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RESEARCH ARTICLE

Role of PGPR in modulating feeding efficacy, growth and development of *Spodoptera litura* in Okra

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Abstract

Okra (*Abelmoschus esculentus*) is an important crop often targeted by *Spodoptera litura*, a destructive pest that damages the leaves and impairs plant growth, ultimately affecting yield. Plant growth-promoting rhizobacteria (PGPR) have emerged as a promising alternative to chemical pesticides for sustainable pest management. This study evaluated the impact of various PGPR strains, including *Bacillus subtilis* Bbv57, on the growth and development of *S. litura* larvae feeding on okra. Controlled laboratory experiments and biochemical analyses were conducted to assess the consumption, digestion and utilization of PGPR-treated plant materials by *S. litura*. The results showed that PGPR treatments significantly reduced larval consumption and weight gain compared to untreated controls. Additionally, PGPR-treated plants resulted in shorter feeding periods, lower consumption indices, growth rates and conversion efficiencies of ingested and digested food. Faecal output was also reduced in larvae fed on PGPR-treated leaves. These findings suggest that PGPR can enhance plant defence mechanisms, leading to a reduction in pest feeding efficiency. The study highlights the potential of PGPR in inducing systemic resistance and biochemical responses that contribute to pest management. Therefore, this research supports the integration of PGPR in sustainable pest management strategies, offering both environmental and economic benefits in agriculture.

Keywords: *Bacillus*; defence; growth; pest; resistance

Introduction

Okra (*Abelmoschus esculentus* L.), a nutrient-rich vegetable from the Malvaceae family, is a valuable dietary component providing carbohydrates, proteins, fats, vitamins A, C, B6 and folic acid, as well as essential minerals like calcium, magnesium, potassium, iron, zinc, phosphorus, β-carotene, riboflavin and dietary fiber (1). Thriving mainly in summer under optimal conditions of 30-35 °C, pH 6-7 and sandy loam soil. Okra is cultivated on approximately 1.26 million hectares globally, yielding 22.29 million tonnes at a productivity rate of 15.10 t/ha (2). Despite its nutritional benefits and dietary importance, okra farming faces significant challenges, especially from pest infestations, necessitating proactive and effective management strategies (3–5). Okra is vulnerable to various insect pests from the vegetative through reproductive phases, causing substantial damage, with around 72 insect species recorded on this crop (6). These pests include both sucking and chewing types.

Among chewing pests, the leafworm *Spodoptera litura* (Fab.) is notably destructive, targeting okra in its early vegetative state (7). This sporadic pest can cause crop losses ranging from 25.8 % to 100 %, depending on the crop stage and infestation level (8). *S. litura* also infests various crops, including brassicas, maize, cotton, flax, lucerne, rice, soybeans, tobacco, jute, tea, cucurbits, potatoes, capsicum, tomatoes, eggplants, cauliflowers, radishes, peanuts and other legumes (9). Feeding in groups, these pests strip leaves, leaving only the midribs (10). In the Asia-Pacific region, *S. litura* is particularly destructive due to its high reproductive capacity and significant infestation levels. Recent advances have explored biological (11, 12) and bio-pesticidal (13, 14) methods to manage major crop pests. However, for immediate and accessible pest control, toxic insecticides remain widely used, although they present environmental risks such as crop residues, pest resistance and resurgence (15, 16). To balance effective pest control with environmental safety, alternative methods are essential.

Biological control, such as using microorganisms to combat pests, offers an eco-friendly solution (17). Beneficial rhizobacteria colonize plant roots, utilizing root exudates and lysates (18, 19). Certain non-pathogenic rhizobacteria can activate systemic resistance (ISR) in plants, strengthening defences against fungal, bacterial and viral pathogens, as well as against insect and nematode pests (20). Around 2–5 % of rhizobacteria, when reintroduced into soils with competitive microflora, can enhance plant growth and are classified as plant growth-promoting rhizobacteria (PGPR) (21). These plant

growth-promoting rhizobacteria (PGPR) include strains like *Pseudomonas* and *Bacillus*, which act as biofertilizers and support plant growth and pest resistance both directly and indirectly (20, 22, 23). PGPR possess essential characteristics, including the ability to colonize the root surface, survive and multiply effectively and compete with other microorganisms during their activity period (24).

Directly, PGPR aids plant growth through improved nitrogen uptake, phytohormone synthesis, mineral solubilization and iron chelation (25). Additionally, some PGPR suppress soil-borne pathogens by producing siderophores, antimicrobial compounds, or by outcompeting for nutrients and niches (23). Indirectly, certain PGPR enhance plant defences against leaf-feeding pathogens and pests by inducing physical and chemical defence barriers, a process known as ISR (18, 26, 27). Hence, PGPR would be of great value, especially to conserve natural enemies and to avoid potential problems encountered when some insecticides fail to control populations that have developed resistance (28). This research, therefore, aims to examine PGPR's role in regulating the feeding behaviour, growth and development of *S. litura* on okra.

Materials and Methods

Okra F1 hybrid COBh4 seeds were treated with talc-based formulations of each PGPR strain, standardized to a concentration of 1×10^8 CFU/g, at a rate of 10 g per kg of seed and sown in earthen pots. Before sowing, each PGPR formulation was incorporated into the soil at a rate of 5 g per pot, supplemented with 100 g of well-decomposed farmyard manure. At 30 days after emergence (DAE), the potted okra plants were sprayed with the respective PGPR formulations at a concentration of 5 g/L using a hand atomizer. The experiment followed a Completely Randomized Design (CRD) with seven treatments, each replicated three times. The treatments consisted of seed treatment (ST) with 10 g/kg of seed, soil application (SA) at 2.5 kg/ha and foliar spray (FS) at 5 g/l of water with talc formulations containing $1x10^8$ CFU/g of *Bacillus subtilis* Bbv57 (T1), *Bacillus amyloliquefaciens* (T2), *Rhizobium pusense* (T3), *Ensifer* sp. (T4), *Siphanobacter* sp. (T5) and an imidacloprid seed treatment at 7 g/kg of seed (T6) along with an untreated control (T7). The talc formulations of *B. subtilis* Bbv57 and *B. amyloliquefaciens* were sourced from the Department of Plant Pathology at Tamil Nadu Agricultural University, Coimbatore, while *R. pusense*, *Ensifer* sp. and *Siphanobacter* sp. were obtained from the Microbiology Unit of the Department of Soil Science and Agricultural Chemistry at the Agricultural College and Research Institute, Killikulam.

Studies on food consumption indices

Laboratory studies were conducted to evaluate the impact of PGPR on the growth and development of *S. litura* in okra. The consumption, digestion and utilization of PGPR-treated plant materials by *S. litura* were analyzed under controlled conditions of 33 ± 2 °C temperature and 75 ± 5 % relative humidity. Each treatment included three replications, with ten larvae per replicate. Third instar larvae, starved for four hrs, were fed okra leaves harvested from potted plants three days after foliar application of PGPR formulations. Fresh weights of the larvae, the food provided, the remaining food after feeding and the faecal output were recorded at 24 hr intervals using a balance. Food ingestion was calculated as the difference between the initial and leftover food weights, while larval weight gain was determined as the difference between the initial and final larval weights. The mean weight of the larvae was obtained by averaging their initial and final weights (29). The growth indices for *S. litura* were computed as per a previous study(30).

$$\text{Consumption index (CI)} = \frac{\text{Weight of food eaten}}{\text{Feeding period x Mean weight of larva during feeding period}}$$

$$\text{Growth rate (GR)} = \frac{\text{Weight gain of the larva during feeding period}}{\text{Feeding period x Mean weight of larva during feeding period}}$$

$$\text{Efficiency of conversion of ingested food (ECI)} = \frac{\text{Weight gained}}{\text{Weight of food ingested}} \times 100$$

$$\text{Efficiency of conversion of digested food (ECD)} = \frac{\text{Weight gained}}{\text{Weight of food ingested - Weight of faces}} \times 100$$

$$\text{Approximate digestibility (AD)} = \frac{\text{Weight of food ingested - Weight of faces}}{\text{Weight of food ingested}} \times 100$$

Studies on biochemical analysis

The biochemical analysis involved estimating total phenol, tannin and defense enzyme activities such as peroxidase, polyphenol oxidase and phenylalanine ammonia lyase (PAL) following standard protocols. Leaf samples were collected 30 days after emergence (DAE) from five randomly selected plants for biochemical and defense enzyme estimations. Additionally, the induction of these biochemical and defense enzyme activities was assessed 72 hr after the foliar application of PGPR formulations.

Estimation of biochemicals

Total phenol

Total phenol content was determined using the method an earlier research (31). Leaf samples (500 mg) were collected, weighed and ground using a mortar and pestle with 10 mL of 80 % alcohol for homogenization. The extracts were centrifuged at 10000 rpm for 20 min, after which the residue was discarded and the supernatant was evaporated. Six milliliters of distilled water were added to the sample and 0.5 mL of the sample was pipetted into test tubes, with the volume adjusted to 3 mL using distilled water. Subsequently, 0.5 mL of Folin-Ciocalteu reagent was added, followed by 2 mL of 20 % sodium carbonate solution after 3 min. The mixture was heated in a boiling water bath for one minute, cooled and the absorbance was measured at 650 nm using a UV-VIS spectrophotometer (Agilent Cary Win®). The total phenol

content was expressed in milligrams per gram of fresh weight. *Tannin:* Tannin content was determined using the AOAC method with slight modifications (32). Folin-Denis reagent and saturated sodium carbonate were used for the assay and tannin levels were expressed as milligrams of Tannic Acid Equivalence (TAE) per 100 g of dry weight.

Estimation of defense enzymes

Leaf samples from each treatment were collected in a chiller box and brought to the laboratory for enzyme extraction. One gram of the sample was homogenized in 5 mL of 0.1 M sodium phosphate buffer (pH 7.0) and centrifuged at 10000 rpm for 20 min at 4 °C. The supernatant was used to determine the activities of defense enzymes such as peroxidase (PO), polyphenol oxidase (PPO) and phenylalanine ammonia lyase (PAL).

Peroxidase (PO)

Peroxidase activity was analyzed using an earlier research (33). The reaction mixture contained 3.5 mL of sodium phosphate buffer (pH 6.5), 200 µL of enzyme extract and 0.1 mL of freshly prepared o-dianisidine solution. The reaction was initiated by adding 0.2 mL of 0.2 M hydrogen peroxide. Changes in absorbance at 430 nm were recorded at 30 s intervals for three minutes using a UV-VIS spectrophotometer (Agilent Cary Win®). The enzyme activity was expressed as changes in absorbance per minute per gram of tissue.

Polyphenol Oxidase (PPO)

The procedure described by Augustin, Ghazali (34) was followed to determine PPO activity. The reaction mixture comprised 1 mL of 0.05 M catechol and 4.5 mL of 0.2 M phosphate buffer (pH 6.8, 30 °C). The reaction was initiated by adding 0.5 mL of enzyme extract. Absorbance changes at 410 nm were recorded every 30 s for 3 min using a UV-VIS spectrophotometer (Agilent Cary Win®). The enzyme activity was expressed as units per minute per gram of tissue.

Phenylalanine Ammonia Lyase (PAL)

PAL activity was estimated following the method described in a previous study (35). The reaction mixture included 0.5 mL of buffer, 0.2 mL of enzyme solution and 1.3 mL of distilled water. The reaction was initiated by adding 1 mL of L-phenylalanine, followed by incubation at 32 °C for 30 min. The reaction was stopped by adding 0.5 mL of 1 M trichloroacetic acid. The absorbance was measured at 290 nm using a UV-VIS spectrophotometer (Agilent Cary Win®). Enzyme activity was expressed as micromoles per minute per gram of tissue.

Statistical analysis

Data on consumption indices and biochemical parameters were square-root transformed for analysis. Statistical analyses were conducted using R software and treatment means were compared using the least significant difference (LSD) test at a 5 % probability level.

Results

Effect of PGPR-treated okra plants on consumption, digestion and utilization of *E. vittella*

The feeding experiment showed that the PGPR treatments significantly reduced the consumption, digestion and utilization of *S. litura* over the untreated plants (Fig. 1 & Table 1). *S. litura* consumed 1.68 g of leaves collected from plants treated with *B. subtilis* Bbv57 and more consumption of leaves on a fresh weight basis was observed in untreated plants (2.02 g), followed by imidacloprid treatment (2.01 g of leaves). The faecal weight was also low when larvae fed on *B. subtilis* Bbv57 treatment (0.78g larva^{-1}) followed by *B. amyloliquefaciens* (0.80 g larva^{-1}) compared to the larva fed on untreated (0.90 g larva^{-1}) and imidacloprid treated leaves (0.90 g larva^{-1}). There was a significant difference in the weight gain by *S. litura* larvae when fed on untreated plants than PGPR-treated leaves. Among the treatments, *B. subtilis* Bbv57 treatment recorded lower weight gain (0.47g larva^{-1}), followed by larvae provided with leaves from *B. amyloliquefaciens* treated plants (0.50 g larva^{-1}). The average weight gain per larva was high on untreated plants (0.64 g larva^{-1}) and on leaves collected from imidacloprid-treated plants (0.63 g larva^{-1}). The feeding period also varied significantly among the treatments. The feeding period was low for *B. subtilis* Bbv57-treated leaves (8.96 days) compared to imidacloprid treatment (9.99 days) and untreated plants (10.01 days). The consumption index (0.0562), growth rate (0.0162), efficiency of conversion of the digested food (ECD) (52.22 %), efficiency of conversion of the ingested food (ECI) (27.98 %) and the approximate digestibility (AD) (53.57 %) were low when *S. litura* fed with leaves collected from plants treated with *B. subtilis* Bbv57. Similarly, the CI (0.0691), GR (0.0201), ECD (53.76 %), ECI (28.90 %) and AD (53.76 %) were lower for the larvae fed on *B. amyloliquefaciens*-treated plant leaves. The untreated plants recorded high CI (0.0932), GR (0.0294), ECD (57.14 %), ECI (31.68 %) and AD (55.45 %).

Table 1. Consumption, digestion and utilization of PGPR treated okra leaves by *S. litura*

S.No	Treatments	Total food consumed/ larva (g)	Weight of faeces voided/ larva (g)	Weight gain (g)	Feeding period (days)	Consumption index (CI)	Growth rate (GR)	ECD %	ECI %	AD %
T_1	*Bacillus subtilis* Bbv57	1.68^{a}	0.78^{a}	0.47^{a}	8.96^{a}	0.0562^{a}	0.0162^{a}	52.22^{a}	27.98^{a}	53.57^{a}
T_2	*Bacillus amyloliquefaciens*	1.73^{a}	0.80^{a}	0.50^{a}	9.02^{a}	0.0691^{a}	0.0201^{a}	53.76^{ab}	28.90^{ab}	53.76^{ab}
T_3	*Rhizobium pusense*	1.97^{b}	0.89^{b}	0.59^{b}	9.76^{b}	0.0850^{b}	0.0250^{b}	54.63^{abc}	29.95^{bcd}	54.82^{b}
T_4	*Ensifer* sp.	1.95^{b}	0.89^{b}	0.58^{b}	9.66^{b}	0.0833^{b}	0.0254^{b}	54.72^{bcd}	29.74^{bc}	54.36^{b}
T_5	*Siphanobacter* sp.	1.96^{b}	0.88^{b}	0.60^{b}	9.78^{b}	0.0861^{b}	0.0263^{b}	55.56^{bcd}	30.61^{cde}	55.10^{b}
T_6	Imidacloprid 48FS	2.01^{b}	0.90^{b}	0.63^{b}	9.99^{b}	0.0894^{b}	0.0281^{b}	56.76^{cd}	31.34^{de}	55.22^{b}
T_7	Untreated control	2.02^{b}	0.90^{b}	0.64^{b}	10.01^{b}	0.0932^{b}	0.0294^{b}	57.14^{d}	31.68^{e}	55.45^{b}
	CD (P = 0.05)	0.15**	0.075**	0.052**	0.39**	0.0071*	0.0021*	2.46**	1.51**	1.09**

In a column, means followed by common letters are not significantly different by LSD (P=0.05)

Fig. 1. Laboratory experiments on the effect of PGPR on growth indices of *S. litura*.

T1 - Bacillus subtilis Bbv57; T2 - Bacillus amyloliquefaciens; T3 - Rhizobium pusense; T4 - Ensifer sp.; T5 - Siphanobacter sp.; T6 - Imidacloprid 48 FS and T7 - Untreated control.

Effect of PGPR-treated okra plants in enhancing biochemical activity

The application of PGPR significantly improved the production of secondary metabolites and defense enzyme activities (Tables 2 & 3).

Estimation of biochemicals: During Rabi 2020, foliar application of PGPR at 30 DAE notably increased phenol and tannin levels compared to untreated plants. *B. subtilis Bbv57* recorded the highest phenol (1.96 mg g^{-1}) and tannin (1.98 mg 100 g^{-1}) contents 72 hr after treatment, followed by *B. amyloliquefaciens* with phenol and tannin levels of 1.11 mg g^{-1} and 1.49 mg 100 g^{-1}, respectively. Conversely, imidacloprid-treated plants showed lower phenol (0.66 mg g^{-1}) and tannin (1.05 mg 100 g^{-1}) levels, with untreated plants also recording low phenol (0.53 mg g^{-1}) and tannin (0.99 mg 100 g^{-1}) contents (Table 2).

In summer 2021, the biochemical analysis showed a significant rise in phenol and tannin levels in PGPR-treated plants compared to controls. Plants treated with *B. subtilis Bbv57* exhibited the highest phenol (2.54 mg g^{-1}) and tannin (2.37 mg g^{-1}) levels, followed by *B. amyloliquefaciens* with 1.71 mg g^{-1} phenol and 1.49 mg g^{-1} tannin. Untreated plants and those treated with imidacloprid had lower levels of phenol (1.18 mg g^{-1} and 1.28 mg g^{-1}, respectively) and tannin (1.18 mg g^{-1} and 1.28 mg g^{-1}, respectively) (Table 3).

Estimation of Defense Enzymes: Defense enzyme activity was also significantly elevated during Rabi 2020 after PGPR application (Table 3). *B. subtilis* Bbv57-treated plants demonstrated the highest peroxidase (14.72 min^{-1} g^{-1}), polyphenol oxidase (16.01 min^{-1} g^{-1}) and phenylalanine ammonia lyase (PAL) (113.64 µM min^{-1} g^{-1}) activities. In comparison, untreated plants had lower enzyme activities, with peroxidase (2.09 min^{-1} g^{-1}), polyphenol oxidase (3.44 min^{-1} g^{-1}) and PAL (50.39 µM min^{-1} g^{-1}). Imidacloprid-treated plants also exhibited lower activities of peroxidase (3.88 min^{-1} g^{-1}), polyphenol oxidase (6.92 min^{-1} g^{-1}) and PAL (60.31 µM min^{-1} g^{-1}) (Table 2).

A similar trend was observed in summer 2021 (Table 3), where PGPR treatments enhanced the activity of all defense enzymes. *B. subtilis* Bbv57-treated plants recorded the highest activities for peroxidase (16.82 min^{-1} g^{-1}), polyphenol oxidase (18.16 min^{-1} g^{-1}) and PAL (117.79 µM min^{-1} g^{-1}). By contrast, untreated plants and imidacloprid-treated plants showed lower enzymatic activities, with peroxidase (2.71 min^{-1} g^{-1} and 4.22 min^{-1} g^{-1}), polyphenol oxidase (8.71 min^{-1} g^{-1} and 11.31 min^{-1} g^{-1}) and PAL (54.08 µM min^{-1} g^{-1} and 85.64 µM min^{-1} g^{-1}), respectively.

Discussion

The feeding ability of an insect and the nutrient content of the food determine the growth and developmental rate of the insect. The feeding efficiency of an insect and the nutrient composition of its food significantly influence its growth and developmental rates. Consumption, digestion and utilization indices could be used as indicators for the presence of antinutritional factors in the food material (36). The results of the present study indicated that significant reduction in the growth and development indices of *S. litura* in all PGPR treatments compared to the untreated control. Likewise, the amount of food ingested by *S. litura* larvae was significantly low in all PGPR treatments. In general, competition for nutrients, niche exclusion, induced systemic resistance and antifungal metabolites production are the chief modes of biocontrol activity in PGPR. Interaction of some rhizobacteria with the plant roots can result in plant resistance against *S. litura* by a phenomenon called Induced Systemic Resistance (ISR) (17).

The reduction in consumption and growth indices may be attributed to the elevated levels of biochemicals and enhanced defence enzyme activity induced by PGPR application. These findings align with those of an earlier research (37). In this study, biochemical analysis revealed significantly higher total phenol, tannin content and defence enzyme activity, including peroxidase, polyphenol oxidase and phenylalanine ammonia lyase, in PGPR-treated okra plants compared to untreated plants. Among the PGPR treatments, *B. subtilis Bbv57* demonstrated the highest increase in biochemical levels in okra plants during both the Rabi 2020

Table 2. Effect of PGPR on biochemicals and defence enzyme activity in okra during Rabi 2020

S.No.	Treatments	Phenol content* mg g^{-1} fresh weight		Tannin content* mg 100 g^{-1} dry weight		Peroxidase activity* min^{-1} g^{-1}		Polyphenol Oxidase* activity min^{-1} g^{-1}		PAL activity* µM min^{-1}g^{-1}	
		30 DAE	72 HAT	30 DAE	72 HAT	30 DAE	72 HAT	30 DAE	72 HAT	30 DAE	72 HAT
T_1	*Bacillus subtilis* Bbv57(ST-SA-FS)	1.36 (1.36)^{a}	1.96 (1.57)^{a}	1.39 (1.37)^{a}	1.98 (1.58)^{a}	4.68 (2.28)^{a}	14.72 (3.90)^{a}	10.35 (3.29)^{a}	16.01 (4.06)^{a}	110.37 (10.53)^{a}	113.64 (10.68)^{a}
T_2	*Bacillus amyloliquefaciens* (ST-SA-FS)	1.01 (1.23)^{b}	1.11 (1.27)^{bc}	1.28 (1.33)^{bc}	1.49 (1.41)^{b}	3.77 (2.07)^{b}	11.63 (3.48)^{b}	9.64 (3.18)^{b}	12.67 (3.63)^{c}	94.49 (9.75)^{b}	96.84 (9.86)^{b}
T_3	*Rhizobium pusense* (ST-SA-FS)	0.60 (1.05)^{de}	0.91 (1.19)^{c}	0.91 (1.19)^{f}	1.03 (1.24)^{e}	2.95 (1.86)^{c}	9.01 (3.08)^{e}	8.04 (2.92)^{c}	12.21 (3.56)^{bc}	55.86 (7.51)^{e}	58.80 (7.70)^{e}
T_4	*Ensifer* sp. (ST-SA-FS)	0.88 (1.17)^{bc}	0.65 (1.07)^{d}	1.20 (1.30)^{c}	1.27 (1.33)^{d}	2.65 (1.77)^{d}	11.19 (3.42)^{c}	10.18 (3.27)^{a}	10.14 (3.26)^{d}	72.27 (8.53)^{c}	75.93 (8.74)^{c}
T_5	*Siphanobacter* sp. (ST-SA-FS)	0.78 (1.13)^{cd}	1.18 (1.3)^{b}	1.12 (1.27)^{d}	1.37 (1.37)^{c}	4.55 (2.25)^{a}	10.17 (3.27)^{d}	7.79 (2.88)^{c}	13.32 (3.72)^{b}	69.85 (8.39)^{c}	71.16 (8.46)^{d}
T_6	Imidacloprid 48FS (ST alone)	0.63 (1.06)^{de}	0.66 (1.08)^{d}	0.98 (1.22)^{e}	1.05 (1.24)^{e}	2.88 (1.84)^{c}	3.88 (2.09)^{f}	6.74 (2.69)^{d}	6.92 (2.72)^{e}	60.22 (7.79)^{d}	60.31 (7.80)^{e}
T_7	Untreated control	0.50 (0.99)^{e}	0.53 (1.01)^{d}	0.80 (1.14)^{g}	0.99 (1.22)^{e}	2.01 (1.58)^{e}	2.09 (1.61)^{g}	3.11 (1.90)^{e}	3.44 (1.98)^{f}	50.15 (7.12)^{f}	50.39 (7.13)^{f}
	CD (P=0.05)	0.06**	0.09**	0.02**	0.03**	0.04**	0.05**	0.04**	0.09**	0.14**	0.17**

DAE – Days after emergence; HAT – Hours after treatment; ST- Seed treatment; SA- Soil application; FS- Foliar spray; *-Mean of three replications; Figures in parentheses $\sqrt{x+0.5}$ are transformed values. In a column, means followed by common letters are not significantly different by LSD (P=0.05)

Table 3. Effect of PGPR on biochemicals and defence enzyme activity in okra during summer 2021

S.No.	Treatments	Phenol content* mg g^{-1} fresh weight		Tannin content* mg 100g^{-1} dry weight		Peroxidase activity* min^{-1} g^{-1}		Polyphenol Oxidase* activity min^{-1} g^{-1}		PAL activity* µM min^{-1}g^{-1}	
		30 DAE	72 HAT	30 DAE	72 HAT	30 DAE	72 HAT	30 DAE	72 HAT	30 DAE	72 HAT
T_1	*Bacillus subtilis* Bbv57(ST-SA-FS)	1.48 (1.41)^{a}	2.54 (1.74)^{a}	1.66 (1.47)^{a}	2.37 (1.69)^{a}	5.81 (2.51)^{a}	16.82 (4.16)^{a}	15.27 (3.97)^{a}	18.16 (4.32)^{a}	113.28 (10.67)^{a}	117.79 (10.88)^{a}
T_2	*Bacillus amyloliquefaciens* (ST-SA-FS)	1.21 (1.31)^{a}	1.71 (1.49)^{b}	1.37 (1.37)^{ab}	1.88 (1.54)^{b}	2.36 (1.69)^{de}	13.21 (3.70)^{b}	10.94 (3.38)^{b}	12.89 (3.66)^{b}	97.25 (9.89)a^{b}	101.65 (10.11)^{ab}
T_3	*Rhizobium pusense* (ST-SA-FS)	0.77 (1.13)^{bcd}	1.13 (1.28)^{c}	1.16 (1.29)^{b}	1.47 (1.4)^{c}	4.28 (2.19)^{b}	11.47 (3.46)^{bc}	9.34 (3.14)^{bc}	10.59 (3.33)^{bc}	58.37 (7.67)^{cd}	61.05 (7.84)^{cde}
T_4	*Ensifer* sp. (ST-SA-FS)	0.95 (1.2)^{b}	1.44 (1.39)^{b}	1.34 (1.36)^{b}	1.69 (1.48)^{bc}	3.54 (2.01)^{bc}	13.01 (3.68)^{b}	11.06 (3.40)^{b}	12.51 (3.61)^{b}	76.18 (8.76)^{bc}	79.14 (8.92)^{bc}
T_5	*Siphanobacter* sp. (ST-SA-FS)	0.82 (1.15)^{bc}	1.11 (1.27)^{c}	1.22 (1.31)^{b}	1.37 (1.37)^{c}	2.96 (1.86)^{cd}	10.22 (3.27)^{c}	9.07 (3.09)^{bc}	10.98 (3.39)^{bc}	72.09 (8.52)^{c}	74.30 (8.65)^{cd}
T_6	Imidacloprid 48FS (ST alone)	0.65 (1.07)^{cd}	0.69 (1.09)^{d}	0.55 (1.02)^{c}	0.59 (1.04)^{d}	2.02 (1.59)^{ef}	3.11 (1.90)^{d}	7.12 (2.76)^{cd}	8.01 (2.92)^{c}	57.16 (7.59)^{cd}	58.06 (7.65)^{de}
T_7	Untreated control	0.60 (1.04)^{d}	0.68 (1.08)^{d}	0.43 (0.96)^{c}	0.48 (0.98)^{d}	1.64 (1.44)^{f}	2.17 (1.61)^{e}	6.08 (2.52)^{d}	8.71 (2.97)^{c}	53.33 (7.17)^{d}	54.08 (7.22)^{e}
	CD (P=0.05)	0.10**	0.11**	0.11**	0.12**	0.20**	0.24**	0.421**	0.50**	1.30**	1.27**

DAE – Days after emergence; HAT – Hours after treatment; ST- Seed treatment; SA- Soil application; FS- Foliar spray; *-Mean of three replications; Figures in parentheses $\sqrt{x+0.5}$ are transformed values. In a column, means followed by common letters are not significantly different by LSD (P=0.05)

and summer 2021 seasons.

Untreated plants consistently exhibited lower induction of biochemicals and defence enzymes compared to all other PGPR treatments across both seasons. The enhanced biochemical levels and defence enzyme activity induced by PGPR likely contributed to the reduced insect pest incidence on treated okra plants. Previous studies have also reported that increased biochemical levels and defence enzyme activity lead to physiological changes in crop plants, adversely affecting the growth and development of insect pests, ultimately resulting in lower pest populations in PGPR-treated plants (38).

PGPR-induced chemical defence exhibits the increased levels of biochemicals and defence enzymes activity. Mainly, enhanced levels of phenols, tannins and defence enzymes in PGPR-treated plant parts could have contributed to the reduced intake of the given feed (37, 39). The results were relevant with findings of earlier research which reported increased levels of polyphenol and terpenoid in cotton plants treated with *Pseudomonas gladioli* and the increase in polyphenol and terpenoid reduced the growth rate, CI and ECD of *Helicoverpa armigera* (Hüb) (39). Consistent with earlier studies which reported a notable reduction in the growth and development of *E. vittella* when feeding on okra plants inoculated with *Pseudomonas fluorescens*, this study also observed significantly lower food intake by *E. vittella* larvae in all PGPR treatments (40).

The reduction in consumption and growth indices could be due to the multifaceted mechanisms by which PGPR promote plant growth, including enhancing plant tolerance to biotic and abiotic stresses, optimizing plant growth factors, ISR, an immune response in plants (1-3, 17). ISR mainly involves the enhancement of plant defences by inducing physical and chemical defence barriers against *S. litura* (22, 26, 41). Moreover, ISR involves jasmonate and ethylene signaling within the plant and these hormones stimulate the host plant's defence responses against a variety of plant pathogens (42). Many individual bacterial components induce ISR, such as lipopolysaccharides (LPS), flagella, siderophores, cyclic lipopeptides, 2,4-diacetylphloroglucinol, homoserine lactones and volatiles like acetoin and 2,3-butanediol (17).

Conclusion

The study demonstrated that PGPR application significantly reduced the growth and development of *Spodoptera litura* in okra by lowering consumption, digestion and utilization indices compared to controls. *Bacillus subtilis* Bbv57 was most effective, reducing larval feeding and growth through induced systemic resistance (ISR), enhanced biochemical defences and antifungal metabolite production. ISR, mediated by jasmonate and ethylene pathways, increased phenols, tannins and defence enzymes, bolstering plant defences. PGPR offers a sustainable alternative to chemical pesticides, though further studies should explore strain optimization, molecular mechanisms, field validation and integration with IPM. Research on its long-term effects on soil health, pest resistance and cost-effectiveness is essential for broader adoption.

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Authors' contributions

RAM carried out the research and performed the statistical analysis. MR participated in the conceptualization and design of the study. AS revised and drafted the manuscript. BJP edited the manuscript. GP edited the manuscript. All authors read and approved the final manuscript.

Compliance with ethical standards

Conflict of interest: Authors do not have any conflict of interest to declare.

Ethical issues: None

References

1. Varmudy V. Need to boost okra exports. Facts For You. 2011;31 (5):21–23.
2. Ray A, Ray R, Sreevidya E. How many wild edible plants do we eat-their diversity, use and implications for sustainable food system: An exploratory analysis in India. Front Sustain Food Syst. 2020;4:56. https://doi.org/10.3389/fsufs.2020.00056
3. Ali A, Desneux N, Lu Y, Liu B, Wu K. Characterization of the natural enemy community attacking cotton aphid in the Bt cotton ecosystem in Northern China. Sci Rep. 2016;6(1):24273. https://doi.org/10.1038/srep24273
4. Kumawat R, Pareek B, Meena B. Seasonal incidence of jassid and whitefly on okra and their correlation with abiotic factors. Annals Bio. 2000;16(2):167-69.
5. Bhatt B, Joshi S, Karnatak A. Biodiversity of insect pests and their predators on okra agroecosystem. J Pharmacogn Phytochem. 2018;7(4):84–86. https://doi.org/10.20546/ijcmas.2018.709.091
6. Rahman MM, Uddin MM, Shahjahan M. Management of okra shoot and fruit borer, *Earias vittella* (Fabricius) using chemical and botanical insecticides for different okra varieties. Int Res J Appl Life Sci. 2013;2(1).
7. Kumar S, Dagnoko S, Haougui A, Ratnadass A, Pasternak N, Kouame C. Okra (*Abelmoschus* spp.) in West and Central Africa: Potential and progress on its improvement. Afr J Agricl Res. 2010;5(25):3590-98.
8. Dhir B, Mohapatra H, Senapati B. Assessment of crop loss in groundnut due to tobacco caterpillar, *Spodoptera litura* (F.). Indian J Plant Prot. 1992;20(2):215–17.
9. Zhou Z, Chen Z, Xu Z. Potential of trap crops for integrated management of the tropical armyworm, *Spodoptera litura* in tobacco. J Insect Sci. 2010;10(1):117. https://doi.org/10.1673/031.010.11701
10. Ahmad M, Ghaffar A, Rafiq M. Host plants of leaf worm, *Spodoptera litura* (Fabricius) (Lepidoptera: Noctuidae) in Pakistan. Asian J Agric Biol. 2013;1(1):23–28.
11. Ali H, Muhammad A, Bala NS, Wang G, Chen Z, Peng Z, et al. Genomic evaluations of Wolbachia and mtDNA in the population of coconut hispine beetle, *Brontispa longissima* (Coleoptera: Chrysomelidae). Molecular phylogenetics and evolution. 2018;127:1000–09. https://doi.org/10.1016/j.ympev.2018.07.003

12. Qasim M, Husain D, Islam SU, Ali H, Islam W, Hussain M, et al. Effectiveness of *Trichogramma chilonis* Ishii against spiny bollworm in Okra and susceptibility to insecticides. J Entomol Zool Stud. 2018;6(1):1576–81.
13. Ali H, Qasim M, Saqib HSA, Arif M, Islam S. Synergetic effects of various plant extracts as bio-pesticide against wheat aphid (*Diurophous noxia* L.) (Hemiptera: Aphididae). Afr J Agric Sci Technol. 2015;3(7):310–15.
14. Shakeel M, Ali H, Ahmad S, Said F, Khan KA, Bashir MA, et al. Insect pollinators' diversity and abundance in *Eruca sativa* Mill.(Arugula) and *Brassica rapa* L. (Field mustard) crops. Saudi J Biol Sci. 2019;26(7):1704–09. https://doi.org/10.1016/j.sjbs.2018.08.012
15. Patil S, Lande G, Awasthi NS, Barkhade U. Effect of different doses of newer insecticides against sucking pests of okra. The Bioscan. 2014;9(4):1597–600.
16. Suman S, Choudhary R, Naveen S, Yadav N. Efficacy of advanced insecticides against sucking pests of okra. The Pharma Innov J. 2021;10(11):1925–28.
17. Lugtenberg B, Kamilova F. Plant-growth-promoting rhizobacteria. Annual review of microbiology. 2009;63(1):541–56. https://doi.org/10.1146/annurev.micro.62.081307.162918
18. Pieterse C, Van Wees S, Ton J, Van Pelt J, Van Loon L. Signalling in *Rhizobacteria*-induced systemic resistance in *Arabidopsis thaliana*. Plant Biol. 2002;4(05):535–44. https://doi.org/10.1055/s-2002-35441
19. Antoun H, Prévost D. Ecology of plant growth-promoting rhizobacteria. PGPR: Biocontrol and biofertilization. 2006:1–38. https://doi.org/10.1007/1-4020-4152-7_1
20. Kennedy IR, Choudhury A, Kecskés ML. Non-symbiotic bacterial diazotrophs in crop-farming systems: Can their potential for plant growth promotion be better exploited? Soil Biol Biochem. 2004;36 (8):1229–44. https://doi.org/10.1016/j.soilbio.2004.04.006
21. Kloepper JW, Leong J, Teintze M, Schroth MN. Enhanced plant growth by siderophores produced by plant growth-promoting rhizobacteria. Nature. 1980;286(5776):885–86. https://doi.org/10.1038/286885a0
22. Persello-Cartieaux F, Nussaume L, Robaglia C. Tales from the underground: Molecular plant–rhizobacteria interactions. Plant, Cell & Environment. 2003;26(2):189–99. https://doi.org/10.1046/j.1365-3040.2003.00956.x
23. Nelson LM. Plant growth-promoting rhizobacteria (PGPR): prospects for new inoculants. Crop management. 2004;3(1):1–7. https://doi.org/10.1094/CM-2010-0707-02-RS
24. Kloepper JW, Okon Y. Plant growth-promoting rhizobacteria (other systems). *Azospirillum*/plant associations. 1994;187:137–66.
25. Bowen G, Rovira A. The rhizosphere and its management to improve plant growth. Advances in agronomy. 1999;66:1–102. https://doi.org/10.1016/S0065-2113(08)60425-3
26. Bostock RM. Signal crosstalk and induced resistance: straddling the line between cost and benefit. Annu Rev Phytopathol. 2005;43(1):545-80. https://doi.org/10.1146/annurev.phyto.41.052002.095505
27. Ryu CM, Hu CH, Reddy M, Kloepper JW. Different signalling pathways of induced resistance by rhizobacteria in *Arabidopsis thaliana* against two pathovars of *Pseudomonas syringae*. New Phytologist. 2003;160(2):413–20. https://doi.org/10.1046/j.1469-8137.2003.00883.x
28. Wang K-Y, Liu T-X, Yu C-H, Jiang X-Y, Yi M-Q. Resistance of *Aphis gossypii* (Homoptera: Aphididae) to fenvalerate and imidacloprid and activities of detoxification enzymes on cotton and cucumber. J Econ Entomol. 2002;95(2):407–13. https://doi.org/10.1603/0022-0493-95.2.407
29. Dhandapani N. Consumption digestion and utilisation of bhendi varieties by Earias vittella Fabricius. Madras Agric J. 1986;73 (12):676-78.
30. Waldbauer G. The consumption and utilization of food by insects. Adv Insect Physiol. 5: Elsevier; 1968. p. 229–88. https://doi.org/10.1016/S0065-2806(08)60230-1
31. Malik CP, Singh M. Plant enzymology and histo-enzymology. Rome: Food and Agricultural Organisation of the United Nations (FAO); 1980:393–417.
32. AOAC. Official methods of analysis of the Association of Official Analytical Chemists: Washington (DC): Association of Official Analytical Chemists.; 1931.
33. Pütter J. Peroxidases. In: Bergmeyer HU, editor. Methods of enzymatic analysis: Vol. 2. New York; Elsevier; 1974. p. 685–90. https://doi.org/10.1016/B978-0-12-091302-2.50033-5
34. Augustin M, Ghazali HM, Hashim H. Polyphenoloxidase from guava (*Psidium guajava* L.). J Sci Food Agric. 1985;36(12):1259–65. https://doi.org/10.1002/jsfa.2740361209
35. Brueske CH. Phenylalanine ammonia lyase activity in tomato roots infected and resistant to the root-knot nematode, *Meloidogyne incognita*. Physiol Plant Pathol. 1980;16(3):409–14. https://doi.org/10.1016/S0048-4059(80)80012-9
36. Nathan SS, Kalaivani K. Efficacy of nucleopolyhedrovirus and azadirachtin on *Spodoptera litura* Fabricius (Lepidoptera: Noctuidae). Biol Control. 2005;34(1):93–98. https://doi.org/10.1016/j.biocontrol.2005.03.001
37. Thiruveni T, Shanthi M, Baskaran RM, Raguchander T. Field Evaluation of Microbial Consortia Mediated Resistance against Okra Shoot and Fruit Borer, *Earias vittella*. Madras Agric J. 2012;99 (Jan-Mar):1. https://doi.org/10.29321/MAJ.10.100025
38. Ramamoorthy V, Viswanathan R, Raguchander T, Prakasam V, Samiyappan R. Induction of systemic resistance by plant growth-promoting rhizobacteria in crop plants against pests and diseases. Crop Prot. 2001;20(1):1–11. https://doi.org/10.1016/S0261-2194(00)00056-9
39. Qingwen Z, Ping L, Gang W, Qingnian C. On the biochemical mechanism of induced resistance of cotton to cotton bollworm by cutting off young seedlings at the plumular axis. Acta Phytophylacica Sinica. 1998;25(3):209–12.
40. Murugan M, Dhandapani N, Devanathan M. Bottom-up and top-down effect of induced resistance in okra against insect pests. Ann Plant Physiol. 2005;19:106-13.
41. Kloepper JW, Ryu C-M, Zhang S. Induced systemic resistance and promotion of plant growth by *Bacillus* spp. Phytopathology. 2004;94(11):1259-66. https://doi.org/10.1094/PHYTO.2004.94.11.1259
42. Glick BR. Plant growth-promoting bacteria: Mechanisms and applications. Scientifica. (Cairo) 2012;2012(1):963401. https://doi.org/10.6064/2012/963401

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