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RESEARCH

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Enhancing chili pepper (*Capsicum annuum* L.) resistance and yield against powdery mildew (*Leveillula taurica*) with beneficial bacteria

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Abstract

Background *Leveillula taurica* is an obligate pathogen that causes powdery mildew on chili pepper (*Capsicum annuum* L.) which is considered one of the most serious diseases for the crop.

Results *Leveillula taurica* was isolated from infected pepper plants in Assiut Governorate, Egypt. Pathogenicity test was performed, and it was found that the pathogen can cause the symptoms of powdery mildew on the pepper plant. Under greenhouse conditions, treatment with *Bacillus thuringiensis* MW740161.1, *Pseudomonas fluorescens,* and *Bacillus subtilis* cultures resulted in a significant reduction in conidial germination of the pathogen (69.07, 29.55, and 19.58%, respectively). Spraying chili pepper plants with the microorganisms effectively reduced the powdery mildew's disease severity. Also, treatment with the bacterial strains resulted in a significant (*P* 0.05%) increase in the yield of chili pepper. Based on the findings, it appears that the use of *B. thuringiensis,* as foliar spraying, significantly induced resistance of chili pepper plants against *L. taurica* and stimulated many biochemical functions in the plant. Also, it increased the crop yield compared to all other treatments.

Conclusions This study recommends *B. thuringiensis* as a viable alternative to harmful pesticides, and it is feasible to formulate an appropriate fungicide for the sustainable green production of chili peppers. The *B. thuringiensis* can increase the resistance of chili pepper plant to *L. taurica* the causal pathogen of powdery mildew.

Keywords *Capsicum annuum*, *Leveillula taurica*, *Bacillus thuringiensis* MW740161.1, *Pseudomonas fluorescens*, Induce resistance, Biocontrol

Background

Chili pepper (*Capsicum annuum* L.) is a major crop in Egypt, with 1.055.605 tons produced in 2020 (FAO 2021). Chili pepper is susceptible to a variety of diseases caused by fungi, bacteria, and viruses. Powdery mildew, anthracnose, and leaf spot are the most frequent type of fungal infections in chili pepper production, resulting in yield loss leading to considerable foliage losses reduction in the size and number of fruits per plant, which may reach up to 20% (Abdul Kareem et al 2020).

The most prevalent microorganisms that injure the pepper crop worldwide, generating millions of annual losses, are *Leveillula taurica, Fusarium solani,*

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Phytophthora capsici, and *Rhizoctonia solani* (Abdel-Kader et al. 2012). *Leveillula taurica* causes powdery mildew, which is one of the most important and harmful plant diseases associated with the highest losses in productivity of chili pepper in the greenhouse (Karkanis et al. 2012).

It is commonly acknowledged that chemical plant disease control pollutes the environment and increases the accumulation of hazardous substances in the human food chain. Disease management also can be achieved using environmentally friendly ways (Awad et al. 2012)**.** Bioagents and chemical inducers are being studied extensively as alternative strategies for controlling plant diseases by induced resistance. Chemical inducers and bioactive substances have been successfully employed by several researchers to control many plant diseases (Hussein et al. 2018). Biological products can be used instead of some fungicides, especially if the fungicide has failed.

As indicated by multiple *Bacillus* species, the bacteria appear to defend plants against a lot of diseases, and the potential for commercial use is promising. When pathogens are controlled with a fungal biocontrol agent, such as the well-studied *Trichoderma* spp., infection and reproduction are reduced. In the greenhouse and experiments in the field, several researchers have used fungal and bacterial antagonists to successfully control powdery mildew in pepper, cucumber, and other vegetable crops (Abo-Elyousr et al. 2022a). According to Elsisi (2019), alternative eco-friendly ways to reduce plant disease damage, such as the employment of biocontrol measures, including naturally existing biocontrol agents, must be adopted. Bioactive compounds have been effectively used by many researchers to control many diseases of crops (Radwan and Gad 2021).

The use of bioagents such as *B. subtilis* and *P. fluorescens* in combination has been proposed as a simple, safe, and cost-effective control technique (Karkanis et al. 2012). Biological control was discovered to be a good method for protecting chili pepper without leaving behind a hazardous residue in the product. Powdery mildew can be controlled with several pathogens such as fungi, bacteria, and actinomyces (Abo-Elyousr et al 2022b).

Bacillus spp., such as *B. subtilis* and *B. thuringiensis* MW740161.1, were effective against the causative agent of pepper diseases such as powdery mildew in three laboratory trials and under greenhouse circumstances using the foliar spray with varying quantities. Spraying bioagent *B. thuringiensis* on pepper plants, alone or in combinations, greatly reduced disease severity and increased yield (Alharbi and Alawlaqi 2014).. The biological control of *L. taurica* using *P. fluorescens* was successful at the regular dose. It was as successful as the standard fungicide alone when mixed with a half reduction in fungicide dose. Plants treated with *P. fluorescens* + azoxystrobin showed a doubled rise in phenolics, phenylalanine, polyphenol oxidase, and peroxidase activities (Anand et al. 2010). *Pseudomonas fluorescens* bioagents were found to be efficient in comparison to the fungicidal therapies in lowering disease severity (Hareesh et al. 2016).

After exposure to a range of bioagents, defense-related enzymes such as polyphenol oxidase and peroxidase can improve disease and stress resistance. They can also help plants develop induced systemic resistance (Elsisi 2019). Phenolic compounds as plant metabolites are biosynthesized because of bioagent treatments, which improve plant resistance (Prasad et al. 2019). *Bacillus* sp. and *Pseudomonas* sp. bacteria can cause systemic resistance in plants. *P. fluorescens* treatment increased gene expression of peroxidase, phenol oxidase, and chitinase in tests involving the resistance induction of the vine powdery mildew caused by *Uncinula necator* (Sendhilvel et al 2007). In chili pepper infected with *L. taurica*, treatment with *P. fluorescens* caused an increasing accumulation of total phenolic contents. This reaction supports systemic resistance induced by *P. fluorescens* treatment (Anand et al 2010).

The primary objective of this study was to explore optimal strategies for managing powdery mildew in chili pepper plants under greenhouse conditions. This investigation aimed to assess the efficacy of various microorganisms, including *B. thuringiensis* MW740161.1, *B. subtilis*, and *P. fluorescens*, in the treatment of chili pepper plants. Additionally, the study looked into how systemic resistance is induced in chili pepper plants and how it affects yield enhancement.

Methods

Powdery mildew of chili pepper pathogen identification

An alteration in chili pepper leaves was found in the Assiut Governorate, Egypt, characterized by symptoms of powdery mildew, and then collected. The disease's causal pathogen was identified using morphological properties, such as the positioning of mycelium on leaves, the presence of dimorphic conidia, the branching of the conidiophore, and the size and form of the conidia. The identification steps were followed as mentioned by Correll et al. (1987): Conidia were removed from the host tissue with a piece of transparent tape then, transferred to microscope slide, stored at 4 °C in the laboratory, and counted within 72 h. A total of 100 conidia were counted on conidia and conidiophore shape as a step of identification.

Pathogenicity test

The experiments were conducted in the greenhouse of the Plant Pathology Department, Assiut University, Assiut, Egypt. Powdery mildew on naturally infected chili pepper plants was collected from growing plants in fields and was used to harvest the fungal growth. Before being used as an inoculum source, host tissues with indications of sporulation and infections were gathered, under cool conditions stored in plastic bags, and then incubated for 24–48 h at 30 °C. Two seedlings for each of the five pots were transplanted from chili pepper plants, each pot containing 5 kg of sand and clay soil (1/1, v/v), and the experiment was repeated three times. At the time of blooming, ten seedlings were infected. The conidial suspension was sprayed on the pepper leaves. Four isolates were used for inoculation.

After being inoculated, the plants were brought to the greenhouse. Humidity levels were kept above 80% for 12-h. Then, they were incubated at a day/night regime of 28°/22°C, respectively, for four weeks of inoculation, symptoms developed that were observed as mentioned by Correll et al. (1987).

In vivo infection

The disease symptoms were obtained and incubated on the leaves of chili pepper as previously described. Methods of Sutton and Shane (1983) were used to make *L. taurica* conidial suspensions. Conidia were gathered from diseased leaves after they were saturated three times with sterile distilled water. Using two layers of cheesecloth, the conidial suspension was stressed twice at 4000 rpm for 30 min. Using sterilized distilled water, the conidial concentration of the solution was adjusted to 5×10^4 conidia per ml (De Souza and Café-Filho 2003). After, 60-day-old healthy chili pepper in the greenhouse was sprayed with 30 ml of spore suspension per plant. They were then sealed in plastic bags for 24 h to keep the humidity 80% high enough for disease growth, under a day/night regime of 28°/22°C.

Antagonistic test against *L. taurica* in vivo

The bioagents (*Pseudomonas fluorescens* ON202985, *Bacillus thuringiensis* MW740161.1, and *B. subtilis* MW740159.1) were obtained from the Department of Plant Pathology, Assiut University, Egypt.

Chili pepper seeds were planted in peat trays ($10 \times 20 \times 40$ cm). The seedlings were transplanted to mud pots four weeks after germination (diameter 30 cm) and filled with garden-land soil (two seedlings for each of five pots). Insect-proof cages were used to keep seedlings in pots. During flowering, the lowest leaves surfaces were followed by spraying with *L. taurica* conidial suspension (5×10^4 conidia per ml). *P. fluorescens, B. thuringiensis*, and *B. subtilis* were tested which proved promising antagonistic bioagents in the greenhouse. The previous isolates were obtained from the Plant Pathology, Assiut University, Egypt. Three replicates were used for each treatment in a randomized block pattern. Spraying by *P. fluorescens, B. thuringiensis*, and *B. subtilis* (1×10^6 CFU/ml) was done as soon as disease symptoms began to develop (Vidhyasekaran et al. 1995). Control water spray was used. As previously mentioned, disease severity was monitored weekly until the harvest stage. After the final harvest, the total yield was estimated. Yield at harvest time, the average accumulated yield was calculated for all applied treatments and control as well. All plants from each replicate were pulled for assessment the yield of each treatment (kg per plant). In a complete randomized design, four plants were used for each treatment, which was reproduced three times.

As mentioned by Reuveni et al. (1998), the disease severity of the pathogen was measured 15 days, following the inoculation by randomly evaluating leaves from each treatment and ranking them on a scale of 0 to 4, with 0 indicating no symptoms and 4 indicating severe disease. 1 = 1–10% of the leaf area is damaged; 2 = 11–25% leaf area is damaged; 3 = 26–50% leaf area is impacted; and 4 = ≥ 50% leaf area is affected. The disease index was calculated as the next formula:

$$\mathrm{DI\%} = \Sigma \text{ rated groups} / (\text{Total plants} \times 100/\text{Maximum Category})$$

Estimation of induced resistance of the host plant

Three seedlings of chili pepper per pot were cultivated in 30-cm-diameter clay pots with vermiculite and peat soil (1:1v/v) in the greenhouse. In this experiment, flowering plants were used. Cell suspension of *B. thuringiensis, P. fluorescens*, and *B. subtilis* was utilized and only water foliar spray as control. The foliar spray was done on the upper surface of each plant's leaf with a hand sprayer until runoff was reached. A couple of days following treatment, *L. taurica* (5×10^4 conidia/ml) from the greenhouse preserved stock was taken and sprayed. Monitoring disease progression followed under greenhouse conditions as mentioned by Reuveni et al. (1998). Each treatment was maintained by nine seedlings upon three replicates in the complete random design. The severity of the disease was measured on a 0–4 scale 10 days before harvesting was completed, as stated previously, and the disease index was calculated.

Biochemical experiments

Samples of leaf from various treatments under glasshouse conditions were taken 2, 4, and 6 days after spraying and used for biochemical analysis. For enzyme extraction, leaf samples from each treatment were powdered separately in 5 ml of 0.1 M sodium phosphate buffer (pH 7.0). The pulverized materials were centrifuged for 15 min at 10,000 rpm, and the supernatant was then employed as an enzyme source.

Phenol content determination

A total of 500 mg sample of leaves was extracted in 80% ethanol 10 ml. For 10 min, the ethanolic extract was heated at 65°C. With 80% ethanol, the supernatant volume was increased to 10 ml. In a hot water bath, 100 µl of ethanolic extract were evaporated. A mixture of six milliliters of water and 500 ml of Folin–Ciocalteu reagent was mixed and kept for ten min. The total phenolic content was measured in mg/g of fresh tissue and reported as catechol equivalents (Bray and Thorpe 1954).

Peroxidase (PO) assay

PO was assayed by estimating the absorbance change at 470 nm of guaiacol oxidation in existence of H_2O_2 and the enzyme sample every 30-s intervals. The change in absorbance at 470 nm/min/mg protein was used to measure peroxidase activity (Hammerschmidt et al. 1982). The protein content was calculated as described by Bradford (1976).

Polyphenol oxidase (PPO) assay

The activity of polyphenol oxidase was measured using Srivastava's technique (Srivastava 1987). The protein content was calculated as described by Bradford (1976).

Statistical analysis

The experiments were repeated twice, the resulting data were amalgamated, and means were calculated. Experiments conducted under greenhouse conditions were performed under a randomized complete block design with six replicates. The data from disease severity were transformed arcsine values, and a one-way analysis of variance (ANOVA) was performed using MSTAT-C (version 2.1). According to Gomez and Gomez, the means were compared using the least significant difference (LSD) test at $p < 0.05$ (Gomez and Gomez 1984).

Results

Powdery mildew of chili pepper pathogen identification

The microscopic methods were used to examine the pathogen of chili powdery mildew to reveal its morphological characteristics. Endophytic mycelium and dimorphic conidia were among the traits observed (pyriform to obclavate). On branched conidiophores, conidia were borne singly. The pathogenic strains from chilies had morphological traits that were like *Ovalariopsis taurica* Lev. Chili pepper powdery fungus based on its endophytic partial feature was identified as *L. taurica*, and the normal conidiophore emerges from stomata, piercing mycelia and ramifying within the leaf mesophyll. Conidia were singular, and conidiophore sizes ranged from 50 to 125 µm in diameter, or 4.6 to 5.7 µm. Primary conidia had a tapering end and were pyriform (65.1 18.4 µm), whereas secondary conidia were more cylindrical (55.5 17.6 µm). Mature conidia were hyaline, pyriform, obclavate, lacking prominent fibrosin bodies, and having reticulated wall wrinkles , which were found in this study.

Pathogenicity test

The virulence of the fungus was investigated on 70-day-old healthy chili pepper plants in the glass house. Within 5–9 days of inoculation, typical powdery mildew signs appeared. Within 7 days of the original infection, white powdery outgrowth had covered the whole lowest surface of the leaves. The symptoms and conidial features of naturally infected chili pepper plants were identical. The pathogenicity test showed that *L. taurica* 1 gave the highest disease symptoms in plants (Table 1).

Effect of three bacterial strains against *L. taurica* under greenhouse conditions

In the research study, *Bacillus thuringiensis*, *Pseudomonas fluorescens*, and *Bacillus subtilis* were evaluated for their effectiveness in reducing disease incidence in a greenhouse environment. The results of the study indicated that *B. thuringiensis* had the most significant impact on disease reduction, with a remarkable reduction of 69.07% compared to control conditions. *P. fluorescens* also exhibited a notable reduction in disease incidence, albeit to lesser extent than *B. thuringiensis*. The disease reduction attributed to *P. fluorescens* was measured at 29.55%, indicating its moderate efficacy in managing diseases in the greenhouse setting. *B. subtilis*, on the other hand, demonstrated a lower disease reduction rate compared to the other two microorganisms. The reduction achieved with *B.*

Table 1 Pathogenicity test of powdery mildew on chili pepper plants under greenhouse conditions

Isolates no	Disease severity %
Leveillula taurica1	67.5^{a}
L. taurica 2	50.0^{b}
L. taurica 3	12.25^{d}
L. taurica 4	22.5^{c}
Control	0.00^{e}

Columns followed by the same letter were not significantly different at $p < 0.05$. ± S.E

Table 2 Effect of treatments with biotreatments on disease severity and reduction of powdery mildew in greenhouse

Treatments	Disease severity (%)	Reduction %
Pseudomonas fluorescens	51.25 [c]	29.55
Bacillus subtilis	58.5[b]	19.58
Bacillus thuringiensis	22.5[d]	69.07
Infected control	72.75 [a]	-
Healthy control	0[e]	100

Columns followed by the same letter are not significantly different at $p<0.05$

Table 3 Effect of treatments with biotreatments on yield of chili pepper plants

Treatments	Yield weight per plant in Kg
Pseudomonas fluorescens	0.345 ± 0.02[b]
Bacillus subtilis	0.254 ± 0.001[c]
Bacillus thuringiensis	0.598 ± 0.026[a]
Infected control	0.195 ± 0.024[d]
Healthy control	0.568 ± 0[a]

Values are the mean of three replicates ± standard deviation (SD). Columns followed by the same letter are not significantly different at $p<0.05$

subtilis was 19.58%, which, while still beneficial, it was the least effective among the three evaluated organisms (Table 2).

Impact of biotreatments on chili pepper yield

The maximum yield per plant was 598 g as an outcome of the application of *Bacillus thuringiensis* followed *P. fluorescens* (345 g), while the lowest yield was achieved by *B. subtilis* (254 g) as shown in Table 3. Although, none of the treatments was as effective as a fungicide in reducing disease severity, where the maximum yield by *B. thuringiensis* was recorded as the highest treatments followed by *P. fluorescens* (Table 3) after 90 days from transplanting.

Induced systemic resistance in plant by biotreatments

Phenolic contents

All treatments had a significant increase in the total phenolic content. Spraying with the causal pathogens and *B. subtilis* yielded a high total phenolic content (62 mg), followed by *P. fluorescens* (58 mg), while the least phenolic content treatment (46 mg) was in the case of *B. thuringiensis*, and a healthy control with 32 mg/100 g as determined (Fig. 1).

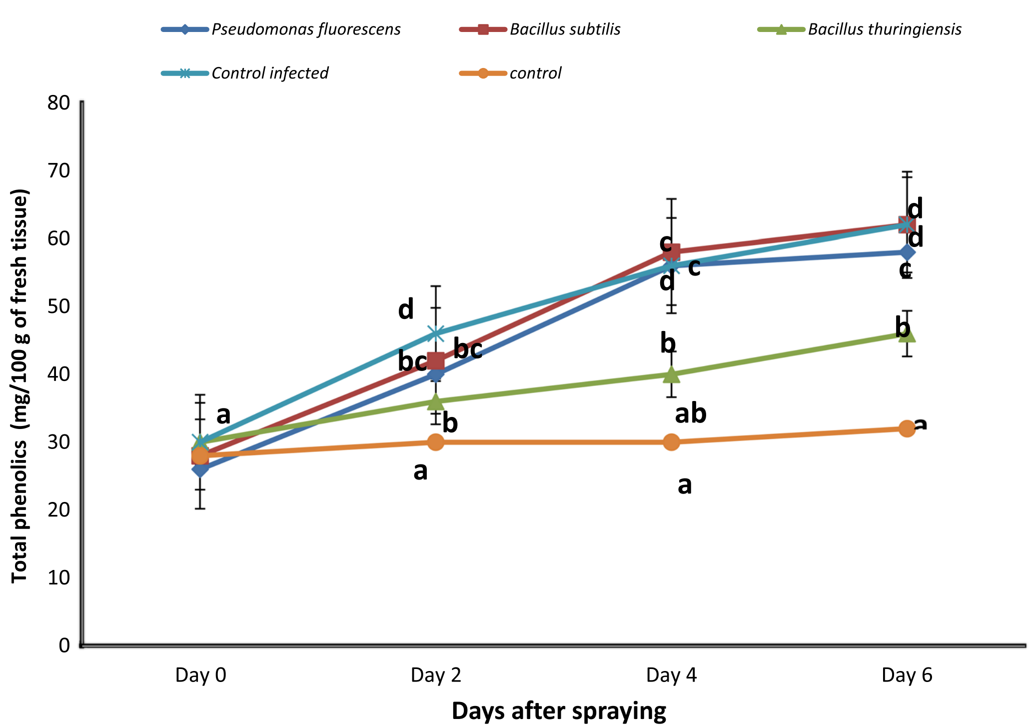

Fig. 1 Effect of treatment with biotreatments on total phenolic contents of infected plants with powdery mildew. Vertical bars represent the standard error ($n=3$). Marks on the same line and followed by the same letter are not significantly different at $p<0.05$

Polyphenol oxidase

Polyphenol oxidase represented when it is exposed to causal pathogens such *L. Taurica*. Polyphenol oxidase activity was significantly heightened by all our treatments, which recorded 0.55 mg by spraying with *B. thuringiensis*; however, *B. subtilis* and infected control resulted in 0.44 and 0.40 mg, respectively. That value by *B. subtilis* was followed by *P. fluorescens* (0.38 mg), while the least activity of polyphenol oxidase was detected in healthy control (0.22 absorb/g/min) (Fig. 2).

Peroxidase activity

When compared with the infected control, all treatments had significantly high peroxidase activity. Peroxidase activity was very high in the infected control (0.56 mg), followed by *P. fluorescens* and *B. subtilis* with the same value (0.55 mg). This was followed by *B. thuringiensis* (0.45 mg), while the lowest peroxidase activity was detected in the healthy control (0.14 absorb/g/min). These data are presented in Fig. 3.

Discussion

There is evidence that natural biological management protects against a variety of foliar diseases. The remarkable reduction in powdery mildew severity on chili pepper produced by phyllosphere application of *P. fluorescens*, called pseudobactin, it was also widely acknowledged among potential antagonists which produce antibiotic material (Hegde et al. 2022). Ali and Ayoub (2017) found that in terms of biological control, data illustrated that utilizing *B. subtilis* reduced pathogen incidence. Interaction between low planting density with *B. subtilis* or mono-potassium phosphate treatment reduced powdery mildew disease incidence and severity. Derbalah et al. (2012) recorded that treating with *B. subtilis* was the most effective application against powdery mildew. Also, *B. subtilis* filtrate showed significant activity against *L. taurica* on chili pepper. Sudha and Lakshmanan (2009) recorded that *P. fluorescens* showed a substantial disease reduction result in the greenhouse, which was likewise observed in the field. The maximum yield for this treatment was 7.5–7.7 tons/ha.

Ali and Ayoub (2017) found that maximum values of the vegetative growth characteristics, fruit quality, and yield were recorded in a foliar application with *B. subtilis*. A significant effect on vegetative growth characteristics, early yield, number of fruits per plant, and yield was recorded with this interaction. Similar results were also found by Alharbi and Alawlaqi (2014). These results might be the result of the effect of bioagents on reducing the powdery mildew disease incidence of chili pepper.

By considering induced resistance as an impact on reducing disease, Fofana et al. (2002) outlined the various antagonists' modes of action. The outcomes are identical to the results of the present experiments. Reduced primary inoculum and proper use of effective fungicides such as benzimidazole, sulfur, and sterol biosynthesis inhibitors have been highlighted by several writers as the key strategies for managing diseases of powdery mildew in the open field (Reuveni et al. 1998). Punitha et al.

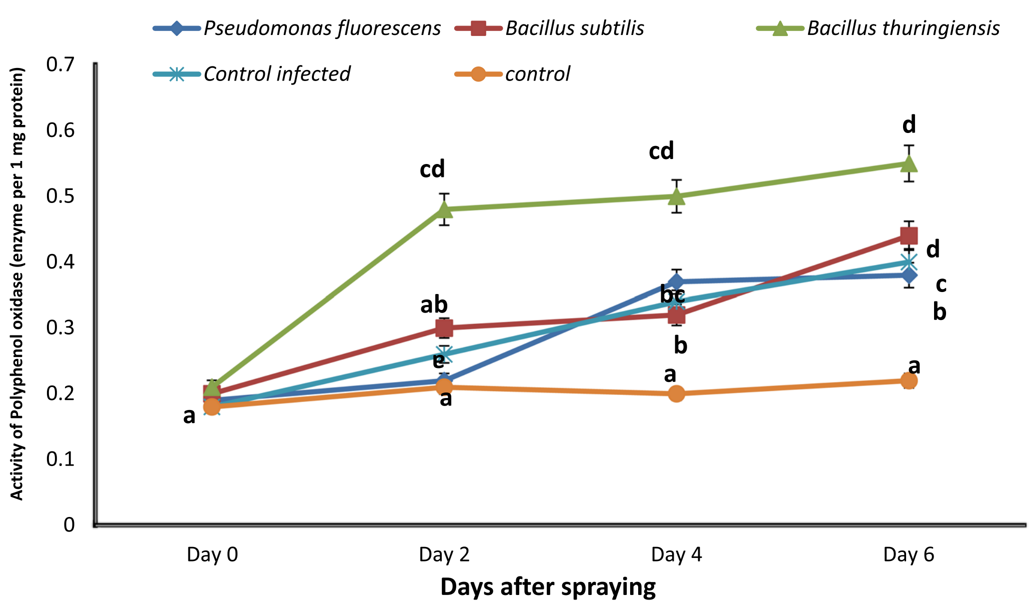

Fig. 2 Effect of treatment with biotreatment on polyphenol oxidase (PPO) activity of infected plants with powdery mildew. Vertical bar represents represent the standard error ($n = 3$). Marks on the same line and followed by the same letter(s) are not significant different at $p < 0.05$

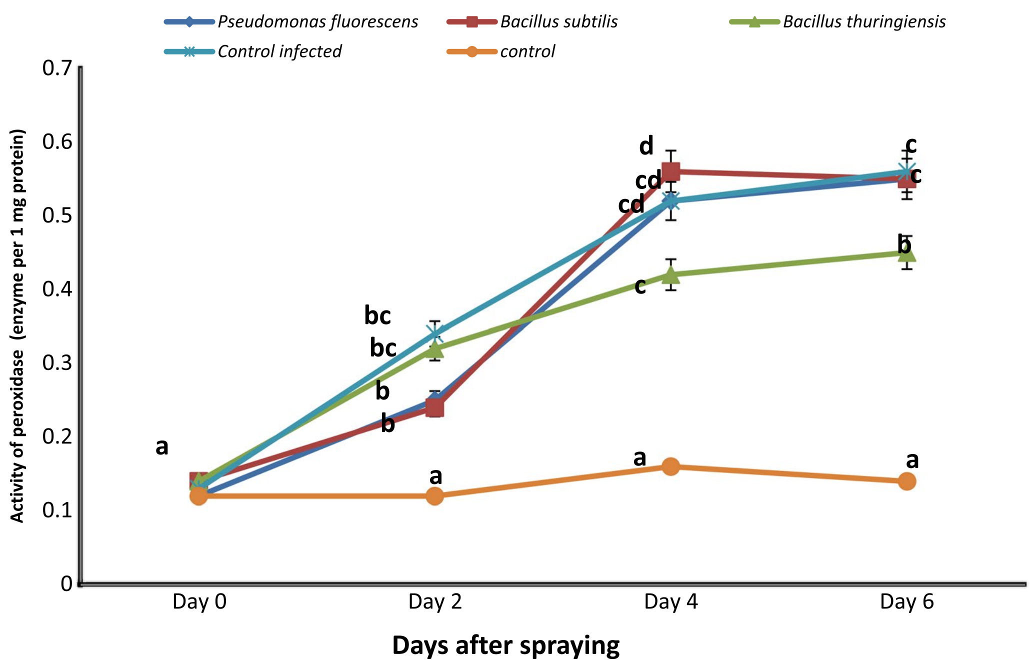

Fig. 3 Effect of treatment with biotreatments on total peroxidase activity of infected plants with powdery mildew. Vertical bars represent the standard error ($n = 3$). Marks on the same line and followed by the same letter(s) are not significantly different at $p < 0.05$

(2016) mentioned that the higher phenolic concentration in the same treatment resulted in fewer infections. Ali and Ayoub (2017) found that disease control was favorably connected with the total amount of phenols and sugars in treated plants' leaves, according to laboratory data. In all treatments examined, the phenolic content of treated plants was higher than that of control plants. The mechanism could be related to the tested antagonist's direct action on the pathogen, as well as the fact that it stimulates plants to resist pathogens by creating active phenols (Cheri et al. 2007).

Total phenol, polyphenol oxidase, and peroxidase levels in chili pepper leaves increased significantly after being sprayed with the bioagents. This could be because of the developed resistance to *L. taurica*. Several researchers have reported on the contribution of these molecules in resistance to diseases in diverse crops (Yadav et al. 2021). According to Avis and Belanger (2001), its act alters the fluidity of cell membranes. As numerous authors have stated, one of the most important disadvantages of utilizing biological antagonists in practical biocontrol is that they quickly lose efficacy below 85–90% relative humidity (Lahlali et al 2022). Many researchers have reported the efficacy of natural treatments such as essential oils, plant extracts, and microbial agents in laboratory and greenhouse, and tested culture filtrates against the powdery mildew pathogen showed a great reduction of the disease incidence. According to Ali and Ayoub (2017), this will result in a high early fruit output. When the most successful therapy (*B. subtilis*) was compared to the control, the relationship between the reduced incidences of the disease and increased chlorophyll, total phenol, and total sugar concentrations was very evident.

Conclusions

The use of fungicides from the same family raised the chance of promoting a disease population's resistance. Reduced pesticide levels on food crops emphasize the need for integrated disease control, especially when commercially suitable resistant cultivars are unavailable. Powdery mildew biological control will continue to be a challenge for further study and development. The findings thus far have shown some promise in concerning practical biocontrol of several powdery mildew diseases, particularly in many hosts and especially pepper and chilies, but further research is needed to verify the efficiency of these approaches in horticultural practice. Our study recommends the implementation of pathogens especially *B. thuringiensis* MW740161.1 as a prospective bacterium bioagent to protect chili pepper against the incidence of powdery mildew, and it is a potential part of the green farming strategy.

Abbreviations

AgNPs Silver nanoparticles
PDA Potato dextrose Agar

TPC Total phenol content
PO Peroxidase
SD Standard deviation
LSD Least significant difference

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Author contributions
Abo-Elyousr and Moustafa were involved in conceptualization, methodology, formal analysis, and writing—original draft. Mousa and Rawa were involved in supervision and review and editing. Abdel-Aal and Hussein were involved in conceptualization, formal analysis, and review and editing.

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Not applicable.

Declarations

Ethics approval and consent to participate
This manuscript is in accordance with the guide for authors available on the journal's website. Also, this work has not been published previously and is approved by all authors and host authorities.

Consent for publication
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Competing interests
No potential conflict of interest was reported by the authors.

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