.* (2007) showed that the inoculation of *P. putida* strain UW4 comprising the ACC deaminase enzyme in the presence of salt considerably enhanced canola growth. In

addition, various studies have reported that PGPR inoculation increases the photosynthetic pigments in different plant species (Kohler *et al.*, 2009; Bhattacharyya and Jha, 2012). Similarly, this study also found higher chlorophyll content in canola plants treated with PGPR than untreated control plants. Furthermore, chlorophyll content was enhanced when plants were treated with SA in the current research, which is consistent with the results of Yildirim *et al.* (2008), who demonstrated that the foliar application of SA stimulated plant growth and chlorophyll content. The positive effects of SA application on chlorophyll accumulation in *Wolffia arrhiza* (L.) have also been reported by Czerpak *et al.* (2002). Moreover, glucosinolates, phenolics, and flavonoids in *B. rapa* were responsive to phytohormone elicitor-mediated enhancement (Thiruvengadam *et al.*, 2015). Increases in the chlorophyll content of the leaves of PGPR- and SA-treated plants could be due to the greater availability of nutrients and augmented organic matter in the rhizosphere (Esitken *et al.*, 2006; Nadeem *et al.*, 2007). However, some studies have shown that the long-term treatment of plants with SA decreased the chlorophyll content in barley (Pancheva *et al.*, 1996) and basil (Karalija and Parić, 2017). The efficiency of exogenous application of SA can differ depending upon the plant species, growth stage, application technique, and SA concentration (Borsani *et al.*, 2001). In addition, the helpful effect of the combined *P. putida* and SA application on plant growth indices was significantly obvious in the current research. Khan *et al.* (2018) demonstrated that the integrated application of PGPR and SA considerably increased the leaf phenolics compounds and chlorophyll contents. In fact, their findings showed that SA combined with PGPR acted synergistically for the elimination of heavy metals and plant growth. Several studies have demonstrated that PGPR/SA in canola plant resulted in multiple benefits on plant growth and yield due to its role in integrated nutrient management and root proliferation plus exopolysaccharide production (Khan *et al.*, 2018, 2019; Naseem *et al.*, 2018). Elhamahmy *et al.* (2016) have also shown that SA at low concentrations had positive effects on decreasing aphid population on inflorescence and increasing the growth and productivity of canola.

In summary, canola plants treated by *P. putida* + SA with the highest levels of glucosinolates, total phenol, and flavonoids in leaves were more resistant to the cabbage aphid. Furthermore, the separate application of *P. putida* and SA treatments can be recommended on canola because of the lower performance of the aphid on these treatments compared with the control. These results will be helpful in finding ways to induce resistance in canola against *B. brassicae* and, as a result, might cause reduced reliance on synthetic insecticides for pest control. Because elicitors may change the chemical composition of the treated plant material, there are risks of altered crop quality by the increased level of some secondary metabolites (Holopainen *et al.*, 2009). Therefore, similar wide safety testing for pesticides will be required for the application of elicitors in the programs of crop management. However, the advantages of using elicitor treatments based on growth chamber and greenhouse experiments or small-scale field trials could include: (1) reduced damage from herbivorous pests and fungal infection (De Meyer and Höfte, 1997; Cooper *et al.*, 2004; Peng *et al.*, 2004; Elhamahmy *et al.*, 2016); (2) the lower environmental hazards of elicitors compared with pesticides (Holopainen *et al.*, 2009); (3) attraction of some natural enemies of pest insects by inducing plant volatiles (De Boer and Dicke, 2004; James and Grasswitz, 2005; Degen *et al.*, 2012); (4) the lower ecological risks of applying elicitors compared with the genetically modified plants (Poppy and Wilkinson, 2005).

The current study is evidence that SA elicitor and PGPR could be considered in the future as an alternative to conventional pesticides for the control of the cabbage aphid. Further research, including field experiments, is required to achieve more accurate results for the effective and sustainable management of canola pests.

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